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An Exploration of Visuomotor and

Perceptual Mechanisms in Humans

and Rats

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Abstract

Neuropsychological, neurophysiological and psychophysical evidence support the notion of two separate and largely independent cortical visual systems: a dorsal system mediating visually guided action and a ventral system mediating object perception and recognition (Goodale & Milner, 1992). This thesis is divided into three parts that explore questions related to the two-visual-systems model, two in humans and one in rats.

The first part explores whether dorsal representations are based on the veridical properties of the stimuli or whether they include information produced by filling-in mechanisms of cortical visual areas. All human experiments were carried out with the ELITE and SMART motion tracking systems. Kinematic analysis showed that grasping Kanizsa illusory squares and partly-occluded objects was as accurate as grasping luminance-defined targets and it is concluded that information about interpolated regions is available to the dorsal system for the calibration of the movement parameters. A Vernier acuity task confirmed that the perceptual localization of Kanizsa and luminance-defined contours is not equally accurate in the ventral visual system.

The second part explores the effect of target dimensionality on grasping, focusing on the possibility that actions aimed at targets that contain two-dimensional information could be modulated by ventral visual mechanisms. The Diagonal Illusion (DI) was chosen to investigate this possibility because it is entirely the product of three-dimensional objects. The DI exerted an effect on both perception and action, although the latter was smaller, suggesting that the effects of illusions on action previously reported are not attributable to the presence of 2D information and, by implication, that 2D information in the target array does not elicit modulation by the ventral visual system. These conclusions were confirmed by a study that found similar kinematic

profiles from grasps aimed at 3D, 2D and 2D-enhanced targets. Control studies ruled out potential confounding effects resulting from curvatures of the stimuli that could have acted as obstacles and from differences in haptic feedback. It is concluded that object-directed action is mediated by dorsal visual mechanisms, irrespective of target dimensionality.

The third part seeks to find evidence of ventral visual processing in rats by measuring the perception of visual illusions and object recognition in this species. The aim is to establish whether rats could provide a suitable model to further investigate the dorsal and ventral visual systems. An automated apparatus with a touch-screen and computer generated stimuli was developed to train the animals. The results from the illusion studies are not conclusive as only one out of three groups of rats was able to solve a discrimination with Kanizsa illusory figures. The preliminary results from the object recognition studies are however clearer. Rats were able to use aspect ratio to solve a discrimination with stimuli that varied in size and location suggesting that size- and location-independent object recognition occurs in this species. Probe trials confirmed these results. It is concluded that rats may have visual processes comparable to those occurring in the ventral visual system of humans and primates.

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Publications and Conference Presentations

Journal Abstracts

Minini, L., & Wattam-Bell, J. (2005). Contour interpolation in the dorsal visual system: Accurate grasping with Kanizsa squares. *Perception, 34*(S), 218.

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Minini, L., Reed, P., & Wattam-Bell, J. (2002). Rats see visual illusions. European Association for Behaviour Group, Annual London Conference, 25-26 March.

Poster Conference Presentations

Minini, L., & Wattam-Bell, J. (2005). Contour interpolation in the dorsal visual system: Accurate grasping with Kanizsa squares. 28 European Conference on Visual Perception, A Coruña, 22-26 August 2005.

Minini, L., Wattam-Bell, J., & Jeffery, K.J. (2005). Shape discrimination in rats. British Psychological Society Quinquennial Conference, Manchester, 30 March – 2 April 2005.

Minini, L., & Wattam-Bell, J. (2003). Grasping partly occluded objects. 26 European Conference on Visual Perception, Paris, 1-5 September 2003.

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1. Two Cortical Visual Systems

1.1. Introduction

Most of us have the conception of perceiving and interacting with a unitary visual world. Contrary to this impression, recent evidence strongly suggests that in both the primate and human brains visual information is processed largely independently and in parallel by two separate visual systems: The ventral and dorsal visual systems (Milner & Goodale, 1995; see Figure 1.1).

This subdivision between the two systems is supported by anatomical, physiological, psychophysical and neuropsychological evidence. More specifically, a large number of studies suggest that both the dorsal and ventral systems process the location, orientation, shape and size of objects within the visual field, but that they do so independently and in different ways, according to the output requirements of their systems (e.g., Goodale & Humphreys, 1998). In the present review the evidence for Milner and Goodale's (1995) model will be presented and some of the properties of the dorsal and ventral systems will be explored.
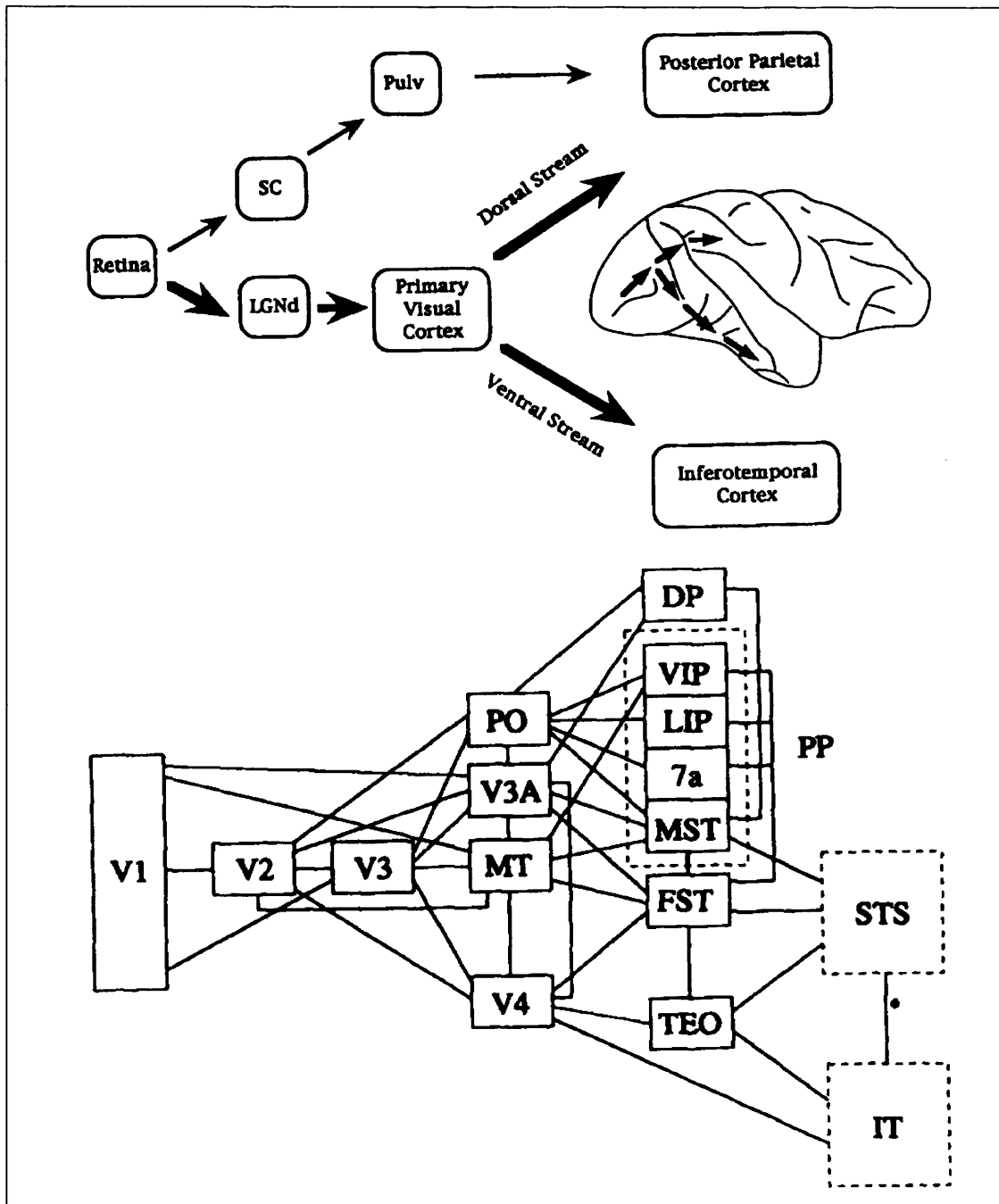
Figure 1.1. Top: Schematic diagram of the dorsal and ventral routes that take retinal information to the inferotemporal (IT) and posterior parietal (PP) cortices, respectively. Bottom: The major known projections to these areas. Adapted from Milner and Goodale (1995).

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1.2. Modularity of Vision in Other Species

A major debate in vision science is whether the visual system constructs a general-purpose representation of the world that closely represents it and that mediates any interaction of the organism with the environment, including thought and action. A major question related to this approach is whether experiential perception is necessary for interacting with a visual world. Goodale (1996) has argued that this monolithic and indirect approach to vision confuses vision with sight. Specifically, he argued that whereas the latter is what humans generally associate with the conscious perception of visual stimuli the former, which is a more direct processing of the visual input, is also possible and does not require conscious perception. This opinion is shared by several other authors (Horridge, 1987; Ingle, 1991).

There is little doubt that visual processing has evolved primarily to detect luminance discontinuities in the environment to subserve vital physiological functions (Horridge, 1987). For instance, photosynthetic bacteria that reverse their swimming direction when they encounter decreases in ambient light possess a simple servomechanism that is sufficient to keep them in illuminated areas (Goodale. 1996). Similar mechanisms are also present in more complex multicellular organisms. For instance, the shell-closure reflex in barnacles is triggered by the detection of luminance changes resulting from the shadow cast by potential predators on a few photoreceptors (Horridge, 1987). Examples of this kind are also found in more complex animals that move such as insects (Horridge, 1987). Vision in these latter organisms clearly subserves the pursuit of prey and mates and that of collision avoidance. Importantly, this relatively complex visually guided behaviour is found in organisms with small brains and that lack cortical structures suggesting that vision without sight, specifically vision that allows interaction with the environment without experiencing sight, is present in several species (Goodale, 1996; Horridge, 1987; Ingle, 1991).

More complex vertebrates have of course a larger repertoire of behaviours. However several studies suggest that seemingly complex behaviour in amphibian and rodents is also mediated by relatively simple, hard-wired and specialised circuits that are not too dissimilar from the servomechanisms described above. Particularly, these studies suggest that the visual system, at least in some species, is modular and that complex visual behaviour can be mediated by several specialised subsystems that work independently and separately. Moreover, these studies support the view that vision primarily evolved to detect the relative motion of objects in the background and to mediate locomotion and that conscious sight developed later in phylogeny (Goodale, 1996; Horridge, 1987).

1.2.1. Amphibia

"Rewiring" studies in the frog (*Rana pipiens*, Ingle 1973), where specific pathways are transected and induced to regrow at different brain locations, provide evidence for the modularity of the visual system in amphibia. In a series of compelling studies, Ingle (Ingle, 1973, 1982, 1991) demonstrated that visually elicited prey catching, visually driven escape from looming targets and visually guided locomotion around barriers are guided by separate and largely independent systems.

Ingle (1973), after removing the optic tectum in one side of the frog brain, transected the projections from the retina that originally were connected to this region. These projections eventually crossed the midline and reconnected with the remaining optic tectum on the other side of the brain. After "rewiring" had occurred the frogs displayed mirror-symmetrical responses to flying prey and looming stimuli. Instead of turning and jumping towards the prey they would respond to a mirror-like location in the opposite direction. Similarly, instead of jumping away from potentially threatening looming stimuli they would jump towards them. These responses suggest that the rewired retinotectal pathway mediates these two types of responses in the frog. Surprisingly, when these animals had to escape a tactile stimulus by moving around a barrier, they

were able to avoid this obstacle regardless of its position in the visual field. Importantly, they could avoid the barrier even when it was positioned in the "rewired" visual field.

In subsequent studies Ingle identified other projections that from the retina terminated in the pretectal nuclei (e.g., Ingle, 1982) and he was eventually able to "rewire" the pretectum leaving the otpic tectum intact (personal communication, cited in Goodale, 1996). In these latter animals, Ingle observed the opposite behaviour: These frogs displayed mirror-reversed visually guided barrier avoidance but normal prey catching and avoidance of looming stimuli. Taken together, these results constitute a double dissociation and suggest that, in the frog, there are at least two independent visual systems. Visually guided prey catching and avoidance of looming stimuli are mediated by the tectal system whereas the visually guided avoidance of barriers appears to be guided by the pretectal system.

1.2.2. Rodents

1.2.2.1. The Rat Visual System

Rats are nocturnal animals and, unlike humans and primates, use olfactory rather than visual cues as a primary source of sensory information. In agreement with this observation, there are several differences at various stages of visual processing between rats and diurnal mammals such as humans and primates that rely more heavily on visual information. These differences result in a poorer visual apparatus, and ultimately in a lower visual acuity in rats (around 1.5 cyc/deg; Keller, Strasburger, Cerutti & Sabel, 2000; Prusky, West & Douglas, 2000) than in humans and primates.

Compared to humans and primates, some of the major differences at a retinal level are that rats have afoveate retinas with a substantially smaller number of cones and ganglion cells. These latter are relatively evenly distributed with a ratio of 5:1 from the highest (3000 cells mm^2) to the lowest (600 cells mm^2) densely populated regions

(Perry, 1979) and the size of their receptive fields does not significantly increase as a function of retinal eccentricity (for review see Sefton & Dreher, 1995). These figures stand in contrast with the 300:1 ratio (foveal density of 80,000 to 100,000 mm^2; Rolls & Cowey, 1970) and with the smaller receptive field size recorded at the fovea (Hubel & Wiesel, 1974) reported for monkeys. Moreover, rats seem to have lenses that do not accommodate and appear to have a small number of cones (7%) that are sensitive to ultraviolet light (Sefton & Dreher, 1995). In addition, rats' laterally placed eyes provide a panoramic view but reduce the size of the binocular field (estimated to be between 40-60%, Sefton & Dreher, 1995) relative to frontally placed eyes.

Of course, differences are also found at a cortical level. Most notably rats have a smaller and less differentiated visual cortex than humans and primates and with different retinofugal projections (Sefton & Dreher, 1995). Notably, whereas in these latter species the large majority of retinal ganglion cells project to the geniculostriate system and only a small proportion to the superior colliculus (about 90% and 10%, respectively, in macaque monkeys), in rats about 90% of ganglion cells project to the superior colliculus and only between 20% and 50% of these cells have collateral projections to the dorsal lateral geniculate nucleus (Sefton & Dreher, 1985). Thus, whereas visual processing in humans and primates is largely mediated by the geniculostriate pathway, in rats it is dominated by the retinotectal system.

However, there are also similarities between these species. For instance, the rat contrast sensitivity function has an inverted-U shape that is qualitatively comparable to that of humans and primates although maximum contrast sensitivity is lower and limited to low spatial frequencies (Keller et al., 2000). Moreover, albeit with afoveate vision, rats posses an *area centralis* that, as suggested by eye-orienting movements elicited by electrical stimulation of the superior colliculus (see review in the next sections), seems to have some functional equivalence with the fovea. Most importantly, rats have a relatively highly developed visual cortex that is larger and more functionally differentiated than originally thought (Montero, 1993). For instance, Montero (1993)

identified 10 extrastriate areas in this species including a retinotopically organized primary visual cortex. Thus, rats seem to have a relatively well developed visual system. In accordance with these findings, these animals partly rely on vision for a variety of biologically relevant tasks such as prey and predator recognition and navigation.

1.2.2.2. Subcortical Visual Systems

The subcortical parcellation of function outlined above for amphibians has also been found in the organization of visually guided behaviour in rodents. Schneider (1969) first proposed that the visual cortex and superior colliculus (the homologue of the optic tectum) of rodents respectively mediate the identification and localization of objects. Localization in Schneider's (1969) model served the purpose of orienting head and body toward stationary visual stimuli. These conclusions were based on the findings that hamsters with lesions to the superior colliculus were unable to (head) orient towards sunflower seeds whereas this behaviour was not affected in animals with cortical lesions. By contrast, decorticate but not colliculotomized animals were impaired in visual discrimination tasks.

Schneider's (1969) definition of "orientation behaviour" has been shown to be too broad (Goodale & Carey, 1990; Goodale & Milner, 1982) and, as outlined below, there is now evidence that not all orienting responses are mediated by the superior colliculus. However, in general, lesions to the superior colliculus in a variety of rodents have been found to significantly impair the ability to orient towards visual targets, in particularly when presented in the visual periphery (for review, see Goodale & Milner, 1982). Moreover, studies that pharmacologically or electrically stimulated this structure elicited orienting-like behaviour for eyes, head, limbs and body (for review, see Dean, Redgrave & Westby, 1989) or in some cases biting and gnawing movements (Kilpatrick, Collingridge & Starr, 1982). These orienting responses have been characterised as a "*visual* grasp reflex" (Hess, Bürgi & Bucher, 1946; cited in Milner &

Goodale, 1995), although several authors have proposed that in afoveate species with a poorly developed area centralis, such as rats, this orienting behaviour is more likely to serve the purpose of facilitating responses such as locomotion towards the stimuli or their olfactory and tactile exploration rather than serving an exclusively *visual* (identification) function (Goodale & Carey, 1990; Milner & Goodale, 1995). Nevertheless, the retinal projections to the superior colliculus in rodents, as in amphibia, seem to mediate orienting movements of the eye, head and body towards visual targets for feeding behaviour.

Moreover, in rodents as in amphibia, a different set of projections from the retina to the superior colliculus seems to mediate visually elicited escape responses. For instance, lesions to the superior colliculus significantly impair escape responses to threatening visual stimuli (Ellard & Goodale, 1988). In addition, electrical or pharmacological stimulation of this region elicits either "freezing" or startle responses similar to those observed in escape procedures in this species (Ellard & Goodale, 1988). Finally, there is evidence that, in rodents as in amphibia, the visually guided avoidance of barriers is mediated by a pretectal system (Goodale & Carey 1990). Specifically, lesions to the gerbil pretectum were found to impair the avoidance of a barrier that partially obstructed a target entrance to a greater extent than lesions to the superior colliculus.

The above studies suggest that, like amphibia, rodents have a dual-purpose optic tectum mediating visually elicited feeding and escape responses. In addition, like in amphibia, the rodent pretectum seems to mediate the visually guided avoidance of barriers. More generally, they clearly suggest that visually guided behaviour in rodents is mediated by dedicated and largely separate visual networks.

1.2.2.3. Cortical Visual Systems

Goodale and Milner (1982) and Goodale and Carey (1990), after an extensive review of the deficits resulting from collicular and cortical lesions, argued that not all visually

guided behaviour is mediated by the superior colliculus as initially proposed but that cortical networks might modulate some of these responses. For instance, Goodale and Murison (1975) trained rats to run towards a small light in an apparatus where two rectangular chambers were connected by a tunnel. When the rat ran through the tunnel, one of the five lights on one of the two walls of the chambers would turn on and the task of the animal was to collect the reward behind the target. Goodale and Murison (1975) videotaped the task and compared the spatial and temporal properties of the movements relative to stimulus onset and location. It was found that normal, sham operated and colliculectomized rats (with large and bilateral lesions) ran directly towards the light as soon as they entered the open chamber, displaying therefore normal behaviour. In fact, the colliculectomized rats showed "supernormal performance" in that they did not stop when exiting the tunnel, as it was common in this task, and had consequently smoother paths. Goodale and Milner (1982) suggested that these rats might have been less distracted by task-irrelevant stimuli. By contrast, rats with large lesions to posterior neocortex were clearly impaired at this task as these animals ran towards the central door irrespective of target location. These results clearly show that the superior colliculus is not essential for visually guided locomotion towards stationary stimuli in rodents, even when this entails orientation behaviour of the type described by Schneider (1969). Similar results have been reported by other authors (Dyer, Marino, Johnson & Kruggel, 1976).

The supernormal performance observed in colliculectomized animals was further explored by Goodale, Foreman and Milner (1978) who set out to establish whether it underlined a "distraction" deficit and whether it was field-dependent. Goodale et al. (1978) replicated Goodale and Murison's (1975) task with 16 additional "distracting" overhead flashing lights that were turned on when the photobeam in the tunnel was broken. Measurements of response latency as a function of distractor location revealed increased latencies for sham and visual-decorticate animals with all distractors except for those presented directly behind the animals. Behaviours such as freezing, rearing and head orienting towards the overhead lights also indicated that these animals were

distracted by these stimuli. Colliculectomized rats showed similar responses but only when the lights were presented within 40° from their midline. No effects were observed for lights presented between 40° and 160°. Failure to orient towards the novel stimuli presented in the visual periphery by these latter rats is in agreement with the general functional role attributed to the superior colliculus. However, their normal head orienting responses towards lights presented in the central visual field suggests that this subcortical structure does not mediated all orienting behaviour. Although at present it remains unclear which areas mediate this behaviour in the rat, evidence that in Mongolian gerbils this extratectal ability is abolished after lesions to the striate cortex (Ingle, 1982; Milner & Goodale, 1984) suggests that cortical mechanisms might be a probable structure (Goodale & Carey, 1990; Goodale & Milner, 1982). Taken together, the studies by Goodale and Murison's (1975) and Goodale et al. (1978) suggest that in rodents, as in humans and primates (Milner & Goodale, 1995), some visually guided behaviour is mediated by the cortical visual system.

1.2.2.4. Visuomotor and Visuocognitive Systems

Of course, the visuomotor mechanisms described above are not sufficient to mediate all visually guided behaviour of many complex animals. For instance, a large number of visually elicited responses depend on learning, memory and planning and visual stimuli can have meaning and causal relationships attached to them. This type of behaviour is likely to be mediated by some kind of representation of the world and by visuocognitive mechanisms, probably mediated by cortical networks (Goodale, 1996).

Carey, Goodale and Sprowl (1990) provide evidence for the existence of visuomotor and visuocognitive mechanisms in rodents. These authors used the finding that Mongolian gerbils are very good jumpers and that they very rapidly calibrate their jump just enough to clear the gap between two platforms, as indicated by highly significant correlations between gap size and distance jumped (Ellard, Goodale & Timney, 1984). Carey et al. (1990) used this experimental procedure to establish that gerbils calibrate

their jumps according to the retinal size of the platform. Retinal image size is a direct function of object size but also an inverse function of its distance from the observer: The greater the distance the smaller the retinal image. Carey et al. (1990) argued that over a series of trials with the same platform presented at various distances, gerbils could learn the invariant relationship between object size and retinal size and could eventually predict the distance of the platform from retinal sizes that were within the experienced range.

This claim was tested by inserting "probe" trials during which the landing platform was either smaller or bigger than the training platform (Figure 1.2). As predicted, gerbils overjumped the smaller platform as if it was further away whereas they underjumped the larger platform as if it was nearer. These results suggest that gerbils interpreted the retinal image size according to the calibrated relationship between object size and distance that was acquired during training and used this to compute the distance to jump in the probe trials. Importantly, lesions to the geniculostriate pathway, primary visual cortex or peristriate regions did not significantly affect this behaviour. These results are in sharp contrast to those obtained with animals with large striate lesions in size discrimination tasks where subjects could not discriminate between two platforms of different sizes (Carey et al., 1990), a task easily solved by gerbils with intact brains (Goodale, 1996).
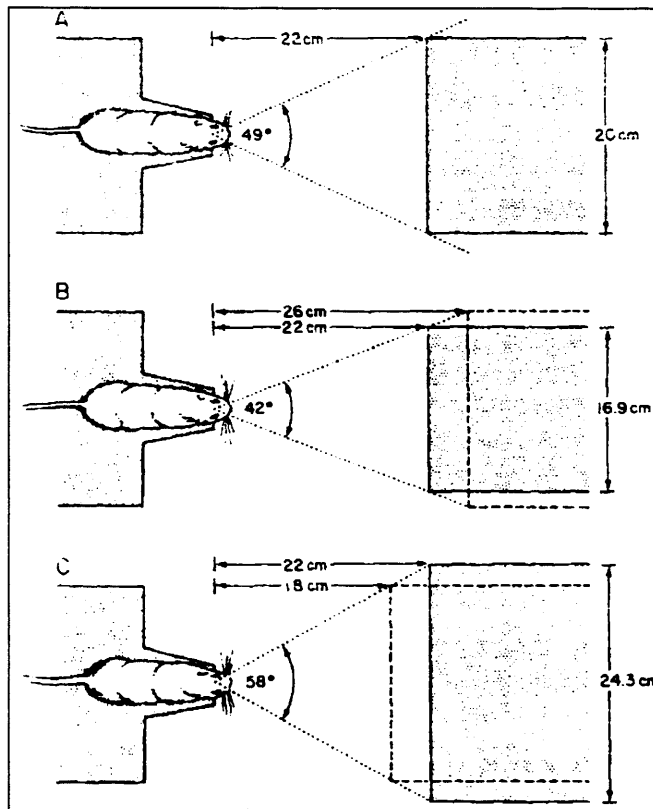
Figure 1.2. Schematic diagram of the platforms used by Carey et al. (1990). (A) the platform used during training. (B) the narrower platform used in probe trials. (B) the wider platform used in probe trials. Note that the gap distance (22 cm) is the same in all conditions. The dotted lines represent the apparent location of the platform used by the animal to compute the jump parameters.

Thus, gerbils with lesions to their geniculostriate system can use retinal size information to calibrate the amplitude of their jump (a visuomotor task) but can not use the same information to solve a simple discrimination (perceptual) task. Goodale (1996) argued that, in this latter task, the visual properties of the stimulus become arbitrarily associated with reward and that this kind of visual processing is likely to be mediated by visuocognitive cortical networks that probably use some kind of representation of the world. By contrast, the relationship between retinal size and distance is not arbitrary as specific targets are always instances of the general case. Therefore, this behaviour could be mediated by relatively simple, dedicated, phylogenetically older visuomotor

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mechanisms after the calibration of the specific instance has occurred, perhaps after as little as a single exposure to the target (Goodale, 1996).

In summary, the above results provide evidence for a dissociation in rodents between visual networks that mediate visuomotor responses and other, more cognitive, visually guided behaviours that might require more complex representations of the world (Goodale, 1996). Whether these representational visual networks might be comparable to some extent to the processes known to occur in the ventral visual system of humans and primates still remains unclear and it is one of the questions explored in this thesis.

1.2.3. Modularity of Vision in Primates

Several behavioural and neurophysiological studies suggest a modular organization in the primate visual system. These studies found that post-training lesions to the primate temporal region result in a severe impairment in a variety of object recognition tasks based on shape, colour and texture but not on visuomotor tasks like visually guided reaching and grasping or judging which of two stimuli is nearer to a landmark (the landmark task). The inverse pattern of results is observed with post-training lesions to the primate parietal cortex (for review, see Ungerleider & Mishkin, 1982).

Single cell studies also support this functional subdivision between the two systems. Neurones in areas that belong to the occipitotemporal system (e.g., V1, V2, V4, the superior temporal sulcus, SCS, and inferotemporal cortex, IT) selectively respond to visual features that are relevant for object recognition such as shape or colour. By contrast, neurones in areas known to belong to the occipitoparietal system (e.g., V1, V2, V3, middle temporal area MT, medial superior temporal area, MST, and the anterior intraparietal area, AIP) have been found to selectively respond to spatiotemporal properties of the stimuli such as velocity and direction of motion or to properties necessary for object directed action (for reviews, see Milner & Goodale, 1995; Ungerleider & Haxby, 1994).

The above findings strongly suggest that the occipitoparietal system processes visual information for visuomotor tasks whereas the occipitotemporal system is more concerned with processing visual information for object recognition. Although several differences between monkey and human neuroanatomy suggest that analogies between the two systems should be drawn with caution (Crick & Jones, 1993), the following sections will present evidence that the distinction between the occipitotemporal and occipitoparietal visual systems is structured in a very similar way in the human brain (Milner & Goodale, 1995).

1.3. Experimental Paradigm: Measuring the Kinematic Profile of Manual Prehension

In most of the visuomotor research that will be presented below the properties of the visuomotor system have been investigated by comparing the kinematic profile of prehension obtained under normal conditions with either the profiles from neurological patients or with the profiles obtained from experimentally manipulated conditions. It is therefore necessary to give a brief review of the normal kinematic profile of prehension.

In the act of prehension 3 components can be clearly identified. First, the hand and arm have to be transported to the location of the target, second the hand has to preshape prior to contact and finally the object has to be manipulated. Most visuomotor research has explored the first two of these components, the transport or reaching and the grasping components, respectively.

Jeannerod (1981, 1984) was among the first to investigate the kinematic profile of prehension and to propose that this distinction is not merely descriptive but that it is quantifiable and that it reflects two separate underlying visuomotor mechanisms. The transport and grasping distinction is closely mapped onto the intrinsic and extrinsic properties of the object to be grasped. Extrinsic properties like orientation, location in

the frontal plane and direction and velocity of a moving target are properties that emerge from the behavioural context and are clearly distinct from properties like size, shape, colour or texture that are intrinsic to the object.

The "classical model" proposed by Jeannerod (1981) claims that the transport component is concerned with the extrinsic properties whereas the grasping component is concerned with the intrinsic properties of the target. Although not without criticism (e.g., Smeets & Brenner, 1999), the classical model is to some extent supported by anatomical evidence that suggests that the two systems for transport and grasping are separated anatomically. For instance, several lesions studies in primates have shown that damage to the parieto-occipital junction result in selective damage to the transport component whereas more widespread damage that includes the superior parietal lobe affects both the transport and grasping components (for review, see Jakobson & Goodale, 1991). In addition, evidence from human infants suggests that transport and grip formation have different developmental profiles (for review, see Atkinson, 2000).

A direct prediction of the classical model is that distance and shape/size should selectively affect the transport and grasping components, respectively. In agreement with this prediction, Jeannerod (1981) found that varying the distance between the start position of the hand and the target affected the transport but not the grasping component. Maximum velocity increased almost linearly with distance. Because higher velocities were used for longer distances no effect of distance was observed on movement duration. The transport component was formed by two distinct phases, the acceleration and deceleration phase, separated by a sharp change in the slope of the velocity-against-time curve (see Figure 1.3). After peak velocity, most subjects decelerated gradually although a few participants maintained a constant velocity plateau and then abruptly stopped at the end of movement.

By contrast, Jeannerod (1981) found that manipulations of the object size affected the grasping but not the transport component. Maximum Grip Aperture (hereafter MGA)

was a function of object size, although larger than the actual size, and occurred at a constant time during movement execution, regardless of target size. The above results provide evidence for the independence of transport and grasping in that these two components are selectively affected by different properties of the target. However, it should be noted that there is a strong temporal interdependence between them. As shown in Figure 1.3, MGA mostly occurred at the initiation of the deceleration phase and had a fixed time position with respect to movement duration.

In agreement with the classical prediction a further study that measured changes of target shape, obtained with a semi-reflective mirror, revealed that these manipulations affected the grasping but not the transport component. The above results led Jeannerod (1981) to propose that transport and grasping are two separate and independent components of prehension, although the strong temporal coupling between them suggests that they are modulated by a higher-order common mechanism.

The above findings have been largely replicated and refined by several subsequent studies (e.g., Jeannerod, 1984; Jakobson & Goodale, 1991). For instance, Jeannerod (1984) found that the initiation of the deceleration phase occurred at about 75% of movement duration whereas MGA occurred between 74% and 81%.

However, recent evidence suggests that the selective effect of the extrinsic and intrinsic properties of the target on transport and grasping is not so clear as initially described by the classical model. In disagreement with Jeannerod's (1981, 1984) claims Jakobson and Goodale (1991) found that manipulations of object size affected peak velocity and overall movement duration whereas manipulations of distance affected MGA. In addition, relative time to peak velocity was affected both by size and distance as it occurred proportionally sooner for larger or more distant objects. Finally, relative time to MGA was affected by distance as it occurred proportionately later for more distant objects. These results are in disagreement with the predictions made by Jaennerod's

(1981, 1984) original model of prehension and suggest that the transport and grasping components are more interdependent than originally claimed.

Although the specific effect that different target properties like distance and size have on the kinematics of grasping is still a matter of ongoing research (e.g., Hu & Goodale, 1999; Servos, Goodale & Jakobson, 1998.), the above studies have revealed a clear kinematic profile of normal prehension, for instance that MGA occurs at about 75% of movement duration and that it is a function of target size. In several of the studies presented below this normal kinematic profile has been used to either identify visuomotor impairments in neurological patients or to test the effect of laboratory manipulations in neurologically intact individuals.

Finally, it should be noted that whereas early analyses of prehension were carried out with video techniques (e.g., Jeannerod, 1981) more recent studies (e.g., Jakobson & Goodale, 1991) used optoelectronic equipment that allows a more detailed and accurate analysis of the kinematic profile. In these latter systems, the movement kinematics of interest are derived by tracking and plotting the position of either infra-red-light-emitting diodes (IREDs) or infra-red-light-reflecting markers that are generally placed on the thumb, index finger and wrist. Normally, the grasping component is measured using the markers on the thumb and index finger whereas the transport parameters are obtained from the marker on the wrist. The greater accuracy of the optoelectronic measurements could account for the discrepancy between Jeannerod's (1981, 1984) and Jakobson and Goodale's (1991) results.
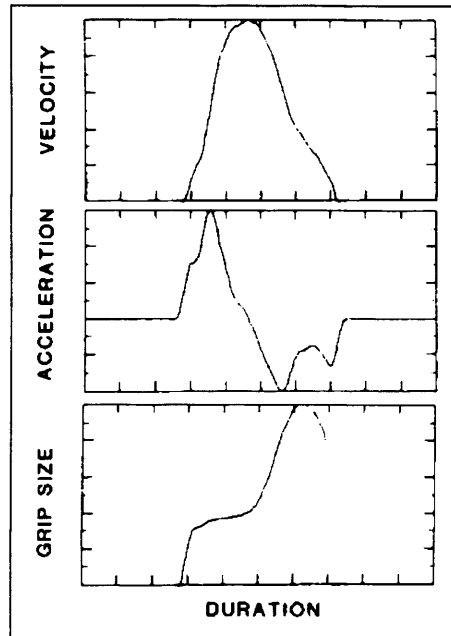
Figure 1.3. Graphs illustrating the temporal relationship between the transport and grasping components. Note that MGA occurs soon after maximum velocity and it coincides with minimum acceleration. Adapted from Jeannerod (1988).

1.4. Modularity of Vision in Humans: Neuropsychological Evidence

Evidence for the functional distinction between the dorsal and ventral visual systems in humans comes from neuropsychological studies with neurological patients and psychophysical studies with neurologically intact individuals. In the intact human brain the two systems usually work in collaboration and, as it will be seen later, only under carefully manipulated laboratory conditions is it possible to observe the functional distinction between them. Patients with selective brain damage to either the occipitotemporal or the occipitoparietal areas offer a rare opportunity to observe the functional specialization and some of the properties of the undamaged system.

Two types of neurological patients, with optic ataxia and visual form agnosia, have been identified as having selective damage to the dorsal and ventral streams, respectively. Several studies with these patients in the last two decades have revealed that both visual systems compute the location, orientation, shape and size of the stimuli but that they do so independently and separately. A review of these studies is given below.

1.4.1. Visual Form Agnosia: Dissociating Orientation and Size

Goodale, Milner, Jakobson and Carey (1991) conducted an investigation of the perceptual and visuomotor abilities of DF, a 35-year-old woman who was left with visual form agnosia after carbon monoxide poisoning. DF's damage spared most of area 17 (primary visual cortex) although it involved the parasagittal occipitoparietal region, extensive ventral damage to the lateral occipital region (mostly areas 18 and 19) and some localized damage to the basal ganglia. DF's perception of orientation and shape either conveyed by luminosity, colour, stereopsis, or motion was significantly impaired.

Goodale et al. (1991) tested DF and 2 neurologically intact individuals on perceptual and visuomotor tests of orientation and size. Perception of orientation was tested in three ways. In the first perceptual task the patient had to choose which of 4 luminance-defined lines of different orientations printed on a card matched the orientation of a large slot in an upright disk (Perening & Vighetto, 1988, used a very similar apparatus; see Figure 1.4). In the second, she had to match the orientation of a hand held card with the orientation of the slot and in the third she had to say verbally the orientation of a 3-D rectangular shape place in front of her. Orientation accuracy processed by the visuomotor system was tested in a posting task where DF had to insert a card into the slot described above that was positioned at different orientations.

DF was very accurate in the posting task suggesting that she could use orientation to insert the card in the slot as well as the control subjects. By contrast, DF performed very

poorly in the perceptual tasks. For instance, she was much worse than the controls at matching the orientation of the hand-held card to the orientation of the slot.

A similar dissociation between the processing of size for perception and action was found in this patient. In this second part of the study, DF and the 2 controls were presented with five pairs of white shapes of equal area but different dimensions. In one of two perceptual tasks participants were presented with pairs of these shapes and were asked whether the shapes were the same or different, in the other task the shapes were presented individually and participants had to match the 'front-to-back extent' with their thumb and index finger. In the visuomotor task participants were asked to pick up the targets using their thumb and index finger. The position of the fingers during movement execution was recorded with optoelectronic equipment.

The maximum grip apertures of DF and the controls in the grasping task were positively correlated with the size of the targets indicating that DF's visuomotor system was able to process the size of the objects to be grasped to calibrate her grip size. Control participants performed similarly in the manual estimation task. However, DF's aperture in this latter task was not correlated with the target size and her trial-to-trial variability was much greater than in the visuomotor task. DF's performance in the same/different perceptual task was nearly at chance level (52%) whereas controls had no difficulty in this task.

The above results strongly suggest that DF, a patient with damage to the ventral visual system, can process size and orientation for object directed action but can not process these attributes of the stimulus for perceptual tasks. These results provide clear evidence that the dorsal system processes orientation and size in addition to the location of objects as originally postulated by Ungerleider and Mishkin (1982). More specifically, these results, taken together with the findings presented below by Jakobson, Archibald, Carey and Goodale (1991) and by Perenin and Vighetto (1988), provide evidence for a double dissociation in the processing of size and orientation, respectively, in patients

with optic ataxia and visual form agnosia. They suggest that size and orientation are processed independently and separately by the dorsal and ventral visual systems.

1.4.2. Optic Ataxia

Optic ataxia has been described as a disorder of "coordination and accuracy of visually elicited hand movements not related to motor, somatosensory, visual acuity or visual field defects" (Perenin & Vighetto, 1988, p.643) that is often observed after unilateral lesions to the posterior parietal cortex (PPC). It is important to note that these patients show visuomotor deficits not associated with purely visual, proprioceptive or motor deficits. They often have normal visual acuity, normal visual space perception and largely normal visual fields. In addition, eye movements, most elementary motor capacities and somatosensory functions, as assessed by tactile or position sense tests, are also within the normal ranges.

Although optic ataxic patients are often impaired in reaching with either hand for objects located in the contralesional hemifield (i.e., they show a field effect), some patients have been reported that were impaired only for reaching with 1 hand in 1 hemifield and occasionally some others have been found to have a hand effect (i.e., they showed an impairment in reaching with the contralesional hand, irrespective of the location of the stimuli in the visual field). Finally, optic ataxia can occasionally be observed after bilateral lesions to the PPC (for review, see Perenin & Vighetto, 1988).

1.4.3. Optic Ataxia: Orientation is Processed by the Dorsal Stream

Perenin and Vighetto (1988) were among the first to systematically investigate the visuomotor and perceptual deficits in optic ataxic patients and to propose that these patients have a specific visuomotor disorder that is independent from their perception of the visual space. Thus, these authors were among the first to make a clear distinction between visuomotor and perceptual deficits in these patients. Perenin and Vighetto

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(1988) used video analysis to test ten patients with optic ataxia and five neurologically intact individuals with a visual space perception task and a task that required orientation of the hand.

Perception of orientation was tested by presenting bars at different orientations with respect to the horizontal axis. After each trial participants had to indicate verbally the number of a card that corresponded to the test stimulus just presented. Orientation of the hand was tested with the apparatus shown in Figure 1.4. Participants had to insert their hand into an oval hole that could be positioned at different orientations with respect to its main axis (horizontal, vertical or 45°). Both the perceptual and visuomotor tasks were tested in the ipsilesional and contralesional hemifields.

Perenin and Vighetto (1988) found that all but one of the patients performed within the normal range in the perceptual task when the stimuli where presented in the ipsilesional hemifield, although some patients made more errors with contralesional stimuli. By contrast, in the visuomotor task both spatial and orientation errors were observed, mainly for stimuli in the contralesional field, although the former were usually small and often corrected.

A careful analysis revealed that the magnitude of the orientation errors was much larger than that of the perceptual errors for several patients and that these two types of errors did not appear to be correlated. Furthermore, perceptual impairment was not observed in all the patients whereas visuomotor impairment was. Perenin and Vighetto (1988) concluded that perceptual errors do not have a substantial role in optic ataxia and that this condition is characterized by an impairment that is visuomotor in nature. Perceptual errors in these patients could have been the result of lesions that marginally extended to other, perhaps ventral, areas involved in visual perception.

Overall, the above results suggest that these patients could use the orientation of bars to solve a perceptual task but could not use the orientation of an oval hole to adjust the

orientation of their hand during a posting task. These findings taken together with the results from DF (Goodale et al., 1991) constitute a double dissociation: Patients with optic ataxia can use orientation to solve perceptual tasks but not visuomotor tasks whereas the inverse pattern is observed with patients with visual form agnosia. Taken together these results suggest that the orientation of visual stimuli in the environment is processed independently and separately by the dorsal and ventral visual systems.
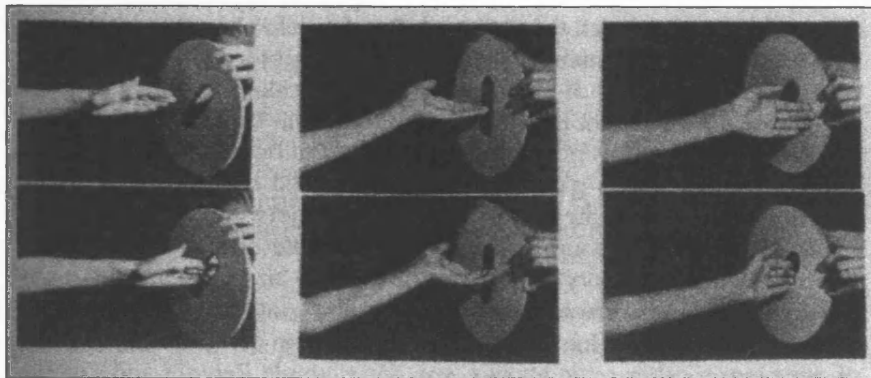
Figure 1.4. The apparatus used by Perenin and Vighetto (1988). From left to right: Responses from a control subject and orientation and localization errors from a patient with optic ataxia.

1.4.4. Optic Ataxia: Size is Processed by the Dorsal Stream

The majority of published work on optic ataxia, in particular work prior to Milner and Goodale's (1995) reinterpretation of the dorsal and ventral visual systems' functional roles, did not use techniques that allowed a careful analysis of the kinematic profile of these patients. Few exceptions are studies that used video analysis (e.g., Jeannerod, 1986; Perenin & Vighetto, 1988) to derive measures like hand velocity and grip aperture. However, Jakobson, Archibald, Carey and Goodale (1991) were among the first to carry out a systematic kinematic analysis of optic ataxic patients with optoelectronic and therefore more accurate equipment.

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Jakobson et al. (1991) measured pointing and grasping in VK, a 68-year-old woman with optic ataxia, and in 2 neurologically intact control subjects. To prevent stereotypical movements, in the pointing condition participants had to point to light targets presented at 5 different locations, but the analysis was carried out only on the targets presented centrally. In the grasping task participants had to grasp 3 rectangular shapes of different sizes presented at different distances but always located in the central field of vision. Both pointing and grasping were carried out in full light conditions (i.e., closed loop) and without vision of the hand and target (i.e., open loop).

In the pointing task under closed loop conditions, although movement initiation occurred slightly later in VK than in the normal controls, acceleration, peak velocity and duration were all within the normal range. A greater disruption was observed in the movement kinematics of VK's grasping responses. VK showed an abnormally long deceleration phase but most importantly, her maximum grip aperture was 60-70% greater than that of the normal controls. In addition, although the mean scores on this variable were weakly scaled to the size of the object to be grasped, there was a much greater variability in VK's responses as she often opened her hand wider with the smallest of the targets than when asked to grasp the larger objects. In addition, VK's trial-to-trial variability for time to maximum grip aperture was also greater than the normal values and frequently and unusually she readjusted the position of her fingers during the deceleration phase. This final pattern was exacerbated by the removal of visual feedback.

Jakobson et al. (1991) provide first direct evidence that patients with optic ataxia, with a lesioned visuomotor system, show various abnormal movement kinematics but most importantly they can not calibrate the size of their grip according to the size of the target to be grasped. Conversely, normal controls could perform this task effortlessly. Although Jakobson et al. (1991) did not test VK's ability to solve perceptual tasks using size, it is well documented that these patients do not have difficulties in solving

same/different discrimination tasks based on this property of the stimulus (for review, see Milner & Goodale, 1995).

1.4.5. Shape is Processed by Both the Ventral and Dorsal Streams

Goodale, Meenan, Bülthoff, Nicolle, Murphy and Racicot (1994) provide evidence that shape is processed independently by both the ventral and the dorsal systems. Goodale et al. (1994) used the set of shapes illustrated in Figure 1.5 as these stimuli lack clear symmetry and have only smooth contours. The authors argued that due to these characteristics, in a grasping task, the computation of the landing points on these targets would need to consider the entire contour envelope, i.e., the entire shape of the target. Goodale et al. (1994) compared the performance of DF, the visual form agnosic introduced above and RV, a 55-year-old woman who developed optic ataxia after bilateral occipitoparietal lesions with that of a neurologically intact control subject.

In the discrimination task participants were presented with pairs of the shapes in Figure 1.5 and were asked to judge whether these stimuli were the same or different. The two shapes simultaneously presented could have the same or a different orientation. This latter arrangement increased the difficulty of the discrimination test. The results revealed that the control performed perfectly with the same- and differently-oriented shapes and that RV, although slightly more impaired with the differently-oriented shapes (80% correct), performed nearly perfectly with the easier version of the test (90% correct). By contrast, DF performed nearly at chance level (< 60% correct) in both versions of the test.

A different pattern of results was observed in the grasping task where participants were required to pick up the stimuli using their thumb and index finger. The authors argued that, given the asymmetrical shapes of the targets, participants had to position their thumb and index finger on particular points on the circumference of the stimuli to allow a stable grasp. The determination of the stable landing points on the targets had to

necessarily follow a computation of the entire contours envelope. The results were quite conclusive. Figure 1.5 illustrates the straight lines joining the two landing points of the thumb and index finger in each precision grip performed by the 3 participants. It can be clearly seen that whereas all the landing points chosen by DF resulted in stable grasps and are very similar to those used by the control subject, RV often chose unstable points for her grasps. This observation was confirmed by a quantitative analysis of this data. Goodale et al. (1994) measured the shortest distance between the grasp lines and the centre of mass of each target and as predicted, no significant differences were found between the values obtained for DF and the control subject whereas they both significantly differed from RV's responses. The authors concluded that RV was unable to choose stable grasp points on the targets because the computation of their overall shape in the dorsal visual stream was impaired by her lesions to the parietal region.

Taken together the above results provide a double dissociation and clear evidence that shape is computed independently and separately for perception and action. DF, a patient with lesions largely localised to her ventral visual stream was able to use shape to guide her visuomotor performance but was unable to use this property of the stimuli to solve a simple discrimination task. Conversely, RV a patient with lesions largely confined to her dorsal stream was able to use shape to solve the discrimination task but was not able to use this property to guide her visuomotor performance. These results strongly suggest that in addition to location, orientation and size, shape is processed independently and separately by both the dorsal and ventral visual systems.
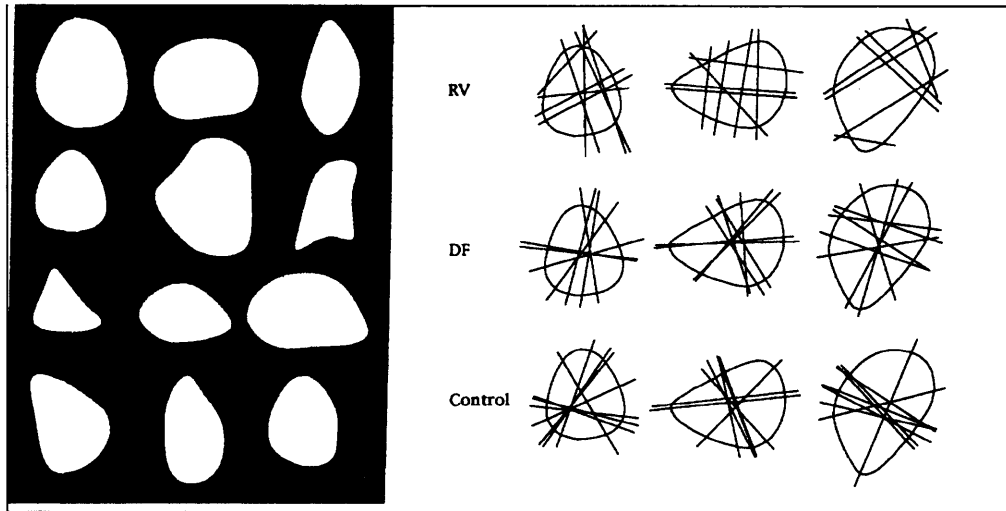
Figure 1.5. The asymmetrical shapes used by Goodale et al. (1994). Right: The straight lines joining the two landing points of the thumb and index finger.

1.5. Psychophysical Evidence in Normal Subjects

As seen above the dual-systems hypothesis proposed by Milner and Goodale (1995) is largely supported by neurophysiological studies in other species, in particular primates, and by neuropsychological studies with neurological patients. In addition to this, in the last few years a large number of studies carried out with neurologically intact subjects have provided further evidence for a dorsal/ventral functional specialization of visual processing in normal individuals. These studies found that various types of visual illusion affect perceptual performance but do not affect visuomotor responses.

1.5.1. Illusion of Size: The Ebbinghaus Illusion

In a widely cited study Aglioti, DeSouza and Goodale (1995) were among the first to provided clear evidence of a differential illusory size effect on perception and action in normal individuals.

Aglioti et al. (1995) tested participants with a modified (bottom Figure 1.6) and the original version (top Figure 1.6) of the Ebbinghaus illusion. In the top part of Figure 1.6 the central circles are of equal size but due to the different surrounding circles (hereafter referred to as annuli) the left central circle generally appears to be larger. In the modified version of this illusion the right central circle has been physically enlarged so that it appears to be equivalent in size to the left central circle. Thus, the two central circles are physically the same but perceptually different in the top part of the figure whereas they are physically different but perceptually the same in the bottom display. Finally, in Aglioti et al. (1995) the central circles were always three-dimensional whereas the annuli were two-dimensional and printed on paper.

Participants were presented with either the top or the bottom part of the display in Figure 1.6 and were asked to pick up the left circle if the two central circles appeared to be the same and to pick up the right circles if they appeared to be of different sizes. Maximum grip aperture, computed with optoelectronic equipment was used as a measure of the computation of size in the visuomotor system whereas the modified same/different discrimination task provided a measure of the accuracy of size perception.

The kinematic analysis revealed that participants adjusted their grip aperture as a function of the veridical size of the targets. MGAs were larger for the physically larger target in the bottom of Figure 1.6 whereas they were the same for the two targets in the top display of the figure. A different pattern was observed in the perceptual task where participants were more likely to judge as similar the two targets in the bottom display and as different the targets in the top version of the illusion. Aglioti et al. (1995) quantified the illusory effect on action by computing the difference between the MGAs for the two target disks in the perceptually-different displays. A small difference was found (less than 1.5mm) suggesting that action was not entirely immune to this illusion as originally predicted. However further analysis revealed that this difference was statistically smaller and more variable than the difference in disk size (about 2.5mm)

that participants required to judge the two targets as equivalent (i.e., a measure of the illusory effect on perception).

Taken together Aglioti et al. (1995) provide first direct evidence that the Ebbinghaus illusion, a size-contrast illusion, differentially affects perception and action. Participants were more likely to judge the two targets in the top of Figure 1.6 as perceptually different however they calibrated their grip according to the veridical size of the targets when they were asked to grasp them. Similar effects were observed with the bottom display. Most importantly, these results provide further support for the dual-systems hypothesis as they strongly suggest that the two systems differently process the visual information available from this type of display. They also suggest that in neurologically intact individuals visual information is processed separately and independently by the dorsal and ventral systems and that this phenomenon can be measured if the right conditions are created.
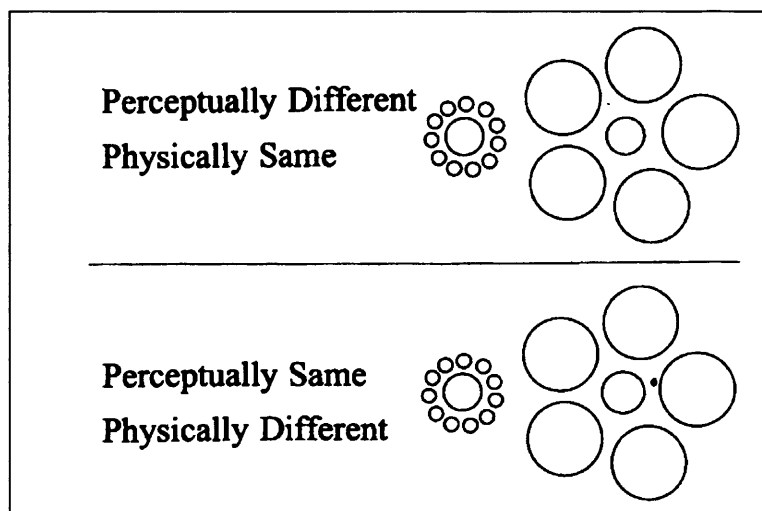
Figure 1.6. The Ebbinghaus illusion used by Aglioti et al. (1995). Bottom: The right central circle has been physically enlarged so that it appears to be equal to the left central circle.

1.5.2. Visual Feedback Cannot Account for a Differential Effect of the Ebbinghaus Illusion

In the last few years several authors, most notably Goodale, Haffenden and colleagues (e.g., Haffenden & Goodale, 1998) have successfully replicated the study by Aglioti et al. (1995). They have also controlled for two potentially confounding variables.

First, in Aglioti et al. (1995) the task was carried out in closed loop, that is with full vision of the hand and target. This could have allowed participants to adjust the aperture of their grip according to the size of the target during movement execution, reducing the effect of the illusion on action. The effect of on-line visual feedback will be further addressed in Section 1.7. Here it suffices to say that Aglioti et al. (1995) considered and discarded this possibility on the grounds that some evidence (e.g., Jeannerod, 1984) suggests that changes in the size and shape of the target need at least 500 msec to be processed and to affect movement. Given that MGA occurs at about 420 msec after movement initiation (Jeannerod, 1984), Aglioti et al. (1995) concluded that on-line visual comparison of hand and target could not be responsible for the accurate scaling of the grip aperture in this study. As we will see later, and as pointed out by Haffenden and Goodale (1998), other studies (e.g., Castiello & Jeannerod, 1991) have found that movement adjustments to changes in target size during movement execution only required 320 msec. These results open the possibility that the accurate visuomotor performance observed in Aglioti et al's (1995) study was, at least partly, due to the available visual feedback. The second criticism made by Haffenden and Goodale (1998) is that in Aglioti et al. (1995) perceptual performance was measured as a dichotomous variable (i.e., same/different task) whereas visuomotor performance was measured as a continuous variable (i.e., MGA).

Haffenden and Goodale (1998) replicated the study by Aglioti et al. (1995) under open loop conditions and using a continuous measure of perceptual performance, a manual estimation task. In this task participants were asked to provide a "manual read-out" of

the size of the target. The authors argued that this task, despite having a motor component, is largely driven by ventral representations. The evidence in support of this claim will be presented in Section 1.8.

In agreement with Aglioti et al. (1995), Haffenden and Goodale (1998) found that under open loop conditions MGA was not significantly affected by the Ebbinghaus illusion. Participants used significantly wider grip apertures when grasping the larger inner circles in the physically-different display and used the same apertures for both targets in the physically-identical display. An opposite pattern of results was found in the manual estimation task where the grip aperture was the same for both targets in the physically-different display and it was larger for the target surrounded by the smaller annulus in the physically-identical display.

Haffenden and Goodale's (1998) results further support the claim that the Ebbinghaus illusion has a differential effect on perception and action. More importantly, they rule out the possibility that the lack of an illusory effect on action is simply the result of adjustments of the grip aperture in-flight as a result of visual feedback from the moving hand and target. Finally, they provide further evidence that action *per se* is a necessary but not sufficient condition for activating the dorsal system. In this study, matching responses had a motor component but were nonetheless affected by the illusion suggesting that this kind of task is largely driven by ventral representations.

1.5.3. More Differential Effects on Perception and Action: The Müller-Lyer Illusion

Following the seminal work of Aglioti et al. (1995) a large number of studies have sought to find a dissociation between perception and action with a variety of visual illusions in neurologically intact individuals. As predicted by the results with the Ebbinghaus illusion, the large majority of these studies found that perception is

generally affected by visual illusions whereas action is not. A brief review of these studies is given below.
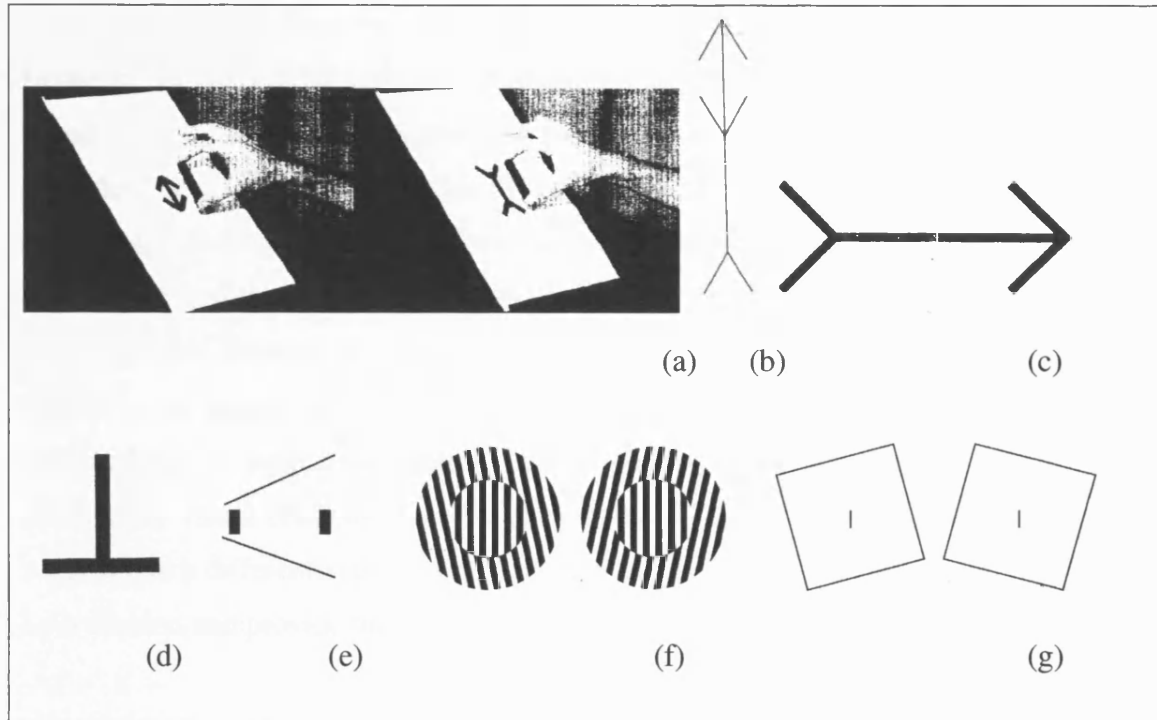
Figure 1.7. (a) The Müller-Lyer illusion, (b) the Brentano version of the Müller-Lyer illusion, (c) the Judd illusion, (d) the Horizontal-Vertical illusion, (e) the Ponzo illusion, (f) the Simultaneous-Tilt illusion and (g) the Rod-and-Frame illusion.

Together with the Ebbinghaus illusion, the Müller-Lyer illusion (see Figure 1.7) is one of the most investigated geometrical illusions. In this illusion, the two shafts between the arrows are of equal length although the shaft between the two arrowheads turned inwards is perceived to be shorter than the shaft between the arrowheads turned outwards.

Otto-de Haart, Carey and Milne (1999) investigated grasping and matching performance under binocular and monocular conditions with a 3D version of the Müller-Lyer illusion where a wooden bar was superimposed on the shaft of the display. Otto-de Haart et al.

(1999) directly compared performance in the open and closed configurations of this illusion that were presented simultaneously. These authors found that in the matching task, performed under both binocular and monocular conditions, the mean grip aperture was significantly greater for the open configuration than for the closed configuration. However, in agreement with the dual-systems hypothesis, no such a difference was found in the grasping task performed under binocular conditions. Under monocular conditions a marginally significant difference was found although this illusion effect was lost if a Bonferroni correction was applied to the significance level. Moreover, this latter effect can be accounted for by the claim that actions carried out under monocular conditions are likely to be driven by ventral networks (see Section 1.9). If this is the case, it is not surprising that Otto-de Haart et al. (1999) found an effect of the illusion on this type of actions as ventrally driven visuomotor responses are known to be affected by visual illusions. Thus, taken together Otto-de Haart et al.'s (1999) results suggest that a differential effect on perception and action can be found with the Müller-Lyer illusion and provide further support for the dual-systems hypothesis.

Similar results were found by Post and Welch (1996) who compared the accuracy of pointing responses towards the three crucial locations in the Brentano version of the Müller-Lyer illusion (see Figure 1.7) with responses towards the three corresponding locations in a control display. The display was created by black tape on Mylar and participants viewed the stimuli through a mirror. Post and Welch (1996) found that there was no significant difference between the mean pointing responses towards the Müller-Lyer and the control displays and concluded that pointing responses are not affected by this illusion. A measure of perceptual judgement was also taken and, in agreement with the dual-systems hypothesis, this revealed an illusion effect in the predicted direction.

1.5.4. More Differential Effects on Perception and Action: The Ponzo Illusion

The dissociation between perception and action has also been found with the Ponzo illusion. The Ponzo illusion (see Figure 1.7) is an illusion of size where two identical stimuli framed by two converging straight lines appear to be of different sizes, more specifically the element closer to the converging point appears to be bigger. Brenner and Smeets (1996) recently investigated the effect of the Ponzo illusion on the two visual systems. MGA was measured during a grasping task towards a circle either positioned nearer the converging point of the Ponzo inducing background or nearer the diverging point. In agreement with Milner and Goodale's (1995) model Brenner and Smeets (1996) found no effect of this illusion on action.

Similar results were found by Westwood, Dubrowski, Carnahan and Roy (2000) who compared the effect of the Ponzo illusion on perception and action with a manual estimation and a grasping task, respectively. MGA in the matching but not in the grasping task was affected by the illusion as apertures for the targets at the converging end of the Ponzo background were much larger than apertures resulting from grasping the same target positioned at the diverging side of the display. Similar results were subsequently reported by Jackson and Shaw (2000).

Taken together the above findings suggest that the Ponzo illusion has a differential effect on perception and action and provide further support for the dual-systems hypothesis.

1.5.5. Equivalent Illusory Effects on Perception and Action: The Müller-Lyer Illusion

In disagreement with Milner and Goodale's (1995) model, a number of studies in the last few years have reported that a variety of visual illusions affect both perception and action. The authors of these studies suggest that perception and action are guided by the same system, as it is more unlikely that two systems would be equally affected by the

same phenomenon. Importantly, they suggest that psychophysical evidence from studies with visual illusions do not provide evidence for the ventral and dorsal distinction in neurologically intact individuals. A review of some of these studies is given below.

Daprati and Gentilucci (1997) used a Müller-Lyer display with a 3D wooden bar superimposed on the shaft and compared the performance between two perceptual tasks, drawing and manual estimation, and a grasping task. As expected, an illusion effect was found in the two perceptual tasks. However, more surprisingly, MGA in the grasping tasks also revealed an illusion effect.

A similar effect of the Müller-Lyer illusion was also found on a pointing task reported by Gentilucci, Chieffi, Daprati, Saetti and Toni (1996). These authors presented participants with the two Müller-Lyer configurations plus an additional control display in which the fins at the end of the central bar were substituted by small lines orthogonal to the central bar. Participants had to execute a pointing movement from a starting disk to the more distant vertex of the stimulus and movement amplitude was measured as an index of the effect of the illusion. The analysis revealed that participants significantly undershot the closed configuration with respect to the control display. This suggests that the visuomotor system computed the movement for a closer location in the former display as the length of the shaft was underestimated in this stimulus. The converse pattern was observed for the open display. Participants significantly overshot this target with respect to the control stimuli suggesting that the movement was computed for a more distant location due to an overestimation of the length of the shaft. These patters of result are in agreement with the effect of this illusion generally found in perceptual tasks and suggest that the pointing task was affected by the Müller-Lyer display.

Taken together, the above findings are in disagreement with the dual-system hypothesis as they suggest that the Müller-Lyer illusion has an effect on action. However, it should be noted that in Daprati and Gentilucci (1997) the effect in the grasping task was much smaller than in the two perceptual tasks. More specifically, across-task comparisons

revealed that the illusion effect for the closed configuration was significantly smaller in the grasping task than in the manual estimation task, although this trend was not significant for the open configuration. Thus, to some extent, a differential effect on perception and action was found in this study. Moreover, none of the other kinematic parameters (e.g., maximum velocity) showed a significant effect of the illusion in the grasping task. Therefore, although these latter findings are not sufficient to reconcile Daprati and Gentilucci's (1997) results with Milner and Goodale's (1995) proposal, they suggest that more evidence is needed to draw clearer conclusion on the effects of the Müller-Lyer illusion on grasping.

1.5.6. Equivalent Illusory Effects on Perception and Action: The Judd and the Horizontal-Vertical Illusions

The dissociation between perception and action has also been investigated with the Judd illusion (see Figure 1.7), a variation of the Müller-Lyer illusion in which participants inaccurately bisect the shaft between two arrowheads that point in the same direction. The centre is misperceived to be more towards the opposite direction of the side in which the arrowheads point (Coren, 1986).

Ellis, Flanagan and Lederman (1999) used a 2D Judd display with a metal bar superimposed on the central segment joining the two arrowheads. In the perceptual task participants were asked to guide the experimenter in moving a marker to the centre of the metal bar whereas in the visuomotor task they had to grasp the metal bar at its centre. The position of the fingers on the bar was recorded with marked double sided tape that was transferred from the index finger to the bar during the task. Ellis et al. (1999) found an illusion effect on both perception and action as in both tasks participants were more likely to use a centre that was judged to be significantly displaced, with respect to the true centre, towards the opposite side of the direction of the arrowheads. However, similarly to Daprati and Gentilucci (1997), further analysis revealed that the illusion effect on perception was significantly greater than the effect on

action. Thus, Ellis et al.'s (1999) found a differential effect of the Judd illusion on perception and action.

More recently, Mon-Williams and Bull (2000) used stimuli and a data collection method similar to those used by Ellis et al.'s (1999) to investigate the effect of the Judd illusion on perceptual judgements and pointing under closed and open loop conditions. In the pointing task participants had to point to the middle of the bar reaching it from under a table. In agreement with Ellis et al. (1999), the statistical analysis revealed that, under closed loop conditions, although there was an illusion effect on pointing, it was significantly smaller than the effect on perceptual judgement. However, this difference was not found under open loop conditions and the difference between the illusion effects on the open and closed loop pointing tasks was significant. Mon-Williams and Bull (2000) concluded that a reduced effect of the illusion was found under closed loop because during reaching part of the illusory display became occluded by the limb, reducing the effect of the illusion. These authors claim that partial occlusion of the illusory display during reaching under closed loop conditions could also account for the reduced or non-existent effect of illusions on action found in several other studies.

Although this claim makes a valid criticism that should be investigated further, it can not account for previous studies that did not find an illusory effect on action under open loop conditions (e.g., Haffenden & Goodale, 1998: Kwok & Braddick, 2003). Moreover, it is not clear whether the type of movement chosen in their open loop condition, that is reaching from under a table, is a natural movement comparable to the visuomotor task used in their closed loop condition. As pointed out by Carey (2001), there should be concern about movements that are directed at targets that do not involve a "standard sensorimotor mapping" (p. 111). In reaching from under a table the movement initiates on a plane further away from the subject than the plane where the target lies. Given that it is not clear yet whether this type of movement involves a standard sensorimotor mapping, caution should be used in generalising the results obtained with this type of visuomotor responses.

Finally, the Horizontal-Vertical illusion (Avery & Day, 1969; see Figure 1.7) is another illusion of size that has been used to investigate the dual-systems hypothesis. In this display, where two orthogonal identical bars are positioned to form an inverted T display, the majority of participants report that the vertical line appears to be longer than the horizontal line. Vishton, Rea, Cutting and Nuñez (1999) measured grasping and perceptual performance under open loop conditions with a 2D version of the Horizontal-Vertical illusion. In disagreement with the dual-system hypothesis Vishton et al. (1999) found a small but significant effect of the illusion on action.

However, Vishton et al. (1999) used 2D and not 3D stimuli in the grasping task. As it will be discussed in Section 1.10, it is not clear yet whether visuomotor responses towards 2D targets are guided by dorsal representations. If actions towards 2D targets are guided by ventral representations, then it should not be surprising that this type of response is affected by visual illusions. This potential methodological bias taken together with the finding that the illusion effect on perception was much greater than the effect observed on action suggest that overall this study does not provide conclusive evidence against the dual-systems hypothesis.

1.5.7. Equivalent Illusory Effects on Perception and Action: Attentional Differences

Two recent studies (Franz, Gegenfurtner, Bülthoff & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti & Farnè, 1999) have made a significant criticism to the experimental paradigm used by Aglioti et al. (1995) and by Haffenden and Goodale (1998). Both Pavani et al. (1999) and Franz et al. (2000) suggested that the differential effect of the illusion on perception and action found in the above studies could be the result of attentional differences in the two tasks and not due to the fact that illusions are independently and differently processed by the dorsal and ventral systems. More specifically, Pavani et al. (1999) claimed that in the perceptual task used by Aglioti et al. (1995) and Haffenden and Goodale (1998) participants were asked to decide which

target was smaller or larger, that is they were asked to make a direct comparison between the two inner circles and determine the relative size of the target. By contrast, in the visuomotor task participants were asked to pick up only one target. Pavani et al. (1999) claimed that there is a different distribution of attention in the two conditions as in the former attention had to be divided between two targets whereas in the latter attention could be focussed on only one target. These authors claimed that this difference could account for the differential effect of the Ebbinghaus illusion on perception and action and devised an experimental paradigm to test this hypothesis.

Pavani et al. (1999) measured grasping and perceptual performance towards the two configurations of the traditional version of the Ebbinghaus illusion (top Figure 1.6) that were presented individually. In addition, participants were also presented with a "neutral" configuration in which the diameter of the target, the diameter of each circles in the annulus and their distance was of equal size. This latter display did not induce any size-contrast illusion and was used to test the degree to which the size-contrast inducing annuli altered the target size (that is, the effect of the illusion) in the traditional Ebbinghaus configurations.

An analysis of the data from the neutral configurations revealed that in the perceptual judgement task participants were more than 70% accurate. Similarly, MGA in the grasping task was significantly scaled according to the veridical size of the target to be grasped. These results suggested that when the size-contrast-illusion-inducing annulus was not present, participants were accurate at both estimating the size of the targets and at calibrating their grip aperture to grasp them. However, different results were found when the data from the neutral condition were compared with the results from the illusory inducing displays. In disagreement with the dual-system hypothesis, an effect of annulus type was found in the perceptual judgement task and in the grasping task. It is worth noting that the effects on action were either equal or greater than the effects found on perception.

Taken together Pavani et al.'s (1999) results provide evidence that, when presented individually, the configurations of the Ebbinghaus illusion can elicit very similar effects on both perception and action. Most importantly, they suggest that the differential illusory effect observed in previous studies (e.g., Aglioti et al., 1995) could be explained by the different attentional demands in the perceptual and visuomotor tasks.

Similar results were reported by Franz et al. (2000) who also found an effect of the Ebbinghaus illusion on perception and action when the two configurations were presented individually. Taken together the studies by Franz et al. (2000) and Pavani et al. (1999) do not support the dual-system hypothesis. More specifically, these results suggest that the differential illusion effect found on perception and action is not due to the existence of two separate visual systems but due to differences in the attentional demands in the perceptual and visuomotor tasks. When attentional demands were equal in the two tasks, the illusory effect on perception and action was very similar suggesting that these two responses are likely to be guided by a common visual system.

1.5.8. The Ebbinghaus Illusion Does Not Affect Action: The Effect of Annulus Distance and Obstacles

Haffenden, Schiff and Goodale (2001) subsequently investigated Franz et al.'s (2000) and Pavani et al.'s (1999) claim and reached different conclusions. Haffenden et al. (2001) proposed that the large illusion effect on action observed in these two studies could have been due differences in the distance between annuli and targets present in the traditional Ebbinghaus display. Franz et al.'s (2000) and Pavani et al.'s (1999) used the traditional version of the Ebbinghaus illusion where the distance between the inner edge of the large annulus and the circumference of the target disk it surrounds is much greater than the distance between the inner edge of the small annulus and the circumference of its target disk. Importantly, in the configuration with the large annulus there is a finger-width gap between the target and the annulus whereas this gap is much smaller in the configuration with the small annulus. Evidence suggests that MGAs from

precision grips towards targets that are separated by the surrounding elements by a finger-width gap are generally smaller than MGAs obtained from grasping either the target presented alone (Haffenden & Goodale, 1998) or a target separated by its surrounding elements by a smaller gap (Haffenden & Goodale, 2000a). Haffenden et al. (2001) suggested that the different MGAs obtained in Franz et al. (2000) and Pavani et al. (1999) could have been due not to an illusory effect on action but to the fact that participants opened their hand less in the Ebbinghaus configuration with the larger annulus, that is with the finger-width gap.

Haffenden et al. (2001) tested this hypothesis by comparing the MGAs obtained with the two traditional Ebbinghaus configurations and with a new (the "adjusted small") configuration where the small annulus was positioned in such a way that the distance between its inner diameter and the target was equivalent to the corresponding distance in the large annulus display. Importantly, both displays resulted in a finger-width gap. To further test the attentional account proposed by Franz et al. (2000) and by Pavani et al. (1999) these three configurations were presented individually and were tested in a manual estimation and grasping task.

An analysis of the MGAs from the manual estimation task revealed that participants opened their grips according to the expected size-contrast illusion. MGAs were wider for targets surrounded by the small annuli, regardless of the gap between the target and the inner edge of the annulus. By contrast, MGAs in the grasping task revealed no significant difference between the grip used for targets in the large annulus and in the adjusted small configurations. In agreement with the prediction, larger grips were used for the traditional small annulus configuration.

These results suggest that the illusion effect on action observed in Franz et al. (2000) and Pavani et al. (1999) was not the result of equal attentional demands in the perceptual and visuomotor tasks but due to differences in the distance between annuli and targets in the traditional Ebbinghaus display. A recent study by Kwok and Braddick

(2003) further support this claim as these authors did not find an illusion effect on grasping when the two configurations of the Ebbinghaus illusion had the same gap between the target and the inner edge of the annuli.

1.5.9. High-Level and Low-Level Illusions

In a recent article, Dyde and Milner (2002) proposed a modified version of the original dual-system hypothesis that could account for the effects of illusions on action found in some of the studies presented above. These authors pointed out that visual illusions are not a homogeneous phenomenon and that they can differ in many aspects, most importantly in the areas of the visual cortex where they are generated. Visual illusions largely generated in early visual cortex are likely the result of relatively simple visual mechanisms and are therefore often referred to as low-level illusions. By contrast, visual illusions largely processed in high-level visual areas are likely to depend on more complex mechanisms and are therefore referred to as high-level illusions. Dyde and Milner (2002) pointed out that because the anatomical separation between the dorsal and ventral visual systems is known to occur after V1, the effect of visual illusions generated in early visual cortex (i.e., low-level illusions) should be broadcast to both the dorsal and ventral systems. Consequently, this effect should be observed on both perception and action. By contrast, visual illusions generated in high level visual areas that belong largely to one (e.g., ventral) system should affect only tasks processed by this system (e.g., perception).

Dyde and Milner (2002) tested this hypothesis by measuring perceptual and visuomotor performance towards the 'simultaneous-tilt-illusion' (STI, see Figure 1.7) and the 'rod-and-frame' illusion (RFI, see Figure 1.7), a low- and a high-level illusion, respectively. In agreement with their predictions, the authors found an illusion effect on perception and action with the STI. An across subjects analysis further strengthened the claim that the effects of this illusion on perception and action was the result of the same mechanisms as a strong positive correlation between the magnitudes of the two effects

was found. The results from the RFI were also in agreement with the prediction as its effect was found only on the matching task, a measure of perceptual performance. Finally, a direct comparison between the effects of this high-level illusion on the two tasks was also statistically significant and a correlation analysis of the magnitudes of these effects did not reveal a shared component between these two measures.

These findings provide strong evidence that illusions thought to be generated at different levels of the visual system can differentially affect perception and action. In particular, visual illusions generated in early visual cortex, that is in areas common to the dorsal and ventral systems, are likely to be broadcast to both systems and to affect both perception and action. By contrast, illusions generated in high level areas of the ventral system like the RFI are likely to have a significant effect on perception only. Thus, this revised version of the dual-systems hypothesis can account for the effect of visual illusions on visuomotor responses, provided that these illusions are generated, or partly generated, in early visual cortex. This revised model can therefore account for some of the illusion effects found in several of the studies described above.

1.5.10. Conclusions from the Illusions Studies

The above review suggests that the large majority of studies that investigated the effects of illusions on perception and action are in agreement with the dual-system hypothesis. Visual illusions affect perception but not action.

The few studies that found an effect of a variety of illusions on action are not easily reconcilable with the claim that the dorsal system uses the veridical properties of the target to guide visuomotor performance. However, it can be argued that these findings do not provide conclusive evidence against the dual-system hypothesis. Firstly, it should be noted that in several of these studies the effect observed on action was smaller than the effect observed on perception (Daprati & Gentilucci, 1997; Ellis et al., 1999; Vishton et al., 1999). Thus, in agreement with the claim that visual information for

perception and action is processed by two different visual systems, a differential illusion effect was observed in these studies. Secondly, as discussed above, other factors such as the dimensionality (2D/3D) of the targets used for the visuomotor task (e.g., in Vishton et al., 1999) or whether the movement involved a standard sensorimotor mapping (e.g., in Mon-Williams & Bull, 2000) could account for the effect of illusions on visuomotor responses. Finally, the modified version of the dual-system hypothesis presented by Dyde and Milner (2002) could also account for some of the illusion effects in the above studies as it is likely that some of the illusions used are processed, at least partly, in early visual cortex.

Until these research questions are fully understood, for instance until clearer conclusions can be drawn on whether actions towards 2D stimuli are guided by the visuomotor system, the above results should be interpreted with caution. In particular, it should not be concluded that they provide conclusive evidence against the dual-system hypothesis.

1.6. The Role of Visual Feedback

A significant question that has been widely considered in visuomotor research is whether in a grasping task visual feedback of the hand, target or surrounding environment (e.g., distal objects) can affect the kinematic profile observed in prehension. In particular, it is of interest to establish whether the movement is pre-planned in advance of movement initiation or whether visual feedback modulates the adjustment of the parameters during movement execution. Several studies have investigated this question by comparing movements executed under full vision (i.e., closed loop) and under no vision of the hand, target or a combination of both (i.e., open loop).

Jeannerod (1981, 1984) was among the first to investigate this question by measuring the effect of distance and size on the transport and grasping components under both

open and closed loop conditions. Under open loop the hand was occluded from view by a semi-reflective mirror, but ambient light was left on and participants could see the stimuli reflected in the mirror. Various comparisons between the closed and open loop conditions did not reveal any significant difference in various movement kinematics. In a second study, Jeannerod (1984) compared closed loop with no-visual feedback (with occlusion of the hand only, as described above) and with a no-vision condition where both the hand and target were occluded during movement execution. Again, no significant differences were recorded except for a longer movement duration and deceleration phase in the closed loop condition. Importantly, the timing of the transport and grasping components remained unaffected by the manipulation of feedback and MGA continued to be scaled according to target size in all conditions. These results led Jeannerod (1984) to conclude that the coordination between the transport and grasping components observed in prehension is largely pre-programmed, that very little, if any, correction is carried out during movement execution and that the deceleration phase does not have an exclusive corrective function based on visual feedback as previously proposed.

More recently, Gentilucci, Toni, Chieffi and Pavesi (1994) used a mirror apparatus similar to that used by Jeannerod (1981, 1984) and found significant greater duration and MGAs in the no-visual-feedback condition. However, differences between the two studies could account for these discrepant results. Firstly, the kinematic variables in Jeannerod (1981, 1984) were measured with a video-camera-analysis whereas Gentilucci et al. (1994) used more reliable optoelectronic equipment. Secondly, Gentilucci et al. (1994) randomly varied the position of the target over 3 distances for all participants in all conditions whereas this was not the case in the Jeannerod's studies where distance was either varied only for a subset of the participants (Jeannerod, 1984) or only in one session (Jeannerod, 1981).

In Gentilucci et al. (1994) and in Jeannerod (1981), only the hand was occluded during movement execution and participants could see the target. Several other researchers

have compared the movement kinematics under full vision with those obtained from movements where vision of both the hand and the target was prevented. For instance, in Jakobson and Goodale (1991) a fluorescent light illuminating the experimental surface was turned off as soon as the movement was initiated. These authors found that removing visual feedback resulted in greater MGAs (on average 8 mm greater in open loop) and that MGA and maximum wrist height were achieved proportionately sooner in time.

Similar results were found in a study by Berthier, Clifton, Gullapalli, McCall and Robin (1996) who systematically investigated the contribution of visual feedback in a full vision condition, in a vision-of-target-only condition (obtained using a glow-in-the-dark object) and in a no-vision condition. In agreement with the above results it was found that reducing visual feedback yielded greater MGAs that occurred significantly earlier, smaller peak velocities and longer durations. Thus, in disagreement with the initial studies by Jeannerod (1981, 1984), recent evidence suggest that on-line visual information from the target and moving hand is used to adjust the grasp parameters.

It is worth noting that a possible confounding variable in the studies by Jakobson and Goodale (1991) and by Berthier et al. (1996), and necessarily so in any other study that created the open loop condition by switching off the light source, is the difference in ambient light between the open and closed loop conditions. Alterations in ambient light are likely to affect the information available to compute properties of the target like location (or even size and shape) allocentrically, that is with respect to the surrounding environment. A recent study by Connolly and Goodale (1999) controlled for this possibility and provide more conclusive evidence of the effect of visual feedback from the moving limb only. These authors found that when ambient light was equal in both the open and closed loop conditions, there were longer durations, acceleration and deceleration phases, and that MGA occurred significantly later under open loop. However, in disagreement with the above results no significant differences were found in the MGAs and maximum velocity from these two conditions.

Taken together, the above results do not provide conclusive evidence that preventing vision of the hand or hand and target during movement execution affects maximum grip aperture although there is some agreement that open loop conditions increase movement duration. As pointed out by Connolly and Goodale (1999), several possible confounding variables like ambient light and view of initial hand position could account for these discrepant results. Particularly, these differences could account for these discrepancies if a recently proposed model of manual prehension is considered. Glover (2004) proposes that manual prehension is mediated by two temporally overlapping stages: planning and control. The planning stage occurs prior to movement execution and, as proposed by the two-visual-system model of Milner and Goodale (1995), uses a large number of visual and cognitive factors to select a suitable target and how to grasp it according to its function. However, unlike the two-visual-systems model, Glover (2004) proposes that planning "also determines the initial kinematic parametrization of the movements, including their timing and velocity" (Glover, 2004; p.4). During movement execution, the kinematic parameters become increasingly and gradually dependent on the control stage, which is affected only by the spatial properties (i.e., real metrics) of the target. Importantly, in Glover's (2004) model, the initial kinematic parametrization of the movement can be affected by factors such as: (1) the distance between the effector and target, (2) the distance between the target and other objects and (3) the visual context surrounding the target object. Moreover, in Glover's (2004) model inaccuracies in the initial kinematic parametrization of the movement that arise from the planning phase can be corrected in the control stage, if there is sufficient time for this latter to fully control the movement.

Whether Glover's (2004) model provides a more accurate account of manual prehension than Milner and Goodale's (1995) model remains to be seen, and it is currently a topic of active debate (for full review see Glover, 2004). However, it is of interest to note that this model could account for some of the discrepancies observed in the above findings as factors such as the distance between the effector and target, the distance between this latter and other objects and the visual context surrounding it were not kept constant

across studies. Future research investigating the effect of visual feedback on manual prehension should carefully control for these factors. Moreover, the temporal dependency of the correction mechanisms suggests that these studies should also control for the potential confounding effect of differences in movement duration, for instance arising from differences in hand velocity or target location.

Other possible confounding variables such as propioceptive and haptic feedback should also be taken into account by future investigations. As it will be seen in the next section, proprioception and haptic feedback affect the movement parameters of prehension. When grasping in the dark (open loop) participants often misreach the target generating different haptic and proprioceptive signals than in the closed loop condition. These potential differences should be taken into consideration when measuring the effect of visual feedback.

1.7. The Role of Proprioception and Haptic Feedback

A detailed study of the role of proprioception in grasping was recently carried out by Gentilucci, Toni, Chieffi and Pavesi (1994). These authors compared the grasping responses of MB, a deafferented patient, with that of 5 normal control patients. Responses were studied under closed and open loop, in this latter condition vision of the moving limb was not available.

The comparison between the controls and MB revealed that, although there were no significant differences in the opening phase of the hand, the closure phase differed in several aspects, notably the variability of MB's grip aperture and duration were significantly greater than in the controls. This patient frequently reopened her fingers during the deceleration phase. In the transport component, acceleration and velocity up to peak velocity were similar to those of the controls whereas trajectory variability was much greater in MB. These results are in agreement with Jeannerod, Michel and Prablanc (1984) who found that the prehension profile of a deafferented patient was

normal only up to the first velocity peak. After this point the hand "wandered" and the grasp was not formed.

These findings suggest that proprioception is an important factor in modulating the deceleration phase of prehension. Notably, the finding that MB was still able to increase the aperture of her grip in the no-vision condition, that is in the absence of either visual or proprioceptive feedback, suggest that the aperture in the acceleration phase must be the result of feedforward processes only. These results are in agreement with the claim that the first part of the movement is preprogrammed whereas the deceleration phase is executed largely online (Gentilucci et al., 1994).

Gentilucci, Toni, Daprati and Gangitano (1997) provide evidence for the role of haptic feedback in prehension. These authors compared the kinematic profiles of neurologically intact individuals under normal open loop conditions and in open loop conditions where the distal phalanges of their index finger and thumb were anaesthetised. Tactile anaesthesia of the fingers removed haptic feedback but left proprioception unaffected. The results showed that anaesthesia affected the finger-opening phase of grasping as MGA and time to MGA significantly increased in this condition. Interestingly, the duration of the deceleration phase was only mildly affected. The transport component was also affected, as there was an increase in trajectory variability mostly in the deceleration phase.

The above results suggest that tactile signals are used by the visuomotor system to control the parameters of prehension. These conclusions are particularly relevant to studies that investigated the effect of visual manipulations on the kinematics of grasping. If, as seen above, haptic and proprioceptive feedback have an effect on the movement parameters, then this should be taken into account when designing studies that compare conditions that could differ in these aspects. For instance, it is often the case that under open loop conditions participants misreach the target, generating different haptic and proprioceptive feedback than under closed loop conditions. A

similar problem is present in the manual estimation task as this necessarily generates different haptic and proprioceptive feedback. Although some studies have controlled for these variables, for instance by asking participants to grasp the target after each manual estimation, the vast majority of research did not implement this procedure. Thus, it could be the case that some of the kinematic differences observed when comparing open and closed loop profiles or grasping and manual estimation responses could be partly due to differences in haptic and proprioceptive feedback. Future research investigating the effect of visual information on movement parameters should ensure that these potentially confounding variables are carefully controlled.

1.8. Pantomimed Action and Manual Estimation

The dual-systems hypothesis proposes that the visuomotor system processes visual information required for object-directed action whereas the visuocognitive system processes visual information for perception. However, it should be noted that action *per se* is a necessary but not sufficient condition for engaging the visuomotor system. At present, 3 types of actions have been identified that despite having a motor component they seem to be guided by ventral representations. Pantomimed-displaced actions, pantomimed-delayed actions and manual estimations suggest that in order to activate the dorsal system, action has to be immediate and object directed.

Goodale, Jakobson and Keillor (1994) provided the first systematic investigation of the kinematic profile of pantomimed-delayed actions in DF, the patient with visual form agnosia, and in normal sujects. In their first experiment, after a short initial viewing, normal participants were prevented from viewing the target for 2 sec during which the target was either removed or left in the same position. In the latter condition participants had to grasp the target (normal action) whereas in the former they had to pretend to grasp the target and direct the movement at the same location where the target was, prior to removal (pantomimed-delayed actions). The results showed that pantomimed-delayed actions yielded smaller MGAs that occurred proportionally earlier, lower peak

velocities, more curvilinear trajectories and tended to undershoot the target. These results suggest that pantomimed-delayed actions are not guided by the same representations that guide normal action. The observation that viewing the target after the 2 sec delay was sufficient to return to a normal kinematic profiles strongly suggests that the visuomotor parameters are computed *de novo* immediately before each action.

In a second experiment, Goodale et al. (1994) used a very similar procedure and compared the performance of normal subjects with DF, the visual form agnosic. They predicted that if pantomimed-delayed actions are largely modulated by representations within the ventral system, then DF should be impaired in this type of task. In agreement with the prediction, whereas DF's performance in the normal trials was within the normal range, she produced abnormal kinematic profiles in the pantomimed-delayed condition. In these latter trials, DF did not show any anticipatory hand shaping and failed to adjust her grip aperture according to the size of the target. These results can not be accounted for by the fact that in the delay condition there was no visual feedback from the removed target as DF can normally shape her hand in grasping tasks performed under open loop conditions. Further, the authors also tested the normal subjects and DF in a pantomimed-delayed condition with a 30 sec delay. No significant differences were found between the 2 sec delay and the 30 sec delay conditions for either normal subjects or DF further suggesting that the movement parameters in pantomimed-delayed actions, like in normal actions, are computed immediately before movement execution. If not, some deteriorating effect should have been observed in the 30 sec delay condition.

Taken together the above results suggest that pantomimed-delayed actions are guided by ventral representations as they produce kinematic profiles very different from those obtained with normal actions and DF, a patient known to have damage to her ventral stream is significantly impaired at this task. Moreover, they suggest that the movement parameters are computed *de novo* immediately before each pantomimed-delayed or normal action.

In the two experiments presented above pantomimed-delayed action is defined as delayed action towards the location of a removed target. However this procedure introduces a delay that alone could be responsible for the different kinematic profile obtained in this task. Goodale et al. (1994) provide first direct evidence that immediate actions to a location adjacent to the target are also guided by ventral representation. These authors found that when participants had to "imagine grasping an object" positioned nearby the target, they produced very different kinematic profiles than during normal grasps. Pantomimed-displaced grasps resulted in smaller MGAs and peak velocities, longer durations and greater displacements in the trajectory. The data from DF's responses strongly suggest that this type of action is also modulated by the ventral stream. Although she was slightly less impaired than in the pantomimed-delayed task, her performance in these pantomimed-displaced grasps was far from normal. Taken together, these results suggest that immediate action *per se* is not sufficient to engage the dorsal system and that action needs to be object directed.

Evidence from manual estimation tasks further support this latter claim. In this type of task participants are asked to estimate the size of the target by adjusting the distance between their index finger and thumb. It is important to note that in this task, although action is immediate, the hand remains either at or just above the starting point and it is not transported towards the target.

Goodale et al. (1994) provide evidence that manual estimation is dependent on ventral representations. These authors found that, although the manual estimations of normal subjects were scaled according to the size of the target, DF was unable to make correct estimations. Specifically, her grip aperture was not related to the size of the target suggesting that this task is largely modulated by the ventral stream, which is damaged in this patient. In addition, a large number of studies with visual illusions (see Section 1.5) further support this claim as manual estimation, like more traditional ventral tasks, is affected by visual illusions.

In summary, the above evidence suggests that action *per se* is a necessary but not sufficient condition to engage visuomotor representations. Actions must be immediate and object directed in order to be driven by the dorsal system. The ventral system takes over the control of actions that are either directed towards a location different from the location of the target or that are executed when a short delay is introduced between target offset and movement initiation.

Interestingly, the only study that tested whether pantomimed actions are affected by visual illusions used pantomimed-delayed actions (Westwood, Chapman & Roy, 2000). In agreement with the claim that pantomimed-delayed actions are driven by ventral representation, Westwood et al. (2000) found that these actions were affected by the Müller-Lyer illusion. As proposed below, it would be of interest to investigate whether pantomimed-displaced actions would also be affected by visual illusions.

1.9. The Role of Binocular Information

It is a well known fact that neurones in V1 and V2 are sensitive to binocular disparity (Poggio, Gonzalez & Krause, 1988). However, more recent neurophysiological evidence suggests that neurones in the parietal (e.g., Tsuitsui, Jiang, Yara, Sakata & Taira, 2001) and temporal (Uka, Tanaka, Yoshiyama, Kato & Fujita, 2000) association cortices also respond to binocular disparity signals. Given that some of these areas in the parietal cortex are part of the dorsal visual system, a number of authors have asked whether binocular vision is necessary for object directed action. Binocular cues could have several functional roles for prehension. For instance, they could contribute to the computation of target size and distances in the planning of movement. Additionally, during movement execution these cues could have a role for the computation of the location of potential obstacles and the position of the hand in space with respect to the target.

Servos, Goodale and Jakobson (1992) were among the first to find substantial difference in the kinematic parameters of prehension under monocular and binocular vision. Specifically, these authors found that monocular grasps resulted in smaller MGAs, lower peak velocities, longer durations and proportionally longer deceleration phases. Servos et al. (1992) concluded that subjects were underestimating the distance, and consequently the size, of the target under monocular viewing. Similar results were found by Marotta, Perrot, Nicolel, Servos and Goodale (1995) and by Servos (2000).

Neuropsychological studies with patients with visual form agnosia provide further evidence for the significant role of binocular cues in visuomotor behaviour. Marotta, Behrmann and Goodale (1997) investigated the grasping parameters of two patients with visual form agnosia, DF and JW, and of four control subjects under binocular and monocular vision. As discussed above visual form agnosics have damage to their ventral stream combined with normal visuomotor abilities. As seen in Servos et al. (1992), neurologically intact individuals performed more accurate grasping under binocular conditions. However, it is important to note that these subjects were able to grasp objects with no great difficulty under monocular conditions and could adjust their grip size according to the size of the target. Marotta et al. (1997) argued that under monocular conditions normal participants can use pictorial depth cues such as linear perspective, occlusion, texture gradient and shading to compute distance for visuomotor tasks. These pictorial cues available under monocular conditions are thought to be computed by the ventral system. Marotta et al. (1997) argued that if that was the case, patients with visual agnosia, known to be impaired at tasks that require the modulation of ventral mechanisms, should show an impairment under monocular conditions.

As expected, Marotta et al. (1997) found that under binocular conditions all subjects, control and agnosics, were able to scale their grip apertures according to object size. However, under monocular conditions the patients were much more impaired than the controls. Although DF's grip scaling was slightly better than JW's, her trial-to-trial variability was significantly increased. JW's performance was markedly deteriorated

under monocular conditions and both patients seemed to use retinal size to adjust their grip aperture in these conditions, for instance they used wider grips for nearer objects.

Taken together the above findings suggest that the visuomotor system uses binocular depth cues to compute the movement parameters (e.g., distance) under normal conditions. When binocular cues are not available, movement parameters can be adjusted according to pictorial cues that are processed by the ventral system. In agreement with these conclusions, patients with visual form agnosia show a greater impairment under monocular conditions as they are unable to use ventral stream processes.

Marotta, DeSouza, Haffenden and Goodale (1998) provide further evidence for the above conclusions as these authors found an effect of the Ebbinghaus illusion on both perception and action under monocular conditions. These results suggest that under monocular conditions, when binocular cues were not available, distance was computed using pictorial cues that were processed by the ventral system and that gave rise to the illusion. Further research should investigate whether this illusion effect observed under monocular condition is present with other pictorial illusions.

1.10. The Role of Target Dimensionality

Although a few studies have use 2D stimuli to investigate the functional properties of the dorsal system (e.g., Dyde and Milner, 2002; Vishton et al., 1999), a recent question in visuomotor research is whether actions towards 2D stimuli engage this system. It should be noted that visuomotor responses do not automatically activate the dorsal system, for example, as seen in Section 1.8. pantomimed actions are likely to be guided by the ventral system. Given that visuomotor responses such as grasping never occur towards 2D stimuli in the natural environment, it could be possible that the dorsal system has evolved to process only task-relevant, that is 3D, stimuli. From an

evolutionary perspective it would be computationally advantageous for the dorsal system to selectively process only task-relevant stimuli.

Westwood, Danckert, Servos and Goodale (2002) addressed this question directly by presenting DF, the visual form agnosic, and five control subjects with a set of 3D rectangles (the 3D condition), with a set of computer generated 2D images identical to the top surface or the 3D set (the 2D condition), and with a set of images of the 3D set taken with a digital camera (2D-enhanced condition). In the grasping task participants had to pick up, or pretend to pick up in the case of 2D and 2D-enhanced stimuli, the target. An analysis of this data revealed that DF's maximum grip aperture was significantly and linearly related to the veridical size of the target in all 3 conditions. In addition, these MGAs did not significantly differ from each other. Given that DF is severely impaired in tasks guided by the ventral system, the above results suggest that DF used dorsal mechanisms to guide her movements with the 2D stimuli. In agreement with previous findings, the results from the manual estimation task revealed that DF's MGAs were not correlated with the veridical size of the object in any of the three conditions.

Different results were obtained for the control participants. Although MGA was related to the veridical size of the target in all conditions for both the perceptual and visuomotor tasks, in the grasping task the MGAs from the 2D and 2D-enhanced conditions were significantly smaller than the MGAs from the 3D targets. However, this effect was found only for three participants. Westwood et al (2002) concluded that, at least in DF, actions towards 2D targets are guided by the dorsal system and that this does not substantially discriminate between 2D and 3D targets. However, the pattern of results from the normal subjects suggests that there are some quantitative differences between actions towards 2D and 3D targets. Westwood et al. (2002) proposed that at the response selection phase, before movement execution, some participants chose to use 'natural' movements with 2D and 2D-enhanced targets. By contrast, some other

participants recognized that they could not generate a natural grasp with these stimuli and chose to use as pantomimed grasp that was guided by ventral representations.

More recently, Kwok and Braddick (2003) investigated the movement kinematics of a grasping and a manual estimation task with the Ebbinghaus illusion where the central targets were either 3D or 2D. Kwok and Braddick (2003) found that, irrespective of dimensionality (2D or 3D), an illusion effect was found for manual estimation but not for grasping. Given the similar effect of the illusion, these authors concluded that the mechanisms used to guide actions towards 2D and 3D stimuli are fundamentally the same. However, it should be noted that, similarly to Westwood et al. (2002), Kwok and Braddick (2003) found that the MGAs obtained in the 3D condition were significantly larger than those obtained with the 2D targets suggesting that there are some quantitative, if not qualitative, differences between the kinematic profiles obtained with these two types of targets.

Hu, Eagleson and Goodale (1999) provide some compelling evidence that the 3D structure of the target plays a significant role in prehension. These authors presented participants with 3D objects of different dimensions that were aligned either according to the bottom or top surface on the horizontal plane or according to the far or near surface on the vertical plane (see Figure 1.8). Participants were instructed to grasp the target along its width, the only 'relevant' dimension of the target. Hu et al. (1999) found that maximum grip aperture increased as a function of target width, regardless of alignment, however it also changed according to target height, in this task an irrelevant dimension. Moreover, hand elevation also varied as a function of object height, but only when the targets were aligned along the bottom surface. This effect was not found when the targets were aligned according to their top surface. Hu et al. (1999) proposed that the increase in hand elevation ensured that the index finger and thumb did not collide with the top of the target during movement execution. This would explain why the same elevation was used when objects of different heights were aligned along their top surface. Importantly, these results suggest that hand elevation varied not as a function of

target height but as a function of the location of the top surface in a 3D space. Finally, maximum wrist velocity was found to be dependent on the location of the far surface of the target. These latter results were also reported by Servos, Goodale and Jakobson (1998).

Hu et al. (1999) argued that the above results could be possible only if the visuomotor system took the entire geometry of the target and its location in 3D space into consideration when computing the movement parameters. Most importantly, they suggest that 3D structure has a substantial role in prehension. If this is the case, it could be possible that actions towards stimuli that lack such a 3D structure (e.g., 2D stimuli) are guided by the ventral system. Although this explanation could neither account for the absence of an illusion effect for grasps aimed at 2D stimuli (Kwok & Braddick, 2003) nor for DF's ability to adjust grip aperture according to the size of these stimuli (Westwood et al., 2002), it could explain the smaller MGAs reported for this condition by both groups.

Taken together the above evidence does not allow clear conclusions to be drawn on whether 2D stimuli engage the dorsal visual system. Further research will hopefully provide some answers for this important methodological question.
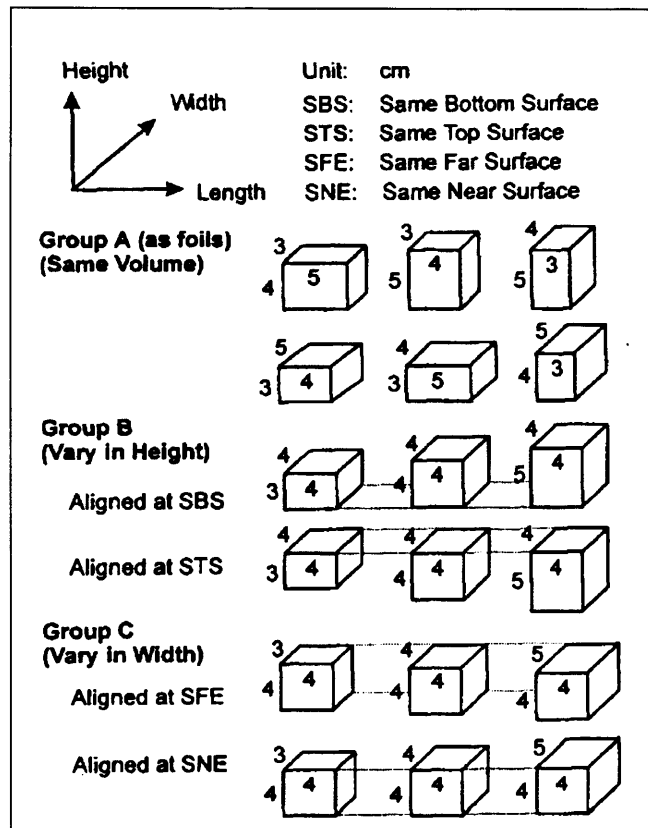
Figure 1.8. The stimuli used by Hu et al. (1999) illustrating the alignments according to top and bottom surfaces (middle rows) and near and far surfaces (bottom rows).

1.11. Is Colour Processed by the Dorsal Visual Stream?

Whether colour affects visuomotor tasks is of primary importance as area V4, the "colour centre" identified in the macaque brain (Zeki, 1993) is unambiguously seen as part of the ventral rather than the dorsal system (Milner & Goodale, 1995). In addition to this anatomical distinction, colour does not seem to have a significant functional role for object directed action in that it is difficult to see how different colours would change movement parameters like grip aperture or maximum velocity.

Some recent evidence from single cells studies in the macaques suggests that chromatic input can modulate the responses of directionally selective neurones in the middle temporal cortex (MT), an area that belongs to the dorsal system (e.g., Thiele, Dobkins & Albright, 1999). In addition, Blum (1995) found colour sensitive cells in area 7a of the inferior parietal lobe in rhesus monkeys, an undisputedly dorsal area. Thus, the above evidence suggests that colour is processed to some extent by the dorsal system and that it could affect the movement parameters not indirectly, via ventral representations as suggested by some authors (e.g., Haffenden & Goodale, 2000b) but more directly, because it is represented in this system.

Gentilucci, Benuzzi, Bertolani and Gangitano (2001) provide some evidence for this claim. These authors investigated the effect of chromaticity on the transport and grasping components, more specifically they predicted that colour, as an intrinsic property, would affect more grasping than reaching. Gentilucci et al. (2001) used psychophysical findings that suggest that red objects are often estimated to be larger than green objects (e.g., Tedford, Bergquist & Flyn, 1977) and predicted that if the visuomotor system represents chromaticity, then the same effect should be observed on grip apertures. In agreement with the prediction, when the stimuli had identical lightness values and differed only in chromaticity, MGA was significantly greater for red than for green targets and no effect of colour was found for the transport component. Moreover, no effects on grasping and reaching were found for stimuli that differed in lightness but not in chromaticity. Taken together these results suggest that chromaticity affects the grasp parameters of prehension, in particular maximum grip aperture. Most importantly, they suggest that colour is not exclusively processed by the ventral stream but that it is represented by dorsal representations.

1.12. Experimental Questions Addressed in the Thesis

This thesis is broadly divided into three parts that explore questions related to the two-visual-systems model.

The first part investigates whether the dorsal system processes only the veridical properties of the target object or whether it has access to information resulting from filling-in cortical processing. Specifically, Experiment 1 tests the claim that visual illusions generated in cortical areas that precede the anatomical separation between the two systems should affect both perception and action (Dyde & Milner, 2002). This is assessed by measuring whether information about Kanizsa illusory contours is used in manual prehension by comparing the kinematic parameters from grasps to 2D luminance-defined and Kanizsa squares. Two control conditions assess the effect of target dimensionality and the possibility that the luminance-defined contours in the Kanizsa display are sufficient to correctly adjust grip aperture. This experiment assesses the localization accuracy of luminance-defined and interpolated contours as represented in the dorsal visual system. However, another possibility is that these contours are localised in the ventral system and then made available to the dorsal system for the control of the movement. Such an account would require that the localization of interpolated and luminance-defined contours is equally accurate in the ventral visual system. This possibility is explored in Experiment 2 with a three-line Vernier acuity task with reference elements consisting of luminance-defined lines, pacmen or crosses. Finally, Experiment 3 explores whether another type of visual interpolation, the interpolation of occluded regions in partially occluded objects, is available to the dorsal system for the computation of the kinematic parameters in manual prehension. This is assessed by comparing the kinematic parameters of grasps to entirely visible and partially occluded targets. In this latter condition, the contact point on the shape for the index finger is occluded, thus, correct adjustment of grip aperture with these stimuli would suggest that the dorsal system has access to an interpolated representation of the target object that includes the occluded region. One additional condition controls for the effect of removing haptic feedback from the index finger and another assesses whether the interpolation of the missing region occurs in the absence of occlusion cues.

The second part of the thesis explores the effect of target dimensionality on grasping. Specifically, Experiment 4 examines the possibility that the illusion effect on action

previously reported by some authors could be due to additional ventral stream participation in the visuomotor task that could have been recruited by the presence of 2D inducing element in the illusion display. This possibility is assessed by measuring the effect of the Diagonal Illusion (DI) on grasping. The DI is generated by a display that is entirely three-dimensional, thus an illusion effect on grasping with these stimuli would rule out the possibility that the illusion effects on action previously reported could be exclusively due to the presence of 2D inducing elements in the display. However, in this experiment the two shapes generating the DI differ in some of their physical dimensions and this could affect the kinematic variables. Experiment 5 controls for this possibility by replicating Experiment 4 with a DI display where the graspable elements of the display are identical for the two shapes. Experiment 6 directly compares the kinematic parameters from grasps to 3D, 2D and 2D-enhanced (2D with added pictorial depth cues) versions of the DI to explore whether the dorsal system is equally engaged by these stimuli.

Finally, Experiment 7 explores two methodological questions still unaddressed in visuomotor research. First, whether differences in haptic feedback in manual estimation and prehension could account for some of the differences observed in these tasks is assessed by comparing maximum grip apertures from manual estimations with manual estimations followed by grasping the shape. This latter condition introduces regular haptic feedback comparable to that found in a grasping task. Second, the experiment explores the possibility that misreaching in open loop grasping tasks could result in different haptic feedback and therefore account for some of the differences reported between this task and closed loop grasping. This question is examined by comparing the traditional version of an open loop grasping task with the same task in which each trial is followed by closed loop grasping. This latter condition introduces regular haptic feedback comparable to that generated in closed loop grasping.

The third part of the thesis seeks to find evidence of ventral visual processing in rats as a preliminary attempt to establish whether these subjects could provide a suitable model

for further investigating the dorsal and ventral visual systems. In its original form, the two-visual-systems model suggests that in humans visual illusions are processed by the ventral but not by the dorsal visual system. Thus, evidence that rats perceive visual illusions would provide preliminary support for the claim that ventral visual processing comparable to that postulated for humans occurs in this species. Experiment 8 tests this claim with a manually operated dual-discrimination box by measuring whether rats perceive Kanizsa illusions. Experiments 9 and 10a replicate this experiment with a more stringent counterbalancing procedure and an automated discrimination box with a touch-screen and computer generated stimuli, respectively.

Experiments 10b, 10c, and 11 use the automated apparatus developed for Experiment 10a to explore whether rats are capable of object recognition qualitatively similar to that found in humans. Specifically, these experiments measure whether rotation-, size- and location-independent object recognition occurs in this species. In the two-visual-systems model, shape constancy is observed only in ventral visual processing, where the representations of objects are allocentrically coded and based on relative metrics. Thus, evidence of shape constancy in rats would provide preliminary evidence that this species is capable of visual processing comparable to that known to occur in the human ventral visual system.

2. Experiment 1 – Grasping Kanizsa Squares: Contour Interpolation in Manual Prehension I

2.1. Introduction

The aim of this experiment was to establish whether information about Kanizsa illusory contours is used in visually guided manual prehension.

As discussed in Chapter 1, the equivalent effect of visual illusions on perception and action reported by some studies (Daprati & Gentilucci, 1997; Ellis et al., 1999; Franz et al., 2000; Mon-Williams & Bull, 2000; Pavani et al., 1999; Vishton et al., 1999) is not easily accounted for by the two-visual-systems model in its initial form. In particular, these results are difficult to reconcile with the model's prediction that, due to the need for accuracy in functional visually guided action, the dorsal system processes only the veridical properties of the target (Milner & Goodale, 1995). However, as pointed out by Dyde and Milner (2002) and Milner and Dyde (2003), this prediction rests on the assumption that visual illusions operate in high level visual areas that belong exclusively to the ventral visual system. These authors recently argued that visual illusions are not a homogeneous phenomenon and that illusions generated in areas that are common to both systems, for instance because they precede their anatomical separation, should affect both perception and action. In support of this claim, Dyde and Milner (2002) found that the rod-and-frame illusion (RFI), an illusion thought to be largely the result of contextual influences operating in the ventral system, affected only perception. By contrast, also as predicted, the simultaneous-tilt-illusion (STI), a phenomenon thought to be the result of short-range inhibitory interactions in V1, affected both perception and action.

Dyde and Milner's (2002) results provide the first direct evidence that visual illusions generated in areas that are common to both systems can affect both perception and action and could therefore account for some of the illusion effects on action reported by previous studies. More importantly, Dyde and Milner's (2002) findings clearly demonstrate that the dorsal system is not limited to processing the veridical properties of the target, that is, properties directly derivable from the luminance distribution on the retina, but that it can process other signals generated by cortical visual processing if these occur in early areas. This is a significant finding as it opens the possibility that other visual illusions, or phenomena, not explicitly represented at a retinal level could be used in the control of visually guided action.

The present experiment further explores Dyde and Milner's (2002) claim by measuring whether Kanizsa contours, a visual illusion thought to be largely the result of mechanisms operating in V1 and V2 (Peterhans & von der Heydt, 1989), are used in the control of manual prehension.

2.1.1. Kanizsa Contours as a Low-level Phenomenon

Real static contours are perceived at regions of discontinuity in luminance, chrominance, or texture between two adjacent surfaces. Kanizsa contours (Kanizsa, 1979; Figure 2.2a) are illusory as they are perceived in the absence of a discontinuity in any of these stimulus parameters. At present the relative contribution made by low- and high-level factors to the perception of illusory contours is still a matter of debate (Davis & Driver, 1998; Lesher, 1995; Petry & Meyer, 1987; Spillman & Dresp, 1995), however, converging evidence suggests that low-level mechanisms are likely to play a major role in generating this phenomenon.

For instance, psychophysical studies have found that the strength of the illusory contour is affected by low-level factors such as the support ratio (i.e., the ratio between the luminance-defined contour supported by the inducers and the total contour; Shipley & Kellman, 1992) and the luminance contrast between inducers and background (Shapley

& Gordon, 1985). Moreover, as discussed in Chapter 3, Vernier acuity studies suggest that illusory contours interact with real contours in the hyperacuity range in ways that could be accounted for by early visual mechanisms (Danilova & Kojo, 2001; Dresp & Bonnett, 1991, 1993, 1995; Greene & Brown, 1996).

Evidence that monkeys (Grosof et al, 1993; Ramsden et al., 2001; Peterhans & von der Heydt, 1989) cats (Bravo, Blake & Morrison, 1988; De Weerd, Vandenbussche, De Bruyn and Orban, 1990), owls (Nieder & Wagner, 1999) and honeybees (Horridge, Zhang & O'Carrol, 1992; van Hateren, Srinivasan & Wait, 1990) behaviourally respond to illusory contours further support a low-level account as these studies suggest that the perception of illusory contours might be a general capability across species and present in organisms with arguably simpler high-level mechanisms (for reviews, see Nieder, 2002; Ohzawa, 1999).

Single cell neurophysiology provides more direct evidence for the role of early visual areas in the representation of illusory contours as responses to illusory contours in areas V1 and V2 have been reported in monkeys (e.g., Grosof et al, 1993; Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; Ramsden et al., 2001; Peterhans & von der Heydt, 1989) and cats (Redies, Crook & Creutzfeldt, 1986; Redies, 1989; Sheth, Sharma, Rao & Sur, 1996). Peterhans and von der Heydt (1989) proposed one of the most influential and complete neurophysiological models of illusory contour perception. These authors found that a good proportion (32%) of orientation-selective cells in V2 of behaving monkeys showed selective activation for both luminance-defined and 'anomalous contours' as shown in Figure 2.1b, although activity had different strengths and often different orientation selectivity for the two types of contours. Peterhans and von der Heydt (1989) proposed that these "contour cells" could sum two different signals generating from the same patch of the retina. Specifically, one signal generating from oriented cells selective for luminance-defined lines and the other from end-stopped neurons. These latter are known to respond to line-ends or corners (Hubel & Wiesel, 1968) and in the model they would activate the contour cell only when active in pairs. Figure 2.1b shows how the inducers of a Kanizsa display could activate end-stopped

neurons. Peterhans and von der Heydt's (1989) model suggests that inducer collinearity and edge alignment play a major role in the perception of illusory contours.
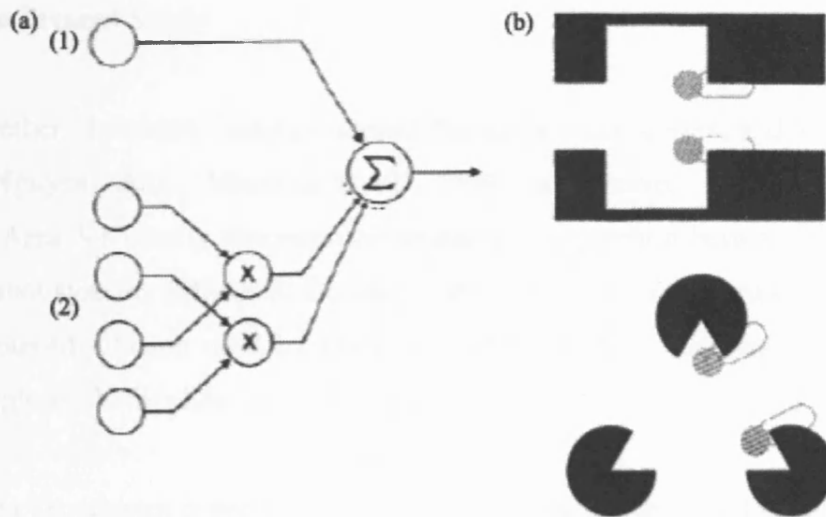
Figure 2.1. (a) Schematic representation of Peterhans and von der Heydt's (1989) model. The "contour cell" (Σ) receives input from an orientation-selective cell (1) and from a pair of end-stopped cells (2). (b) Top: An example of the stimuli used by Peterhans and von der Heydt (1989). Bottom: Diagram illustrating how Kanizsa inducers could activate end-stopped cells. Adapted from Peterhans and von der Heydt (1989).

More recently, Lee and Nguyen (2001) found selective activation for Kanizsa contours in V1 of monkeys, although these cells responded to a lesser extent and with a greater latency than V2 (120-190 msec and 70 msec, respectively). Lee and Nguyen (2001) proposed a 2-stage model in which illusory contours would be initially processed in V2, where large receptive fields could easily integrate information from pools of cells, and then fed back to V1, where neurones with smaller receptive fields could construct a more accurate spatial representation.

In agreement with the above findings, a recent functional neuroimaging study found retinotopic specific activation in human V1 and V2 upon presentation of Kanizsa shapes

(Mendola, Dale, Fischl, Liu & Tootel, 1999). Although in this study the signal was stronger in higher areas (V3A, V7, V4v and V8), these results clearly strengthen the claim that early visual cortex is involved in the processing of Kanizsa illusions.

2.1.2. The Present Study

Taken together, the above findings suggest that early visual cortex, and V1 in particular (Lee & Nguyen, 2001; Mendola et al., 1999), is involved in processing illusory contours. Area V1 clearly precedes the anatomical separation between the dorsal and ventral visual systems (Milner & Goodale, 1995), therefore, in an analogous way to the simultaneous-tilt-illusion used by Dyde and Milner (2002), Kanizsa contours can be used to explore whether low-level illusions affect the control of visually guided action.

The present experiment tested this claim by comparing grasps aimed at Kanizsa (Figure 2.2a) and 2D luminance-defined squares (Figure 2.2b). In these conditions, grip aperture had to be adjusted relative to an illusory and luminance border, respectively. Specifically, participants had to grasp the Kanizsa squares along their illusory borders, that is, along the illusory brightness contours generated by the illusion, and the 2D luminance-defined squares along their luminance gradient. Grip aperture is known to be related to the veridical size of the target when this is specified by a luminance gradient (Jeannerod, 1981). Thus, a lack of differences between these two conditions would suggest that grip aperture was scaled according to the size of the illusory shape with the Kanizsa stimuli and, by implication, that the interpolated signal was available to the dorsal visual system for the calibration of the kinematic parameters.

Three-dimensional Kanizsa figures have been previously used (Kojo, Liinasuo & Rovamo, 1994), however these stimuli require carefully controlled viewing and lighting conditions. In this study, it was decided to retain natural unconstrained movements and accordingly, 2D Kanizsa stimuli were used. In order to maintain the same haptic feedback, 2D luminance-defined squares rather than 3D stimuli were used for the comparison. However, performance with 3D squares was also measured and compared

with the 2D luminance-defined stimuli in order to assess the effects of target dimensionality (2D vs 3D) and haptic feedback. As discussed in Chapter 1, both factors have been found to affect the kinematic parameters of manual prehension (Gentilucci et al., 1997; Westwood et al., 2002).

A final set of stimuli (Crosses, Figure 2.2c) controlled for the possibility that the supported contour in the Kanizsa display could have been sufficient for the accurate calibration of the grasp. These stimuli had the same supported contours as the Kanizsa stimuli but did not generate the illusory squares and grip aperture had to be adjusted according to an imagined prolongation of the inner contours of the horizontal elements forming the crosses. Accordingly, grip aperture with these stimuli should have been less related to the size of the target. Finally, in order to assess the effect of visual feedback grasping was recorded under both open and closed loop conditions.

2.2. Method

2.2.1. Design

This was a repeated measures design as participants performed in all conditions. Conditions were individually presented in blocks of 24 trials consisting of 8 trials for each of the 3 sizes. Stimulus presentation followed a different pseudorandom order for each block with the constraint that the same size was not repeated for more than 3 consecutive trials. Conditions were grouped under closed and open loop sets and their order of presentation was counterbalanced across subjects. Within these sets, conditions were further counterbalanced according to the same Latin Square arrangement. In total, each participant performed 192 trials, 96 for each viewing set.

2.2.2. Participants

Thirteen participants took part in the study. Of these, four were discarded due to loss of marker values. The data analysis was carried out on 9 participants (4 females and 5 males, age range 20 - 39 years). They all had normal or corrected-to-normal self-reported visual acuity, stereo vision ≤ 120 min arc (TNO, Laméris, Utrecht) and were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave informed consent and were paid to participate in the study.

2.2.3. Apparatus and Materials

2.2.3.1. Stimuli

Kanizsa condition: The stimuli in this condition consisted of four black circles each having a missing quadrant (the inducers) and positioned with these latter facing each other (Figure 2.2a). The circles were printed on a white background and their configuration created the impression that they were partly occluded by a white square (hereafter referred to as the Kanizsa square). The diameter of the notched circles was 18.45, 23.06 or 27.68 mm and the linear distance between the centres of a pair of these inducers was 40, 50 or 60 mm, respectively. These measurements resulted in the same support ratio (4.6, see Section 2.1) for the three sizes. The stimuli were printed on white squared paper cards ($160g/m^2$) whose side was varied according to the size of the Kanizsa square to maintain the distance between the side of the square and the nearest edge of the card constant at 7 cm, irrespective of target size. Accordingly, the cards used with the 40, 50 and 60 mm Kanizsa squares had a side of 180, 190 and 200 mm, respectively. The inducers were positioned so that the Kanizsa square was centred on the card.
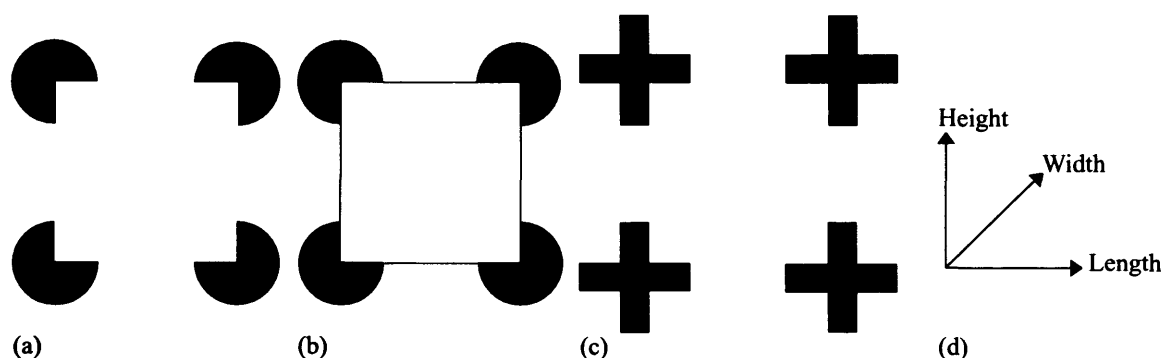
Figure 2.2. Stimuli used in the (a) Kanizsa, (b) 2D luminance-defined and (c) Crosses conditions for the 60 mm targets. In the 3D condition a clear Perspex square was superimposed to the 2D stimuli. (d) A reference system showing the grip axis (width).

2D (luminance-defined) condition: The stimuli in this condition were as in the Kanizsa condition except that the inducers were joined by black lines 0.28 mm wide (Figure 2.2b).

3D condition: The stimuli in this condition were identical to the 2D stimuli except that squares made of clear 6 mm thick Perspex were superimposed to the printed 2D squares. A thin black line (approximately 1 mm wide) marked the contours of the Perspex squares.

Crosses condition: The stimuli in this condition were obtained as in the Kanizsa condition except that the inducers were replaced by crosses (Figure 2.2c). The orthogonal distance between the internal contours of the arms forming the crosses was 40, 50 or 60 mm and this corresponded to the "size" of the imaginary square. The width and length of the arms for the 3 sizes were varied to maintain the ratio of these measures to the side of the imaginary square constant for all stimuli (0.15 and 0.61, respectively). As for the Kanizsa stimuli, the support ratio was 4.6 for all sizes and the distance between the side of the imaginary square and the nearest edge of the card was 7 cm. The crosses were positioned so that the imaginary square was centred on the card.

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2.2.3.2. Apparatus and Set-up

The positions of the index finger, thumb and wrist during movement execution were recorded with an ELITE (BTS, Milan) motion tracking system. Two infrared light-emitting cameras recorded the barycentre of infrared light-reflecting hemispherical markers, 6 mm in diameter, that were placed on the index finger, thumb and wrist. The positions of the markers were sampled at a frequency of 50 Hz and their 3D position was reconstructed off-line. The resolution of the ELITE varies as a function of marker size and of their distance from the cameras. In this study the spatial resolution of the system was assessed with a method suggested by Haggard and Wing (1990). Two markers attached to a flat disk were moved and recorded for 500 msec for a total of 8 trials. The mean maximum variation of the distance between the 2 markers was used as the spatial resolution of the system and this was calculated to be 0.43 mm. A schematic representation of the set-up is shown in Figure 2.3.

2.2.4. General Procedure

For all participants stereoscopic vision and handedness were assessed at the beginning of the session. The stimulus cards were aligned along the vertical midline of a white experimental surface (908 × 648 mm) so that their lower edge was 150 mm from the centre of the Start button (18 mm in diameter). Participants stood in front of the table to allow a "bird's eye view" of the workspace with the stimuli centred along their midsagittal plane.

Three 6-mm markers were placed with surgical tape on the inner corner of the nail of the index finger and thumb and on the wrist, approximately at the location of the styloid process of the radius. Movements were recorded for 2 seconds, from shortly before the verbal cue signalling movement initiation was given, and analysed off-line. The emphasis was placed on performing movements as naturally and as accurately as possible, in particular on using a natural speed.

At the beginning of each condition, participants performed 6 practice trials, two for each of the three sizes. In a pre-test phase, participants were presented with the Kanizsa stimuli and asked to report what they saw. This procedure ascertained that all participants perceived the illusory squares before testing. The open and the closed loop blocks were separated by a 5-minute break.

2.2.4.1. Closed Loop Grasping (CL)

In the closed loop procedure the task was performed under normal lighting conditions with full vision of the hand and stimuli throughout the movement. At the start of each trial, the participant grasped the Start button with the index finger and thumb close together and kept his/he eyes closed. At the verbal cue "go", the participant was instructed to open the eyes and to look at the stimuli and "as soon as ready" begin the movement. The participant's task was to reach out and grasp the square front-to-back (Figures 2.2.d and 2.3), using a precision grip. In the 3D and 2D conditions the participant was instructed to grasp, or pretend to grasp in the case of the 2D stimuli, the Perspex and 2D printed square, respectively. In the Kanizsa and Crosses conditions the participant was instructed to pretend to grasp the imaginary square formed by the prolongation of the horizontal edges of the pacmen or of the inner edges of the horizontal elements of the crosses, respectively (Figure 2.3). After each grasp, the index finger and thumb were maintained on the target until the verbal instruction "ok" signalled the end of trial and that the participant could return to the Start position.
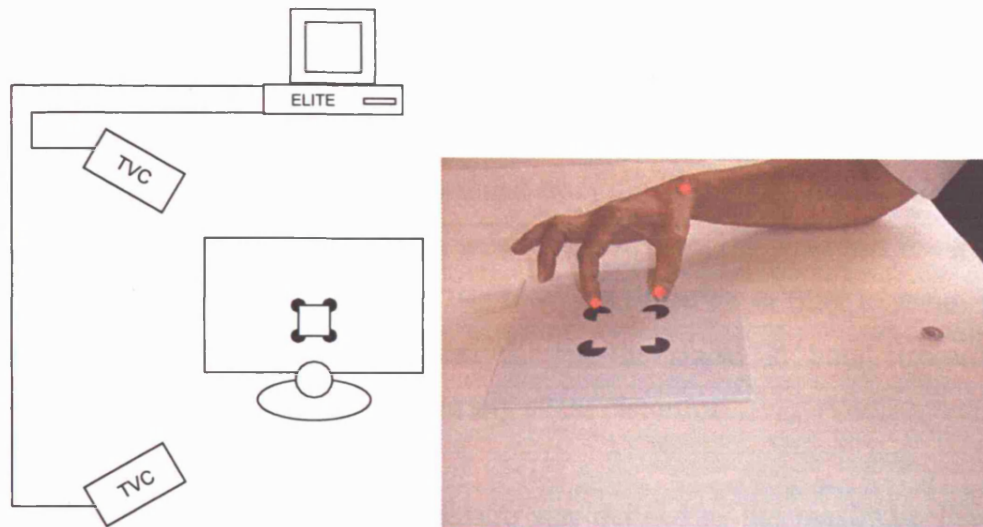
Figure 2.3. Schematic representation of the experimental set-up. Righ: A participant performing the task with a Kanizsa square. The markers are highlighted in red.

2.2.4.2. Open Loop Grasping (OL)

This condition was identical to the closed loop condition except that the only source of light in the room was provided by a lamp activated by a switch button operated by the participant. At the start of the trial the participant pressed down the switch with the palm of the hand while maintaining the grasp on the Start button. As soon as the hand was lifted to initiate the movement, the switch was released and the lamp was turned off. This procedure ensured that participants did not see their hand or the target during movement execution. The distance between the switch and the Start button was adjusted for individual participants according to the size of the hand to allow a comfortable position.

2.2.5. Data Collection and Variables

For all conditions, 9 kinematic measures of interest were recorded. These were maximum grip aperture (MGA, mm), time to maximum grip aperture (msec), percent time to maximum grip aperture (%), maximum wrist velocity (MWV, mm sec^{-1}), time

to maximum wrist velocity (msec), percent time to maximum wrist velocity (%), maximum wrist displacement (mm), maximum wrist height (mm) and movement duration (msec). Maximum grip aperture, time to maximum grip aperture and percent time to maximum grip aperture were obtained from the markers on the index finger and thumb whereas the remaining variables were obtained from the wrist marker. The data were filtered off-line using a 5th order 7Hz low-pass Butterworth filter to remove noise above 7Hz. The Matlab function used filtered the signal in both forwards and backwards directions therefore removing any phase distortion.

Grasp component: Maximum grip aperture was defined as the maximum Euclidean distance between the markers on the thumb and index finger that occurred during movement execution. A velocity of 50 mm sec^{-1} was used as the cut-off point to determine the start and end of movement. The movement was considered to start on the first of 5 consecutive frames where the velocity exceeded 50 mm sec^{-1}. Similarly, the movement was considered to end on the first of 5 consecutive frames where the velocity fell below this cut-off point. The 50 mm sec^{-1} cut-off point was chosen as it has been previously used to calculate the start and end of movement in this type of analysis (Goodale et al., 1994). Time to maximum grip aperture was defined as the time elapsed from movement initiation to the point where grip aperture was at its maximum. Percent time to maximum grip aperture expressed this measure as a percentage of total movement duration.

Transport component: The velocity profile was obtained from the wrist marker and maximum wrist velocity was defined as the maximum velocity value that occurred during movement execution. Time and percent time to maximum wrist velocity were obtained as for maximum grip aperture. Maximum wrist displacement was the Euclidean distance between the position of the wrist marker at the start and at the end of movement whereas maximum wrist height was the maximum displacement of this marker on the vertical axis. Movement duration was calculated as the time elapsed between the start and end of movement.

2.3. Results

Participants performed 8 trials for each of the 3 sizes in each condition in both open and closed loop, resulting in a total of 192 trials. The means entered in the analysis were computed from a minimum of 3 trials. To reach this criterion, for a small number of trials (0.8%) a linear interpolation procedure was carried out off-line to estimate the position of missing markers, with the constraint that data were interpolated only if missing for one frame (i.e., 20 msec) that did not occur at the start or end of movement. A linear interpolation was chosen as it has been previously used in this type of analysis (Westwood, Dubrowski, Carnahan & Roy, 2000). Trials for which markers positions were missing for longer periods of time were discarded from the analysis. Where not otherwise specified, an alpha level of 0.05 was used for the tests of significance and where necessary, Geisser-Greenhouse adjustments were made to the degrees of freedom. Simple comparisons were analysed with repeated measures t-tests and Bonferroni correction.

The individual kinematic variables were analysed in a series of $2 \times 4 \times 3$ repeated measures ANOVA with Loop (closed/open), Contour (3D/2D/Kanizsa/crosses) and Size (40/50/60 mm) as factors.

2.3.1. Kinematic Profiles

Figure 2.4 shows representative grip aperture and velocity profiles for the 4 conditions. In agreement with the typical kinematic profiles observed in manual prehension (Jeannerod, 1981), it can be seen that the transport component has clear acceleration and deceleration phases for all targets. Similarly, the grasp component resulted in biphasic curves, with finger-opening and finger-closure phases in all conditions, although these were more pronounced for the 3D targets. The grip aperture profiles show that fingers were stretched to increase the grip size to a maximum point after which they were flexed again to match grip aperture to the size of the target. Finally, in agreement with

the typical temporal coupling between the transport and grasp components (e.g., Jeannerod, 1981) maximum grip aperture occurred soon after maximum wrist velocity for all targets.
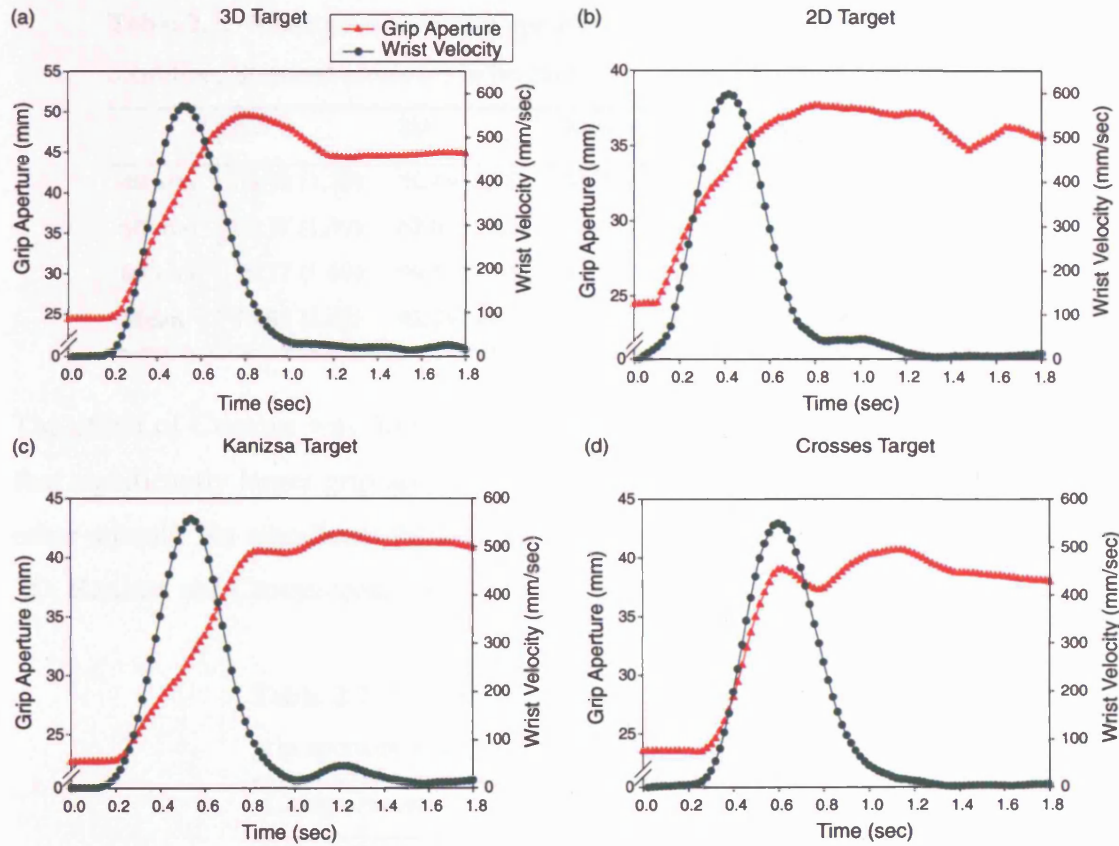
Figure 2.4. Representative grip aperture and velocity profiles from one participant for a 40 mm target in the (a) 3D, (b) 2D, (c) Kanizsa and (d) Crosses conditions.

2.3.2. Grasp Component

2.3.2.1. Maximum Grip Aperture

The analysis of maximum grip aperture revealed significant main effects of Contour ($F_{(3,24)}$ = 7.199, p = .012) and Size ($F_{(2,16)}$ = 455.084, p < .001) but a non-significant main effect of Loop ($F_{(1,8)}$ = 2.529, p = .150) and non-significant interactions (p > .05

for all interactions). Accordingly, the data from the closed and open loop conditions were combined for the simple effect analysis of the other factors. The group means are shown in Table 2.1 and Figure 2.5.

Table 2.1. Mean maximum grip aperture (mm) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	63.18 (1.20)	56.49 (2.77)	54.39 (2.22)	56.48 (2.88)	**57.64 (1.97)**
50 mm	70.17 (1.59)	62.62 (2.61)	61.45 (2.32)	63.14 (3.10)	**64.35 (2.03)**
60 mm	76.72 (1.60)	69.17 (2.61)	67.52 (2.51)	67.67 (2.44)	**70.27 (1.89)**
Mean	**70.02 (1.40)**	**62.76 (2.62)**	**61.12 (2.31)**	**62.43 (2.78)**	

The effect of Contour was further explored with planned comparisons. These revealed that significantly larger grip apertures were used for the 3D targets than for any of the other stimuli. No significant differences were found between the grip apertures in the 2D, Kanizsa and Crosses conditions. These comparisons are reported in Table 2.2.

Table 2.2. Planned comparisons exploring maximum grip aperture as a function of contour type.

Comparison	$t_{(8)}$	p
3D - 2D	-2.724	.026
3D – Kanizsa	3.363	.010
3D – Crosses	2.604	.031
2D – Kanizsa	1.951	.087
2D – Crosses	.0211	.838
Kanizsa – Crosses	-1.177	.273

Despite the lack of a Contour × Size interaction, in order to assess whether grip aperture was scaled according to target size with all stimuli the effect of Size was analysed for each condition separately. Repeated measures *t*-tests revealed that grip aperture

significantly increased from the 40 to the 50 mm targets and from the 50 to the 60 mm targets in all conditions, irrespective of contour type (p < .001 for all comparisons).
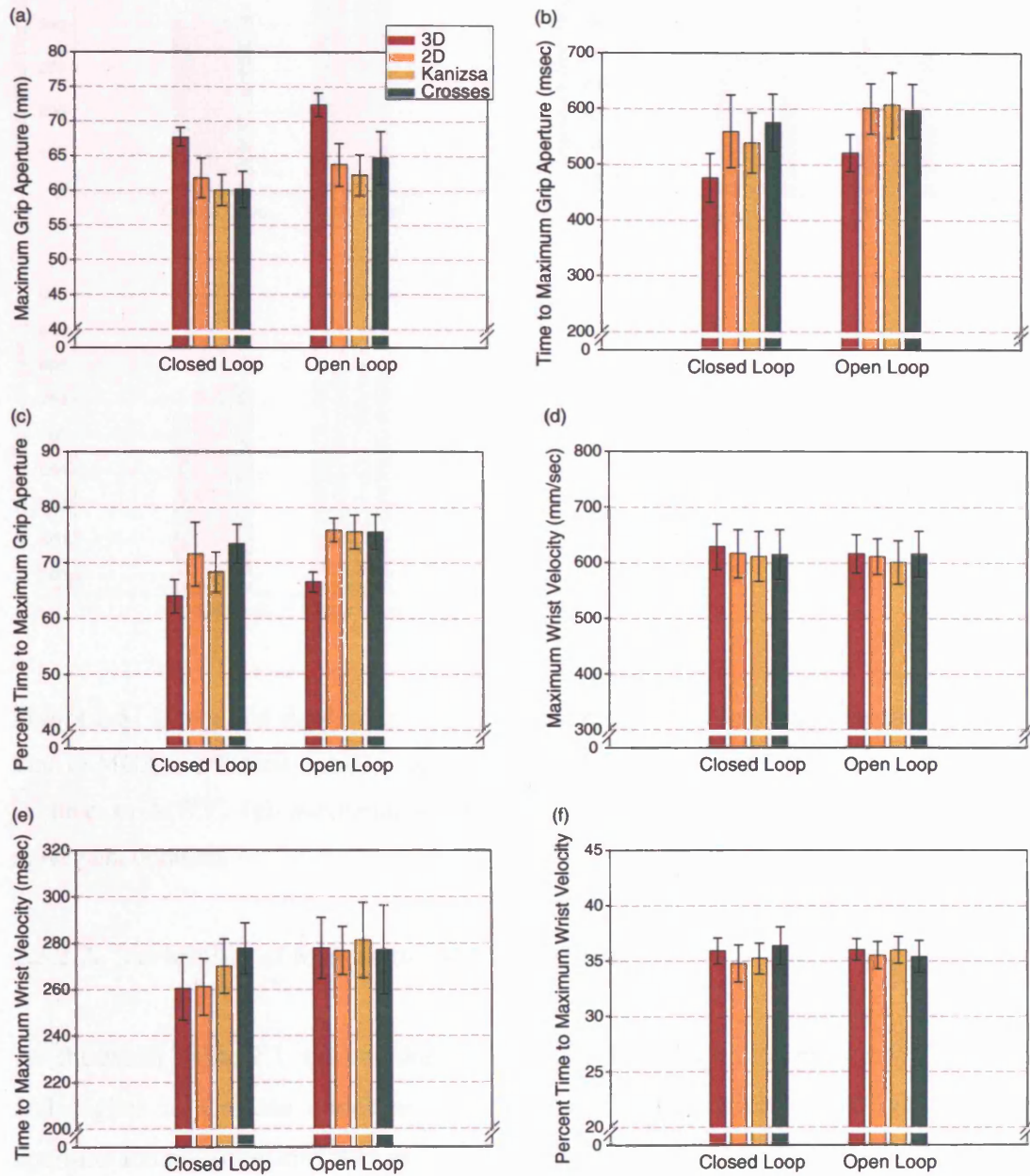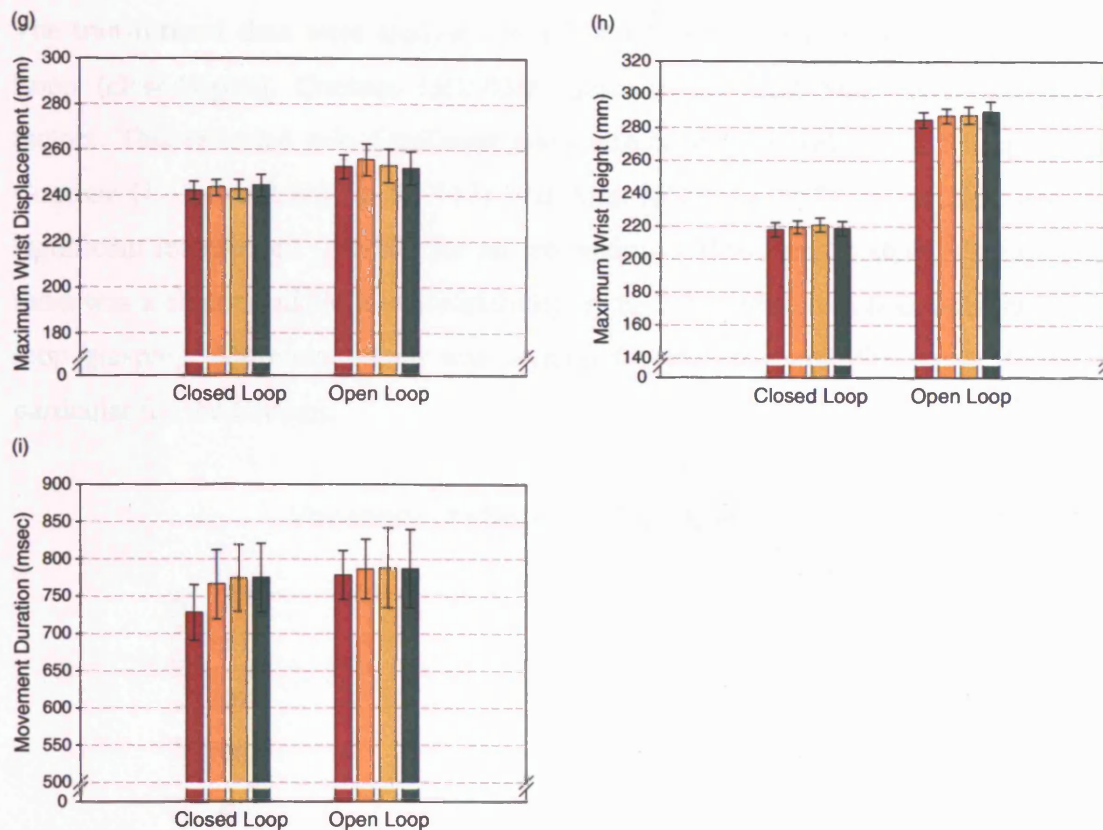
Figure 2.5. Means and standard errors (error bars) for: (a) maximum grip aperture (MGA), (b) time to MGA, (c) % time to MGA, (d) maximum wrist velocity (MWV), (e) time to MWV, (f) % time to MWV, (g) maximum wrist displacement, (h) maximum wrist height and (i) movement duration.

2.3.2.2. Variability of Maximum Grip Aperture

As shown in Table 2.1, the standard errors were found to be lower in the 3D condition and higher in Crosses conditions. Differences in the variability of maximum grip aperture across conditions was measured using the transform method of O'Brien (1981, r transformation). With this transformation, group variances can be analysed with ANOVA in a procedure similar to that used for the group means. This method has been previously used to analyse variability of maximum grip aperture (Castiello, 1996).

The transformed data were analysed in a 2 × 4 × 3 repeated measures ANOVA with Loop (closed/open), Contour (3D/2D/Kanizsa/crosses) and Size (40/50/60 mm) as factors. This revealed non-significant main effects of Loop ($F_{(1,8)} = 1.530$, p = .251), Contour ($F_{(3,24)} = 2.212$, p = .113) and Size ($F_{(2,16)} = 1.577$, p = .237) and non-significant interactions (p > .05 for all interactions). However, as shown in Figure 2.6, there was a clear trend for lower variability in the 3D condition in both open and closed loop grasping. Moreover, there was a trend for greater variability in the former, in particular for the Crosses.
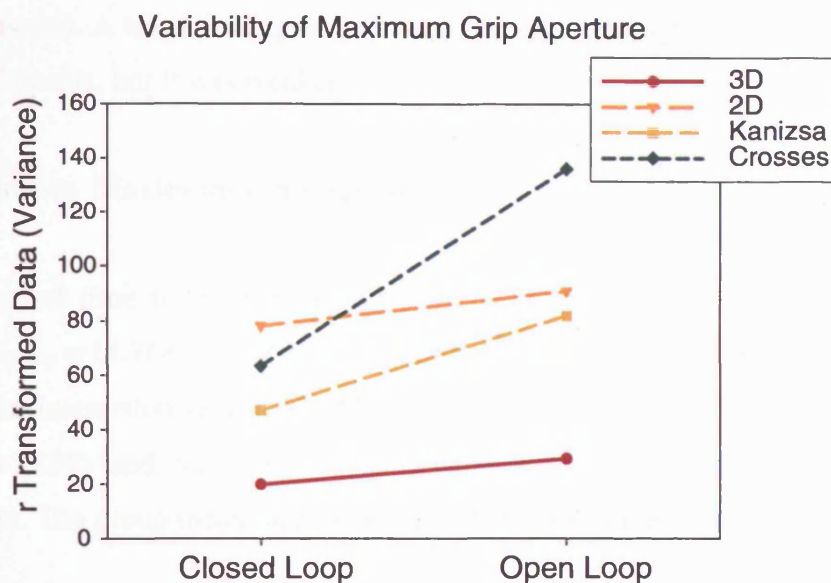
Figure 2.6. Variability as a function of contour and viewing condition.

The O'Brien (1981) transform was also used to assess the trial-to-trial variability across condition for individual participants. The transform was applied to raw data points and the resulting data were analysed with a 2 × 4 × 3 repeated measures ANOVA with Loop (closed/open), Contour (3D/2D/Kanizsa/crosses) and Size (40/50/60 mm) as factors. Because some trials were discarded due to the loss of markers positions, individual variables did not contain the same number of data points. To maintain homogeneity of size across variables, only the data points that corresponded to the size of the variable with the smallest number of cells were used for the transformation.

The analysis revealed that, overall, although there was a trend for lower variability in the 3D condition for 7 of the 9 participants, trial-to-trial variability did not significantly vary across conditions. The main effect of Contour was found to be significant only for 2 participants. Visual inspection of the data indicated that these effects were due to smaller variability in the 3D condition for one participant and to increased variability in the 2D condition in closed loop for the other. However, for both participants, post-hoc comparisons revealed that none of these differences were significant after the Bonferroni correction (p $\geq$ .021 and p $\geq$ .005 for the two participants, respectively, for all comparisons). A trend for higher variability in open loop grasping was also present across participants, but it was weaker.

2.3.2.3. Time to Maximum Grip Aperture

The analysis of time to maximum grip aperture revealed significant main effects of Contour ($F_{(3,24)} = 11.768$, p < .001) and Size ($F_{(2,16)} = 14.676$, p < .001) and a significant Loop $\times$ Size interaction ($F_{(2,16)} = 6.511$, p = .009). The main effect of Loop ($F_{(1,8)} = 1.964$, p = .199) and the other interactions were non-significant (p > .05 for all interactions). The group means are shown in Table 2.3 and Figure 2.5.

Table 2.3. Mean time to maximum grip aperture (msec) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	478 (31.8)	546 (48.1)	534 (58.7)	559 (54.7)	**529 (47.0)**
50 mm	502 (34.8)	583 (53.9)	581 (56.5)	588 (37.4)	**564 (44.2)**
60 mm	513 (42.6)	609 (54.8)	601 (48.6)	609 (50.7)	**583 (47.9)**
Mean	**498 (36.3)**	**580 (50.8)**	**572 (52.9)**	**585 (47.1)**	

The data from the closed and open loop conditions were combined for the simple effect analysis of Contour. This revealed that maximum grip aperture occurred significantly earlier in the 3D condition than in any of the other conditions. No significant differences

were found between the timing of maximum grip aperture in the 2D, Kanizsa and Crosses conditions. These comparisons are reported in Table 2.4.

Table 2.4. Simple comparisons exploring time to maximum grip aperture as a function of contour type. Corrected $\alpha = .008$.

Comparison	$t_{(8)}$	p
3D - 2D	4.059	.004
3D – Kanizsa	-3.695	.006
3D – Crosses	-4.342	.002
2D – Kanizsa	0.635	.543
2D – Crosses	-0.393	.705
Kanizsa – Crosses	-0.985	.354

The effect of Size was separately analysed for each viewing condition. Repeated measures t-tests revealed that maximum grip aperture occurred significantly earlier for with the 40 mm targets in closed loop, relative to the 50 mm targets ($t_{(8)}$ = -4.342, p = .002). No significant differences were observed for any of the other comparisons (p > .05).

2.3.2.4. Percent Time to Maximum Grip Aperture

Similar results were found for the analysis of percent time to maximum grip aperture. This revealed significant main effects of Contour ($F_{(3,24)}$ = 10.559, p < .001) and Size ($F_{(2,16)}$ = 11.631, p = .001) and significant Loop × Size ($F_{(2,16)}$ = 15.826, p < .001) and Loop × Contour × Size ($F_{(6,48)}$ = 2.298, p = .05) interactions. The main effect of Loop ($F_{(1,8)}$ = 1.330, p = .282) and the other interactions were non-significant. The group means are shown in Table 2.5 and Figure 2.5.

Table 2.5. Mean percent time to maximum grip aperture (%) for each stimulus size in each condition. Standard errors are in brackets.

		3D	2D	Kanizsa	Crosses	Mean
Closed Loop	40 mm	62.08 (2.32)	66.57 (5.63)	60.75 (5.10)	65.10 (5.14)	**63.62 (4.14)**
	50 mm	64.06 (3.36)	71.68 (7.11)	67.17 (4.76)	76.37 (2.56)	**69.82 (3.74)**
	60 mm	65.81 (4.08)	76.40 (5.54)	77.05 (2.37)	78.73 (4.17)	**74.50 (3.58)**
	Mean	**63.98 (3.03)**	**71.55 (5.78)**	**68.33 (3.64)**	**73.40 (3.54)**	
Open Loop	40 mm	66.38 (1.73)	73.19 (3.19)	74.29 (4.68)	78.03 (3.67)	**72.97 (2.70)**
	50 mm	66.58 (1.90)	78.19 (1.84)	76.75 (2.66)	72.42 (3.72)	**73.48 (1.88)**
	60 mm	66.59 (2.21)	76.22 (2.97)	75.63 (2.78)	76.12 (2.83)	**73.64 (2.36)**
	Mean	**66.52 (1.85)**	**75.87 (2.13)**	**75.56 (3.04)**	**75.52 (3.17)**	

The 3-way interaction was explored by analysing the effect of Contour at each level of Loop. The analysis revealed that maximum grip aperture occurred proportionally earlier in the 3D condition relative to any of the other conditions, but only in the open loop grasping task. As shown in Table 2.6, no significant differences were found in the closed loop task.

Table 2.6. Simple comparisons exploring % time to maximum grip aperture as a function of contour type. Corrected α = .008. "Kan" and "Cros" refer to the Kanizsa and Crosses conditions, respectively.

		3D-2D	3D–Kan	3D–Cros	2D–Kan	2D–Cros	Kan–Cros
Closed Loop	$t_{(8)}$	1.871	-1.917	-3.008	1.063	-0.502	-3.155
	p	.098	.092	.017	.319	.629	.013
	ANOVA:	$F_{(3,24)} = 3.607, p = .028$					
Open Loop	$t_{(8)}$	5.127	-4.391	-3.641	0.207	0.127	0.015
	p	.001	.002	.007	.841	.902	.988
	ANOVA:	$F_{(3,24)} = 8.901, p < .001$					

The effect of target size was also explored separately for each viewing condition. As for time to maximum grip aperture, the analysis revealed that maximum grip aperture

occurred proportionally earlier for with the 40 mm targets relative to the 50 mm targets ($t_{(8)}$ = -4.706, p = .002), but only in the closed loop condition. No significant differences were observed for any of the other comparisons (p > .05).

2.3.3. Transport Component

2.3.3.1. Maximum Wrist Velocity

The analysis of maximum wrist velocity revealed a significant main effect of Size ($F_{(2,16)}$ = 45.571, p < .001) but non-significant main effects of Loop ($F_{(1,8)}$ = 0.173, p = .688) and Contour ($F_{(3,24)}$ = 0.662, p = .583) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 2.7 and Figure 2.5.

Table 2.7. Mean maximum wrist velocity (mm sec^{-1}) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	602.41 (34.47)	592.95 (33.24)	591.61 (39.95)	604.44 (40.96)	**605.03 (43.18)**
50 mm	620.60 (33.71)	606.83 (32.29)	594.06 (38..79)	616.89 (41.81)	**619.51 (45.17)**
60 mm	622.95 (36.84)	631.30 (32.35)	614.04 (39.64)	623.07 (42.75)	**627.13 (43.05)**
Mean	**621.81 (36.88)**	**613.10 (36.49)**	**605.32 (41.71)**	**614.40 (43.11)**	

The effect of Size was further explored with repeated measures t-tests which revealed that significantly slower movements were performed for the 40 mm targets relative to the 50 mm ($t_{(8)}$ = -4.368, p = .002) but that velocity did not increase from these latter to the 60 mm targets ($t_{(8)}$ = -2.163, p = .063).

2.3.3.2. Time to Maximum Wrist Velocity

The analysis of time to maximum wrist velocity revealed non-significant main effects of Loop ($F_{(1,8)}$ = 1.016, p = .343), Contour ($F_{(3,24)}$ = 0.927, p = .443) and Size ($F_{(2,16)}$ = 1.922, p = .179) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 2.8 and Figure 2.5.

Table 2.8. Mean time to maximum wrist velocity (msec) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	274 (14.3)	282 (10.6)	271 (21.6)	266 (21.5)	**269 (11.0)**
50 mm	276 (11.9)	271 (13.1)	292 (16.6)	286 (18.0)	**271 (09.4)**
60 mm	283 (13.8)	277 (10.5)	280 (16.0)	280 (19.5)	**262 (13.7)**
Mean	**269 (12.3)**	**269 (09.6)**	**276 (12.3)**	**277 (13.5)**	

2.3.3.3. Percent Time to Maximum Wrist Velocity

Similar results were obtained for percent time to maximum wrist velocity. The analysis revealed non-significant main effects of Loop ($F_{(1,8)}$ = 0.022, p = .885), Contour ($F_{(3,24)}$ = 0.382, p = .767) and Size ($F_{(2,16)}$ = 2.811, p = .090) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 2.9 and Figure 2.5.

Table 2.9. Mean percent time to maximum wrist velocity (%) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	36.89 (1.22)	35.28 (1.21)	35.21 (1.05)	35.31 (1.21)	**35.67 (1.05)**
50 mm	35.95 (0.93)	35.53 (1.17)	36.12 (1.15)	36.85 (1.75)	**36.11 (1.11)**
60 mm	35.01 (1.22)	34.54 (1.47)	35.39 (1.31)	35.40 (1.60)	**35.09 (1.14)**
Mean	**35.95 (0.99)**	**35.12 (1.22)**	**35.57 (1.05)**	**35.85 (1.46)**	

2.3.3.4. Maximum Wrist Displacement

The analysis of maximum wrist displacement revealed significant main effects of Loop ($F_{(1,8)}$ = 7.223, p = .028) and Size ($F_{(2,16)}$ = 43.163, p < .001) but a non-significant main effect of Contour ($F_{(3,24)}$ = 0.196, p = .898) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 2.10 and Figure 2.5.

Table 2.10. Mean maximum wrist displacement (mm) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	241.97 (4.09)	244.19 (4.94)	239.55 (6.26)	241.73 (5.54)	**241.86 (4.79)**
50 mm	249.08 (4.23)	249.21 (4.94)	248.56 (5.28)	249.13 (6.02)	**248.99 (4.71)**
60 mm	251.25 (4.98)	255.68 (4.80)	255.47 (5.49)	253.78 (5.99)	**254.04 (4.68)**
Mean	**247.43 (4.12)**	**249.69 (4.65)**	**247.86 (5.46)**	**248.21 (5.79)**	

The significant effect of Loop in the absence of any interaction suggests that greater wrist displacements were used in the open loop conditions with all target types. The effect of Size was further explored with repeated measures t-tests which revealed that wrist displacement significantly increased from the 40 to the 50 mm targets ($t_{(8)}$ = -4.758, p = .001) and from these latter to the 60 mm targets ($t_{(8)}$ = -4.963, p = .001).

2.3.3.5. Maximum Wrist Height

Similar results were obtained for maximum wrist height. This analysis revealed significant main effects of Loop ($F_{(1,8)}$ = 1109.632, p < .001) and Size ($F_{(2,16)}$ = 30.378, p < .001) but a non-significant main effect of Contour ($F_{(3,24)}$ = 1.565, p = .224) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 2.11 and Figure 2.5.

Table 2.11. Mean maximum wrist height (mm) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	248.80 (4.36)	250.74 (4.37)	251.78 (4.32)	251.84 (5.12)	**250.79 (4.44)**
50 mm	250.51 (4.54)	252.80 (3.82)	253.09 (5.00)	255.22 (4.78)	**252.91 (4.42)**
60 mm	254.59 (4.35)	256.53 (4.07)	257.86 (4.60)	255.35 (5.48)	**256.08 (4.53)**
Mean	**251.30 (4.39)**	**253.36 (4.05)**	**254.24 (4.58)**	**254.14 (5.09)**	

As for wrist displacement, the significant effect of Loop in the absence of any interaction suggests that greater wrist heights were used in open loop grasping,

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irrespective of target types. The effect of Size was explored with simple comparisons which revealed that significantly greater wrist heights were used for larger targets ($t_{(8)}$ = -6.153, p < .001 and $t_{(8)}$ = -4.815, p = .001 for the 40 – 50 mm and 50 – 60 mm comparisons, respectively).

2.3.3.6. Movement Duration

The analysis of movement duration revealed non-significant main effects of Loop ($F_{(1,8)}$ = 2.043, p = .191) and Contour ($F_{(3,24)}$ = 1.223, p = .323) but a significant main effect of Size ($F_{(2,16)}$ = 4.168, p = .035). None of the interactions were significant (p > .05 for all interactions). The group means are shown in Table 2.12 and Figure 2.5.

Table 2.12. Mean movement duration (msec) for each stimulus size in each condition. Standard errors are in brackets.

	3D	2D	Kanizsa	Crosses	Mean
40 mm	737 (37.0)	776 (39.0)	773 (49.2)	772 (49.2)	**764 (42.4)**
50 mm	760 (29.0)	765 (42.5)	778 (49.2)	788 (45.2)	**773 (40.0)**
60 mm	763 (35.3)	788 (44.1)	792 (49.0)	783 (52.1)	**782 (44.3)**
Mean	**753 (32.9)**	**776 (41.3)**	**781 (48.8)**	**781 (48.5)**	

Although, as shown in Table 2.12, there was a trend for longer movement durations for larger targets, post-hoc comparisons revealed that these differences were not significant ($t_{(8)}$ = -1.157, p = .281 and $t_{(8)}$ = -1.466, p = .181 for the 40-50 mm and 50-60 mm comparisons, respectively).

2.4. Discussion

The aim of this experiment was to establish whether information about Kanizsa illusory contours is used in visually guided manual prehension. This was assessed by measuring whether the kinematic parameters obtained from grasps aimed at Kanizsa squares

differed from the parameters obtained with corresponding 2D luminance-defined targets.

The statistical analysis revealed no significant difference in any of the kinematic variables measured from these two conditions clearly suggesting that information about the Kanizsa contours was available to the dorsal visual system for the calibration of the kinematic parameters in this task. These conclusions are further supported by the analysis of the transformed data which revealed no significant differences in group variability and trial-to-trial variability of grip aperture in the two conditions. These latter give a measure of the stability of grip aperture in the two conditions and suggest that this was equally scaled according to target size with both the luminance-defined and Kanizsa borders. The above conclusions are further supported by the typical kinematic profiles obtained with both types of contours. Maximum grip aperture varied as a function of target size in both conditions and occurred within the expected range, between 60% and 80% of movement execution (Smeets & Brenner, 1999). Moreover, the typical temporal coupling between the transport and grasp components (Jeannerod, 1984) was maintained with the Kanizsa contours as maximum grip aperture occurred soon after maximum wrist velocity, at the start of the deceleration phase, with these stimuli.

The Crosses condition was used to control for the possibility that the luminance-defined contours in the Kanizsa stimuli alone could have accounted for the performance observed with these stimuli. The statistical analysis revealed that the kinematic parameters obtained in this condition did not significantly differ from the 2D luminance-defined and Kanizsa conditions. Similarly, no significant differences were found in the group and trial-to-trial variability of grip apertures in these conditions and typical kinematic profiles were observed with the crosses. Taken together, these results suggest that visuomotor performance with the crosses condition was as accurate as with the 2D luminance-defined and Kanizsa contours.

The above results could be accounted for if the gap between the arms of the crosses was interpolated in early visual cortex and than this information made available to the dorsal visual system for the computation of the kinematic parameters. This account would be in agreement with the claim that inducer collinearity and edge alignment play a major role in the perception of illusory contours and could be accounted by Peterhans and von der Heydt's (1989) model. Specifically, these authors found that "contour cells" in V2 with receptive fields $4°$ from the fovea responded to gaps as wide as $3.5°$. In the present experiment, if an average distance of 80 cm from the stimuli is considered, the gap in the crosses subtended a visual angle of $1.54°$, $1.93°$ and $2.31°$ for the 40, 50 and 60 mm targets, respectively. Of course, the angle subtended by these gaps changed across participants depending on height and variations in head position, however, the 40, 50 and 60 mm targets would have needed to be at a distance of 352, 440 and 528 mm from the stimuli, respectively, to generate a retinal size of $3.5°$. All participants kept a greater distance than this in the study, therefore it can be safely concluded that these gaps could be interpolated by Peterhans and von der Heydt's (1989) cells.

The suggestion that the dorsal visual system may have access to interpolated regions that do not give rise to perceptual experience (i.e., regions that are not processed as interpolated by the ventral visual system) may seem unlikely. However, this possibility is not implausible. As proposed by Kellman and Shipley (1991), and further discussed in Chapters 4 and 15 (General Discussion), contour interpolation can result from the presence of appropriately oriented edges in the display, independently of whether the interpolated region is perceived. These authors suggest that other more high-level visual mechanisms (e.g., mediating depth ordering) will determine the nature of the perception experienced with these displays. Furthermore, the evolutionary advantage and plausibility of having such a distribution of visual processing in discussed in the General Discussion.

An alternative possibility that can not be ruled out by the present study is that participants used the luminance-defined supported contours alone in the crosses to adjust grip aperture. The finding that the same pattern of results was found in the open

loop condition suggests that viewing the supported contours before movement initiation was sufficient for accurate motor control in this condition. However, this account is unlikely as the similar kinematic profiles obtained in the Crosses, 2D and Kanizsa conditions would also suggest that this limited region of the stimuli was used in these latter two conditions. Although at present there is evidence that the Kanizsa and not the supported contour is used in perceptual classification tasks (Gold, Murray, Bennett & Sekuler, 2000), there are no comparable findings for visuomotor tasks as used in this study. Future research could conclusively rule out this account with the use of eye tracking techniques as these could clearly establish the region looked at by the participant before movement initiation. Alternatively, this region could be determined with a response-classification technique, as used by Gold et al. (2000), where performance is correlated with noise introduced at selected regions of the display.

Taken together, the present findings are in agreement with converging evidence from several areas that suggest that the perception of Kanizsa contours largely depends on activity in V1 and V2 (Lee & Nguyen, 2001; Mendola et al., 1999; Peterhans & von der Heydt, 1989), that is, in areas that belong to both the dorsal and ventral visual systems (Milner & Goodale, 1995). With regard to the initial research question addressed by this study, these results provide preliminary evidence that information about interpolated contours is available to the dorsal visual system for the control of visually guided grasping and are therefore in agreement with Dyde and Milner's (2002) claim that the effect of visual illusions generated in areas that precede the anatomical separation between the dorsal and ventral visual systems should affect both perception and action. Thus, these findings provide further evidence that the dorsal visual system can use signals that are not specified on the retina when these are generated in early visual cortex.

The above interpretation is based on the assumption that the signal coding the interpolated contours was broadcast to the dorsal system from early visual areas. However, an alternative explanation that can not be entirely ruled out by the present findings is that information about the interpolated contours was exclusively processed

by the ventral system and that this then contributed to the programming of the movement. As discussed in Chapter 1, the ventral system is known to contribute to motor programming in at least three other instances where the information needed for the computation of the kinematic parameters "cannot be derived directly from the retina" (Goodale & Haffenden, 2003, p.254). Specifically, in the computation of grip and lift forces, of affordances and of other learned associations between metric and non-metric properties with no apparent adaptive function, such as colour (Goodale & Haffenden, 2003). This possibility, however, would require that the borders in the 2D, Kanizsa and Crosses conditions are localized with equal accuracy in the ventral visual system. This question is explored in Experiment 2.

Patients with visual form agnosia could conclusively rule out this possibility as evidence suggests that these patients do not perceive illusory contours. For instance, Milner et al. (1991) reported that DF, a patient with visual form agnosia, when presented with illusory contours resulting from displaced gratings could note that there was a break in the gratings but could not trace or point to the correct line. Similarly, ffytche, Lappin and Philpot (2004) reported that a patient with classical ventral occipito-temporal lesions resulting in achromatopsia, prosopagnosia, alexia and associative visual agnosia failed to detect Kanizsa illusory contours. If accurate responses with the Kanizsa stimuli in the present study were due to the direct processing of interpolated contours in the dorsal visual system, patients with visual form agnosia should be able to scale their grip aperture according to the size of the Kanizsa shapes. By contrast, if the interpolated contours were made available to motor programming by the ventral system, then we would expect grip aperture not to be scaled to target size in these patients.

In this study it was of interest to establish whether action aimed at 2D targets is mediated by the dorsal visual system. Differences were observed between the 3D and the other conditions, however, as discussed later in this thesis, the dorsal visual system is likely to have mediated action towards both 3D and 2D targets. The effects of differences in haptic feedback are discussed in Experiment 7 where it is argued that they do not change the grip aperture profile. Finally, with the exception of earlier grip

aperture for 3D and 40-mm targets in open and closed loop, respectively, and for greater wrist height and displacement in open loop, no other differences were observed as a result of viewing condition. These findings are in agreement with previous reports (Hu, Eagleson & Goodale, 1999; Jeannerod, 1981, 1984) and suggest that the kinematic parameters were largely pre-programmed in this task. However, in agreement with other reports (Berthier et al., 1996; Jakobson & Goodale, 1991) there was a trend for larger and earlier grip apertures in the open loop task.

3. Experiment 2 – The Localization of Luminance-defined and Interpolated Contours in the Ventral Visual System: A Vernier Study

3.1. Introduction

Experiment 1 suggests that information about interpolated contours is available to the dorsal visual system for the computation of the kinematic parameters of manual prehension. Moreover, it suggests that the position discrimination of these contours is as precise as the position discrimination of luminance-defined contours in this visuomotor task. One of the possibilities discussed in Section 2.4 proposes that these contours were interpolated in the ventral visual system and then made available for the programming of the visuomotor task. Of course, this account implies that the localization of interpolated and luminance-defined contours is equally accurate in the ventral visual system. This experiment explores whether this claim is correct.

Surprisingly, to our knowledge, only one study has so far directly compared the localization accuracy of luminance-defined and Kanizsa contours (Pomerantz, Goldberg, Golder & Tetewsky, 1981). Pomerantz et al. (1981) found very small differences in the error rates and reaction times for position judgements of a dot relative to either a luminance-defined or a Kanizsa square. Moreover, both measures were smaller in these conditions than in two control conditions that did not include any contours. These authors found similar results in a second experiment, except that no differences in error rates were also found between the Kanizsa condition and a control condition where outlined pacmen did not form the illusory square. These results suggest that luminance-defined and Kanizsa contours can be localized in the ventral visual

system with similar precision. Moreover, the second experiment suggests that localization was also accurate, albeit slower, when neither illusory nor real contours were present.

In Pomerantz et al. (1981) the lateral offset of the target dot was maintained constant at 8.4′ to either the right or left of the contour. However, Vernier acuity studies have shown that humans can detect displacements as small as 6″ under optimal viewing conditions (Westheimer, 1981). Thus, due to its capacity for detecting very small differences, a Vernier acuity task would provide a more suitable tool for investigating position discrimination in the ventral visual system.

In a typical Vernier acuity task, participants have to report, generally via keyboard presses, the displacement of a target line relative to one or two reference lines. In the former case the target and reference lines can be either abutting or separated by a small distance whereas in the latter case they are generally separated. The point at which the observer can reliably detect the displacement (often set at 75% correct) is referred to as the threshold. In these tasks, humans can detect displacement up to 6″ (Westheimer, 1981) which are much smaller than the resolving power of the visual system. Specifically, Vernier thresholds can be smaller than the minimum recorded diameter of a retinal, LGN, or V1 receptive field (all 2′; de Monasterio & Gouras, 1975; Wiesel & Hubel, 1966 and Poggio, Doty & Talbot, 1977, respectively), the smallest distance between foveal photoreceptors (25″; Regan, 2000) and the 30–35″ resolution obtained when the eye's optics are experimentally bypassed (Westheimer, 1979). For this reason, the ability to detect small offsets is also referred to as "hyperacuity" (Westheimer, 1979). Within the two-visual systems framework, Vernier acuity tasks clearly involve a perceptual response and would therefore measure relative position as coded in the ventral visual system. Vernier studies suggest that the relative position of luminance-defined contours is processed with a high degree of precision in this system.

It is beyond the scope of this experiment and thesis to review the models currently proposed for Vernier acuity, in particular considering that it has been proposed that there might be as many as five different strategies that could be used by the visual system to solve Vernier discriminations, depending on stimulus characteristics (Regan, 2000). In general, however, Vernier acuity models agree on the assumption that the ability to detect Vernier offsets with non-abutting lines must involve some summation of neural activity across different spatial filters, or some other form of neural interpolation, in early visual cortex (Braddick, 1984; Mussap & Levi, 1996; Westheimer & Li, 1996; Regan, 2000). Vernier offsets with abutting lines have been explained in terms of the activity of both single neurons (Wilson, 1991) and of populations of neurons engaged by the diffraction of light at the retina (Morgan, 1992). In this latter case, the light distribution from the small offset would spread over several minutes of arc and could therefore cover several retinal photoreceptors.

The precision of localization within the hyperacuity range of luminance-defined and Kanizsa contours has not yet been directly compared. However, a number of studies have used Vernier acuity tasks to investigate the interaction between these two types of contours (Dresp & Bonnet, 1991, 1993, 1995; Greene & Brown, 1997). These authors have found that illusory contours interact with luminance-defined contours in a very similar way to other luminance-defined borders and have suggested that the localization of real and illusory contours might be mediated by common mechanisms (Greene & Brown, 1997) or that these contours are functionally equivalent in the hyperacuity range (Dresp & Bonnet, 1991, 1993, 1995). Specifically, Dresp and Bonnett (1991, 1993) found that contrast thresholds for the detection of a spot of light increase when near a Kanizsa contour and decrease as a function of their distance from this contour. Very similar results are generally obtained with luminance-defined borders. Dresp and Bonnett (1995) also reported a decrease in the contrast threshold required to detect a luminance-defined line when this is superimposed to a Kanizsa contour. This effect, known as "subthreshold summation" (Dresp & Bonnett, 1995) and thought to depend on

additive neural signals in visual cortex, is also measured when the target line is superimpose on an invisible luminance-defined border.

Greene and Brown (1997) provide further evidence for a common localization mechanism for real and illusory contours of the abutting type. These authors found that, in an analogous way to luminance-defined lines, illusory contours induce attraction and repulsion effects. The attraction effect refers to the findings that, at small flanker-to-target (FTTS) separations (a few min of arc), the target and reference lines in a Vernier task appear closer than reality if the flanker and target line have the same (i.e., positive) contrast polarity. By contrast, at small and large FTTS, the target and reference lines appear farther apart (i.e., repulsion occurs) when the target line and flanker have opposite (i.e., negative) contrast polarity (Badcock & Westheimer, 1985). Greene and Brown (1997) found an attraction effect at small FTTS with illusory and real lines of positive contrast polarity. However, contrary to findings with luminance-defined lines, attraction was also observed for lines with negative contrast polarity. This latter finding was interpreted as evidence that the contrast polarity of the illusory contour is not coded at this stage of visual processing.

Taken together, the above findings suggest that, as proposed by Greene and Brown (1997), common mechanisms might mediate the localization of luminance-defined and illusory contours. If this claim is correct, similar position discrimination thresholds should be measured for these two types of contours. The present experiment tested this prediction with a three-line Vernier acuity task with reference elements consisting of luminance-defined lines, pacmen or crosses. Participants had to judge the offset of a central luminance-defined target line relative to either luminance-defined collinear bars (baseline condition, Figure 3.1a), collinear pacmen that formed a Kanizsa contour (Kanizsa condition, Figure 3.1b), collinear but rotated pacmen that did not form a Kanizsa contour (Rotated condition, Figure 3.1c) and collinear crosses similar to those used in Experiment 1 (Crosses condition, Figure 3.1d). In this study, Vernier position acuity for luminance-defined contours was not directly tested. However, it was argued

that if the gap between the Kanizsa reference elements was perceptually filled in and functionally equivalent to a luminance-defined border, as suggested by the above studies, position thresholds should have been lower in this condition than in any of the other conditions. In the baseline, Rotated and Crosses conditions the target line had to be localized relative to the interpolated contour between the two reference elements without the presence of either a luminance-defined or illusory contour as a reference for localization.

3.2. Method

3.2.1. Participants

Six participants, one of whom was the author (LM), took part in the study (4 females and 2 males, age range 25 - 38 years). They all had normal or corrected-to-normal self-reported visual acuity. All participants gave informed consent and three were paid to participate in the study. One participant (LM) had practiced with the task prior to testing.

3.2.2. Apparatus and Materials

3.2.2.1. Stimuli

All stimuli were generated with a standard PC and a vector-based drawing programme.

Baseline condition: The stimuli in this condition consisted of three collinear black lines (Figure 3.1a). The central comparison line subtended 13.971' (height) by 0.873' (width) whereas the two reference lines subtended 28.815' by 0.873'. The vertical separation between the elements was 21.829'. The central target could have 11 possible lateral positions (offsets) as shown in Figure 3.1a. Specifically, the target line was either

collinear with the reference lines (0′ offset) or displaced laterally by 0.873′, 1.746′, 2.619′, 3.492′ and 4.365′ either to the left or right of the reference lines.
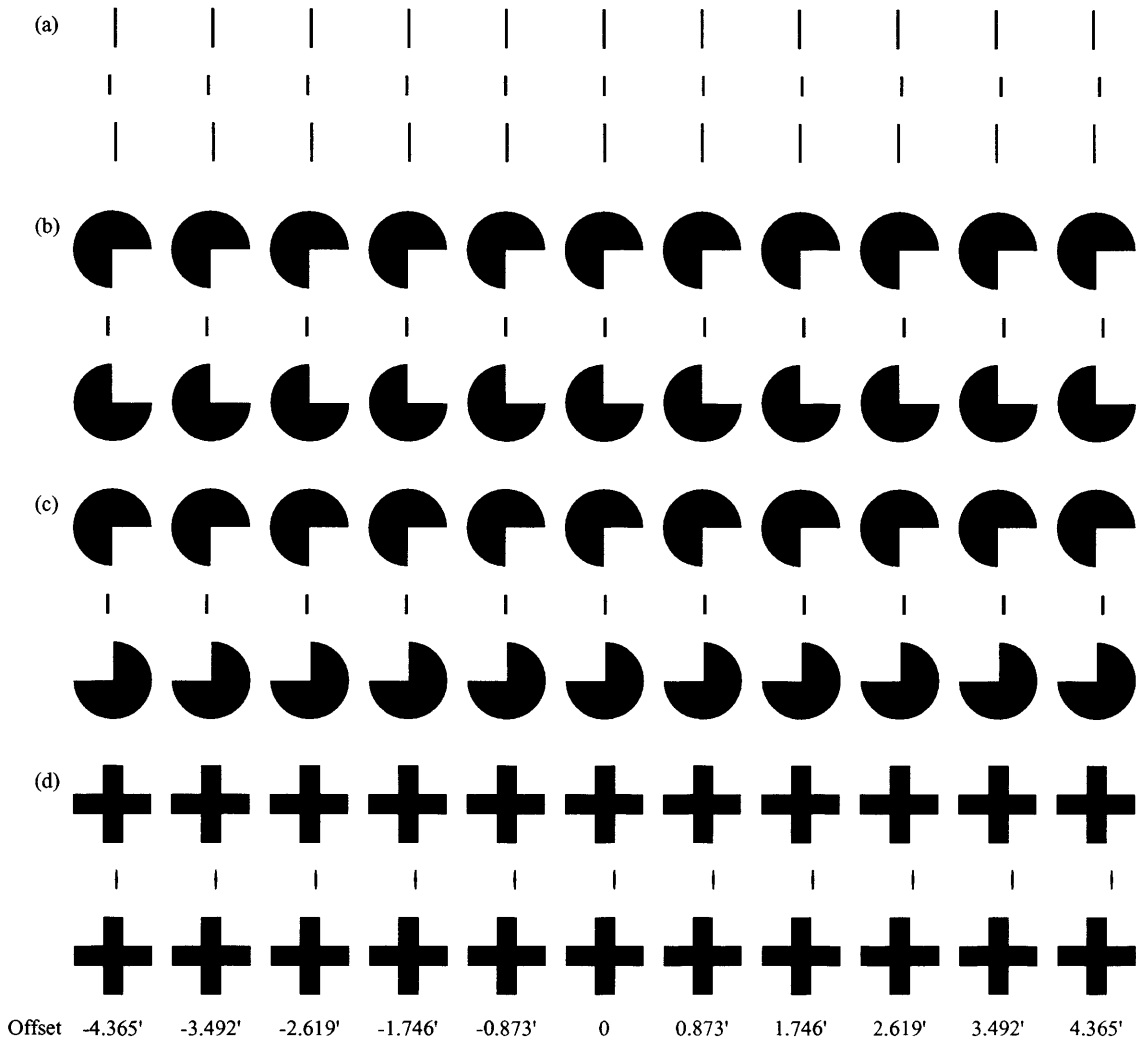
Figure 3.1. The complete set of stimuli (in scale but not in actual size) used in the (a) baseline, (b) Kanizsa (c) Rotated and (d) Crosses conditions.

Kanizsa condition: The stimuli in this condition were as in the baseline condition except that the reference lines were replaced by two black notched circles as shown in Figure 3.1b. The diameter of the notched circles subtended 57.625′ and their vertical separation was also 57.625′. The comparison line was placed halfway between the two

reference elements and at 0′ offset it was collinear with their centres. The length of the vertical edges in the reference elements and their vertical distance from the target line were maintained as in the baseline condition (Figure 3.2).

Rotated condition: The stimuli in this condition were as in the Kanizsa condition except that the bottom notched circle was rotated by 90° anticlockwise (Figure 3.1c).

Crosses condition: The stimuli in this condition were as in the Kanizsa condition except that the notched circles were replaced by crosses (Figure 3.1d). The vertical arms of the crosses subtended 57.625′ by 13.971′ and the horizontal arms were obtained by rotating these by 90°. The right edges of the vertical arms were used as the references lines. The distance between the vertical arms was 57.625′ and as shown in Figure 3.2, the vertical separation between the target line and the reference elements was as in the baseline condition. The length of the arms of the crosses matched the diameter of the inducers in the Kanizsa and Rotated condition. As shown in Figure 3.2, the use of this length and of symmetrical crosses reduced the length of the reference edges to 21.829′. However, this did not constitute a problem as Vernier position thresholds have been found to decrease as a function of line length but only up to about 5′ of arc, after which they are unaffected by further increases in line length (Westeimer & McKee, 1977).
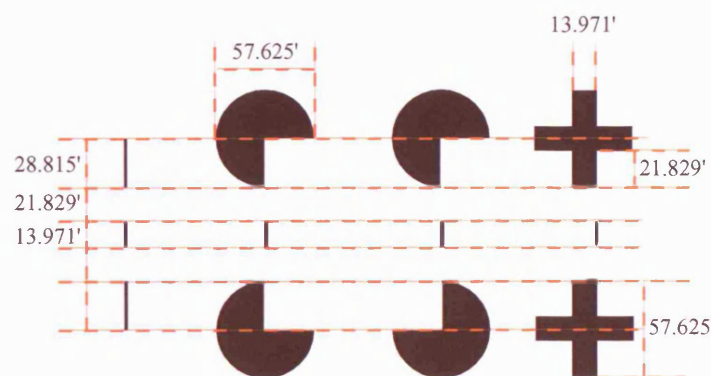
Figure 3.2. The dimensions of the stimuli used in the four conditions.

3.2.2.2. Apparatus and Set-up

The stimuli were displayed on a CRT 17" flat-screen Dell monitor (model P790) with a resolution of 1280 × 768 pixels and a refresh rate of 100 Hz. The participant's head was stabilised with a chinrest that was fixed to a standard office desk. The monitor was positioned 1500 mm from the chinrest and aligned along the sagittal midline. A standard PC and custom made software were used for stimulus presentation and data analysis.

3.2.4. Procedure

This experiment used a standard three-line Vernier task. The two reference elements and the target line of the display were presented simultaneously and viewed binocularly from the chinrest in a darkened room. Participants initiated individual blocks with a button-press. On each trial, the display was presented for 500 msec at the centre of the screen and the participant's task was to press keys # 1 or 3 on a standard keyboard number pad to indicate that the central target line had been perceived to the left or right, respectively, of the two reference elements. Although Westheimer and Li (1997) found that Vernier orientation threshold remained unchanged for a stimulus exposure between 50 and 1050 msec, other studies suggest that the perception of Kanizsa contours requires stimulus durations of at least 100 msec (Reynolds, 1981; Gegenfurtner, Brown & Rieger, 1997) and that the perceived brightness of the contour can increase up to 360 msec (Petry & Gannon, 1987). To ensure that the illusory contour was fully processed at the time of the response, participants were instructed to respond immediately after stimulus offset. Inter-stimulus-interval was set at 3500 msec and only responses that occurred within 2500 msec from stimulus onset were recorded.

The method of constant stimuli was used with a two-alternative forced-choice procedure. Trials were blocked according to stimulus type in sequences of 110 trials each containing 10 presentations for each of the 11 possible offsets. Five blocks were

presented for each stimulus type. The resulting 20 blocks were run in quintuples containing at least one block for each condition and were counterbalanced across subjects according to a Latin Square arrangement. The experiment was completed over 2 sessions of approximately 1 hour each. One subject (TB) participated in 4 blocks per stimulus type and the resulting 16 blocks were distributed across 3 sessions. At the beginning of the first session participants were presented with a 44-trial practice block containing one presentation for each offset from each stimulus type.

3.3. Results

All key presses during stimulus onset were recorded but only the first response was used in the statistical analysis. The psychometric curves for individual participants were obtained from the proportion of responses with the right key. Probit analysis (Finney, 1971) was used to obtain the lateral offset (expressed in min of arc) required to produce 50% and 75% of right key responses. Hereafter, the former is referred to as T_{50} and corresponded to the point of subjective alignment (PSA). The Vernier threshold was obtained by subtracting the PSA from the probit lateral offset corresponding to 75% of right key responses.

The equations obtained from the Probit analysis are shown in Table 3.1 and an example of a comparison between the measured and estimated (Probit) psychometric functions is shown in Figure 3.3.

Table 3.1. Linear regression equations obtained from the Probit analysis for individual participants.

	DB	RK	JT
Baseline	$y = 4.7905 + 1.2143x$	$y = 5.4236 + 0.7314x$	$y = 4.8965 + 0.9508x$
Kanizsa	$y = 5.2255 + 0.8684x$	$y = 5.7053 + 0.3741x$	$y = 5.6523 + 0.7492x$
Rotated	$y = 4.5913 + 0.7186x$	$y = 5.5778 + 0.3904x$	$y = 5.2057 + 0.7123x$
Crosses	$y = 5.2120 + 0.7058x$	$y = 5.6703 + 0.4194x$	$y = 5.9546 + 0.4852x$
	LM	RH	TB
Baseline	$y = 5.2261 + 1.0401x$	$y = 5.0345 + 0.9517x$	$y = 5.4210 + 1.1361x$
Kanizsa	$y = 5.6751 + 0.7036x$	$y = 5.5903 + 0.608x$	$y = 4.9575 + 0.61924x$
Rotated	$y = 4.9555 + 0.6586x$	$y = 5.1300 + 0.5989x$	$y = 3.9392 + 1.00914x$
Crosses	$y = 5.0566 + .07962x$	$y = 5.6413 + 0.5397x$	$y = 4.8134 + 0.81293x$

Measured and Estimated Psychometric Functions for DB
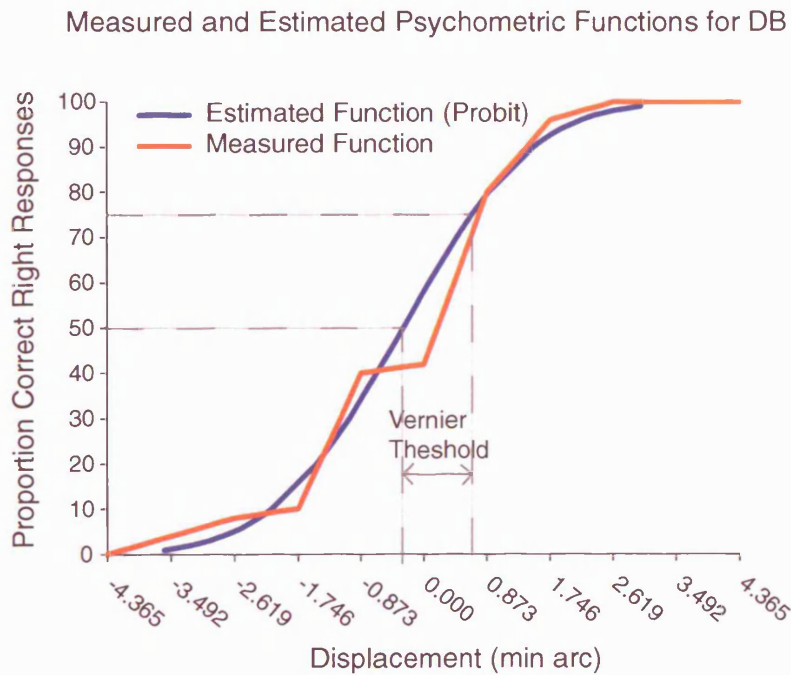
Figure 3.3. Measured and estimated (Probit) psychometric functions obtained in the Crosses condition for subject DB. As shown in the graph, the Vernier threshold corresponded to the lateral offset required to detect the displacement to the right on 75% of the trials measured from

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the PSA. The x- and y-axis indicate the offset of the target line and responses with the right key, respectively.

The T_{50} and Vernier threshold for individual participants for each condition are shown in Figure 3.4. In the baseline condition, it can be clearly seen that for all participants the PSA, that is, when the target and reference lines were perceived as aligned, is clustered around the 0′ offset. The PSA gives a measure of the bias in the perceived alignment and in this condition it indicates that there was no bias: The 0′ offset stimulus was accurately judged to be on the right side of the reference lines on 50% of trials. A similar trend was observed for three participants in the Rotated condition. By contrast, the PSA in the Kanizsa and Crosses conditions was clearly displaced to the left, although this bias was relative small as it remained within 1.746′ except for two cases. The small error bars indicate consistency of performance with all stimuli for all participants.
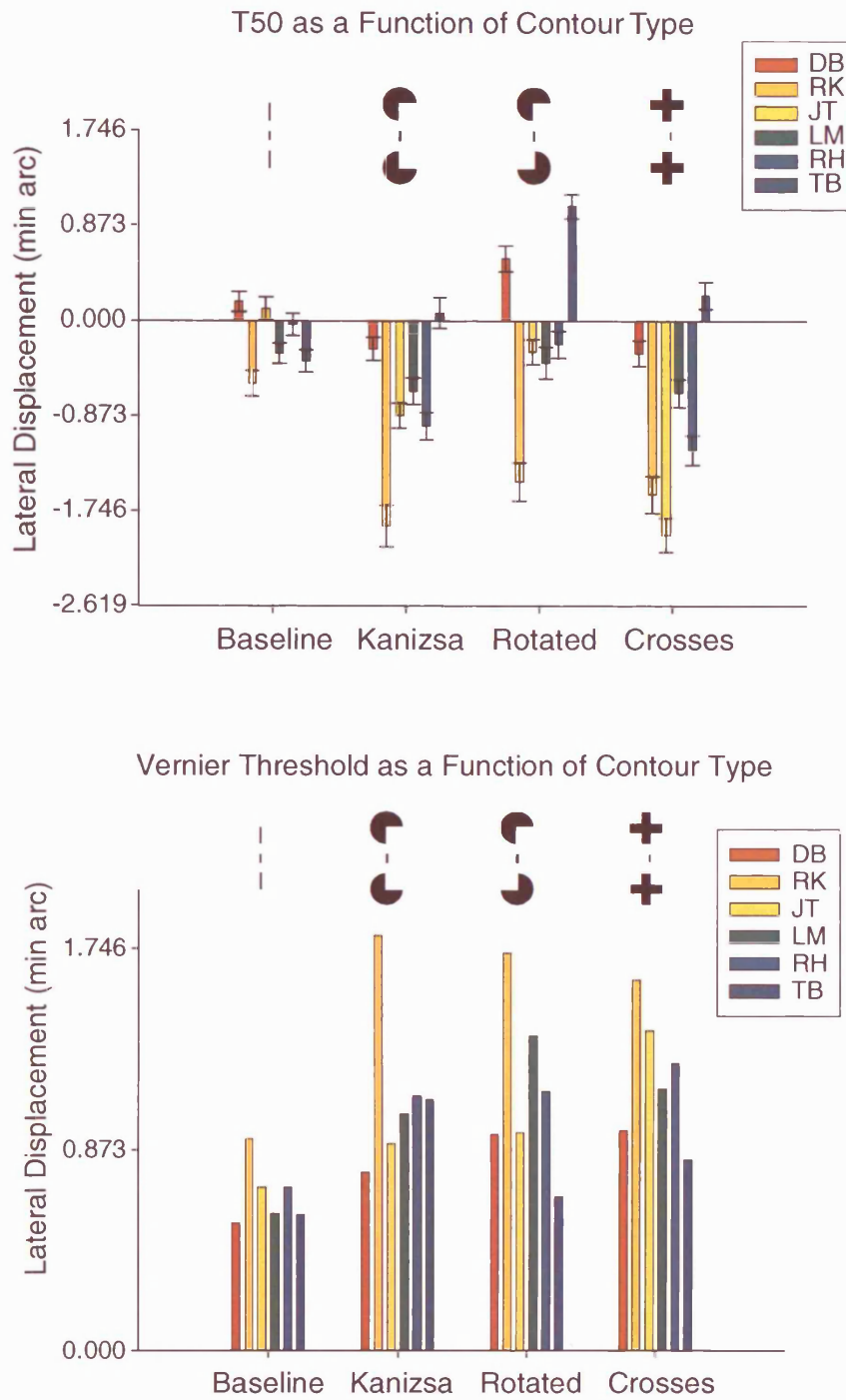
Figure 3.4. T_{50} (top) and Vernier Threshold (bottom) for individual participants in each condition. Error bars are not shown in the latter as the threshold values were adjusted.

The bottom part of Figure 3.4 shows the Vernier threshold. Overall, lower Vernier thresholds were obtained for all participants in the baseline condition where all values except one remained below 0.873'. These results indicate that participants were able to detect the displacement to the right with the smallest lateral offset used in the study with these stimuli. The thresholds in the Kanizsa, Crosses and Rotated conditions were higher and overall clustered around the 0.873' offset, with slightly higher values for the Crosses condition. A similar pattern of results was obtained for RK, however this subject had higher thresholds than the rest of the group. The inter-subject variability observed in this study, in terms of both direction of bias and magnitude of thresholds, is in accordance with previous reports (e.g., Danilova & Kojo, 2001; O'Shea & Mitchell, 1990).

Differences in the PSA and Vernier thresholds were analysed with two separate repeated measures ANOVAs with Contour as a factor (baseline/Kanizsa/Rotated/Crosses). These revealed significant effects for both the T_{50} ($F_{(3,15)}$ = 4.792, p = .016) and Vernier threshold ($F_{(3,15)}$ = 10.780, p < .001). The group means and standard errors in the four conditions are shown in Figure 3.5. In agreement with the individual data, it can be clearly seen that a lower threshold was obtained in the baseline condition indicating that smaller rightward offsets of the target were required to detect the displacement to the right in this condition. In agreement with these observations, planned comparisons revealed that the Vernier threshold was significantly lower in the baseline condition relative to the Kanizsa ($t_{(5)}$ = 4.304; p = .008), Rotated ($t_{(5)}$ = 3.785; p = .013) and Crosses ($t_{(5)}$ = 7.294; p = .001) conditions. None of the other comparisons were significant for this variable (p > .05 for all comparisons). Figure 3.5 shows that the PSA clustered around the 0' offset in the baseline and Rotated conditions indicating no bias with these stimuli. By contrast, a leftward bias was observed for the Kanizsa and Crosses conditions. Planned comparisons confirmed that the bias was significantly smaller in the Rotated condition relative to both the Kanizsa and Crosses conditions ($t_{(5)}$ = -5.735; p = .002 and $t_{(5)}$ = 3.478; p = .018, respectively). The other comparisons were non-significant (p > .05 for all comparisons).
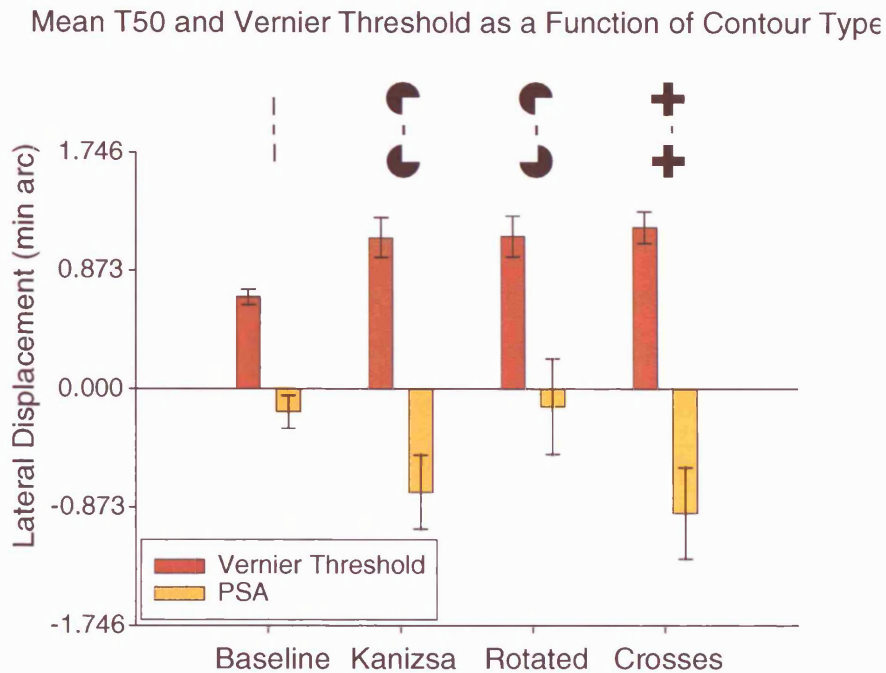
Figure 3.5. Group means and standard errors in the four conditions.

3.4. Discussion

The aim of this study was to establish whether luminance-defined contours, Kanizsa contours and interpolated gaps are localized with similar precision in the ventral visual system. This was measured with a three-line Vernier acuity task by comparing the localization of a luminance-defined bar relative to a standard Vernier configuration (baseline), to pacmen in a Kanizsa configuration or to two control conditions with rotated pacmen and crosses as the reference elements. It was predicted that if Kanizsa and luminance-defined contours are mediated by common mechanisms, the Vernier position threshold in the Kanizsa condition should have been lower than in any of the other conditions as these involved localization relative to interpolated gaps.

The statistical analysis revealed no significant differences between the Vernier thresholds in the Kanizsa, Rotated and Crosses conditions suggesting that the gap

between the reference elements in these stimuli was interpolated with equal accuracy, irrespective of whether the Kanizsa contour was perceived. These findings are in agreement with Pomerantz et al. (1981, Experiment 2) who, as discussed in Section 3.1, found no differences in the number of errors when a dot had to be localized relative to either a Kanizsa contours or to a configuration with outlined inducers that did not generate illusory borders. These results are also in agreement with Westheimer, Crist, Gorski and Gilbert (2001) who found very similar bisection acuity when the position of a luminance-defined line had to be determined when presented at the centre of a Kanizsa square or of a display with the pacmen replaced by diamonds that did not generate an illusory figure.

More importantly, these findings suggest that the mechanisms mediating contour interpolation are separate from those mediating the perception of illusory contours and argue for an early general purpose interpolation mechanism. As discussed in the next chapter, this claim would be in agreement with an influential theory of contour interpolation proposed by Kellman and Shipley (1991; also Kellman, Guttman & Wickens, 2001). Specifically, Kellman et al. (2001) suggested that contour interpolation occurs when appropriately oriented edges are present in the display. Differences in perceptual experience following neural interpolation are likely to depend on subsequent higher-level processes (e.g., mediating depth ordering) that could interact with gap interpolation.

Petherhans and von der Heydt's (1989) "contour neurons" could provide a neural substrate for the interpolation observed in this study. As discussed in Section 2.1, these authors found that "contour cells" in V2 responded to gaps as wide as 3.5°, that is, to gaps much larger than those used in this study (less than 1° of visual angle). Thus, contour cells could account for gap interpolation in the Kanizsa, Rotated and Crosses conditions. Indeed, contour neurons have been already suggested as a plausible mechanism for the mediation of Vernier acuity with non-abutting configurations (Mussap & Levi, 1996).

Contrary to the prediction, lower thresholds were obtained with the baseline condition. At present it is unclear why position accuracy was greater in this condition. However, one possibility is that the position of the target line was judged relative to the position of the reference elements "as a whole" rather than relative to the position of the reference edges. Some evidence suggests that perceptual localization can be based on "shape as a whole" rather than on local features alone and that the position of the shape is calculated relative to its centre of gravity (CoG, Vishwanath & Kowler, 2003). Thus, one possibility is that the localization of the CoG of a large patch, as the reference elements in the Kanizsa, Rotated and Crosses conditions, is inherently less accurate than the localization of thin lines. If, as noted above, the localization of the target line is based on the CoG, these differences in accuracy should be expected to affect the Vernier position thresholds.

Finally, it should be noted that the shorter length of the reference elements in the Crosses condition is unlikely to have affected these results. Position thresholds are known to decrease as a function of line length in configurations with abutting lines but only up to about 5′ of arc (Westeimer & McKee, 1977), after which they remain unaffected by further lengthening of the line. Moreover, non-abutting Vernier lines separated by 2 - 4′ of arc have been found to be unaffected by line length as they can be shrunk to points without any significant changes to the threshold (Westheimer, 1981). Although we are not aware of studies that looked at the effect of target length with separations as large as that used in these stimuli (21.829′), it is unlikely that line length under these conditions had an effect on the thresholds.

Taken together, the present results did not reveal improved position accuracy for the Kanizsa condition suggesting that the localization of interpolated gaps is equally accurate in the ventral visual system, irrespective of whether the gap is filled with an illusory contour. These results are in agreement with an influential theory of contour interpolation and with the postulation of an early general purpose interpolation mechanism (Kellman & Shipley, 1991). Notably, these results are in agreement with

Experiment 1 where no differences were found between the localization of the Kanizsa and the interpolated contours in the Crosses. Thus, although more research is needed to draw firmer conclusions, the same early interpolation mechanism could account for these results and feed the interpolated signals to both the ventral and dorsal visual systems.

In this study, the localization of luminance-defined contours was not directly addressed, therefore no clear conclusions can be drawn on whether these contours would be localized with equal accuracy as the interpolated gaps in this study. The claim that luminance-defined and Kanizsa contours are functionally equivalent and mediated by common mechanisms (Dresp & Bonnet, 1991, 1993, 1995; Greene & Brown, 1997) would suggest that this might be a plausible account. However, this possibility is currently speculative and more research is needed to draw firmer conclusions. Thus, this study cannot entirely answer the question whether the equal accuracy observed in Experiment 1 in the luminance-defined, Kanizsa and Crosses conditions could have been due to a contribution from the ventral system. Although the present results provide evidence that localization accuracy with the Kanizsa and Crosses stimuli is equally accurate in the two visual systems, it cannot conclusively answer this question for luminance-defined contours.

3.4.1. Bias

The point of subjective alignment or T_{50} was clustered around the $0'$ offset in the baseline and Rotated conditions suggesting correct localization judgements with these stimuli. By contrast, a clear leftward bias was found for the Kanizsa and Crosses conditions, although only the comparisons between these and the Rotated condition reached significance. Although this bias was small, within $1.746'$ except for two cases, it was observed for 5 of the 6 subjects.

This pattern of results is likely to depend on the differences in the reference elements. Whereas these consisted of thin lines symmetrically located with respect to the reference border in the baseline condition, they were asymmetrically positioned larger patches in the Kanizsa and Crosses conditions. Due to the rotation of the lower element, the larger patches were "quasi-symmetrically" positioned in the Rotated condition. These differences could account for the bias in a number of ways.

First, these differences could account for the bias if the target line in this task was judged relative to the location of the reference elements as suggested above by Vishwanath and Kowler's (2003) findings. Specifically, the lack of bias in the baseline condition could be accounted for by the symmetry (and probably proximity) of the CoGs of the two reference elements to the reference contour. The quasi-symmetric properties of the pacmen in the Rotated condition could also account for the reduced bias. In these stimuli the CoGs of the two reference elements were at opposite sides of the reference contour and could have therefore "pulled" this latter in opposite directions. This could have reduced the bias if the centre of the reference element was used to make the position judgement as this was likely positioned close to the reference contour. Interestingly, this account would result in a "tilted" contour and could be tested with an orientation discrimination task. By contrast, the CoGs of the two reference elements in the Kanizsa and Crosses conditions were asymmetrically positioned to the left of the reference contour and could have therefore resulted in a leftward bias.

A second possible account is that the right edge of the target line rather then its midpoint was aligned with the edges of the reference elements in the Kanizsa and Crosses conditions. This would have introduced a leftward bias of 0.4365′ (half the width of the target line), which is relatively close, although somewhat smaller, to the bias observed. It could be argued that the bias was not observed in the baseline and Rotated conditions as it is unlikely that such a response strategy would be used with reference elements of the same thickness as the target line or with reference elements of opposite contrast polarity.

A third account that could explain the bias observed is based on differences in the contrast polarity of the reference edges. Specifically, in both the Kanizsa and Crosses conditions the reference edges had a black region extending to the left in both reference elements whereas a white region extended to the left of the bottom reference element in the Rotated stimuli. This difference could account for the bias observed if the opposite contrast polarity of the reference elements generated different attraction effects. As discussed in Section 3.1, flanker studies show that at small flanker-to-target separations, attraction and repulsion effects are observed when the target and flanker have positive and negative contrast polarity, respectively (Badcock & Westheimer, 1985). Thus, the present results could be accounted for if the wide reference elements in the Kanizsa, Crosses and Rotated conditions acted as flankers and exerted attraction and repulsion effects in an analogous way to a standard flanker. Specifically, if the black target line was attracted towards the gap to be interpolated when this had both reference elements with black regions extending to the left (i.e., positive contrast polarity), it would have resulted in a leftward displacement of the PSA in the Kanizsa and Crosses conditions, as it was observed. By contrast, in the Rotated condition the gap to be interpolated had a black (i.e., positive) region on the left of the top reference element but a white (i.e., negative) region on the left of the bottom reference elements. The opposite contrast polarity of the reference elements could have therefore nullified the attraction effect in this condition.

Although still speculative at present, this is not an implausible account for two reasons. First, these elements extended for up to 57.625′ laterally and it is therefore likely that they fell within the spatial integration region known to affect the localization judgement (Danilova & Kojo, 2001). Second, flankers have been found to affect thresholds even at no target-to-flanker separations, a condition analogous to this study where there was continuity between reference edges and the putative flanker region, although maximum interference effects are know to peak at about 2 – 5′ separations (Westheimer & Hauske, 1975).

The phenomenon of "irradiation" could also account for the present results. Irradiation refers to a robust and well reported bias of perceived position resulting from the perceived enlargement of bright areas relative to adjacent dark areas (Mather & Morgan, 1986). Irradiation could account for the present results if in the Kanizsa and Crosses stimuli the white quadrant on the right of the reference edge was perceived as larger than the adjacent dark area. If irradiation occurred with these stimuli it would have shifted the point of subjective alignment to the left, towards the dark region, as it was observed. Irradiation could also account for the smaller leftward bias observed in the baseline and Rotated conditions as in the former no clear white region was present in the reference elements and in the latter the location of the white quadrant was on opposite sides for the two pacmen.

Finally, it should be noted that the lowest thresholds obtained in the present study are in the region of 0.5′ (see Figures 3.4 and 3.5). These are outside the hyperacuity range and could be due to a floor effect resulting from the relatively large offsets used in the study (minimum offset 0.873′). Further research should investigate the localization of Kanizsa contours with smaller offsets as these might reveal lower thresholds but more importantly further differences between conditions that could have been masked by a floor effect in this study. Optimal separations for the elements (2-5′, Westheimer & McKee, 1977) should also be used as position thresholds have been found to be lower under these conditions. Further improvements on the present design would also include the use of a larger sample, a larger number of trials and error feedback.

4. Experiment 3 – Grasping Partially Occluded Targets: Contour Interpolation in Manual Prehension II

4.1. Introduction

In Experiment 1 it was found that information about interpolated gaps and Kanizsa contours is available to the dorsal visual system for the computation of the kinematic parameters in manual prehension. Importantly, Experiment 1 supports Dyde and Milner's (2002) claim that the dorsal visual system can use signals that are not explicitly specified on the retina if generated in early visual cortex.

If the above claim is correct, there might be other instances in nature in which information about interpolated areas could be available to the dorsal visual system for the guidance of object-directed action. The visual interpolation of partially occluded objects could be one of these instances. Partly occluded objects result from the superimposition in depth of opaque objects, or parts of the same object, along the observer's line of sight. Specifically, partial occlusion can result from: (1) self-occlusion, (2) occlusion of a stationary object by another stationary object, (3) occlusion of a stationary object by a moving object, (4) occlusion of a moving object by a stationary object and (5) occlusion of a stationary object due to the observer's motion. These examples suggest that partially occluded objects are pervasive in nature.

There is little doubt that the occluded region of partially occluded targets is interpolated and used for a variety of tasks mediated by the ventral visual system (for reviews see Kellman, Guttman & Wickens, 2001; Kellman & Shipley, 1991; Rensink & Enns,

1998). For instance, Rensink and Enns (1998) found that reaction times for searching a square with a notched corner among complete squares significantly increased when the former contacted a disk as if this latter occluded the notched corner. These results suggest that the notched square adjacent to the disk was perceived as more similar to the complete square and that therefore it was "completed" behind the disk. However, whether the interpolated region of partially occluded objects is available to the dorsal visual system for the mediation of object-directed action has not yet been investigated. Several lines of evidence suggest that this is likely the case.

Due to their ubiquity in nature, partially occluded objects are likely to be relevant for visuomotor processing in at least two ways. First, they are likely to be the target of several object-directed actions. For instance, grasping a glass of milk is a mundane example of an action directed at a self-occluding target. Importantly, in such an action the farthest side of the glass, often the contact point for the index finger, would be occluded by the opaque content. As discussed in Chapter 1, in manual prehension with fully visible targets, kinematic parameters such as hand velocity and grip aperture are functions of the real metrics of the target, in this case target distance and size, respectively. However, in actions with partially occluded targets these stimulus properties are not fully available to the visual apparatus. It is therefore a question of interest to establish how kinematic variables that are known to be based on the target's visual attributes are computed in actions aimed at partially occluded objects, that is, when these attributes are not fully visible. Specifically, it is of interest to establish whether in these actions the dorsal visual system has access to the interpolated occluded region.

A second reason why partially occluded objects are likely to be relevant for visuomotor processing is that these objects are likely to act as obstacles. It has been suggested that organisms must be able to steer away from these objects to achieve effective navigation (Fiorani, De Oliveira, Volchan, Pessoa, Gattass & Rocha-Miranda, 2003). Obstacle avoidance is a function known to be mediated by the dorsal visual system (Milner &

McIntosh, 2004), therefore, the ability to effectively navigate among partially occluded objects observed in several species indirectly suggests that interpolated occluded regions are likely to be represented in the dorsal visual system.

In general, the ability to use the interpolated region of partially occluded objects in visuomotor interactions with the environment would substantially increase the effectiveness of visually guided behaviour in a variety of species. A similar argument has been recently proposed by Fiorani et al. (2003). In agreement with this observation, comparative studies have found that partially occluded objects are completed in several animals such as monkeys (Fujita, 2001), mice (Kanizsa, Renzi, Conte, Compostela & Guerani, 1993), chicks (Regolin & Vallortigara, 1995) and pigeons (Nagasaka, 2003), although other studies have failed to find evidence of visual completion in these latter (Fujita, 2001; Sekuler, Lee & Shettleworth, 1996).

The claim that interpolated occluded regions are used in visuomotor processing is made more plausible by evidence that these interpolation processes might occur, at least partly, in early visual cortex (Fiorani, Rosa, Gattass & Rocha-Miranda, 1992; Greene and Brown 2000; Rensink & Enns, 1998; Sugita, 1999). Fiorani et al. (1992) found that in anesthetised monkeys, visual interpolation occurs as early as V1 and at a single-cell level. When the classical excitatory receptive field (RF) of V1 neurons was masked, and therefore direct input from the visual field was removed, these cells responded to stimulation surrounding the mask in a visuotopic fashion. This expansion of the RF suggests that these cells acted as interpolation regions for the occluded stimuli. More importantly, as noted by Fiorani et al. (1992), expansion occurred without loss of retinotopic order suggesting that the interpolation of the centre of the original RF was accurate. Fiorani et al. (2003) subsequently argued that evidence of similar mechanisms in the opossum striate cortex (Oliveira et al., 1998) indicate that the interpolating properties of these cells might belong to a general mechanism for contour extraction evolved early in phylogeny.

An early locus for these interpolation processes has also been reported by Sugita (1999) in behaving monkeys. Sugita (1999) found that orientation selective cells in V1 stopped responding when a bar crossed a patch that was placed on the receptive field, however, the response was restored when the patch had crossed disparity and appeared in front of the moving bar. These cells were not selective for stimulus disparity alone and did not respond when, due to uncrossed disparity, the patch appeared behind the bar suggesting that their response was specific to the interpolation of the occluded region. Moreover, Sugita (1999) argued that the similar response latencies measured for occluded and unoccluded bars suggest that the V1 response was an early process, either due to lateral connections or to feedback signals from very close areas.

Rensink and Enns (1998) provide psychophysical evidence that in humans the interpolation of occluded regions also occurs at early stages of visual processing. In a visual search task, these authors found that occluded squares were completed within the processing time generally associated with early visual processing and, after a series of control conditions, they proposed that the completed object, and not its constituting fragments, formed the basis of rapid recognition. Finally, psychophysical evidence for an early locus of interpolation processes is provided by Greene and Brown (2000) who found that in a Vernier task the occluded area of a partially occluded bar influenced the localization of a target line as predicted if it was unoccluded, suggesting that the boundary contour was completed at this early stage of visual processing.

Taken together, the above findings suggest that the interpolation of occluded regions occurs, at least partly, in early visual cortex. Moreover, Fiorani et al.'s (1992) results suggest that a good degree of position accuracy is preserved by these interpolation processes. Thus, if Dyde and Milner's (2002) argument is applied to this phenomenon, it would be reasonable to suggest that the signal coding these interpolated regions is likely to be broadcast to both visual systems and therefore could be available for the mediation of object-directed action. As discussed above, it would be evolutionarily

advantageous for visuomotor processing to access these interpolated regions as partially occluded objects are likely to act as both targets and obstacles.

The present experiment explored whether the dorsal visual system accesses the interpolated region of partially occluded objects by comparing the kinematic parameters of grasps aimed at entirely visible and partially occluded targets. Specifically, grasps aimed at Perpex squares (Whole condition) and at the same squares with one corner occluded by a black disk (Occluded condition) where compared. In this latter condition the point of contact of the index finger was not visible. If the dorsal visual system has access to an accurate interpolation of the occluded region no differences should have been observed between the two conditions.

However, because haptic feedback has been found to affect the kinematic profile of prehension, in particular the finger-opening phase (Gentilucci et al., 1997), there was the possibility that the absence of haptic feedback from the occluded corner in the Occluded condition could have confounded the results. This possibility was controlled for with a second baseline condition (Clear condition) in which stimuli identical to the Occluded condition were used with the exception that the occluding disk was made of transparent Perspex. The Clear stimuli provided a better baseline condition than the Whole squares as they allowed full vision of the target but with haptic feedback equal to the Occluded condition. A final set of stimuli (Notched condition) identical to the Whole condition but with the occluded region removed was used to measure whether the interpolation of the missing region occurred in the absence of occlusion.

Finally, the above tasks were also performed with stimuli in which the squares were substituted by corresponding rectangles. It was argued that if the accuracy of the interpolation processes depends on the symmetry of the occluded region, less accurate performance should have been observed with the rectangles relative to the squares.

4.2. Method

4.2.1. Design

This was a repeated measures design as participants performed in all conditions. Conditions were individually presented in blocks of 24 trials consisting of 8 trials for each of the 3 sizes. Stimulus presentation followed a different pseudorandom order for each block with the restrain that the same size was not repeated for more than 3 consecutive trials. Conditions were grouped according to shape (square or rectangle) and the presentation order of these sets was counterbalanced across subjects. Within sets, conditions were further counterbalanced according to the same Latin Square arrangement. In total, each participant performed 192 trials, 96 for each shape.

4.2.2. Participants

Thirteen participants took part in the study. Of these, one was discarded due to stereoscopic vision below criterion. The data analysis was therefore carried out on 12 participants (7 females and 5 males, aged range 19 - 26 years). They all had normal or corrected-to-normal self-reported visual acuity, stereo vision ≤ 120 min arc (TNO, Laméris, Utrecht) and were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave informed consent and were paid to participate in the study.

4.2.3. Apparatus and Materials

4.2.3.1. Stimuli

Whole condition: The stimuli in this condition consisted of squares and rectangles made of 3 mm thick black Perspex with diagonals of either 40, 50 or 60 mm (Figure 4.1a and 4.1e). Accordingly, the squares had a side of either 28.3, 35.4 or 42.4 mm,

respectively, and the rectangles had the following dimensions: 37.1 × 15 mm, 45.8 × 20 mm and 54.5 × 25 mm (height × width), also respectively. Individual stimuli were attached to a 1 mm thick A4 transparent frosted plastic sheet, aligned along the vertical midline and 8.5 cm from the bottom edge (Figure 4.2).
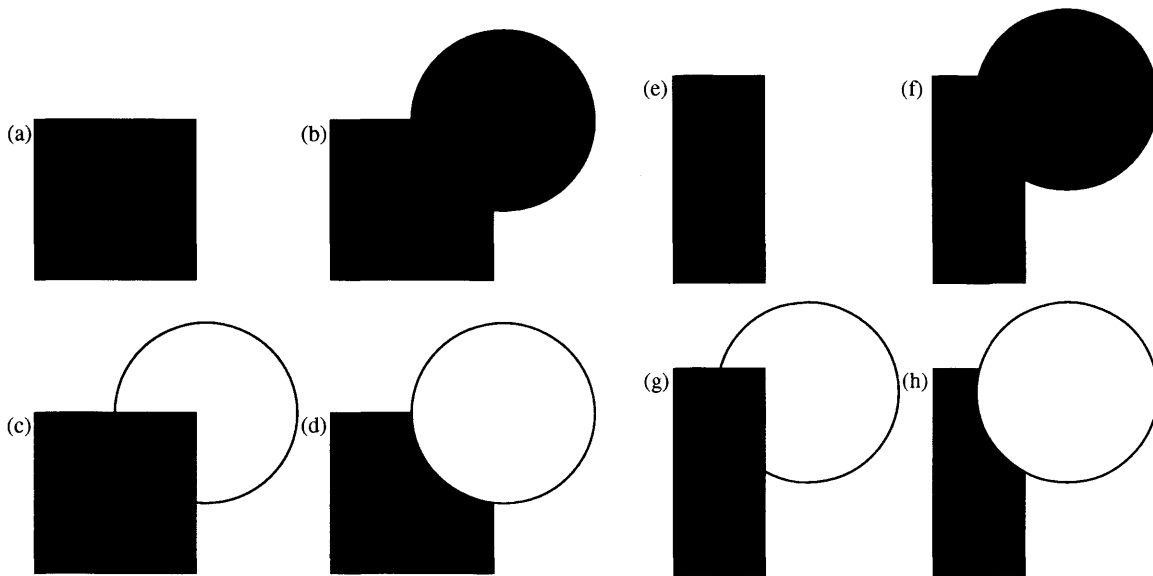
Figure 4.1. The Whole (a), Occluded (b), Clear (c) and Notched (d) squares. Right: The Whole (e), Occluded (f), Clear (g) and Notched (h) rectangles. The circumference of the occluding circles in the Clear and Notched conditions is marked in black for illustrative purposes only. In reality, these circles were made of trasparent Perspex.

Occluded condition: The stimuli in this condition were identical to the Whole stimuli except that the top right corner of the shape was occluded by a 3 mm thick black Perpex circle with a diameter of 40 mm (Figure 4.1b and 4.1f). For both the square and rectangle the occluding circle was positioned so that its circumference intersected the midpoint of the two sides of the occluded shape.

Clear condition: The stimuli in this condition were identical to the Occluded stimuli except that the occluding circle was made of transparent Perspex (Figure 4.1c and 4.1g).

Notched condition: The stimuli in this condition were identical to the Clear stimuli except that the occluded region was removed from the occluded shape. Moreover, the occluding circle was now 6 mm thick and its bottom surface was co-planar with the occluded shape (Figure 4.1d and 4.1h).

4.2.3.2. Apparatus and Set-up

Unless otherwise stated, the apparatus and set-up were as in Experiment 1. In order to reduce interference from shadows, the stimuli were placed on a hollow box (21 x 29.7 x 10.5 cm), as illustrated in Figure 4.2. The hollow box was positioned 11 cm from the bottom edge and along the vertical midline of the table (90.8 × 64.8 mm). The Start button (18 mm diameter) was centred along the midline of a box (11 x 22.5 x 10.5 mm) that was interposed between the stimuli and the edge of the table. The distance between the centre of the Start button and centre of the stimuli was 18.5 cm. A schematic representation of the set-up is shown in Figure 4.2.
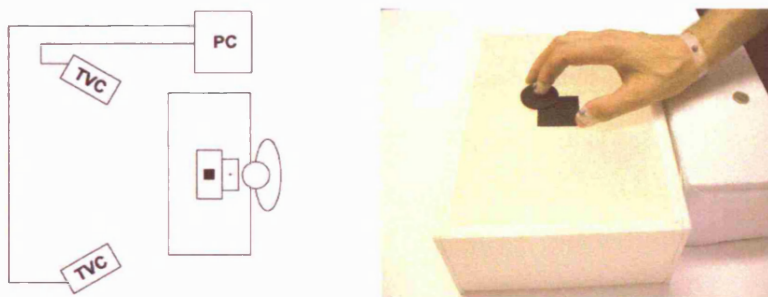
Figure 4.2. Schematic representation of the experimental set up. Right: The grasping task with the Occluded stimuli.

4.2.4. Procedure

Unless otherwise stated the procedure was as in Experiment 1. At the beginning of each condition three practice trials were given, one for each size, and the square and rectangle blocks were separated by a small break. Movements were recorded for 2.5

seconds, from shortly before the verbal cue signalling movement initiation, and analysed off-line. The experiment lasted approximately 1 hour.

Grasping always took place under normal lighting conditions with full vision of the hand and stimuli throughout the task. At the start of each trial, the participant grasped the Start button with the index finger and thumb close together and with the eyes closed. In the Whole condition, at the verbal cue "open", the participant was instructed to open the eyes and to look at the stimuli. After a 3-sec delay, the verbal cue "go" was given and the participant's task was to reach out and grasp the shape using a precision grip. Stimuli were grasped along the diagonal joining the bottom left corner with the top right corner, as shown in Figure 4.2. The participant was instructed to maintain the index finger and thumb on the target until the verbal instruction "ok" signalled the end of the trial and that (s)he could return to the Start position.

The same procedure was used in the Occluded, Clear and Notched conditions except that, due to the absence of a top right "graspable" corner, participants were instructed to reach out and grasp the shape *as if it had both graspable corners*. In the Clear condition the location of the occluded corner was clearly visible. In the Occluded and Notched conditions, participants were instructed that the location of the occluded and missing corner, respectively, was at the intersection of the two sides of the shape, if prolonged.

4.2.5. Data Collection and Variables

Data collection and variables were as described in Experiment 1.

4.3. Results

Participants performed 8 trials for each of the 3 sizes in each condition. The means entered in the analysis were computed from a minimum of 4 trials. A small number of trials (4%) were not included in the analysis due to loss of marker values. Where not

otherwise specified, an alpha level of 0.05 was used for the tests of significance and where necessary, Geisser-Greenhouse adjustments were made to the degrees of freedom. Simple comparisons were analysed with repeated measures t-tests and Bonferroni correction.

The individual kinematic variables were analysed in a series of $2 \times 4 \times 3$ repeated measures ANOVA with Shape (square/rectangle), Occlusion (whole/occluded/clear/notched) and Size (40/50/60 mm) as factors.

4.3.1. Kinematic Profiles

Typical kinematic profiles (Jeannerod, 1981) were obtained in all conditions for both the square and rectangle (Figure 4.3). Specifically, a biphasic grip aperture profile was observed with all stimuli as a finger-opening phase was followed by finger-closure. Moreover, maximum grip aperture occurred within the expected range of movement execution (60% - 80%; Smeets & Brenner, 1999). The velocity profile was also biphasic with clear acceleration and deceleration phases. Finally, the temporal coupling between the transport and grasp components was maintained for all targets as maximum grip aperture occurred soon after maximum velocity.
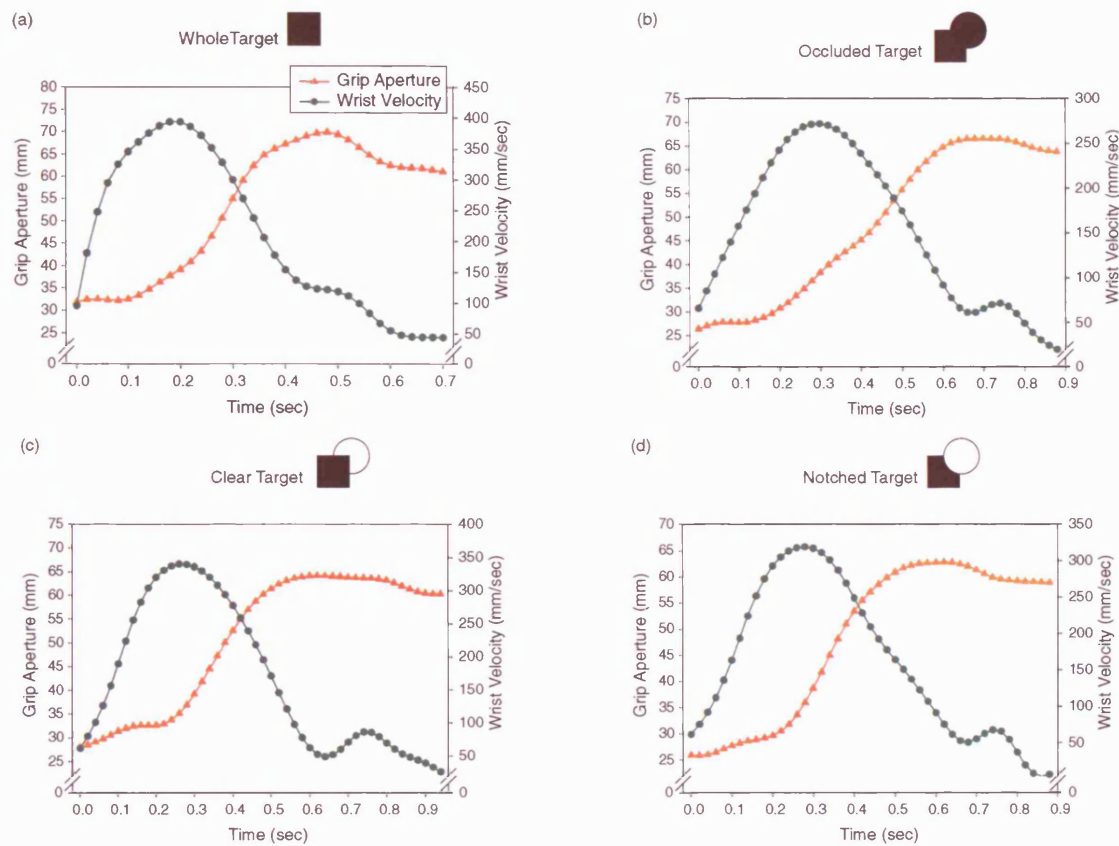
Figure 4.3. Representative grip aperture and velocity profiles from one participant for a 60 mm target in the (a) Whole (b) Occluded, (c) Clear and (d) Notched conditions.

4.3.2. Grasp Component

4.3.2.1. Maximum Grip Aperture

The analysis of maximum grip aperture revealed significant main effects of Occlusion ($F_{(3,33)} = 40.283$, $p < .001$) and Size ($F_{(2,22)} = 488.187$, $p < .001$) and significant Shape × Size ($F_{(2,22)} = 4.051$, $p = .032$) and Occlusion × Size ($F_{(6,66)} = 3.236$, $p = .036$) interactions. The main effect of Shape ($F_{(1,11)} = 0.328$, $p = .579$) and the remaining interactions were not significant ($p > .05$ for all interactions). The group means are shown in Table 4.1 and Figure 4.7.

Table 4.1. Mean maximum grip aperture (mm) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	54.62 (1.058)	50.73 (1.174)	49.73 (1.029)	49.67 (1.043)
Square 50	63.63 (0.830)	59.32 (1.169)	58.36 (1.234)	58.01 (1.169)
Square 60	71.94 (1.230)	67.23 (1.066)	66.96 (1.152)	64.64 (1.121)
Rectangle 40	55.87 (1.055)	51.54 (0.913)	50.67 (1.094)	50.73 (1.085)
Rectangle 50	63.56 (1.052)	59.65 (1.151)	58.42 (1.163)	58.17 (1.211)
Rectangle 60	72.27 (1.125)	66.81 (1.234)	65.62 (1.095)	64.48 (1.282)
Mean	**63.65 (0.886)**	**59.22 (1.006)**	**58.29 (0.988)**	**57.62 (1.038)**

Visual inspection of the data, as shown in Figure 4.4, suggested that the Shape × Size interaction was due to a small convergence of grip apertures for the three sizes that was present for the rectangle but not for the square. This interaction was explored with a simple effect analysis of Size at each level of Shape which revealed that, in agreement with the small difference observed, all comparisons were highly significant ($p < .001$ for all comparisons). These results suggest that grip aperture significantly increased as a function of target size for both shapes. The interaction was also explored with an analysis of Shape at each level of Size. Although mean maximum grip aperture was larger for the 40 and 50 mm rectangles than for the squares, repeated measures t-tests revealed no significant differences for any of the three sizes ($t_{(11)} = -1.760$, $p = .106$; $t_{(11)} = -0.243$, $p = .813$ and $t_{(11)} = 0.828$, $p = .425$ for the 40, 50 and 60 mm targets, respectively).
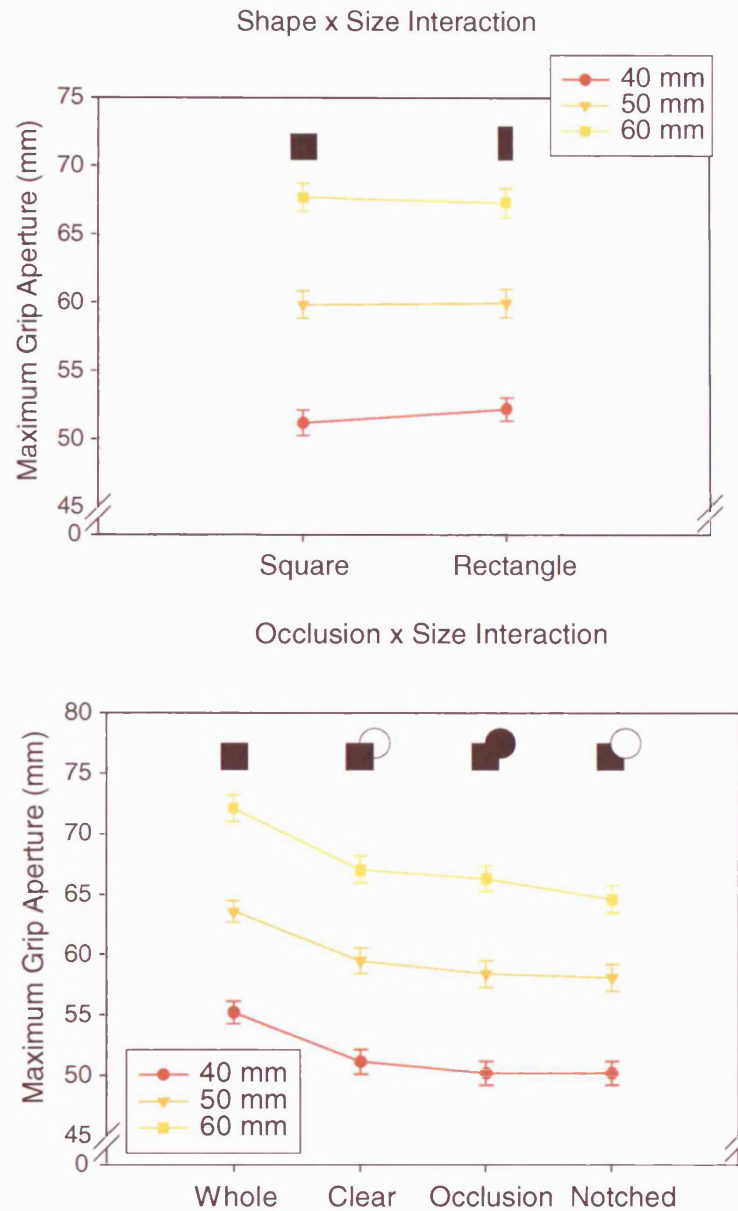
Figure 4.4. Shape × Size interaction. Right: Occlusion × Size interaction. For illustrative purposes the stimuli on the graph are from the square set, however the data refers to both shapes.

The right panel of Figure 4.4 shows that there was a small convergence of maximum grip aperture for the three target sizes in the Notched condition that was not present for the other occlusion levels. This Occlusion × Size interaction was explored with a simple

effect analysis of Occlusion at each level of Size. Repeated measures ANOVAs revealed a significant effect of Occlusion for the 40 mm ($F_{(3, 33)}$ = 19.274, p < .001), 50 mm ($F_{(3,33)}$ = 32.114, p < .001) and 60 mm ($F_{(3,33)}$ = 43.667, p < .001) targets. These effects were further explored with a series of repeated measures t-tests which revealed that significantly larger grip apertures were used in the Whole condition relative to any other condition for all sizes. More crucially, no significant differences were found between the Clear and Occluded conditions in any of the three sizes. Finally, grip apertures in the Notched conditions were found to be significantly smaller than in the Clear condition for the 50 and 60 mm targets. These results are reported in Table 4.2.

Table 4.2. Planned comparisons exploring maximum grip aperture as a function of occlusion and size. df = 11 and α = 0.003 for all comparisons.

Comparison	40 mm	50 mm	60 mm
Whole – Occluded	t = 4.902; p < .001	t = 6.350; p < .001	t = 6.350; p < .001
Whole – Clear	t = 4.448; p = .001	t = 5.460; p < .001	t = 6.442; p < .001
Whole – Notched	t = 6.399; p < .001	t = 7.506; p < .001	t = 7.993; p < .001
Occluded – Clear	t = 1.576; p = .143	t = 2.068; p = .063	t = 2.196; p = .050
Occluded – Notched	t = 0.003; p = .998	t = 0.609; p = .555	t = 3.586; p = .004
Clear – Notched	t = 2.032; p = .067	t = 4.156; p = .002	t = 5.605; p < .001

As expected, the analysis of Size at each level of Occlusion revealed that grip aperture significantly increased as a function of target size in all conditions (p < .001 for all comparisons).

4.3.2.2. Time to Maximum Grip Aperture

The analysis of time to maximum grip aperture revealed significant main effects of Occlusion ($F_{(3,33)}$ = 9.858, p < .001) and Size ($F_{(2,22)}$ = 12.286, p = .004) but a non-significant effect of Shape ($F_{(1,11)}$ = 3.866, p = .075) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 4.3 and Figure 4.7.

Table 4.3. Mean time to maximum grip aperture (msec) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	479 (24.0)	518 (29.9)	528 (34.5)	566 (25.9)
Square 50	510 (22.9)	569 (26.6)	566 (33.1)	611 (30.0)
Square 60	520 (29.7)	578 (24.6)	594 (28.8)	620 (26.1)
Rectangle 40	449 (27.7)	513 (30.1)	527 (32.5)	499 (32.7)
Rectangle 50	475 (20.2)	551 (21.5)	565 (25.0)	529 (28.8)
Rectangle 60	501 (26.2)	585 (22.4)	594 (24.6)	582 (22.0)
Mean	**489 (21.2)**	**552 (21.6)**	**563 (25.6)**	**568 (23.5)**

The effect of Occlusion was explored with planned comparisons which revealed that maximum grip aperture occurred significantly earlier in the Whole condition relative to the Occluded ($t_{(11)}$ = -4.395, p = .001), Clear ($t_{(11)}$ = -3.108, p = .010) and Notched ($t_{(11)}$ = -5.398, p < .001) conditions. No significant differences were measured between these latter three conditions (p > .05 for all comparisons).

The simple effect analysis of Size revealed that maximum grip aperture occurred later with larger targets as both the comparisons between the 40 and 50 mm targets and the 50 and 60 mm targets were significant ($t_{(11)}$ = -3.546, p = .005 and $t_{(11)}$ = -3.062, p = .011, respectively).

4.3.2.3. Percent Time to Maximum Grip Aperture

Similar results were obtained for the analysis of percent time to maximum grip aperture. This revealed a significant main effect of Occlusion ($F_{(3,33)}$ = 10.989, p < .001) and of Size ($F_{(2,22)}$ = 12.540, p = .003) but a non-significant main effect of Shape ($F_{(1,11)}$ = 2.188, p = .167) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 4.4 and Figure 4.7.

Table 4.4. Mean percent time to maximum grip aperture (%) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	67.54 (2.147)	70.27 (3.182)	71.69 (3.809)	75.86 (2.918)
Square 50	70.04 (1.723)	76.64 (2.287)	76.74 (2.807)	80.04 (2.504)
Square 60	71.30 (2.143)	79.01 (1.885)	79.46 (1.984)	82.32 (1.995)
Rectangle 40	63.85 (3.126)	71.10 (3.663)	74.64 (2.942)	68.71 (3.875)
Rectangle 50	67.52 (1.547)	75.75 (2.328)	76.10 (2.276)	72.42 (3.436)
Rectangle 60	70.11 (2.183)	79.11 (2.469)	80.00 (2.150)	79.87 (2.364)
Mean	**68.39 (1.655)**	**75.15 (2.115)**	**76.44 (2.121)**	**76.54 (2.346)**

Planned comparisons exploring the effect of Occlusion revealed that maximum grip aperture occurred significantly earlier in the Whole condition relative to the Occluded ($t_{(11)}$ = -5.427, p < .001), Clear ($t_{(11)}$ = -3.289, p = .007) and Notched ($t_{(11)}$ = -4.550, p = .001) conditions. No significant differences were measured between these latter three conditions (p > .05 for all comparisons).

The analysis of Size revealed that maximum grip aperture occurred proportionally later with larger targets as both the 40-50 mm and the 50-60 mm comparisons were significant ($t_{(11)}$ = -3.570, p = .004 and $t_{(11)}$ = -2.984, p = .012, respectively).

4.3.3. Transport Component

4.3.3.1. Maximum Wrist velocity

The analysis of maximum wrist velocity revealed a main effect of Shape ($F_{(1,11)}$ = 62.886, p < .001) indicating that movements were significantly faster for the rectangles. In addition, the main effect of Occlusion ($F_{(3,33)}$ = 29.577, p < .001) and Size ($F_{(2,22)}$ = 8.280, p = .002) were also significant. None of the interactions were significant (p > .05 for all interactions). The group means are shown in Table 4.5 and Figure 4.7.

Table 4.5. Mean maximum wrist velocity (mm sec^{-1}) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	379.12 (13.30)	354.85 (10.57)	354.83 (13.03)	346.46 (11.72)
Square 50	375.39 (13.42)	361.14 (10.80)	357.10 (10.96)	347.87 (10.28)
Square 60	377.81 (13.59)	368.68 (13.59)	358.41 (13.47)	351.53 (12.17)
Rectangle 40	411.49 (12.19)	381.29 (12.31)	376.87 (10.29)	377.09 (12.59)
Rectangle 50	422.93 (12.73)	392.45 (11.81)	379.41 (12.38)	387.08 (12.27)
Rectangle 60	428.91 (12.90)	390.76 (12.75)	389.83 (11.68)	385.36 (13.50)
Mean	**399.27 (11.04)**	**374.86 (10.93)**	**369.41 (11.53)**	**365.90 (11.27)**

The effect of Occlusion was further explored with planned comparisons which revealed that significantly faster movements were used with the Whole targets relative to the Occluded ($t_{(11)}$ = 8.346, p < .001), Clear ($t_{(11)}$ = 5.414, p < .001) and Notched ($t_{(11)}$ = 6.847, p < .001) conditions. No significant differences were measured between these latter three conditions (p > .05 for all comparisons).

As expected the simple effect analysis of Size revealed that movement velocities increased as a function of target size, however only the 40-50 mm and the 40-60mm comparisons were significant ($t_{(11)}$ = -2.373, p = .037 and $t_{(11)}$ = 3.976, p = .002, respectively).

4.3.3.2. Time to Maximum Wrist Velocity

The analysis of time to maximum wrist velocity revealed a significant main effect of Size ($F_{(2,22)}$ = 5.398, p = .012) but non-significant main effects of Shape ($F_{(1,11)}$ = 0.619, p = .448) and Occlusion ($F_{(3,33)}$ = 0.617, p < .609) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 4.6 and Figure 4.7.

Table 4.6. Mean time to maximum wrist velocity (msec) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	266 (10.7)	267 (11.8)	253 (8.5)	264 (8.5)
Square 50	278 (15.0)	275 (10.7)	257 (9.5)	259 (7.4)
Square 60	271 (16.4)	268 (9.4)	263 (8.5)	271 (8.7)
Rectangle 40	259 (15.3)	261 (9.3)	259 (10.2)	259 (13.3)
Rectangle 50	265 (14.0)	263 (8.9)	265 (11.9)	257 (13.9)
Rectangle 60	261 (14.9)	269 (11.7)	267 (8.6)	262 (12.4)
Mean	**267 (13.3)**	**260 (8.7)**	**267 (9.7)**	**262 (9.4)**

The effect of Size was further explored with planned comparisons. These revealed that although there was a trend for maximum velocity to occur later for larger targets, neither the 40-50 mm ($t_{(11)}$ = -2.098, p = .060) nor the 50-60 mm ($t_{(11)}$ = -0.985, p = .346) comparisons were significant. However, movement velocity significantly increased from the 40 mm to the 60 mm targets ($t_{(11)}$ = -3.363, p = .006).

4.3.3.3. Percent Time to Maximum Wrist Velocity

The analysis of percent time to maximum wrist velocity revealed a significant main effect of Occlusion ($F_{(3,33)}$ = 4.790, p = .007) and a significant Occlusion × Size interaction ($F_{(6,66)}$ = 2.726, p = .020). The main effects of Shape ($F_{(1,11)}$ < .001, p = .989) and Size ($F_{(2,22)}$ = 1.282, p = .297) and all the remaining interactions were non-significant (p > .05 for all interactions). The group means are shown in Table 4.7 and Figure 4.7.

Table 4.7. Mean percent time to maximum wrist velocity (%) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	37.59 (0.937)	36.22 (1.235)	34.30 (0.682)	35.30 (0.932)
Square 50	38.12 (1.389)	37.26 (1.083)	35.14 (0.990)	34.23 (1.050)
Square 60	37.18 (1.188)	36.43 (0.779)	35.36 (0.571)	36.17 (0.732)
Rectangle 40	36.87 (1.085)	36.15 (0.690)	35.06 (0.819)	35.48 (1.166)
Rectangle 50	37.54 (1.092)	36.20 (0.781)	35.73 (1.111)	35.30 (1.486)
Rectangle 60	36.58 (1.224)	36.34 (1.098)	36.05 (0.775)	35.91 (1.019)
Mean	**37.31 (1.063)**	**36.44 (0.805)**	**35.27 (0.638)**	**35.40 (0.698)**

The significant interaction is shown in Figure 4.5 and was explored with repeated measures ANOVAs that analysed the effect Occlusion at each level of Size. These revealed that percent time to maximum velocity significantly varied as a function of occlusion level for the 40 mm ($F_{(3,69)}$ = 6.459, p = .001) and 50 mm targets ($F_{(3,69)}$ = 5.431, p = .007), but not for the 60 mm targets ($F_{(3,69)}$ = 1.119, p = .347). As shown in the right panel of Figure 4.5, post-hoc comparisons revealed that for the 40 and 50 mm targets maximum wrist velocity occurred proportionally later in the Whole condition relative to both the Occluded and Notched conditions but not relative to the Clear condition. In addition, for these 50 mm target maximum velocity occurred proportionally later for the Clear relative to both the Occluded and Notched conditions whereas for the 40 mm target only the former comparison was significant. However, of these comparisons only the Whole-Occluded test for the 40 mm target reached significance after the Bonferroni correction (α = 0.003).
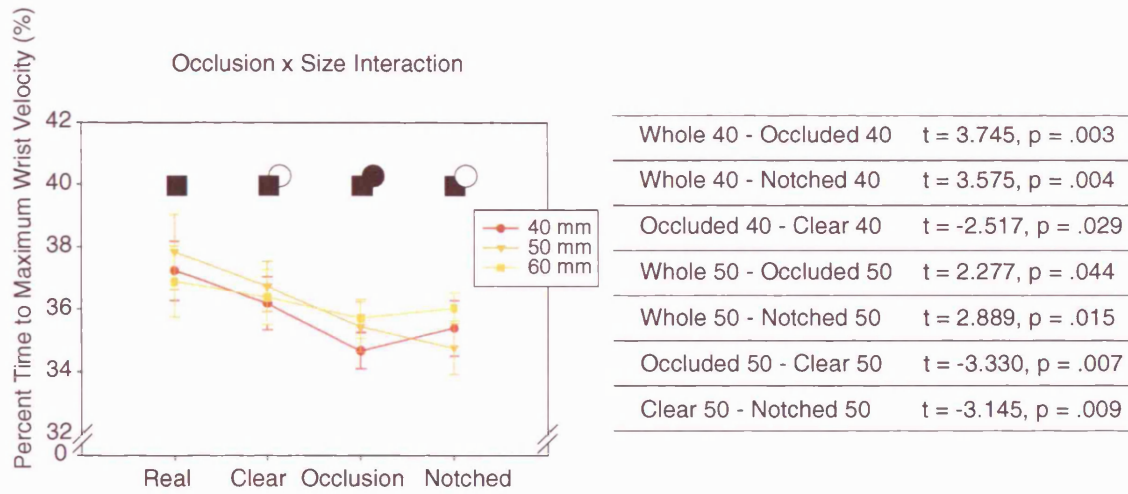
Figure 4.5. Occlusion × Size interaction. As above, the stimuli on the graph are from the square set, however the data refers to both shapes. Right: Comparisons exploring percent time to maximum wrist velocity as a function of occlusion and size. df = 11 for all comparisons.

4.3.3.4. Maximum Wrist Displacement

The analysis of maximum wrist displacement revealed significant main effects of Shape ($F_{(1,11)}$ = 57.671, p < .001), Occlusion ($F_{(3,33)}$ = 13.206, p = .001) and Size ($F_{(2,22)}$ = 295.528, p < .001) and a significant Shape × Size interaction ($F_{(2,22)}$ = 3.650, p = .043). All the remaining interactions were non-significant (p > .05 for all interactions). The group means are shown in Table 4.8 and Figure 4.7.

Table 4.8. Mean maximum wrist displacement (mm) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	153.64 (3.84)	148.54 (2.56)	148.54 (2.73)	146.64 (3.04)
Square 50	156.46 (3.15)	153.36 (2.67)	150.25 (3.01)	149.37 (3.26)
Square 60	158.33 (3.57)	155.66 (2.83)	154.99 (3.07)	153.27 (2.89)
Rectangle 40	164.17 (2.91)	157.81 (2.65)	156.98 (2.29)	155.02 (2.49)
Rectangle 50	168.19 (2.62)	162.56 (2.84)	161.75 (2.30)	158.73 (2.75)
Rectangle 60	174.18 (3.53)	166.07 (3.16)	165.45 (2.43)	164.06 (2.63)
Mean	**162.49 (3.09)**	**157.33 (2.61)**	**156.33 (2.41)**	**154.51 (2.69)**

Visual inspection of the data revealed that, as shown in Figure 4.6, the weak significant interaction was due to larger differences in wrist displacement between different target sizes for the rectangle. However, repeated measure t-tests revealed that the 40-50 mm and the 50-60 mm comparisons were highly significant for both shapes (for all comparisons $p \leq .001$). Similarly, the simple effect analysis of Shape at each level of Size revealed that significantly greater displacements were used for the rectangle than the square for all sizes ($p < .001$ for all comparisons).
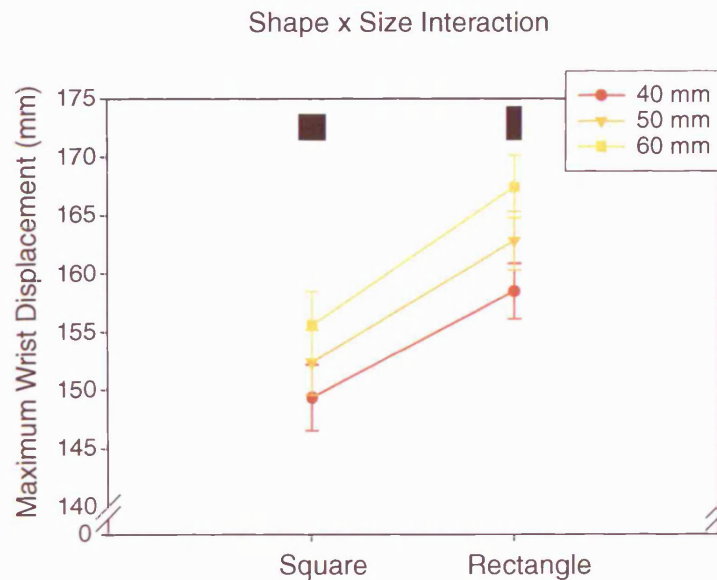
Figure 4.6. Shape × Size interaction for maximum wrist displacement.

Planned comparisons exploring the effect of Occlusion revealed that significantly greater wrist displacements were used in the Whole condition relative to the Occluded $(t_{(11)} = 3.636, p = .004)$, Clear $(t_{(11)} = 2.885, p = .015)$ and Notched $(t_{(11)} = 4.654, p = .001)$ conditions. In addition, the displacements in the Notched condition were significantly smaller than the displacements used in the Occluded $(t_{(11)} = 2.300, p = .042)$ and Clear $(t_{(11)} = 6.441, p < .001)$ conditions.

4.3.3.5. Maximum Wrist Height

The analysis of maximum wrist height revealed a significant main effect of Shape $(F_{(1,11)} = 6.160, p = .030)$ but non-significant effects of Occlusion $(F_{(3,33)} = 2.064, p = .124)$ and Size $(F_{(2,22)} = 0.465, p = .634)$ and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 4.9 and Figure 4.7.

Table 4.9. Mean maximum wrist height (mm) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	518.70 (4.23)	518.20 (4.63)	518.90 (4.07)	516.66 (4.27)
Square 50	517.76 (3.57)	517.72 (4.40)	517.05 (4.00)	517.46 (4.61)
Square 60	518.67 (4.05)	518.33 (4.32)	516.41 (3.87)	516.64 (3.89)
Rectangle 40	524.16 (4.38)	520.59 (4.32)	521.33 (4.42)	519.20 (5.02)
Rectangle 50	524.41 (4.27)	521.52 (4.28)	520.44 (4.48)	520.43 (4.68)
Rectangle 60	525.50 (4.26)	522.52 (4.01)	521.95 (4.37)	519.39 (4.67)
Mean	**521.53 (3.92)**	**519.81 (4.17)**	**519.35 (4.13)**	**518.30 (4.34)**

The main effect of Shape in the absence of any significant interaction suggests that greater wrist heights were used for the rectangle than for the square (means 522 and 518 mm, respectively), irrespective of size or occlusion level.

4.3.3.6. Movement Duration

The analysis of movement duration revealed significant main effects of Occlusion ($F_{(3,33)}$ = 5.344, p = .004) and Size ($F_{(2,22)}$ = 3.897, p = .036) but a non-significant effect of Shape ($F_{(1,11)}$ = 2.425, p = .148) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 4.10 and Figure 4.7.

Table 4.10. Mean movement duration (msec) for each stimulus size in each condition. Standard errors are in brackets.

	Whole	Clear	Occluded	Notched
Square 40	705 (16.5)	733 (17.0)	737 (24.4)	748 (20.2)
Square 50	725 (16.7)	739 (19.3)	733 (24.2)	761 (26.1)
Square 60	724 (22.5)	737 (18.6)	744 (20.7)	752 (24.6)
Rectangle 40	701 (24.3)	721 (15.8)	730 (18.4)	728 (18.6)
Rectangle 50	703 (20.1)	727 (15.5)	742 (19.4)	729 (16.0)
Rectangle 60	711 (18.4)	738 (15.2)	742 (18.2)	729 (17.4)
Mean	**711 (17.1)**	**733 (15.5)**	**738 (19.7)**	**741 (19.4)**

Planned comparisons exploring the effect of Occlusion revealed that movements were shorter in the Whole condition relative to relative to the Occluded ($t_{(11)}$ = -2.869, p = .015, Clear ($t_{(11)}$ = -2.424, p = .034) and Notched ($t_{(11)}$ = -3.576, p = .004) conditions. No significant differences were observed between any of these latter three conditions (p > .05 for all comparisons).

The simple effect analysis of Size revealed that, albeit there was a trend for movement duration to increase with target size, only the 40-60 mm comparison was statistically significant ($t_{(11)}$ = -3.464, p = .005).

(g)

(h)

(i)
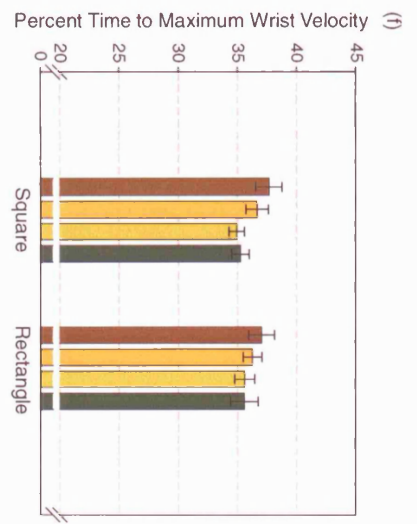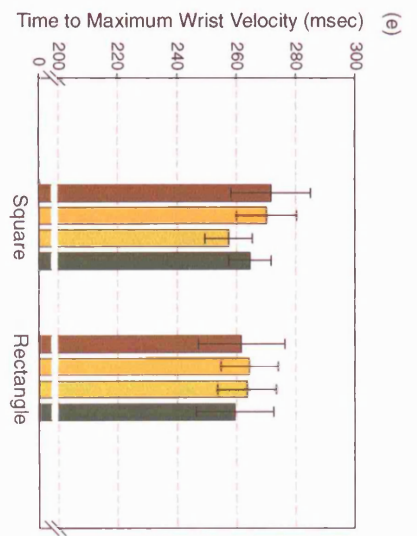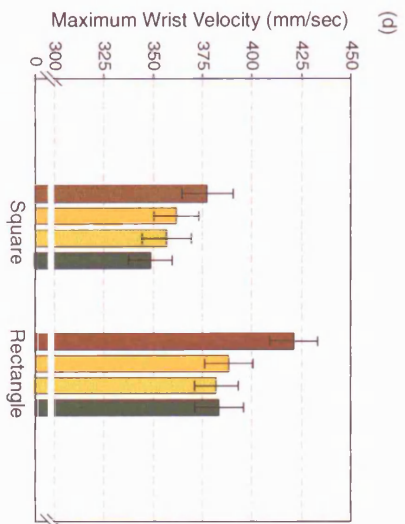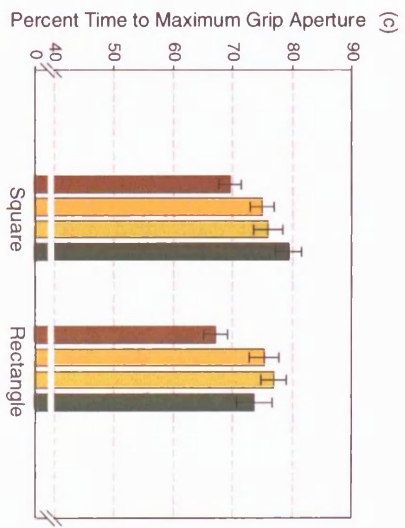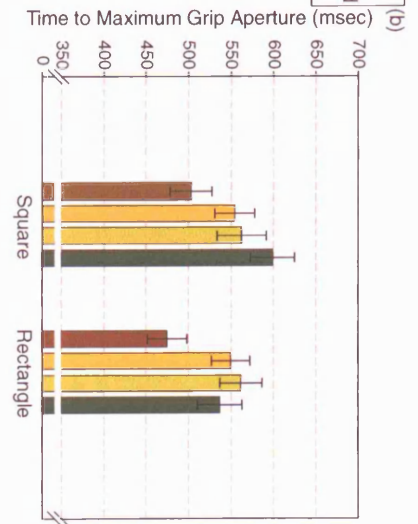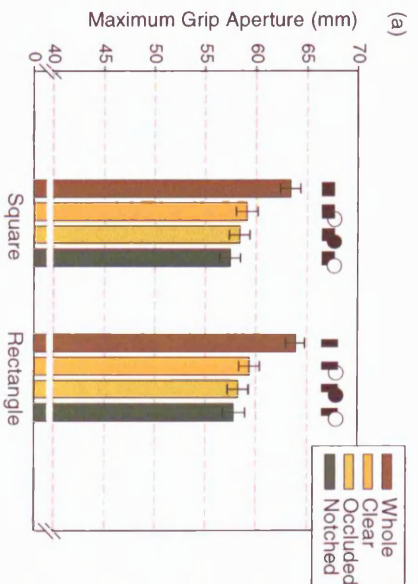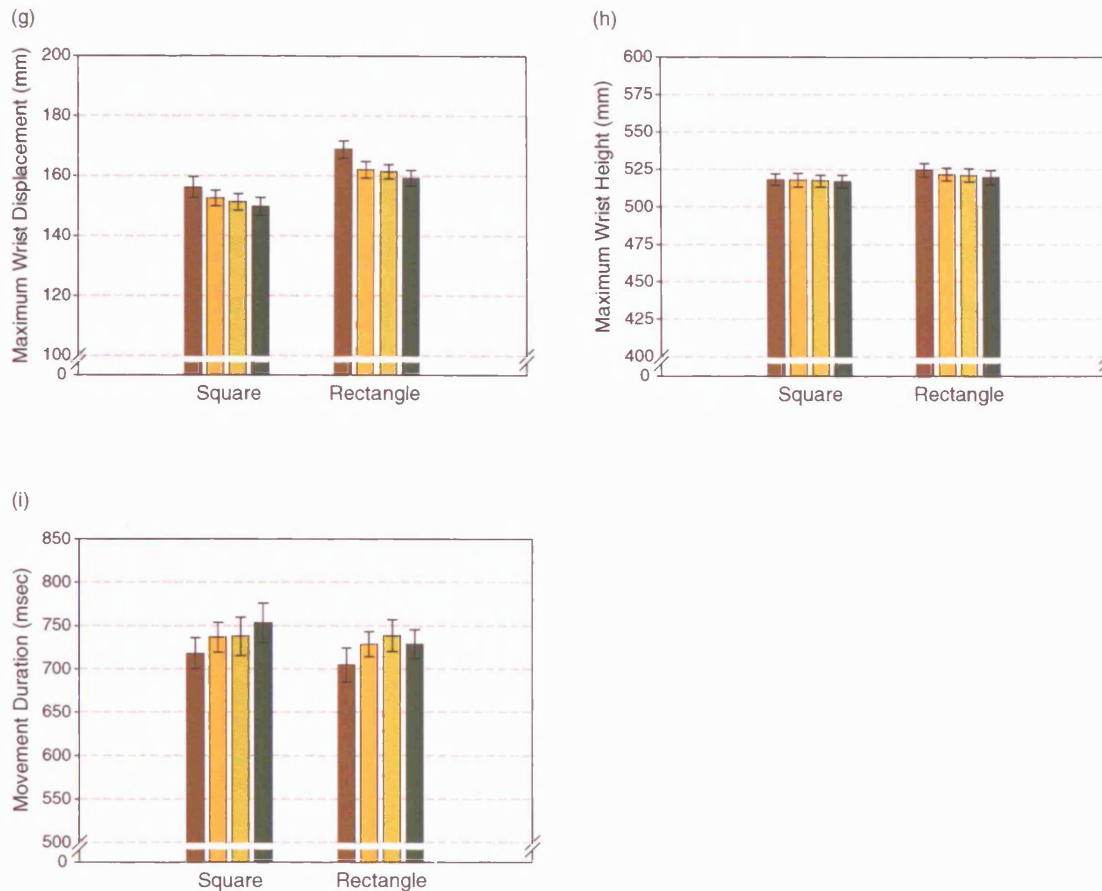
Figure 4.7. Means and standard errors (error bars) for: (a) maximum grip aperture (MGA), (b) time to MGA, (c) % time to MGA, (d) maximum wrist velocity (MWV), (e) time to MWV, (f) % time to MWV, (g) maximum wrist displacement, (h) maximum wrist height and (i) movement duration.

4.3.4 Effects of Removing Haptic and Visual Feedback

Figure 4.7 clearly illustrates that there were systematic ascending and descending trends from the Whole to the Notched conditions. Specifically, the figure shows that maximum grip aperture, maximum wrist velocity, percent time to maximum wrist velocity and maximum wrist displacement systematically decreased whereas time and percent time to maximum grip aperture and movement duration systematically increased. The effects

that removing haptic and visual feedback in isolation had on these kinematic variables was therefore quantified and analysed.

The effect of removing haptic feedback alone was obtained by subtracting the values obtained in the Whole condition from the values obtained in the Clear condition. Similarly, the effect of removing visual information alone was obtained by subtracting the values obtained in the Clear condition from the values obtained in the Occluded condition. Figure 4.8 illustrates these differences.
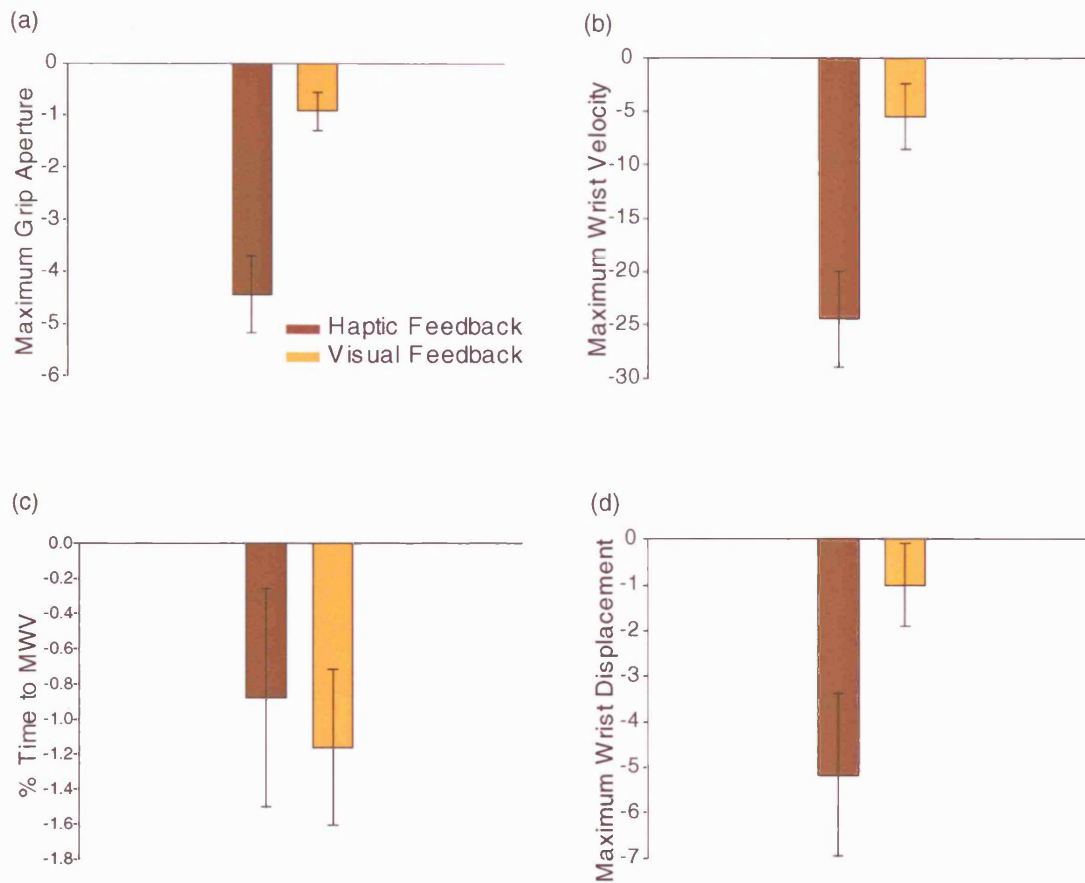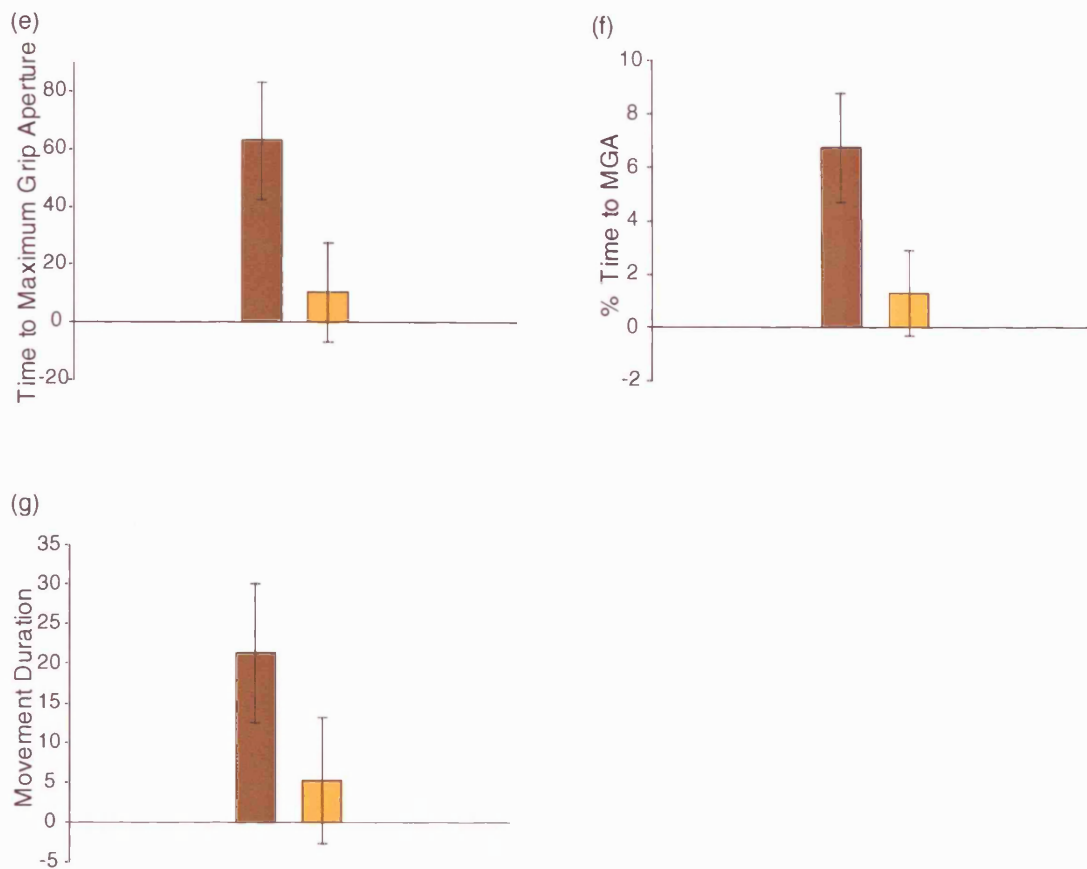
Figure 4.8. Independent effects of removing haptic and visual feedback in isolation for: (a) maximum grip aperture (MGA, mm), (b) maximum wrist velocity (MWV, mm/sec), (c) % time to MWV, (d) maximum wrist displacement (MWD, mm), (e) time to MGA (msec), (f) % time to MGA and (g) movement duration (msec).

Figure 4.8 clearly shows that, except for percent time to maximum wrist velocity, the effect of removing visual feedback had a negligible effect and that the effect of removing haptic feedback was greater. Repeated measures t-tests confirmed that the effect of removing haptic feedback was significantly greater than the effect of removing visual feedback for maximum grip aperture ($t_{(11)}$ = 4.390, p = .001) and for maximum wrist velocity ($t_{(11)}$ = 2.768, p = .018). No significant differences were found for percent time to maximum wrist velocity ($t_{(11)}$ = 0.396, p = .700), maximum wrist displacement ($t_{(11)}$ = -1.829, p = .095), time to maximum grip aperture ($t_{(11)}$ = 1.563, p = .146), percent

time to maximum grip aperture ($t_{(11)}$ = 1.614, p = .135) and movement duration ($t_{(11)}$ = 1.154, p = .273).

4.4. Discussion

The aim of the present experiment was to establish whether the dorsal visual system accesses the interpolated region of partially occluded objects when this is necessary for the computation of the kinematic parameters in manual prehension.

The comparison of interest between the Clear and Occluded conditions revealed no significant differences in any of the kinematic parameters measured suggesting that the removal of visual information did not significantly affect performance. The only exception to this was a trend for maximum wrist velocity to occur later in the Clear condition relative to the Occluded condition for the 40 and 50 mm targets, however these differences did not reach significance. That removing visual information had a small effect was further confirmed in Section 4.3.4 where it was found that, except for percent time to maximum wrist velocity, changes following the introduction of the occluded region were much smaller than the effect of removing haptic feedback. Finally, typical kinematic profiles were obtained with the partially occluded targets further suggesting that no great disruption occurred to visuomotor processing with these stimuli. Taken together these results suggest that the dorsal visual system had access to the interpolated region of the partially occluded targets and that this information was interpolated with a good degree of accuracy.

These results are in agreement with the claim that the occluded region or partially occluded objects is interpolated to a large extent in early visual cortex (Fiorani et al., 1992, 2003; Greene and Brown 2000; Oliveira et al., 1998; Rensink & Enns, 1998; Sugita, 1999). The finding that the interpolated region is available for visuomotor processing taken together with evidence that this information is also available to the ventral visual system (Kellman et al., 2001; Kellman & Shipley, 1991; Rensink & Enns,

1998) provide indirect evidence that the interpolation processes are likely to occur in early areas that are common to both systems. In addition, these findings further corroborate Dyde and Milner's (2002) claim as they clearly suggest that a perceptual phenomenon not explicitly specified at a retinal level but thought to be generated in early visual cortex affects visuomotor performance.

The present findings are also in agreement with the results from Experiment 1 as they provide further evidence that interpolated regions are used by the dorsal visual system for the guidance of object-directed action. It is perhaps of interest to note that whereas this study explored a type of visual completion that in the literature covering ventral visual processing has been referred to as amodal, Experiment 1 explored a type of completion that has been referred to as modal. Both modal and amodal completion refer to perceptual experience in the absence of a physical stimulus, however, whereas in the former the interpolated region acquires sensory characteristics, such as brightness or colour, in the latter the object is completed in the absence of a sensory experience (Michotte, Thines & Crabbe, 1964; cited in Kellman et al., 1991). A clear example of modal completion is visual interpolation at the blind spot. Kanizsa figures, that is the stimuli used in Experiment 1, are another example of modal completion as the illusory figure is generally perceived with clear contours and enhanced brightness (Kellman & Shipley, 1991). By contrast, the perceptual completion of objects behind occluders, that is the targets used in this experiment, is an instance of amodal completion as although the separate regions of the occluded object are perceived as unitary the interpolated region does not acquire sensory properties.

The concept of modal and amodal completion cannot be directly used to describe functions of the dorsal visual system as they refer to perceived visual phenomena and therefore are clearly restricted to ventral visual processing. Moreover, the present results could not be entirely accounted for by this dichotomy, as accurate grasping was observed in the Crosses condition of Experiment 1 and to some extent in the Notched condition in this experiment, that is with phenomena that are known to result in neither

modal nor amodal completion. Nevertheless, it is of interest to give an account of the results within the existing dichotomy and note that the present findings together with Experiment 1 suggest that visual information generated by these two types of interpolation that give rise to different perceptual experience, modal and amodal completion, seems to be available to the dorsal visual system.

This conclusion would be in agreement with an influential theory of contour interpolation proposed by Kellman and Shipley (1991; also Kellman, Guttman & Wickens, 2001) as these authors argue that both modally and amodally completed boundaries are interpolated by the same mechanisms, probably located in early visual cortex (Kellman et al., 2001). Kellman and colleagues refer to this as the *Identity Hypothesis*. Specifically, Kellman and Shipley (1991) suggest that the interpolation process starts with the detection of junctions and corners, called *tangent discontinuities*, in the visible contours. Tangent discontinuities are necessary but not sufficient for contour interpolation as the visible edges in the display must also be *relatable. Contour relatability* is present when a *pair* of edges can be connected continuously and monotonically (with a single inflection) and, if a bent is present, this must not exceed 90°. Essentially, the concept of contour relatability formalises the Gestalt law of good continuation. Importantly, Kellman et al. (2001) argue that the contour is interpolated when these appropriately oriented edges are present in the display, independently of the quality of the perceptual experience generated and, by implication, that the same mechanisms subserve modal and amodal completion at the level of area V1. The perceptual differences experienced with these two types of interpolation are likely to depend on secondary and subsequent processes mediating depth ordering that may interact with the boundary interpolation mechanisms. Evidence for the Identity Hypothesis comes from findings that ratings of clarity for illusory contours are well matched with perceived unity of corresponding occluded displays (Shipley & Kellman, 1992) and from matched accuracy at judging the degree of rotation of Kanizsa and corresponding amodally completed figures (Ringach & Shapley, 1996).

Peterhans and von der Heydt's (1989) contour neurons, discussed in Chapter 2, have been proposed as a possible neural substrate for the detection of tangent discontinuities (Heitger, von der Heydt, Peterhans, Rosenthaler & Kubler 1998), although more recently Kellman, Garrigan and Shipley (2005) have proposed that position and orientation selective neurons in the caudal intraparietal sulcus (cIPS; Sakata, Taira, Kusunoki, Murata & Tanaka, 1997) are a more plausible neural substrate for 3D-relatibility and the contour interpolation of 3D objects. Either account could explain the results from this study and Experiment 1. We have already noted how signals generated in early visual cortex should be expected to be broadcast to the dorsal visual system and therefore account for the findings presented thus far in this thesis. Kellman et al.'s (2005) claim that cIPS neurons mediate contour interpolation would also explain the present findings. cIPS is an area well within the dorsal visual system, therefore, this newly proposed neural substrate would also predict that interpolated regions are used in object-directed action.

Except for greater movement velocity and maximum wrist height and displacement for the rectangle, no other differences were found between grasps aimed at the two shapes. A greater velocity for the rectangle could be accounted for by the fact that this shape extended in length more than the square and that consequently the contact point for the index finger was more distant from the Start position. Specifically, these results could be accounted for by the findings that in manual prehension hand velocity increases as a function of target distance and that this latter is computed relative to the farthest edge of the object (Hu et al., 1999; Servos et al., 1998). It is therefore not surprising that the shape with the more distant far edge, the rectangle, resulted in greater velocities. Greater wrist displacement could also be accounted for by the more extended length of this shape as this variable is clearly a function of target distance. It is less clear why wrist elevation varied as a function of shape. Wrist elevation generally varies as a function of target height (Hu et al., 1999) which in this study was the same for the two shapes. However, given that, as discussed in more detail in Chapter 5, there is evidence that kinematic parameter can be affected by target dimensions not directly relevant for the

task (Cuijpers, Smeets & Brenner, 2004; Hu et al., 1999), it is possible that this variable could also be accounted for by the different length of the two shapes.

The lack of differences in the other variables, in particular in the grasp component, suggests that the occluded region was interpolated with equal accuracy for the two shapes. Thus, a lack of symmetry in the occluded area of the rectangle did not affect the grasp parameters. These results are in agreement with Goodale et al.'s (1994) claim, discussed in Chapter 1, that the entire contour envelope is taken into consideration for the computation of the kinematic parameters. An implication of this proposition is that the symmetry of the whole shape, rather than parts of it, would affect the kinematic parameters. If this is correct, it is not surprising that no differences were found in the grasp parameters for the two shapes as both were symmetric.

Lederman and Wing (2001) provide further evidence that the symmetry of the whole shape affects visuomotor processing. Although Goodale et al. (1994) clearly demonstrate that grasping asymmetric shapes is a function mediated by the dorsal system, Lederman & Wing (2001) found that grasps aimed at symmetric objects result in reduced distance of the grasp-axis from the object centre of mass (known to improve grasp stability) and in less variability in grasp-axis placement than grasps aimed at corresponding asymmetric shapes. Lederman and Wing (2001) proposed that symmetric shapes afford grasp-axes that are more stable (e.g., they are more likely to include parallel surfaces), closer to the natural grasp-axis (estimated to be 10.6° clockwise by these authors) and that require smaller grip apertures. All these factors are thought to facilitate holding the object in place and ease of manipulation once lifted.

Lederman and Wing's (2001) finding that symmetric shapes result in more stereotypical grasp-axis placement opens the possibility that in the present study target symmetry facilitated "accurate" grip apertures in the occluded condition. Specifically, it could be argued that the accuracy of the grasp contact points with the occluded targets was determined to some extent by target symmetry and not by the availability of an

accurately interpolated occluded region. Notably, both square and rectangle were symmetric before completion. The relatively accurate performance in the Notched condition could be interpreted in support of this claim. This possibility could be easily tested by replicating the present study with asymmetric shapes. If the selection of the grasp points with partially occluded objects was due to the availability of an accurately interpolated region in the dorsal visual system, then accurate performance should be observed with asymmetric targets. By contrast, if the selection of the grasp points was largely based on the symmetry of the shape, then performance with asymmetric partially occluded targets should be more variable and less related to the size of the completed shape.

With the exception of wrist displacement which was smaller for the Notched condition relative to all other targets, no other differences were observed between the Notched and Occluded conditions. By contrast, significantly smaller grip apertures were found for the 40 and 50 mm targets in the Notched relative to the Clear condition. These results could be interpreted in three ways. First, it could be argued that the kinematic variable with the most indicative power in this study was maximum grip aperture and that the differences observed suggest that the occluded region was not interpolated in the Notched condition. Second, it could be argued that the lack of differences in the remaining variables indicate that the interpolated occluded region was available in this condition. Notably, these results would be in agreement with Kellman and Shipley's (1991) low-level account of contour interpolation as the appropriately oriented edges postulated in this model were present in the Notched display. As proposed by these authors, perceptual phenomena associated with visual completion are likely to arise from subsequent stages of visual processing. Thus, a possible explanation for these findings is that the interpolation of the "occluded" region in the Notched stimuli occurred in early visual cortex and that this signal was forwarded to later areas of the dorsal system. In addition, the mechanisms that at later stages of visual processing determined that the transparent circle could not occlude part of the square were available to the ventral system only and consequently could not override the

"completion" signal broadcast to this latter. Third, it could be argued that in the Notched condition the transparent occluding circle on the white background was perceived as a white circle occluding the black square. In this case some interpolation would have been expected to occur.

Except for time to maximum wrist velocity and maximum wrist height significant differences were found between the Whole and the Occluded conditions. Grasps with Whole targets resulted in significantly larger apertures that occurred significantly earlier and in faster movements, although in all but one of the comparisons (Whole vs. Occluded at 40 mm) no differences in the duration of the acceleration phase were observed as indicated by percent time to maximum wrist velocity. Moreover, the Whole targets generated larger wrist displacements and shorter movements. The finding that these differences were also present for the Whole-Clear comparisons and that no differences were observed in the Clear-Occluded comparison clearly suggests that they were not due to a reduction of target visual information but were more likely the result of absent haptic feedback from the occluded corner. This conclusion is in agreement with Gentilucci et al.'s (1997) findings that removing haptic feedback lengthens the duration of the finger-opening phase, decreases velocity and increases movement duration. Thus, the differences observed between the Whole and the other conditions are consistent with the possibility that compensation strategies were adopted due to increased uncertainty arising from the removal of haptic feedback. This conclusion is further strengthened by the observation that, as discussed above and explored in Section 4.3.4, removing visual feedback had a smaller effect than removing haptic feedback.

It is perhaps of interest to note that the larger grip apertures observed in the Whole condition are in disagreement with Gentilucci et al. (1997) who found larger apertures after removing haptic feedback. This discrepancy could be accounted for by differences in visual feedback during movement execution in the two studies. Whereas Gentilucci et al. (1997) used an open loop task, subjects in this study had continuous visual feedback of both target and hand throughout movement execution. Given that it has been

suggested that increasing maximum grip aperture is a way to compensate for increased uncertainty (Gentilucci et al., 1997; Jakobson & Goodale, 1991), it is possible that the presence of visual feedback in this study compensated for the removal of haptic feedback in some way that was not available in Gentilucci et al.'s (1997) study. Moreover, larger apertures in the Whole condition could suggest that the visuomotor system was able to determine that the Whole objects were the only truly "graspable" targets in the study. This possibility is further discussed in the General Discussion.

Another explanation that could account for the larger and earlier grip apertures observed in the Whole condition relative to all the three conditions with occlusion (Clear, Occluded and Notched) is that grasping in these latter was of a pantomime type and therefore not mediated by the dorsal system. Specifically, it is possible that because the occluded circle in these three conditions prevented the top right corner of the target to act as a possible landing point for the index finger, this task was construed as pantomimed grasping. As discussed earlier, the evidence suggests that pantomime grasping is mediated by the ventral visual system and results in smaller and earlier maximum grip apertures than dorsally mediated grasping (Goodale et al., 1994). Thus, if this were the case, it would suggest that grasping in the Clear, Occluded and Notched conditions was mediated by the ventral and not by the dorsal visual system. The likelihood of this possibility is difficult to assess as at present we are not aware of any investigation that measured grasping with comparable stimuli. Of course, this is a matter of importance that should be quickly established as if the task in the occlusion conditions was mediated by the ventral visual system it would invalidate our conclusions. Patients with visual form agnosia could be used to test this possibility. These patients cannot preshape their grip aperture according to target size in pantomimed grasping, thus, a similar behaviour should be observed if the grasping task in the three occlusion conditions in this study was of a pantomimed nature. By contrast, DF should display normal grasping parameters if this task depends on dorsal visual processing.

It could be argued that the possibility that the present task was pantomimed grasping could be ruled out by using real occlusion. Specifically, subjects could be asked to grasp a square partially occluded by a circle positioned in front of, but detached from, it. This task would likely engage dorsally mediated grasping, however it would require changes to the experimental paradigm that could affect the naturalness (and perhaps ecological validity) of the task and probably require a motion tracking system with at least 4 cameras. First, in a grasping task aimed at a partly occluded object where the relative position of the occluding and occluded objects is not fixed, small head movements could change the extent of the occluded region. Under these conditions a chinrest should be used to maintain the observer's head position fixed. This possibility was indeed considered but not adopted as the use of a chinrest would have constrained the participant's mobility and could have made the grasp unnatural. In addition, a visuomotor response terminating behind a real occluder is likely to require a motion tracking system with at least 4 cameras, two in front and two behind the occluder to prevent loss of marker values. Despite these difficulties, grasping partially occluded targets with real occlusion would disambiguate the interpretation of the present results and would therefore be of interest. Future research should investigate grasping partly occluded targets under these conditions.

Finally, as discussed in Experiment 1 for the interpolation of illusory contours, the present study can not entirely rule out the possibility that the interpolation of the occluded region was exclusively processed in the ventral visual system (i.e., not broadcast to the dorsal system) and subsequently used for the programming of the visuomotor response in an analogous way to the computation of grip and lift forces, affordances and of other learned associations between metric and non-metric properties (Goodale & Haffenden, 2003). Patients with visual form agnosia could also help to rule out this account. Although the perception of amodally completed stimuli has not been directly tested in patient DF, Milner et al. (1991) reported that she was unable to detect grouping by contiguity suggesting that her deficit includes an inability to bind fragments into whole shapes. Such impairment is likely to affect her ability to perceive

amodally completed figures therefore the above account would predict that DF, and other visual form agnosic patients, should not be able to use the interpolated region to adjust the kinematic parameters in a grasping task. By contrast, if the "accuracy" of the kinematic parameters observed with partially occluded targets in this study was due to the processing of the interpolated region in the dorsal visual system, due to afferent signals from early visual areas, DF's performance should be close to normal.

5. Experiments 4 and 5 – Grasping the Diagonal Illusion: The Effect of Target Dimensionality on Action I

5.1. Introduction to Experiment 4

This second part of the thesis explores the effect of target dimensionality on grasping, focusing on the possibility that actions aimed at targets that are specified, either partly or fully, by 2D information could be modulated by ventral visual mechanisms.

As discussed in Chapter 1, not all visually guided actions are mediated by the dorsal system as pantomimed-delayed and pantomimed-displaced actions are known to be mediated by the ventral visual system (Goodale et al., 1994). Thus, action *per se* is a necessary but not sufficient condition for the mediation of manual prehension by the dorsal visual system. The above findings suggest that changes to procedural parameters such as target location and the time elapsed between stimulus offset and movement initiation can determine which visual system will mediate the visuomotor response. The next three experiments use two approaches to explore whether stimulus properties such as target dimensionality could have a comparable modularity action.

The first experiment explores the possibility that some of the illusion effects on action that have been previously reported could be due to greater participation from the ventral visual system potentially recruited by the presence of 2D information in the display. As seen in Chapter 1, converging evidence suggests that the visuomotor system processes the entire 3D geometry of the target and that kinematic parameters can vary as a function of stimulus properties not directly relevant for the task (Cuijpers et al., 2004;

Hu et al., 1999; Servos et al., 1998). For instance, Hu et al. (1999) found that maximum grip aperture varied as a function of target height when the target had to be grasped along its width. Moreover, these authors found that hand elevation and velocity varied according to target height and size, respectively, but that they were also modulated by alignment. Similar findings have been reported by Cuijpers et al. (2004) and Servos et al. (1998). These studies suggest that the dorsal system has access to the entire geometry of the target and by implication, to information that would be required to differentiate between 2D and 3D targets.

The above conclusions are further supported by findings that actions performed under monocular viewing conditions, that is, in the absence of binocular disparity depth cues, are mediated by the ventral visual system. These studies have found that responses such as grasping and pointing are accurate in visual form agnosics when the target is viewed binocularly, but not monocularly, suggesting that the dorsal visual system modulates only the former type of response (Carey et al., 1998; Marotta et al., 1997). In agreement with these results, monocular grasping in neurologically intact individuals results in smaller maximum grip apertures, lower peak velocities, longer durations and proportionally longer deceleration (Marotta, Perrot, Nicolel, Servos & Goodale, 1995; Servos, 2000; Servos et al., 1992). These results have been interpreted as evidence that target distance, and by implication size, is based on accurate binocular disparity depth cues in the dorsal visual system but on pictorial cues for ventrally mediates grasping. Finally, evidence that visual illusions affect manual prehension under monocular but not binocular viewing conditions (Marotta, DeSouza, Haffenden & Goodale, 1998) further supports this account.

Taken together, the above studies suggest that the dorsal visual system computes the 3D structure of the target and that this plays a major role in the calibration of the kinematic parameters of manual prehension. Moreover, in the absence of binocular depth cues, and presumably of an accurate representation of 3D structure, visually guided action seems to be mediated by the ventral visual system. Given that binocular depth cues from

2D stimuli would not specify 3D structure, it is a question of interest to establish whether the dorsal visual system mediates visuomotor responses aimed at these targets. Importantly, if this were the case, this account could explain some of the illusion effects on action that have been reported.

As discussed in Chapter 1, studies that examined the effect of visual illusions on perception and action have not produced homogeneous results. Although the large majority of authors have found an illusion effect on perception but not on action (Brenner & Smeets, 1996; Haffenden & Goodale, 1998; Haffenden et al., 2001; Jackson & Shaw, 2000; Kwok & Braddick, 2003; Otto-de Haart et al., 1999; Post & Welch, 1996; Westwood et al., 2000), others have reported an illusion effect on both perception and action, although this latter was smaller (Aglioti et al., 1995; Daprati & Gentilucci, 1997; Ellis et al., 1999; Vishton et al., 1999; Westwood, McEachern & Roy, 2001). Moreover, a smaller number of authors have reported an equivalent illusion effect on both tasks (e.g., Franz et al., 2000; Mon-Williams & Bull, 2000; Pavani et al., 1999). These latter studies have been interpreted as evidence against the two-visual-systems model: First, they suggest that metrical distortions can occur in the dorsal visual system or second, that the visual array is processed by the same system for both perception and action.

Illusion studies provide some of the strongest evidence for the two-visual-systems model in neurologically intact individuals, thus it is important to fully account for the illusion effect on action that have been reported. As discussed in Chapter 1, several accounts have been proposed (Bruno, 2001; Carey, 2001; Dyde & Milner 2002; Franz, 2001; Haffenden, Schiff & Goodale, 2001; Milner & Dyde, 2003; Westwood, McEachern & Roy, 2001). These essentially have attributed the discrepancy to either procedural (e.g., attentional) differences (Franz et al., 2000; Pavani et al., 1999) or to properties of the illusion display, such as the annulus distance in the Ebbinghaus illusion (Haffenden et al., 2001). More recently, Dyde and Milner (2002) have suggested that the where an illusion is processed in the visual hierarchy could also

predict its effect on action: Illusions processed in cortical areas that precede the anatomical chiasm between the two systems should be expected to affect both perception and action.

The alternative account for the discrepant illusion studies that is explored in this experiment considers the possibility that the presence of elements that lack 3D structure in the illusion display, that is 2D elements, could increase the participation of ventral visual mechanisms. Given that the ventral visual system is known to process visual illusions, greater participation from this system would likely introduce metric distortions that could be reflected in the kinematic parameters. Indeed, such a possibility has been previously briefly considered by Westwood et al. (2002). If this account is correct, it could explain some of the illusion effects on action reported in previous studies as these displays often combined a 3D "graspable" target object, for instance the central circles in the Ebbinghaus illusion, with 2D inducing elements, for instance the surrounding annuli in the Ebbinghaus illusion (Aglioti et al., 1995; Brenner & Smeets, 1996; Daprati & Gentilucci, 1997; Ellis et al., 1999; Franz et al., 2000; Haffenden & Goodale, 1998; Haffenden et al., 2001; Jackson & Shaw, 2000; Kwok & Braddick, 2003; Otto-de Haart et al., 1999; Pavani et al., 1999; Vishton et al., 1999; Westwood et al., 2000; Westwood et al., 2001). Thus, it is possible that the illusion effects on action reported by these studies could have reflected a contribution of ventral visual processing recruited by the 2D inducing elements rather than the activity of the dorsal visual system.

In this experiment, the above possibility was explored with the Diagonal illusion (Tolansky, 1964; Figure 5.1), an illusion entirely the product of 3D objects and never investigated in this area of research before. In Figure 5.1 the diagonal of the square on the left and of the notched circle (central figure in black) on the right have exactly the same length but the diagonal of this latter is generally perceived as longer. In the present study this illusion was entirely the product of 3D objects because it was generated by the two shapes made of 3 mm thick black Perspex, without the addition of any 2D

elements. Grasping responses were recorded under both closed and open loop and the illusion effect was compared with the effect found on a manual estimation task. It was predicted that, given the lack of a 2D elements in the Diagonal illusion, an illusion effect on grasping with these stimuli would clearly rule out the possibility that the effect on action previously reported could have been the result of greater participation from ventral visual mechanisms engaged by 2D elements in the display.

5.2. Method

5.2.1. Design

This study used a repeated measures design as all participants took part in all three conditions: Grasping in closed loop (CL), grasping in open loop (OL) and manual estimation (ME). Conditions were individually presented in blocks of 48 trials, 8 trials for each of the 2 shapes in the 3 possible sizes, and order of presentation was counterbalanced across subjects according to a Latin Square arrangement. In half of the trials the target was presented on the right of the display and on the other half on the left. Stimulus presentation followed a different pseudorandom order for each block with the constraint that any given size could not be repeated for more than 3 consecutive trials.

5.2.2. Participants

Sixteen participants took part in the study. Of these, one was discarded due to unstable manual estimations (range > 3 mm). The data analysis was carried out on 15 participants (10 females and 5 males, age range 19 - 40 years). They all had normal or corrected-to-normal self-reported visual acuity, stereo vision ≤120 min arc (TNO, Laméris, Utrecht) and were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave informed consent and were paid to participate in the study.

5.2.3. Apparatus and Materials

5.2.3.1. Stimuli

The Diagonal illusion display was obtained by pairing a square with a notched circle with the constraint that the diagonal of the square was of the same length as the diameter of the notched circle. The stimuli were made of 3 mm thick black Perspex and obtained with a computer numerically controlled (CNC) machine.

The length of the diagonal could be either 40, 50 or 60 mm and, accordingly, the squares could have a side of either 28.3, 35.4 or 42.4 mm, respectively. The notched circles were obtained by removing 12, 15 or 18 mm from both sides of circles that had a diameter of 40, 50 or 60 mm, respectively. Thus, the ratio of the width of the removed area to the diameter was 3:5 for all sizes. The notched areas were removed using circles of the same diameter as the notched circle, as illustrated in Figure 5.1.

Each Diagonal illusion display was obtained by attaching the square and corresponding notched circle to a 1 mm thick A4 transparent frosted plastic sheet. The two shapes were aligned along the horizontal midline of the sheet and positioned so that their centres were 70 mm from the centre of the sheet (Figure 5.1).
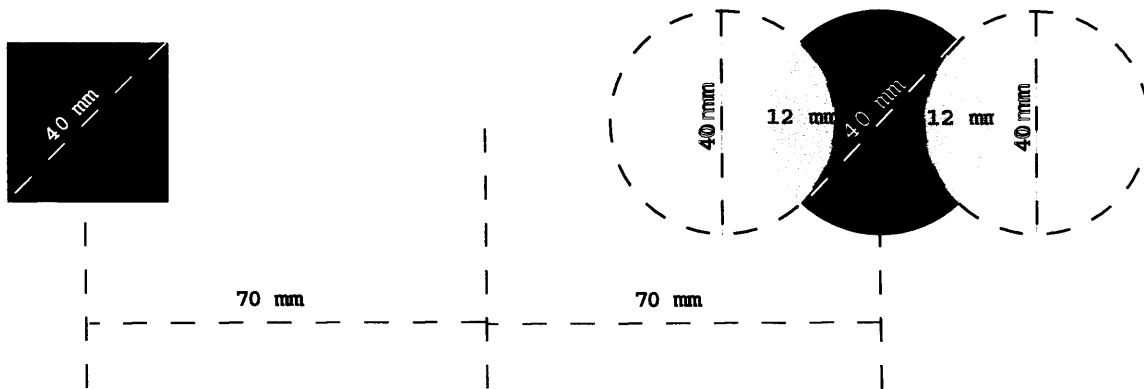
Figure 5.1. A schematic representation of the 40 mm stimuli. The distance between the two shapes is also illustrated. The shapes to be grasped are in black, the circles with the dashed circumference were used to remove the notched areas, which are shown in grey.

5.2.3.2. Apparatus and Set-up

The apparatus and set-up were as in Experiment 3 except that a lamp (60 Watts) was placed on a corner of the experimental table and its switch, interposed between stimuli and participant, was used as the Start button. This latter was raised 10.5 cm above the experimental table and was coplanar with the experimental surface.

In order to reduce interference from shadows, the stimuli were placed on a hollow box (21 x 29.7 x 10.5 cm), as illustrated in Figure 5.2. The box was positioned 11 cm from the bottom edge and along the vertical midline of the table (90.8 x 64.8 mm). The distance between the centre of the Start button and centre of the plastic sheet was 18.5 cm. A representation of the set-up is shown in Figure 5.2.
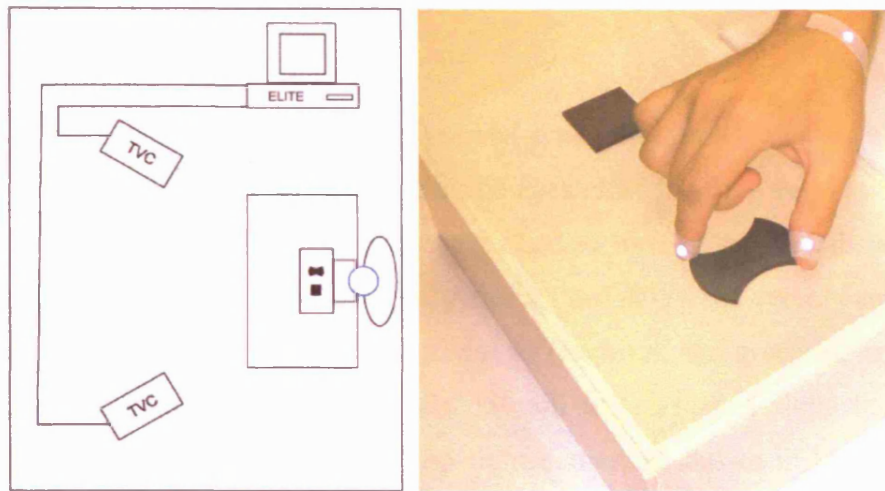
Figure 5.2. A schematic representation of the experimental set-up. Right: The grasping task.

5.2.4. Procedure

Unless otherwise stated, the procedure was as in Experiment 3.

At the beginning of each condition 6 practice trials were given, one for each size for each of the two target shapes. Participants sat in front of the table, with the stimulus display centred along their midsagittal plane. The height of the chair was adjusted to allow a comfortable position as well as a "bird's eye view" of the stimuli.

Three 6-mm hemispherical infrared light reflecting markers were placed with surgical tape on the inner corner of the nail of the index finger and thumb and on the wrist, approximately at the location of the styloid process of the radius. Movements were recorded for 2.5 seconds and analysed off-line. In the grasping tasks the emphasis was put on performing movements as naturally and as accurately as possible, in particular on using a natural speed, and in the manual estimation tasks the emphasis was put on accuracy.

5.2.4.1. Closed Loop Grasping (CL)

At the start of each trial, the participant pressed down the Start button with the index finger and thumb close together and kept his/he eyes closed. At the verbal cue "open", the participant was instructed to open the eyes and to look at the stimuli. They were explicitly instructed to look at both shapes. After a 3-sec delay, the verbal cue "right" or "left" was given and the participant's task was to reach out and grasp the right or left shape, respectively, using a precision grip. Stimuli were grasped along the diagonal joining the bottom left corner with the top right corner, as shown in Figure 5.2. The participant was instructed to maintain the index finger and thumb on the target until the verbal instruction "ok" signalled the end of the trial and that (s)he could return to the Start position. In this condition, the light was kept on and participants could see the stimuli and their hand for the whole duration of the movement.

5.2.4.2. Open Loop Grasping (OL)

This condition was identical to the closed loop grasping condition except that the only source of light in the room was provided by the lamp that was controlled by the Start button. Thus, as soon as the hand was lifted to initiate the movement, the switch was released and the lamp was turned off. This ensured that participant did not see their hand or the target during movement execution.

5.2.4.3. Manual Estimation (ME)

This condition was identical to the open loop grasping condition except that at the verbal cue "right" or "left" participants were instructed to lift the hand above the Start button and to manually estimate the length of the right or left diagonal, respectively. Participants were not allowed to move towards the target and were informed that the task had to be completed within 2.5 seconds.

5.2.5. Data Collection and Variables

For all conditions, data recording started approximately 1 second before the verbal cue signalling the start of trial was given and lasted for 2.5 sec.

For the two grasping tasks (CL and OL), maximum grip aperture (MGA, in mm) was defined as the maximum Euclidean distance between the markers on the index finger and thumb that occurred during movement execution and was recorded as described in Experiment 1.

For the manual estimation condition (ME), the 2.5 sec of data acquisition resulted in 125 measurements of the markers positions. The first 50 frames (corresponding to 1 second) were discarded as this time was largely used to position the hand above the Start button. For the remaining 75 recordings, maximum aperture was calculated as the mean of the 50 consecutive frames (1 second) that had the smallest range and standard deviation. On occasions when the range of these apertures exceeded 3 mm, the sample of frames was gradually reduced in steps of 5 until a sample with a range less than or equal to 3 mm was found. The sample considered had a minimum of 30 frames (0.58 seconds) and trials were discarded if a stable aperture was not found within this sample size. For 2 participants a range of 4 mm was used.

5.3. Results

Participants performed 8 trials for each of the 3 sizes in each condition and right and left side of presentation were combined for the statistical analysis. A small number of trials with missing markers positions were discarded from the analysis. The means entered in the analysis were computed from a minimum of 3 trials. Where not otherwise stated, an alpha level of 0.05 was used for the tests of significance and where necessary, Geisser-Greenhouse adjustments were made to the degrees of freedom. Simple comparisons were analysed with repeated measures t-tests and Bonferroni correction.

5.3.1. Maximum Grip Aperture

Mean maximum grip apertures were analysed in a $3 \times 2 \times 3$ repeated measures ANOVA with Task (CL/OL/ME), Shape (square/notched circle) and Size (40/50/60 mm) as factors. This revealed a significant main effect of Task ($F_{(1.40, 19.58)} = 27.257$, $p < .001$), a significant main effect of Shape ($F_{(1, 14)} = 51.604$, $p < .001$), a significant main effect of Size ($F_{(1.52, 16.12)} = 204.099$, $p < .001$), a significant Task $\times$ Shape interaction ($F_{(1.19, 16.61)} = 7.438$, $p = .012$) and a significant Shape $\times$ Size interaction ($F_{(2, 28)} = 5.036$, $p = .024$). The group means are shown in Table 5.1.

Table 5.1. Mean maximum grip aperture (mm) for each stimulus size in each condition. Standard errors are in brackets.

	Close |Loop	Open Loop	Manual Estimation
Square 40	52.16 (1.16)	57.07 (2.03)	39.87 (1.40)
Square 50	59.83 (1.11)	64.85 (1.71)	47.80 (1.96)
Square 60	67.64 (1.19)	71.98 (1.64)	56.34 (2.71)
Notched Circle 40	54.06 (1.09)	59.89 (1.59)	45.65 (1.73)
Notched Circle 50	62.31 (1.09)	67.53 (1.52)	53.80 (2.47)
Notched Circle 60	70.97 (1.13)	75.48 (1.51)	66.03 (4.42)

The left panel of Figure 5.3 shows the Task $\times$ Shape interaction. It can be clearly seen that the difference in the apertures used for the two shapes increased from the closed loop to the open loop grasping tasks and even more so from this latter to the manual estimation task. This interaction was explored with repeated measures t-tests that analysed the effect of Shape in the 3 conditions separately. Contrary to the above observation, these comparisons revealed that significantly larger grip apertures were used for the notched circle in closed loop grasping ($t_{(14)} = 8.563$, $p < .001$), in open loop grasping ($t_{(14)} = 5.326$, $p < .001$) and in manual estimation ($t_{(14)} = 4.655$, $p = .001$). These results clearly indicate that the Diagonal illusion exerted a significant effect on both perception and action. However, due to the significant interaction, this effect was

further explored by comparing the illusion effects in the 3 conditions and is reported in Section 5.3.2.
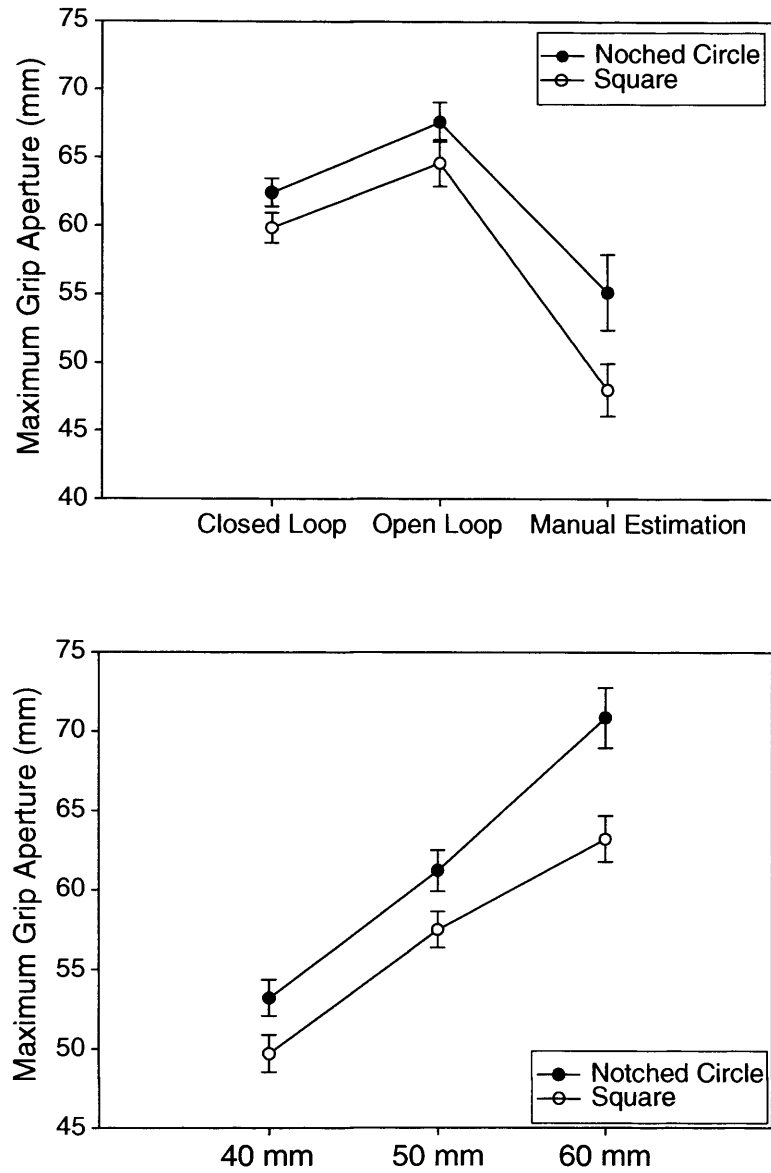
Figure 5.3. Task × Shape interaction: Maximum grip aperture is plotted as a function of task for the two shapes. It can be clearly seen that the discrepancy in grip aperture is greater for the manual estimation task. Right: Shape × Size interaction: Maximum grip apertures is plotted as a function of target size for both shapes.

The Task × Shape interaction was also explored by analysing the effect of Task at each level of Shape. As shown in table 5.2, and in agreement with previous findings (e.g., Jakobson & Goodale, 1991; Kwok & Braddick, 2003), the comparisons were all significant except for the difference between the closed loop and the manual estimation conditions for the notched circle which did not reach significance after the Bonferroni correction.

Table 5.2. Analysis of Task at each level of Shape.

	Target	t-test
CL - OL	■	$t_{(14)} = -3.526$; p = .003
	❚	$t_{(14)} = -4.807$; p < .001
CL - ME	■	$t_{(14)} = 6.220$; p < .001
	❚	$t_{(14)} = 2.651$; p = .019
OL - ME	■	$t_{(14)} = 7.165$; p < .001
	❚	$t_{(14)} = 4.681$; p < .001

The significant Shape × Size interaction was explored with an analysis of the effect of Shape at each level of Size. As shown in Figure 5.3, the difference in the apertures used for the two shapes, that is the illusion effect, was greater for the 60 mm targets. However, repeated measures t-tests revealed that significantly larger apertures were used for the notched circle in all target sizes ($t_{(14)}$ = 7.065, p < .001; $t_{(14)}$ = 6.648, p < .001 and $t_{(14)}$ = 5.602, p < .001 for the 40, 50 and 60 mm targets, respectively).

Finally, as expected, grip aperture was scaled according to target size in all conditions (Figure 5.4). Planned comparisons revealed that grip aperture significantly increased from the 40 to the 50 mm targets and from the 50 to the 60 mm targets for both shapes in all tasks (for all comparisons p < .001).
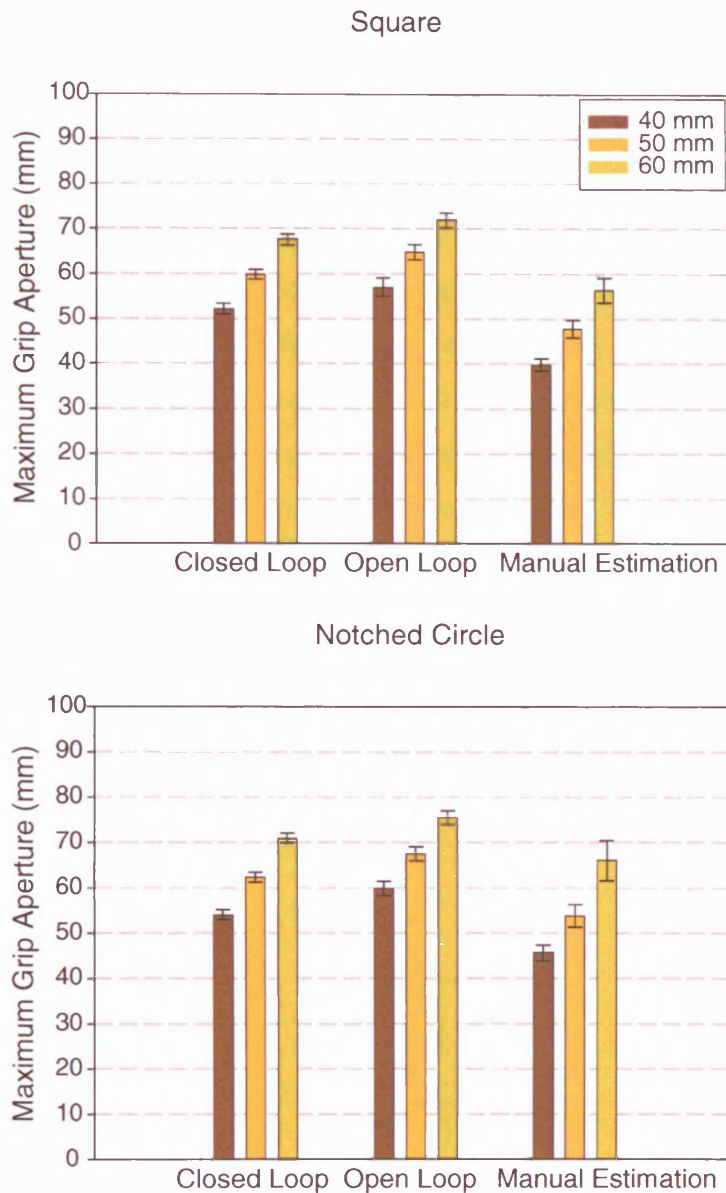
Figure 5.4. Maximum grip aperture plotted as a function of target size for the two shapes in the three conditions.

5.3.2. Illusion Effect

As shown in Figure 5.3 and as revealed by the Task × Shape interaction the difference in the apertures used for the two shapes was greater in the manual estimation task. The magnitude of this illusion effect was quantified for each participant by subtracting the grip aperture obtained with the square from the grip aperture obtained with the notched circle of corresponding size. These data were obtained for the 3 conditions and analysed in a repeated measures ANOVA with Task (CL/OL/ME) as factor.

The analysis revealed a significant main effect of Task ($F_{(1.19, 16.61)}$ = 7.438, p = .012) which was further explored with planned comparisons. These revealed that the difference in the illusion effect in the two grasping tasks was not significant ($t_{(14)}$ = 0.764, p = .457). However, more crucially, the illusion effect in the manual estimation task increased significantly relative to both the closed loop ($t_{(14)}$ = 2.846, p = .013) and the open loop ($t_{(14)}$ = 2.759, p = .015) grasping tasks. The illusion effect as a function of task is shown in Figure 5.5.
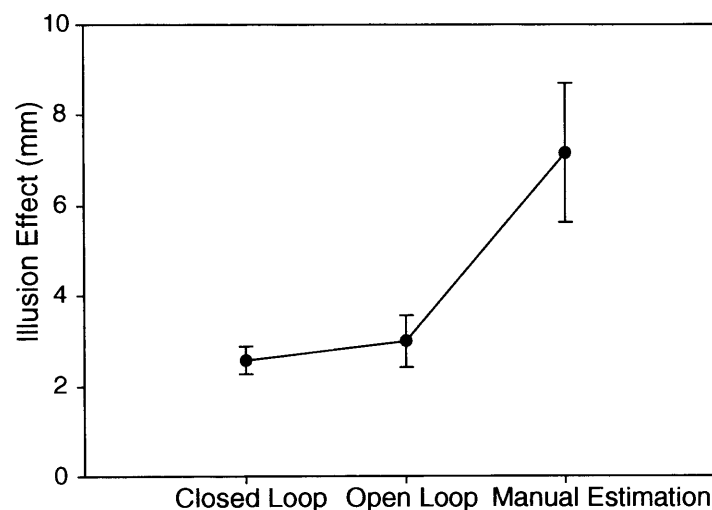
Figure 5.5. The illusion effect plotted as a function of task.

5.4. Discussion

The aim of this study was to examine the effect of the Diagonal illusion, an illusion never investigated before in this area of research and entirely the product of 3D objects, on perception and action. The results from the analysis of the maximum grip apertures showed a significant effect of shape for all three conditions suggesting that greater apertures were used for the notched circle in both grasping and manual estimation. These results suggest that the Diagonal illusion exerted an effect on both grasping and manual estimation.

The illusion effect observed on grasping with these stimuli clearly rules out the possibility that the illusion effect reported by previous studies could have been the result of ventral visual processes recruited in the visuomotor task by 2D inducing elements in the target display. The Diagonal illusion display did not contain 2D information but nevertheless had an effect on grip aperture in this study.

In agreement with the two-visual-systems model (Milner & Goodale, 1995), the comparison of the magnitude of the illusion effect in the three conditions revealed that this was significantly greater for the manual estimation task than for any of the two grasping conditions. Thee findings are therefore in agreement with previous studies that reported an illusion effect on both perception and action, but where the former was significantly greater (Aglioti et al., 1995; Daprati & Gentilucci, 1997; Ellis et al., 1999; Vishton et al., 1999; Westwood et al., 2001). More importantly, the present results support the two-visual-systems model. First, they suggest that the same visual input exerted a differential effect on the perceptual and visuomotor tasks suggesting that the same visual input was differentially processed in the two conditions. Second, the magnitude and direction of the effect in this study is in agreement with the functional role attributed to the two systems. These findings clearly show that, although the dorsal system was not entirely immune to the Diagonal illusion, the effect on grasping was

small suggesting that veridical stimulus properties are more accurately preserved in dorsal representations.

The magnitude of the effect is also in agreement with previous findings. The effect on closed loop, open loop and manual estimation was 2.57 (± 0.30), 3.00 (± 0.56) and 7.16 (± 1.54) mm, respectively. These are in agreement with, among others, Westwood et al. (2001) who reported an illusion effect of 2.7 on closed loop grasping and of 6.5 mm on manual estimation. The finding that maximum grip aperture varied as a function of target size for both shapes is also in agreement with typical findings in this area (e.g., Jeannerod, 1984; Westwood et al., 2001). Finally, the Diagonal illusion exerted a very similar effect on closed loop and open loop grasping. These findings are in agreement with Haffenden and Goodale (1998) and Hu and Goodale (2000), who also found that open loop grasping is not more affected by size-contrast illusions, however they are in disagreement with Westwood et al. (2001) who found that the illusion effect significantly increased when visual feedback was removed in the open loop condition.

The illusion effect found on grasping observed in this study could be accounted for by at least three possibilities. First, the illusion effect could have been exerted directly on dorsal processing, for instance due to the involvement of early visual areas in generating this illusion (Dyde & Milner, 2002; Milner & Dyde, 2003). However this is an unlikely explanation as, although the Diagonal illusion has not been investigated before and its genesis remains therefore presently unclear, it does not appear to be largely based on low-level visual processes. Tolansky (1964), the author who discovered and reported this phenomenon, proposed that the diagonal of the notched circle could be perceived as longer due to (i) the more pronounced convergence effect resulting from the corners in this shape and/or (ii) the perception that the diagonals in this shape appear to intersect at an acute angle due to the asymmetry of the sides. Both factors appear to involve some geometrical and structural property of the stimuli that are unlikely to be processed in early cortical areas preceding the anatomical separation between the two visual systems.

A second account would be that the illusion effect observed on grip aperture was the result of modulatory action by ventral visual processes not related to the 2D component of the display. The present study cannot rule out this possibility. Finally, the larger grip apertures observed for the notched circle in this study could also be accounted for by differences in the physical properties of two target shapes. For instance, curvatures at the two extremities that could have been construed as obstacles were present in the notched circle but absent in the square. This possibility is explored in the next study.

Finally, it should be noted that in agreement with previous findings, grip apertures were significantly larger in the open loop grasping condition (e.g., Jakobson & Goodale, 1991) and significantly smaller in the manual estimation condition (Kwok & Bradddick, 2003). The only exception was the comparison between the closed loop condition and the manual estimation for the notched circle which did not reach significance after the correction to the significance level. However, a strong trend in the same direction was observed in this comparison.

5.5. Introduction to Experiment 5

This experiment explored the possibility that the illusion effect on action observed in Experiment 4 was a methodological artefact resulting from differences in the physical properties of the two target shapes.

It is important to note that in previously reported illusion studies the graspable 3D component of the display was kept the same for the two configurations in the illusion. For instance, in the Ebbinghaus illusion the central graspable target was identical in the configurations with the small and large surrounding annulus. Therefore, in these studies, the illusion effect on grasping could not have been due to differences in the 3D graspable component of the display. By contrast, in the Diagonal illusion used in Experiment 4 the two 3D shapes, the notched circle and square, were physically different. It is therefore of primary importance to rule out the possibility that any

physical difference between the two shapes could have generated different grip apertures and could account for the illusion effect observed.

A physical feature that could have generated larger apertures in grasps aimed at the notched circle is the curvatures at the two extremities of this shape. These curvatures, as indicated in Figure 5.6, were close to the designated contact points of the fingers on the shape and it is therefore possible that they could have been treated as "obstacles" by the visuomotor system.

Several studies suggest that both the grasp and transport components of manual prehension are affected by the presence of non-target objects ("obstacles") when placed in close proximity to the target (Biegstraaten, Smeets & Brenner, 2003; Mon-Williams, Tresilian, Coppard & Carson, 2001; Tresilian, 1998). For instance, Tresilian (1998) found that adding obstacles to a workspace could result, depending on their position and type of grasp, in smaller and earlier maximum grip apertures, lower and earlier velocities and longer durations. Moreover, although the effect of the obstacle was greater when its position was likely to obstruct the movement, the adjustments to the kinematic parameters occurred even if there was no possibility of real collision. Tresilian (1998) concluded that the effects of obstacles on the movement parameters reflect a strategy aimed at maintaining a *minimum preferred distance from non-target objects* as a means to avoid *potential* collision rather than to avoid *certain* collision. Similar results for velocity and grip aperture were reported by Mon-Williams et al. (2001). In agreement with these findings, which indicate common mechanisms in visuomotor control and obstacle avoidance, recent studies suggest that this latter is mediated by the dorsal visual system (Milner & McIntosh, 2004; Schindler, Rice, McIntosh, Rossetti, Vighetto & Milner, 2004).

The above findings suggest that, if the curvatures of the notched circle were construed as obstacles, in order to avoid potential "collision" larger maximum grip apertures could have been generated in grasps aimed at this target. It is important to note that whereas in

Tresilian (1998) and Mon-Williams et al.'s (2001) avoiding contact with the obstacle was achievable by reducing grip aperture, due to differences in target-obstacles location, in Experiment 4 the risk of collision could be minimised only by increasing grip aperture. If this interpretation is correct it could account for the illusion effect observed on grasping in that study. This possibility was tested in the present experiment with a version of the Diagonal illusion constructed by superimposing 3D graspable identical bars, which functioned as the graspable targets, to a 2D version of the square and notched circle. In this study the 3D curvatures could not have acted as obstacles. Therefore, an illusion effect on grasping with these stimuli would have clearly ruled out the possibility that the illusion effect in Experiment 4 was due to the presence of 3D obstacles in the workspace.

In addition to controlling for the effect of obstacles, the stimuli used in this study also examined whether a second non-illusion related factor, namely differences in the physical properties of the two targets, could have accounted for the illusion effect on grasping observed in Experiment 4. As discussed in Section 5.1, there is evidence that geometrical properties of the target not directly related to the grasping task can affect grip aperture. Hu et al. (1999) found that maximum grip aperture increased as a function of object height when the relevant task was to grasp the object along its width. Similar results have been reported by Cuijpers, Smeets and Brenner (2004) who found that maximum grip aperture varied as a function of the length of the grip axis but also as a function of its orthogonal axis. In Experiment 4, the notched circle was taller and wider than the square (e.g., height/width: 60 and 42.4 mm, respectively, for the 60 mm targets). Although it can be argued that because targets were grasped along the diagonal, the axis orthogonal to the grip axis at the point of contact had the same length in both shapes, the possibility that the greater height and width of the notched circle increased grip aperture remains and is worth investigating. The present experiment controlled for this possibility as in this version of the Diagonal illusion the graspable component was identical for both targets.

5.6. Method

5.6.1. Design

This study used a repeated measures design as all participants took part in all three conditions: Grasping in closed loop (CL), grasping in open loop (OL) and manual estimation (ME). Conditions were individually presented in blocks of 48 trials, 8 trials for each of the 2 shapes in the 3 possible sizes. In half of these trials the target was presented on the right of the display and on the other half on the left. Conditions were presented according to a Latin Square arrangement and participants performed a total of 144 trials.

5.6.2. Participants

Sixteen participants took part in the study. Of these, two were discarded due to unstable manual estimations (range > 3 mm). The data analysis was carried out on 14 participants (8 females and 6 males, age range 21 - 40 years). They all had normal or corrected-to-normal self-reported visual acuity, stereo vision ≤120 min arc (TNO, Laméris, Utrecht) and were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave informed consent and were paid to participate in the study.

5.6.3. Apparatus and Materials

5.6.3.1. Stimuli

The target shapes were obtained as in Experiment 4 and had the same dimensions (diagonal 40, 50 and 60 mm long) but were printed in black on white landscape-oriented A3 paper cards. The 3D graspable component of the display functioned as the target and consisted of 3 mm thick and 5 mm wide aluminium bars that were painted in matt black

and superimposed on the diagonal of both shapes, as shown in Figure 5.6. The length of the aluminium bars varied according to the 3 possible sizes of the stimuli. The stimuli were aligned along the horizontal midline of the cards and 70 mm from the centre (Figure 5.6).
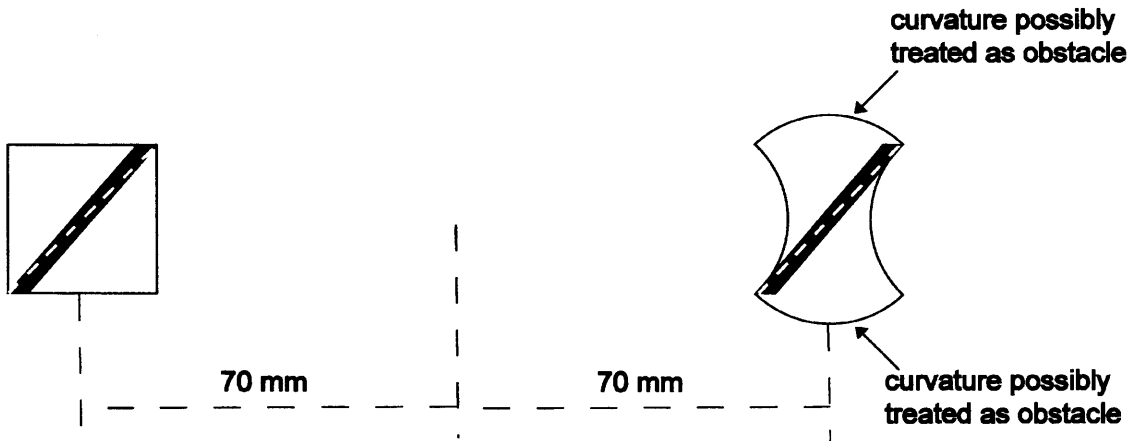
Figure 5.6. Schematic representation of the stimuli. For demonstrative purposes only, the square and the notched circle are drawn in white. In reality, both the shapes and the aluminium bars were in black. The dotted white line shows the grip axis. The arrows indicate the curvatures that could have been construed as obstacles in the 3D version of the illusion.

5.6.3.2. Apparatus and Set-up

The apparatus and set-up were as in Experiment 4 except that the paper cards were now placed on a solid experimental surface (34.7 x 76.2 cm) that was co-planar with the Start button. The distance between the centre of the start button and the centre of the stimuli was maintained as in Experiment 4 at 18.5 cm.

5.6.4. Procedure

The procedure was as in Experiment 4 except that in the two grasping conditions, at the verbal cue "right" or "left", the participant had to grasp either the right or the left

aluminium bar, respectively. Participants were instructed to grasp the bars at the two more distant points, as indicated by the white dotted line in Figure 5.6. Similarly, in the manual estimation condition participants were asked to estimate the length of the bar at the cued location.

5.6.5. Data Collection and Variables

The data collection and variables were as described in Experiment 4.

5.7. Results

Participants performed 8 trials for each of the 3 sizes in each condition and right and left side of presentation were combined for the statistical analysis. A small number of trials with missing markers positions were discarded from the analysis. The means entered in the analysis were computed from a minimum of 3 trials. Where not otherwise stated, an alpha level of 0.05 was used for the tests of significance and where necessary, Geisser-Greenhouse adjustments were made to the degrees of freedom. Simple comparisons were analysed with repeated measures t-tests and Bonferroni correction.

5.7.1. Maximum Grip Aperture

Mean maximum grip apertures were analysed in a $3 \times 2 \times 3$ repeated measures ANOVA with Task (CL/OL/ME), Shape (square/notched circle) and Size (40/50/60 mm) as factors. This revealed a significant main effect of Task ($F_{(2,26)} = 22.553$, p < .001), a significant main effect of Shape ($F_{(1, 13)} = 43.660$, p < .001), a significant main effect of Size ($F_{(2,26)} = 431.742$, p < .001), a significant Task × Shape interaction ($F_{(2, 26)} = 5.482$, p = .010), a significant Task × Size interaction ($F_{(4, 52)} = 3.407$, p = .033) and a significant Shape × Size interaction ($F_{(2, 26)} = 4.181$, p = .027). The group means are illustrated in Table 5.3.

Table 5.3. Mean maximum grip aperture (mm) for each stimulus size in each condition. Standard errors are in brackets.

	Close |Loop		Open Loop		Manual Estimation	
Square 40	58.55 (1.74)		58.35 (1.61)		45.30 (1.79)	
Square 50	67.12 (1.55)		66.35 (1.57)		54.33 (1.88)	
Square 60	73.28 (1.53)		73.59 (1.87)		62.75 (2.20)	
Notched Circle 40	59.68 (1.28)		60.38 (1.65)		48.41 (1.88)	
Notched Circle 50	67.54 (1.47)		68.23 (1.81)		56.61 (2.02)	
Notched Circle 60	76.34 (1.50)		75.07 (1.70)		66.97 (2.35)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean	66.32	67.86	66.09	67.89	54.13	57.33
	(1.55)	(1.37)	(1.59)	(1.65)	(1.89)	(1.98)

As shown in the left panel of Figure 5.7 the difference in the grip aperture used for the two shapes increased from closed loop to open loop grasping and from this latter to manual estimation. The significant Task × Shape interaction confirmed these differences to be significant, therefore repeated measures t-tests were used to further explore the effect of Shape at each level of Task. These revealed that significantly larger grip apertures were used for the notched circle in closed loop grasping ($t_{(13)}$ = 3.268, p = .006), in open loop grasping ($t_{(13)}$ = 3.618, p = .003) and in manual estimation ($t_{(13)}$ = 8.203, p < .001). These results clearly suggest that this version of the Diagonal illusion exerted a significant effect on both grasping and manual estimation. However, as shown in Figure 5.7, the difference in the grip apertures used for the two shapes was larger in the manual estimation task, therefore as in Experiment 4, the strength of the illusion effect in the 3 conditions was further explored. This is reported in Section 5.7.2.
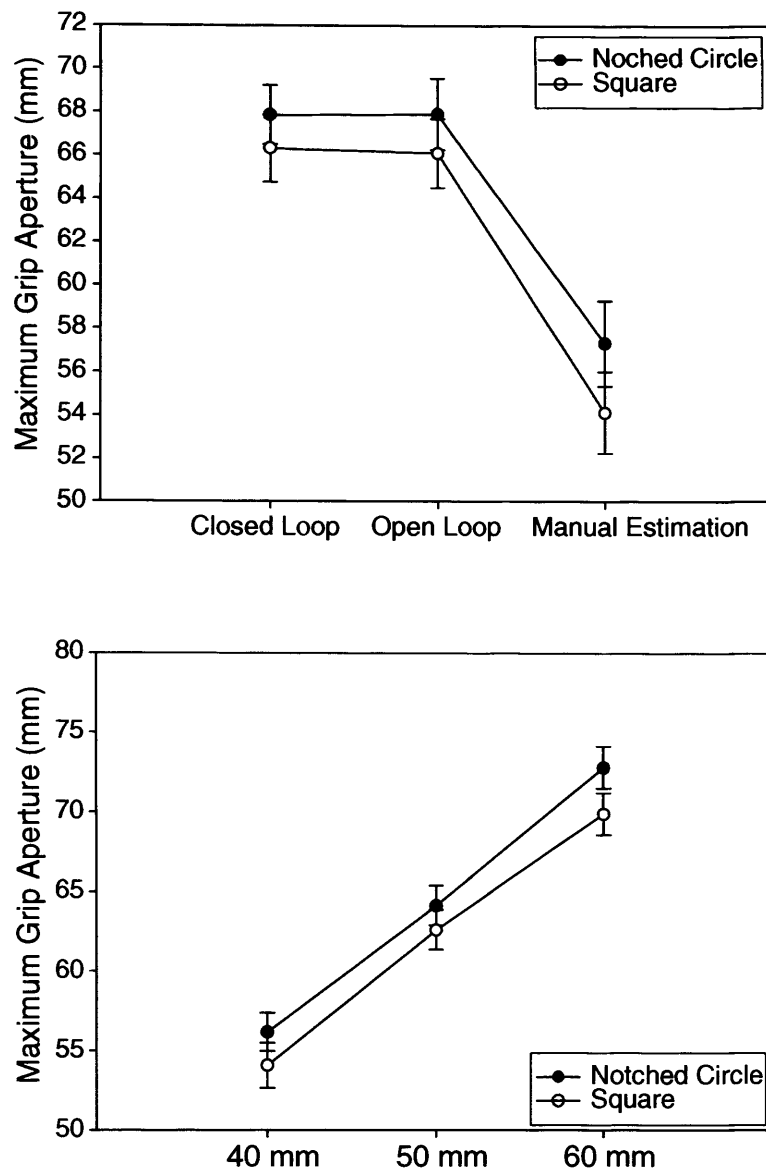
Figure 5.7. Task × Shape interaction: Maximum grip aperture is plotted as a function of task for the two shapes. It can be seen that the discrepancy in grip aperture is greater for the manual estimation task. Right: Shape × Size interaction: Maximum grip apertures is plotted as a function of target size for both shapes.

The Task × Shape interaction was also explored by analysing the effect of Task at each level of Shape. As shown in table 5.4, and in agreement with previous findings (e.g.,

Kwok & Braddick, 2003) and with Experiment 4, smaller grip apertures were used in the manual estimation condition relative to both grasping tasks. However, unlike Experiment 4, but in agreement with findings reported by Jeannerod (1981, 1984), no significant differences were found between the two grasping conditions.

Table 5.4. Analysis of Task at each level of Shape.

	Target	t-test
CL - OL	■	$t_{(13)} = 0.188$; p = .853
	⚋	$t_{(13)} = -0.032$; p = .975
CL - ME	■	$t_{(13)} = 5.664$; p < .001
	⚋	$t_{(13)} = 4.632$; p < .001
OL - ME	■	$t_{(13)} = 5.616$; p < .001
	⚋	$t_{(13)} = 4.286$; p = .001

The significant Shape × Size interaction was explored by measuring the effect of Shape for each target size. As shown in Figure 5.7, the difference in the grip aperture used for the two shapes was slightly greater for the 60 mm targets. However, repeated measures t-tests revealed that significantly larger apertures were used for the notched circle in all target sizes ($t_{(13)} = 4.281$, p = .001; $t_{(13)} = 3.610$, p = .003 and $t_{(14)} = 7.708$, p < .001 for the 40, 50 and 60 mm targets, respectively).

Finally, as expected, grip aperture was scaled according to target size in all conditions (Figure 5.8). Planned comparisons confirmed that grip aperture significantly increased

from the 40 mm to the 50 mm targets and from these latter to the 60 mm targets for both target shapes in all conditions (for all comparisons p < .001).
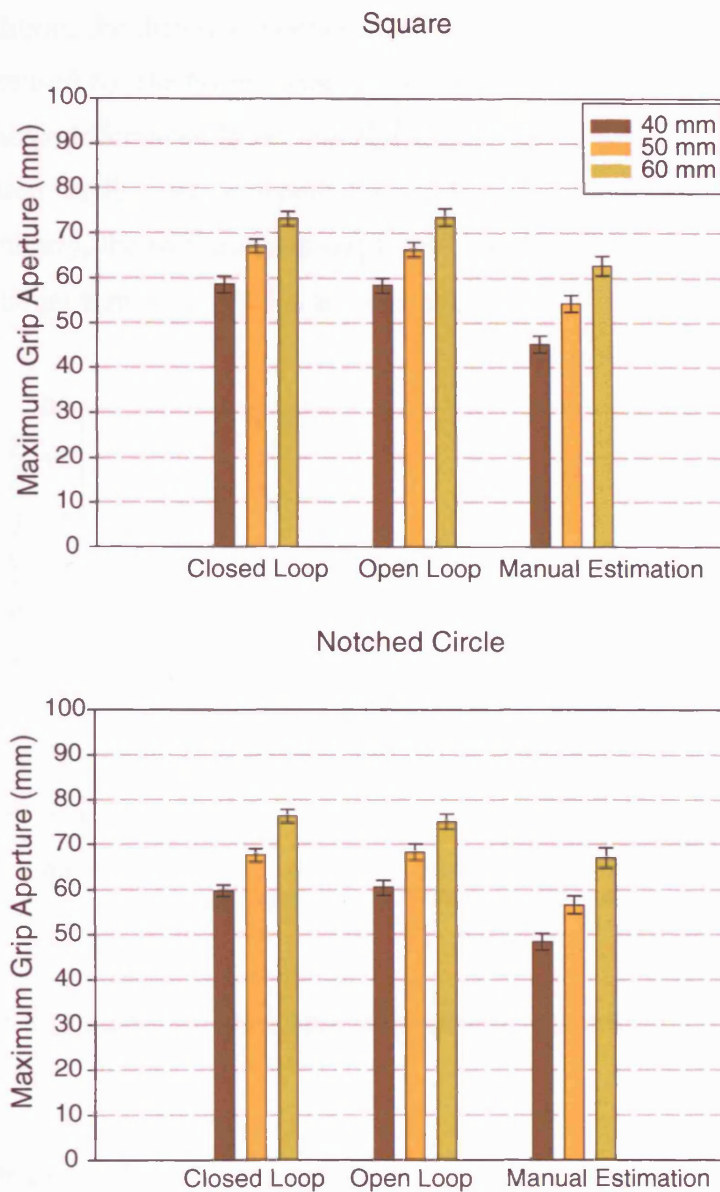
Figure 5.8. Maximum grip aperture plotted as a function of target size for the two shapes in the three conditions.

Unlike in Experiment 4, the Task × Size interaction was significant in this study. This was further explored with an analysis of the effect of Task at each target size. As shown in Figure 5.9, there was a small cross-over effect between the closed and open loop conditions. In addition, the difference between the grasping and the manual estimation tasks slightly decreased for the 60 mm targets. However, a series of repeated measures t-tests revealed these differences to be non-significant. Specifically, very similar grip apertures were used in the two grasping tasks for all target size ($p > .05$ for all comparisons). Similarly, the two grasping conditions significantly differed from manual estimation for all target size ($p \leq .003$ for all comparisons).
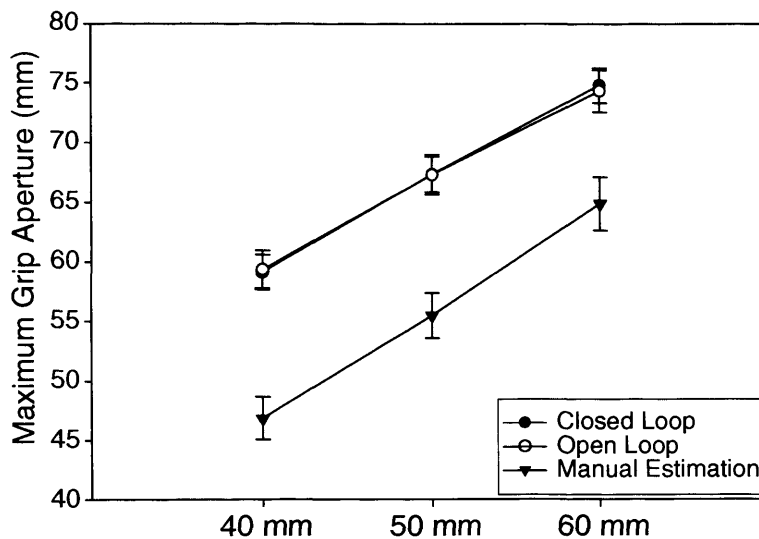
Figure 5.9. Task × Size interaction: Maximum grip aperture is plotted as a function of target size for the three tasks.

5.7.2. Illusion Effect

Both Figure 5.7 and the significant Task × Shape interaction suggest that the difference in the grip apertures used for the two shapes, that is the illusion effect, was greater for the manual estimation task. The magnitude of this effect was quantified as in Experiment 4, by subtracting for each participant the grip aperture obtained with the

square from the grip aperture obtained with the notched circle of corresponding size. These data were obtained for the 3 conditions and analysed with a repeated measures ANOVA with Task (CL/ OL/ME) as a factor.

The analysis revealed a significant main effect of Task ($F_{(2, 26)}$ = 5.482, p = .010) which was further explored with planned comparisons. These revealed that, as expected, the differences between closed and open loop grasping was not significant ($t_{(13)}$ = 0.468, p = 0.647) and that the illusion effect was significantly greater in the manual estimation task, relative to both closed loop ($t_{(13)}$ = 2.957, p = .011) and open loop grasping ($t_{(13)}$ = 2.793, p = .015). Figure 5.10 shows the illusion effect in the three conditions.
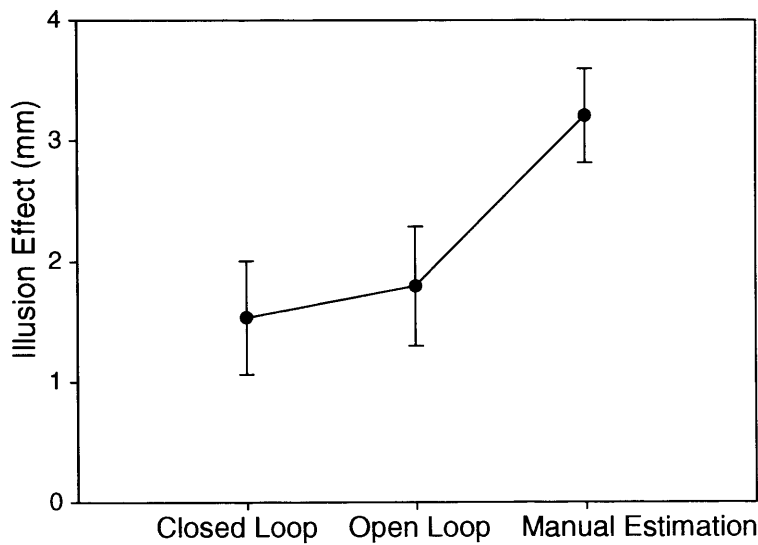
Figure 5.10. The illusion effect plotted as a function of task.

5.7.3. A Comparison of the Illusion Effects in Experiments 4 and 5

In this experiment, 2D elements were introduced in the illusion display. The effect of this manipulation on maximum grip aperture, and therefore on the illusion effect, was explored by comparing the data from this study with the data obtained in Experiment 4,

where the Diagonal illusion was entirely the product of 3D objects. Figure 5.11 shows maximum grip aperture plotted as a function of shape and task in the two experiments. It can be seen that, overall, smaller apertures were used with the 3D version of the illusion in Experiment 4.

These differences were analysed with a mixed model ANOVA with Target-Dimensionality (3D/2D) as the between-subjects factor and Task (CL/OL/ME) and Shape (square/notched circle) as the within-subjects factors. The effect of Target-Dimensionality and the interactions with this factor were of particular interest. In agreement with the individual analysis of the two studies, the ANOVA revealed significant main effects of Task ($F_{(2,54)}$ = 48.035, p < .001) and Shape ($F_{(1,27)}$ = 86.664, p < .001) and a significant Task × Shape ($F_{(2,54)}$ = 11.061, p = .001) interaction. More interestingly, the main effect of Target-Dimensionality ($F_{(1,27)}$ = 4.316, p = .047) and the Shape × Target-Dimensionality ($F_{(1,27)}$ = 8.940, p = .006) interactions were also significant. These significant results suggest that maximum grip aperture differed in the two studies as a function of target shape. Figure 5.11 shown maximum grip aperture plotted as a function of target-dimensionality and task.

Maximum Grip Apertures in Experiments 4 and 5

Illusion Effects in Experiments 4 and 5
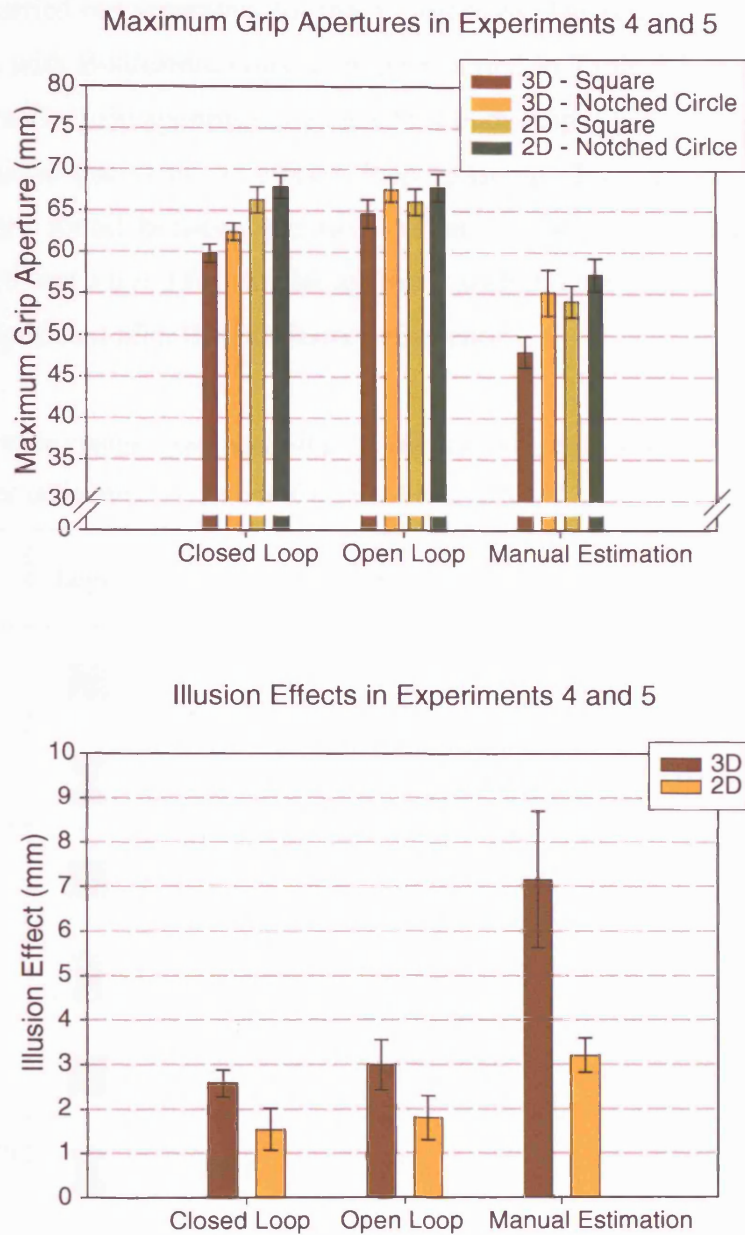
Figure 5.11. Maximum grip aperture plotted as a function of shape and task (let) and the illusion effect plotted as a function of task (right) for the two experiments. 3D and 2D refer to the data from Experiments 4 and 5, respectively.

This interaction was further explored by comparing the grip apertures in the two studies for each of the two target shapes. Despite a non-significant 3-way interaction this

analysis was carried out separately for the 3 conditions. The results of the independent-samples *t*-tests with Bonferroni correction are reported in Table 5.3. It can be seen that significantly smaller grip apertures were used for both shapes with the 3D version of the Diagonal illusion, but only in closed loop grasping. By contrast, no significant differences were found between the two studies in open loop grasping. In manual estimation there was a trend for smaller apertures with the 3D version of the square, but this was not significant after the Bonferroni correction.

Table 5.3. Simple comparisons analysing the effect of Target-Dimensionality at each level of target shape for individual conditions. Corrected $\alpha = .008$.

	Target	Experiment 4	Experiment 5	*t*-test
Closed Loop	■	59.87 (1.10)	66.32 (1.55)	$t_{(27)} = -3.427; p = .002$
	⏳	62.45 (1.03)	67.86 (1.37)	$t_{(27)} = -3.184; p = .004$
Open Loop	■	64.63 (1.70)	66.09 (1.59)	$t_{(27)} = -0.624; p = .538$
	⏳	67.63 (1.46)	67.89 (1.65)	$t_{(27)} = -0.118; p = .907$
Manual Estimation	■	48.00 (1.91)	54.13 (1.89)	$t_{(27)} = -2.274; p = .031$
	⏳	55.16 (2.78)	57.33 (1.98)	$t_{(27)} = -0.629; p = .535$

The differences between the two studies were further explored by comparing the illusion effects obtained with the two versions of the illusion. In Table 5.4 it can be clearly seen that, overall, the effect was larger for the 3D version and that differences between the two studies were much greater for the manual estimation task. However, independent-samples *t*-tests with Bonferroni correction revealed these difference to be non-significant in all conditions ($t_{(27)} = 1.884$, p = .070; $t_{(27)} = 1.990$, p = .123 and $t_{(27)} =$

2.491, p = .024 for CL, OL and ME, respectively). The illusion effect plotted as a function of task in the two studies is shown in Figure 5.11.

Table 5.4. Mean illusion effects (mm) in Experiments 4 and 5.

Illusion Effect	Close |Loop	Open Loop	Manual Estimation
3D (Expt 4)	2.57	3.00	7.16
2D (Expt 5)	1.54	1.80	3.21
Difference	**1.03**	**1.20**	**3.95**

5.8. Discussion

The first aim of this experiment was to establish whether the illusion effect observed on grasping in Experiment 4 could have been the result of illusion-unrelated stimulus properties. Specifically, whether the curvatures at the extremities of the notched circle in the 3D version of the Diagonal illusion could have been construed as obstacles and therefore increased grip aperture in grasps aimed at this shape. In this study, the 3D curvatures were removed, therefore, the analysis of these data allow to clearly establish the contribution made by these features. The second aim of the study was to rule out the possibility that differences in the physical properties of the two targets could have accounted for the illusion effect.

The analysis of maximum grip aperture revealed that significantly larger apertures were used for the notched circle in all conditions. These results clearly suggest that this version of the Diagonal illusion exerted an effect on grasping and rule out the possibility that the 3D curvatures of the notched circle could account for the illusion effect observed in Experiment 4. These conclusions are further supported by the analysis of the illusion effect as very similar patterns were observed in the two studies. Specifically, in this version of the Diagonal illusion, as in Experiment 4, no differences were found between the effects in the closed loop and open loop grasping conditions. Moreover, also as in Experiment 4, the illusion effects on both grasping tasks were

significantly smaller than the effect found on manual estimation. Taken together, these results suggest that the larger grip apertures observed for the notched circle in Experiment 4 were due to the illusion effect exerted by the Diagonal illusion and not to the 3D curvatures construed as obstacles.

Similarly, these results rule out the possibility that the greater dimensions of the notched circle could have accounted for the increase in grip aperture observed with this shape in Experiment 4. As discussed in Section 5.5, maximum grip aperture has been found to increase as a function of target dimensions other than the length of the grip axis (Cuijpers et al., 2004; Hu et al., 1999). The possibility that the greater height and width of the notched circle in Experiment 4 could have accounted for larger grip apertures is ruled out in this study as an illusion effect was found when the dimensions of the graspable component of the two targets were identical.

The above conclusions rest on the assumption that the curvatures of the 2D notched circle in this experiment were not treated as obstacles by the dorsal system. If however these 2D elements were treated as obstacles, the present results cannot rule out that the results from Experiment 4 were due to the presence of 3D curvatures in the notched circle. To our knowledge no study has yet investigated whether 2D elements in the display can act as obstacles, although Haffenden et al. (2001) suggested that this could be a possibility for the 2D annuli of the Ebbinghaus illusion. This question remains unanswered. However, as suggested by the next experiment and discussed in the General Discussion (Chapter 15), although the dorsal system seems to mediate grasping to 2D targets, it also differentiates to some extent between 3D and 2D stimuli indicating that it processes some of the geometric properties of the target. Such a property would not necessarily imply that this system can identify 2D elements as non-obstacles, however this would be a plausible use of geometric information. Further research will perhaps provide more conclusive evidence on this topic.

Finally, it should be noted that unlike Experiment 4, no differences were found in the maximum grip apertures used in closed loop and open loop grasping. These results are however in agreement with Jeannerod (1981, 1984) and Connolly and Goodale (1999) who also reported non-significant differences in maximum grip aperture between closed and open loop grasping. The implications of these results are discussed in the next section. By contrast, the comparisons between manual estimation and the two grasping conditions were in agreement with typical findings (e.g., Kwok & Braddick, 2003) and with Experiment 4 as smaller grip apertures were found in the perceptual task.

5.8.1. A Comparison Between Experiments 4 and 5

Except for minor differences in the experimental surface used and the presence of 2D inducing elements in the illusion display, this experiment was a direct replication of Experiment 4. The former is unlikely to have had an effect on the kinematic parameters, therefore, a comparison of the data from the two studies can be used to examine the effect of introducing 2D information in the target array.

Except for the comparison between closed loop and open loop grasping, a very similar pattern of results was found in the two studies. First, no significant differences were found in the illusion effects between the two studies in any of the three conditions. Second, in agreement with previous findings (e.g., Kwok & Braddick, 2003) grip apertures were significantly smaller in manual estimation than in the two grasping tasks in both studies. The comparison between closed loop and open grasping, however, differed in the two studies. In Experiment 4, where the 3D version of the illusion was used, significantly smaller apertures were observed for both target shapes in closed loop. By contrast, with the 2D version of the illusion no differences were found between closed loop and open loop grasping. As clearly shown in Table 5.3, this latter similarity was due to an increase in grip aperture in the closed loop condition in this study.

This increase in grip aperture could be accounted for by at least two explanations. First, it could be result of introducing 2D elements in the target display. For instance, it could be possible that the 2D elements recruited additional ventral visual mechanisms into the task and that this affected grip aperture. This account however is unlikely given the similarity of the illusion effect in the two studies. Additional ventral modulation should have resulted in an increase in the illusion effect, which was not observed. Moreover, this account is further discounted by the findings of Experiment 6, which also suggest that 2D information in the target array does not result in additional participation from ventral visual processing.

An alternative, more plausible account would be that grasping the thin metal bars in this experiment was construed as a more difficult task than grasping the square and notched circle in Experiment 4. As discussed in more detail in Chapter 6, larger grip apertures have been suggested to result from compensatory mechanisms that ensure that, under suboptimal viewing conditions, the hand is sufficiently open to allow for a greater margin of error in the computation of target size (Connolly & Goodale, 1999; Smeets & Brenner, 1999). This explanation has been proposed to account for the increase in grip aperture often observed under reduced visual feedback in open loop grasping, however it could apply to task difficulty in general. Furthermore, as discussed in more detail in Chapter 6 and in the General Discussion, a recent model of grasping proposed by Smeets and Brenner (1999) suggests that earlier and larger grip apertures should also be obtained when accuracy demands increase due to a recuction of contact surface size. If the above accounts are correct, the greater apertures observed in the closed loop condition of this study could suggest that grasping the metal bars under full vision was treated as having the same degree of difficulty as grasping under suboptimal conditions. This is a very plausible account as the metal bars used in this experiment could have been construed as a difficult target for at least 3 reasons. First, the bars were relatively thin and therefore provided a small contact surface. Second, participants were required to grasp them at their narrow pointed edges which could have been difficult to locate visually. Third, and perhaps more importantly, the black metal bars in this study were

superimposed to a black print-out of the target shapes. Therefore, it is possible that the low contrast resulting from this procedure made it difficult to discriminate the target from the background. Importantly, this interpretation could fully account for the smaller grip apertures observed in the closed loop condition in Experiment 4. Under those conditions, the task was not likely to be construed as difficult as the targets used were more visible due to their larger size and to the clear contrast with the white background.

It should be noted that the possibility that the curvature of the notched circles could have acted as obstacles in the grasping task could have been controlled by using a whole disk rather than a square as the comparison shape. Future research should replicate the present study with such stimuli. However, before grasping aimed at the diagonals of these two shapes can be compared, it should be established whether a perceptual judgement of the length of the two diagonals would result in the Diagonal illusion. At present, to our knowledge no such comparison has been attempted. Moreover, it should also be noted that using a whole disk as the comparison shape for the notched circle would introduce a difference in the surface contact points that would not be present in a comparison with a square. Specifically, whereas corners would be the contact points for the index finger and thumb when grasping the notched circle, a much larger contact surface would be available for grasps to a whole disk. As discussed above, there is evidence that changes in contact surface size can affect kinematic parameters such as the time and magnitude of grip aperture (Smeets & Brenner, 1999). Thus, although comparing grasping notched circles with whole circles rather than squares could remove the possible confounding effect of curvatures differences, it could introduced further discrepancies between the two conditions that could affect the kinematic parameters.

To summarise, the present results clearly rule out the possibility that the illusion effect observed on grasping in Experiment 4 was the result of illusion-unrelated stimulus properties. Specifically, these results suggest that the larger grip apertures observed for the notched circle in Experiment 4 were due to the illusion effect exerted by the Diagonal illusion and not to potential obstacles within the visual display or the different

dimensions of the targets. Additionally, the comparison between this experiment and Experiment 4 suggests that adding 2D elements to the illusion display did not recruit additional ventral visual processing into the grasping task. This latter conclusion is in agreement with the results from Experiment 6 presented in this thesis. More importantly, it has implications for previously reported illusion studies that combined 2D inducing elements with a 3D graspable target (Aglioti et al., 1995; Brenner & Smeets, 1996; Daprati & Gentilucci, 1997; Ellis et al., 1999; Franz et al., 2000; Haffenden & Goodale, 1998; Haffenden et al., 2001; Jackson & Shaw, 2000; Kwok & Braddick, 2003; Otto-de Haart et al., 1999; Pavani et al., 1999; Vishton et al., 1999; Westwood et al., 2000; Westwood et al., 2001) as it suggests that the presence of 2D information in the target display does not recruit additional participation from ventral visual mechanisms.

6. Experiment 6 – Grasping 3D, 2D and 2D-enhanced Targets: The Effect of Target Dimensionality on Manual Prehension II

6.1. Introduction

The illusion effect found with the 3D version of the Diagonal illusion in Experiment 4 clearly rules out the possibility that the presence of 2D elements in an illusion display could recruit additional ventral visual processes into a visuomotor task and, by implication, that 2D elements could fully account for the illusion effects on action reported in previous studies. These conclusions are strengthened by the finding that the illusion effect did not increase when 2D elements where added to the illusion display in Experiment 5. However, neither Experiment 4 nor Experiment 5 explored how targets exclusively specified by 2D information are processed by the dorsal visual system. Specifically, it is still unclear whether the dorsal visual system mediates action only aimed at stimuli with a 3D structure, or whether it does not fundamentally distinguish between 2D and 3D objects.

Another fundamental question closely related to the above is whether the dorsal system accesses a complete 3D volumetric description of the stimuli or whether it uses a more pragmatic representation where only object attributes necessary for setting the relevant kinematic parameters are specified, for instance the landing positions of the fingers on the target in a grasping task (Jeannerod, Arbib, Rizzolatti & Sakata, 1995; Smeets & Brenner, 1999; Westwood, Danckert, Servos & Goodale, 2002). It has been suggested that a 3D structural description of the target must be available at the response selection stage, as the action that an object can afford is likely to depend largely on its structure

(Westwood et al., 2002). The same authors proposed that response selection is likely to be carried out by the ventral visual system, as due to its pivotal role in object recognition this system has probably access to a complete structural description of the target (e.g., Marr & Nishihara, 1978). Thus, there is some consensus that the ventral visual system represents the complete 3D structure of objects.

As discussed in Chapter 5, the evidence suggests that 3D structure is also represented in the dorsal visual system and that this modulates several of the kinematic parameters of manual prehension (Hu, Eagleson and Goodale, 1999). This suggestion is further supported by evidence that grasping performed under monocular vision is mediated by the ventral visual system (Marotta et al., 1995; Marotta et al., 1997; Servos, 2000; Servos et al., 1992). These latter findings suggest that stereoscopically defined depth is necessary for action to be driven by the dorsal system and, by implication, that an accurate representation of distance and probably of 3D target structure play a major role in visually guided action. If these suggestions are correct, it may be possible that actions aimed at objects that lack a 3D structure are not mediated by the dorsal visual system.

This latter suggestion would be in agreement with the observation, also pointed out by other authors (Kwok & Braddick, 2003), that visuomotor responses such as grasping and posting in nature occur exclusively towards 3D objects. An exception to this is pointing, which in nature can occur towards 2D stimuli, for instance it is possible to point at a freckle on the skin or at a spot on a leopard. It is therefore plausible to suggest that visuomotor responses such as grasping and posting aimed at 2D targets would have little functional relevance and that the dorsal visual system could have evolved to mediate visuomotor responses selectively, according to target dimensionality. According to this model, actions towards 2D targets, if functionally irrelevant, would be mediated by the ventral visual system. The dimensionality of the target could be determined at the response selection stage where full access to the volumetric structural description of the target is available. As discussed in more detail below a similar mechanism has been considered by Westwood et al. (2002).

The advantage of a dorsal visual system that selectively mediates action according to the functional relevance of the stimuli is that it would be likely to result in a reduction of computational load. Due to the high refresh rate and the computation of metric information in the dorsal system, dorsal representations are likely to be computationally expensive. Thus, the restricted use of these representations to functionally relevant stimuli could result in a reduction of computation load. This would be a non-trivial outcome, in particular considering that it has been proposed that the parcellation of function between the dorsal and ventral visual systems could have evolved largely due to a preference for computational efficiency within the visual system (Rueckl, Cave & Kosslyn, 1989).

The above model proposes that grasps aimed at targets that lack a 3D structure are mediated by the ventral visual system. If this is correct, the model predicts that the kinematic profiles obtained from these responses should differ from the kinematic profiles obtained from grasps that are known to be mediated by the dorsal visual system. At present, only two studies have directly compared the kinematic profiles of grasps aimed at 2D and 3D targets. As reviewed in Chapter 1, Westwood, Danckert, Servos and Goodale (2002) tested grasping and manual estimation in DF, a patient with visual agnosia, and in 5 neurologically intact subjects with a set of either 3D rectangles (3D condition), computer generated 2D images identical to the top surface or the 3D set (2D condition) or images of the 3D set taken with a digital camera (2D-enhanced condition). These authors found that DF was able to adjust her grip aperture when grasping the three targets and concluded that the dorsal visual system mediated DF's movements with all stimuli. However, although Westwood et al. (2002) found no differences in the kinematic profiles from the three conditions for two of the participants, for the remaining three maximum grip apertures were significantly larger in the 3D condition. The authors concluded that DF's performance suggest that the dorsal system does not substantially differentiate between 2D and 3D targets. However, the quantitative differences between obtained for the control subjects suggest that these tasks could have been mediated by different mechanisms. Specifically, Westwood et al. (2002) suggested

that, at the response selection phase some participants chose to use 'natural' movements with 2D and 2D-enhanced targets whereas other participants recognised that they could not generate a naturalistic grasp with these stimuli and chose to respond as in delayed or displaced actions. That is, grasps aimed at targets lacking a true 3D structure in these latter participants were mediated by the ventral visual system.

More recently, Kwok and Braddick (2003) explored the effect of target dimensionality on manual estimation and prehension with an Ebbinghaus illusion display where the central circles were either in 2D or 3D. Irrespective of dimensionality, an illusion effect was found for manual estimation but not for grasping and the authors concluded that both types of stimuli engaged the dorsal visual system. However, as in Westwood et al. (2002), Kwok and Braddick (2003) found that maximum grip apertures obtained with 3D targets were significantly larger than apertures in the 2D condition confirming that there are some quantitative, if not qualitative, differences between these responses.

The quantitative differences found by Kwok and Braddick (2003) and Westwood et al. (2002) between grasping aimed at 3D and 2D targets warrant further investigation. In particular, if it is taken into account that the decrease in grip apertures observed with 2D targets is comparable to the effect observed for other grasping tasks that are known to be mediated by the ventral visual system. For instance, Goodale et al., (1994) reported that both pantomimed-delayed and pantomimed-displaced grasping result in smaller grip apertures than immediate grasping. A similar reduction has been reported for monocular grasping (Servos, 2000; Servos et al., 1992). Thus, these findings open the possibility that the decrease in grip aperture observed in grasps aimed at 2D targets could also be the result of ventral strem participation in this task. The evidence that DF's grip apertures were scaled according to target size with the 2D and 2D-enhanced targets in Westwood et al. (2002) does not provide conclusive evidence against this claim as it is known that this patient has developed compensation strategies, namely DF can use visuomotor strategies in the solution of perceptual tasks (Murphy, Racicot & Goodale, 1996).

The present study further explores whether the dorsal visual system is engaged by 2D targets by comparing the kinematic profiles from grasps aimed at the Diagonal illusion presented in a 3D, 2D or 2D-enhanced format, this latter with added pictorial depth cues. If grasps towards both 3D and 2D targets are mediated by the dorsal visual system, no significant differences should be observed in the kinematic profiles from these tasks. Moreover, a similar effect of the Diagonal illusion should be observed in the two conditions. By contrast, if grasping 2D targets is largely mediated by the ventral visual system, smaller grip apertures and a greater illusion effect should be observed in this condition. In this latter case, the 2D-enhanced stimuli would allow to explore whether adding pictorial cues to 3D structure could alter any of these effects.

6.2. Method

6.2.1. Design

This study used a repeated measures design as all participants took part in all conditions: 3D, 2D with added pictorial depth cues (2D-enhanced) and 2D. Conditions were individually presented in blocks of 48 trials, 8 trials for each of the 2 target shapes in the 3 sizes, and order of presentation was counterbalanced across subjects according to a Latin Square arrangement. In half of the trials the target was presented on the right of the display and on the other half on the left. Stimulus presentation followed a different pseudorandom order for each block with the only constraint that the same size could not be repeated for more than 3 consecutive trials.

6.2.2. Participants

Sixteen participants took part in the study. Of these, six were discarded due to loss of markers values. The data analysis was carried out on 10 participants (8 females and 2 males, age range 19 - 32 years). They all had normal or corrected-to-normal self-reported visual acuity, stereo vision ≤120 min arc (TNO, Laméris, Utrecht) and were

right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave informed consent and were paid to participate in the study.

6.2.3. Apparatus and Materials

6.2.3.1. Stimuli

3D condition: The stimuli in this condition were the same as in Experiment 4. Therefore, the square and notched circle were made of 3 mm thick black Perspex and the length of their diagonal was either 40, 50 or 60 mm.

Each Diagonal illusion display was obtained by attaching the square and corresponding notched circle to a 1 mm thick transparent clear plastic sheet (24.3 × 32.4 mm). The dimensions of the plastic sheet were chosen so that when superimposed to the 17" monitor it covered the glass entirely. As in Experiment 4, the two shapes were aligned along the horizontal midline of the plastic sheet and positioned so that their centres were 70 mm from the centre of the sheet (and screen). Under the lighting conditions of the laboratory, the luminance of the Perspex shapes was 13 cd/m^2 and they were presented on a white background with a luminance of 71 cd/m^2.

2D-enhanced condition: The stimuli in this condition were created with POV-Ray, a ray-tracing computer programme used for rendering the graphical representation of three-dimensional scenes. The parameters used in the programme were as follows. The positions and sizes of the rendered shapes (Figure 6.1) were kept as in the 3D condition. Specifically, the shapes could have a diagonal of either 40, 50 or 60 mm, were aligned along the horizontal midline of the screen and their centre was kept at a distance of 70 mm from the centre of the screen. The position of the camera was set to correspond to the position of the participant's eyes during the task, that is, at a 40-cm orthogonal distance from the centre of the screen. The camera was set to "look at" the centre of the scene and the light settings were chosen to simulate the lighting conditions of the

laboratory. These parameters resulted in rendered images with added shading and reflections as pictorial depth cues.

It should be noted that the small thickness of the rendered stimuli (3 mm) did not result in conspicuous shadows. Increasing the thickness of the stimuli in POV-Ray would have resulted in more noticeable shadows, however, because the adopted settings were sufficient to distinguish the 2D-enhanced from the 2D images, it was decided to maintain the thickness of the shapes as in the 3D condition. The 2D-enhanced stimuli were rendered in dark grey. The shade of grey was chosen so that these stimuli were equiluminant with the 3D stimuli (13 cd/m^2). The white background was as used in the 3D condition (71 cd/m^2). Finally, the target in each display was signalled by a two-dimensional yellow circle (diameter of 7 mm) displayed above the shape, as shown in Figure 6.1.

Figure 6.1. Example of a rendered image used in the 2D-enhanced condition. The image is shown in scale, but smaller than the actual size. The circle above the notched circle indicates the target.

2D condition: The stimuli in this condition were identical to the stimuli in the 2D-enhanced condition except that the shapes were rendered as flat objects, that is, with zero extension in the depth dimension.

6.2.3.2. Apparatus and Set-up

The positions of the index finger, thumb and wrist during movement execution were recorded with a SMART (eMotion, Padova) motion tracking system with 5 cameras and a sampling rate of 60 Hz. Similarly to the ELITE system, SMART's infrared light-emitting cameras recorded the barycentre of infrared light-reflecting hemispherical markers, 6 mm in diameter, whose 3D position was reconstructed off-line. The resolution of the system during the experiment, as given at the end of each calibration procedure, was ≤ 1 mm.

The 2D and 2D-enhanced stimuli were displayed on a CRT 17" Iiyama monitor (model Vision Master Pro 413) that was placed on a standard pedestal, aligned with the vertical midline of the experimental surface (height: 76.8 cm, length: 121.8 cm and width: 81.5 cm) and 41.5 cm from the lower edge. The Start button was placed at an orthogonal distance of 22 cm from the screen and aligned with its vertical midline. A white paper strip covered the top 5 cm of the screen and was used to maintain the plastic sheet with the 3D stimuli attached to the monitor.

6.2.4. General Procedure

Participants sat in front of the monitor, with the stimuli centred along their midsagittal plane and their eyes aligned with the centre of the screen. This ensured that their viewpoint was as similar as possible to the viewpoint simulated in POV-ray for the 2D-enhanced images. The option of using a chinrest to maintain the eyes aligned with the centre of the screen was considered but not adopted as this would have constrained freedom of movement and could have made the grasp "unnatural".

Three 6-mm hemispherical infrared light reflecting markers were placed with surgical tape on the inner corner of the nail of the index finger and thumb and on the wrist, approximately at the location of the styloid process of the radius. Grasps were recorded

from shortly before movement initiation until contact with the shapes occurred and were analysed off-line. The emphasis was put on performing movements as naturally as possible, in particular on using a natural speed, and on accuracy. Throughout the study the light was kept on and participants could see the stimuli and their hand for the whole duration of the movement. Before testing, a block of 9 practice trials was run, one for each size in each condition. The target shape for these trials was selected randomly.

6.2.4.1. 3D condition

At the start of each trial, the participant pressed the index finger and thumb close together at the Start button with the eyes closed. The plastic sheets with the 3D stimuli were manually attached to the monitor. At the verbal cue "open", the participant was instructed to open the eyes and look at the stimuli. They were explicitly instructed to look at both shapes. After a 3-sec delay, an auditory tone signalled the start of movement and the participant's task was to reach out and grasp, using a precision grip, the shape that was marked by a yellow circle (diameter of 7 mm). This latter was manually placed above the target shape before each trial, as shown in Figure 6.1. Stimuli were grasped along the diagonal joining the bottom left corner with the top right corner, as in Experiments 4 and 5. The participant was instructed to maintain the index finger and thumb on the target until a second auditory tone, played 4 seconds after the tone cueing movement initiation, signalled the end of the trial and that (s)he could return to the Start position. The stimuli were then manually removed from the monitor. A schematic representation of the task is shown in Figure 6.2.
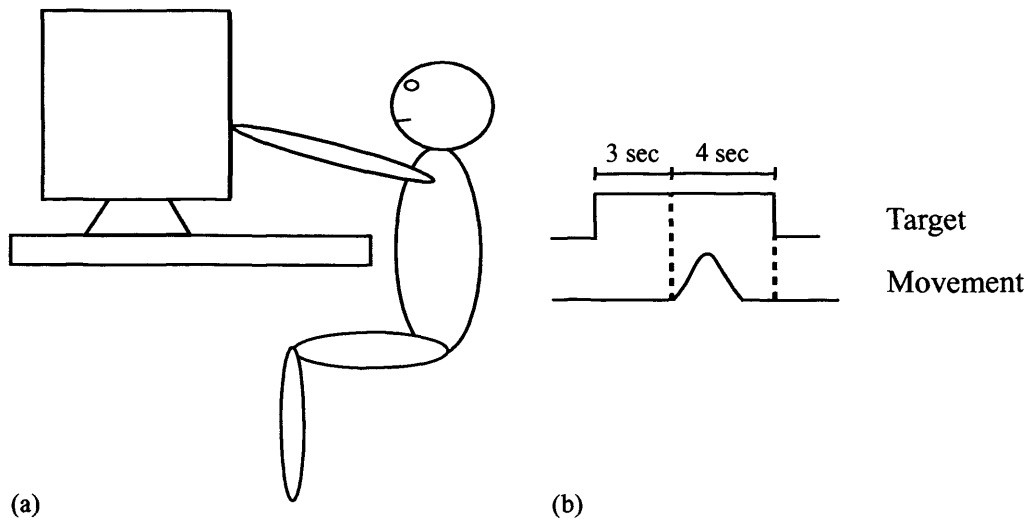
Figure 6.2. A schematic representation (a) and the temporal sequence (b) of the task.

6.2.4.2. 2D-enhanced and 2D conditions

The 2D-enhanced and 2D conditions were identical to the 3D condition except that the onset and offset of the 2D-enhanced and 2D stimuli, respectively, were automatically controlled. Stimulus offset occurred when the second tone signalled the end of trial (i.e., 4 sec after movement initiation).

6.2.5. Data Collection and Variables

For all conditions, 7 kinematic variables of interest were recorded. These were maximum grip aperture (MGA, mm), percent time to maximum grip aperture (%), maximum wrist velocity (MWV, mm sec^{-1}), percent time to maximum wrist velocity (%), movement duration (msec), maximum wrist displacement (mm) and maximum wrist height (mm). These variables were obtained as described in Experiment 1. Data recording started approximately 1 second before the verbal cue signalling the start of trial was given and ended soon after the participant's fingers touched the target.

6.3. Results

Participants performed 8 trials for each of the 3 sizes in each conditions and right and left side of presentation were combined for the statistical analysis. The means entered in the analysis were computed from a minimum of 3 trials. To reach this criterion, for a small number of trials a linear interpolation procedure (as used by Westwood, Dubrowski, Carnahan & Roy, 2000) was carried out off-line to estimate the position of missing markers, with the constraint that data were interpolated only if missing for two or fewer consecutive frames (i.e., 33 msec) that did not occur at the start or end of movement. Interpolated trials constituted less than 3% of all trials. Trials for which markers positions were missing for longer periods of time were discarded from the analysis. For two cells (i.e., 1% of all cells) the means entered in the analysis were computed from 2 trials. Where not otherwise specified, an alpha level of 0.05 was used for the tests of significance and where necessary, Geisser-Greenhouse adjustments were made to the degrees of freedom. Simple comparisons were analysed with repeated measures t-tests and Bonferroni correction.

Individual variables were analysed in a series of $3 \times 2 \times 3$ repeated measures ANOVAs with Dimension (3D/2D-enhanced/2D), Shape (square/notched circle) and Size (40/50/60 mm) as factors.

6.3.1. Kinematic Profiles

Very similar kinematic profiles were found with the three targets. As shown in Figure 6.3, in agreement with the coupling between the transport and grasp components typically observed in manual prehension, maximum wrist velocity preceded maximum grip aperture in all conditions. The typical biphasic curve of grip aperture, with a clear maximum aperture followed by closure of the grip to match target size, was also observed with all targets.
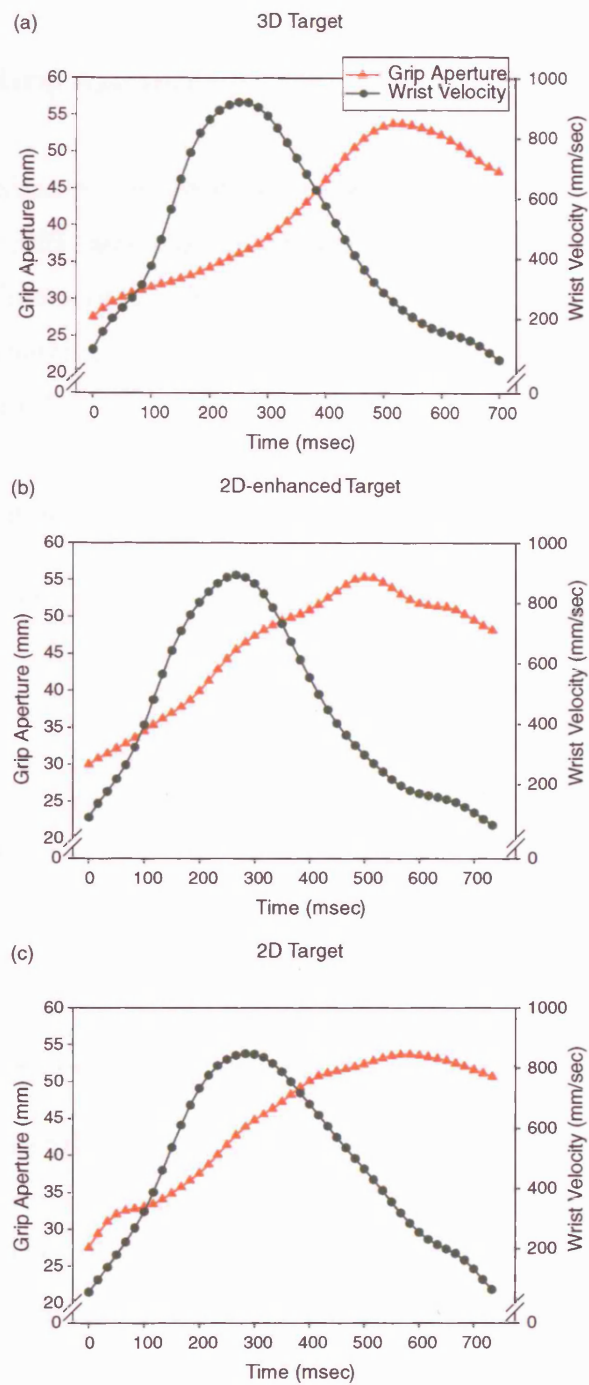
Figure 6.3. Representative grip aperture and velocity profiles in the (a) 3D, (b) 2D-enhanced and (c) 2D conditions with the 40 mm notched circle as a target. The time on the abscissa represents movement duration.

6.3.2. Grasp Component

6.3.2.1. Maximum Grip Aperture

The analysis of maximum grip aperture revealed a significant main effect of Shape ($F_{(1,9)}$ = 17.033, p = .003) and a significant main effect of Size ($F_{(2,18)}$ = 383.530, p < .001). None of the interactions were significant and, more crucially, Dimension was also found to be non-significant ($F_{(2,18)}$ = 1.425, p = 0.267). The group means are shown in Table 6.1 and Figure 6.7.

Table 6.1. Mean maximum grip aperture (mm) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	55.06 (1.96)		53.21 (1.20)		54.60 (1.38)	
Square 50	62.65 (1.81)		62.23 (1.34)		61.79 (1.17)	
Square 60	71.38 (1.28)		70.11 (1.14)		68.65 (1.62)	
Notched Circle 40	57.81 (1.55)		56.51 (1.41)		55.40 (1.20)	
Notched Circle 50	66.36 (1.83)		64.62 (1.50)		63.07 (1.32)	
Notched Circle 60	72.70 (1.65)		71.59 (1.46)		71.45 (1.07)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	63.03	65.62	61.85	64.24	61.68	63.31
	(1.46)	(1.51)	(1.11)	(1.42)	(1.35)	(1.14)

Taken together, the significant main effect of Shape and the lack of a Dimension × Shape interaction indicate that larger grip apertures were used for the notched circle in all three conditions. The effect of Size was further explored with planned comparisons which revealed that grip apertures significantly increased from the 40 to the 50 mm targets ($t_{(9)}$ = 23.011, p < .001) and from the 50 to the 60 mm targets ($t_{(9)}$ = 14.100, p < .001). The lack of a Dimension × Size interaction indicates that maximum grip aperture increased as a function of target size for all three target dimensionalities. The similarity between conditions can be seen in Figure 6.4.
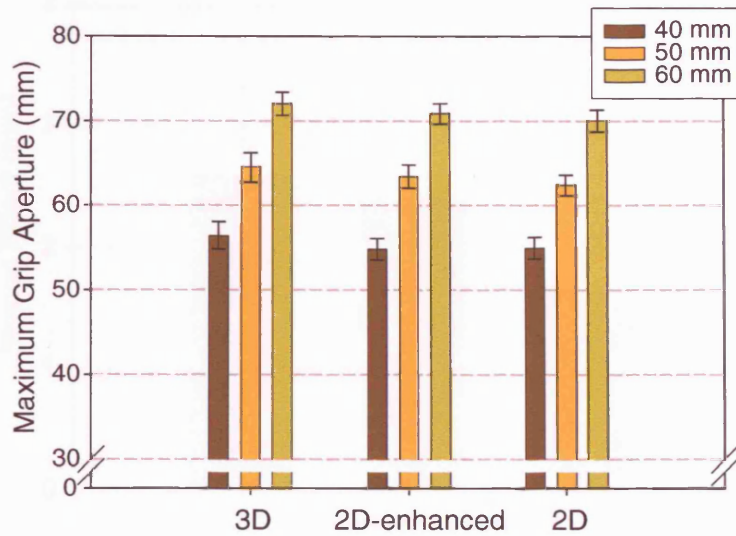
Figure 6.4. Maximum grip aperture plotted as a function of target size.

6.3.2.2. Illusion Effect

The magnitude of the illusion effects was quantified for individual conditions by subtracting the grip aperture obtained with the square from the grip aperture obtained with the notched circle of corresponding size. As shown in Figure 6.5, the illusion effect varied as a function of target dimensionality, as this was 2.59, 2.39 and 1.63 mm for the 3D, 2D-enhanced and 2D targets, respectively. However, a repeated measures ANOVA with Dimension (3D/2D-enhanced/2D) as factor revealed that the differences between the three conditions were not significant ($F_{(2,18)} = 0.900$, p = 0.424).
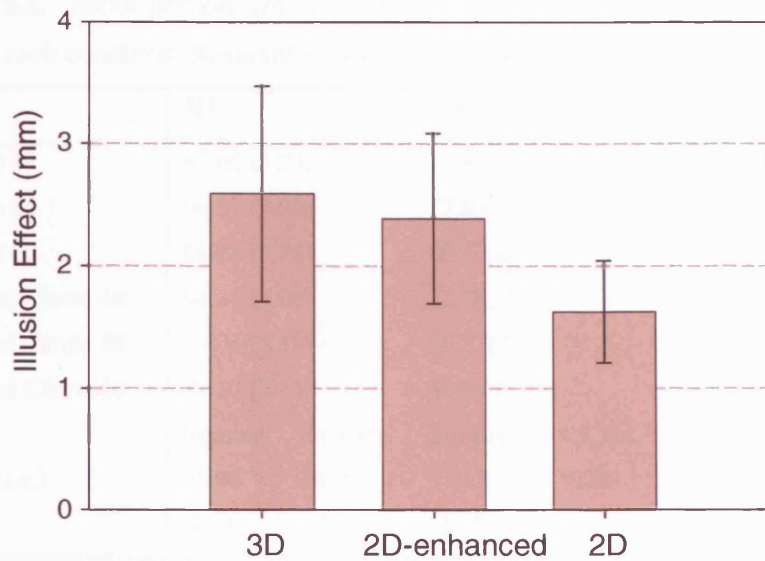
Figure 6.5. The illusion effect plotted as a function of target dimensionality.

6.3.2.3. Percent Time to Maximum Grip Aperture

The analysis of percent time to maximum grip aperture revealed significant main effects of Dimension ($F_{(2,18)}$ = 11.948, p < .001) and of Size ($F_{(2,18)}$ = 8.281, p = .003). None of the interactions were significant and the main effect of Shape was also non-significant ($F_{(1,9)}$ = 0.393, p = 0.546). The group means are shown in Table 6.2 and Figure 6.7.

Table 6.2 shows that maximum grip aperture occurred in the second half of the movement (Jeannerod, 1984) and within the expected range, between 60% and 80% of movement execution (Smeets & Brenner, 1999) for all targets. However, it can also be seen that earlier peak apertures were used for the 3D targets. Planned comparisons confirmed that maximum grip aperture occurred significantly earlier in the 3D condition relative to both the 2d-enhanced ($t_{(9)}$ = 3.670, p = .005) and 2D ($t_{(9)}$ = 3.747, p = .005) conditions. The difference between these latter two conditions was not significant ($t_{(9)}$ = 1.340, p = .213).

Table 6.2. Mean percent time to maximum grip aperture (%) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	65.06 (5.23)		72.84 (4.72)		69.87 (4.17)	
Square 50	66.31 (4.90)		77.83 (3.57)		75.15 (2.53)	
Square 60	66.21 (4.75)		80.70 (3.35)		77.35 (3.22)	
Notched Circle 40	64.21 (3.06)		72.26 (3.02)		67.92 (4.07)	
Notched Circle 50	69.03 (3.19)		76.27(3.45)		78.10 (2.86)	
Notched Circle 60	71.13 (2.15)		80.09 (3.28)		80.42 (1.65)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	65.86	68.12	77.12	76.20	74.12	75.48
	(4.81)	(2.60)	(2.75)	(2.63)	(2.57)	(2.22)

The effect of Size was further explored with planned comparisons which revealed that maximum grip aperture occurred significantly earlier for the 40 mm targets relative to the 50 mm targets ($t_{(9)}$ = 3.078, p = .013) but that this latter did not significantly differ from the 60 mm targets ($t_{(9)}$ = 1.349, p = .210). As shown in Figure 6.6, size modulated the time to maximum grip aperture in all conditions. The effect was lightly smaller for the 3D targets, however the lack of a Dimension × Size interaction indicates that these differences were not significant.
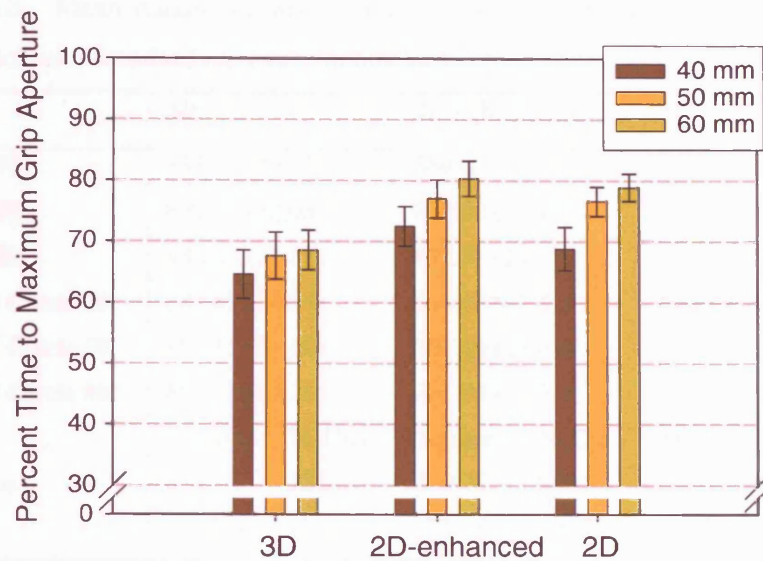
Figure 6.6. Percent time to maximum grip aperture plotted as a function of target size.

6.3.3. Transport Component

6.3.3.1. Maximum Wrist Velocity

The analysis of maximum wrist velocity revealed non-significant main effects of Dimension ($F_{(2, 18)}$ = 3.356, p = .058), Shape ($F_{(1, 9)}$ = 1.204, p = .301) and Size ($F_{(2, 8)}$ = 1.008, p = .385) and non-significant interactions (p > .05 for all interactions). These results suggest that hand velocity was not affected by target dimensionality, shape or size. The group means are shown in Table 6.3 and Figure 6.7.

Table 6.3. Mean maximum wrist velocity (mm sec^{-1}) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	885.05 (40.12)		869.62 (36.85)		904.25 (29.58)	
Square 50	879.27 (32.08)		869.00 (33.46)		887.10 (29.34)	
Square 60	886.87 (37.17)		873.71 (29.77)		899.56 (33.48)	
Notched Circle 40	887.63 (34.34)		860.58 (32.40)		922.71 (30.77)	
Notched Circle 50	885.15 (35.10)		867.10 (27.65)		900.11 (29.58)	
Notched Circle 60	892.83 (40.24)		863.94 (31.31)		905.21 (37.16)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	883.73	888.54	870.78	863.87	896.97	909.34
	(36.00)	(36.02)	(32.72)	(29.70)	(30.03)	(32.16)

6.3.3.2. Percent Time to Maximum Wrist Velocity

Similar results were obtained from the analysis of percent time to maximum wrist velocity as neither of the main effects of Dimension ($F_{(2, 18)}$ = 0.946, p = .407), Shape ($F_{(1, 9)}$ = 0.792, p = .397) and Size ($F_{(2, 8)}$ = 0.599, p = .560) nor any of the interactions were significant (p > .05 for all interactions). These results suggest that peak velocity did not vary as a function of target dimensionality, shape or size. The group means are shown in Table 6.4 and Figure 6.7.

As discussed in Section 6.3.1, Table 6.4 shows that in agreement with the typical coupling between the transport and grasp components observed in manual prehension (e.g., Jeannerod, 1981), maximum wrist velocity occurred proportionally earlier than maximum grip aperture in all conditions.

Table 6.4. Mean percent time to maximum wrist velocity (%) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	33.89 (0.79)		35.89 (1.72)		32.99 (1.37)	
Square 50	33.48 (1.07)		32.90 (1.53)		32.18 (1.06)	
Square 60	34.09 (1.19)		34.28 (1.02)		33.22 (1.01)	
Notched Circle 40	33.55 (0.91)		33.63 (1.41)		31.96 (1.18)	
Notched Circle 50	33.67 (0.93)		34.11 (1.88)		33.09 (1.30)	
Notched Circle 60	33.02 (1.34)		32.82 (1.26)		33.47 (1.37)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	33.82	33.41	34.35	33.52	32.80	32.84
	(0.93)	(0.95)	(1.16)	(1.47)	(1.10)	(1.15)

6.3.3.3. Maximum Wrist Displacement

The analysis of maximum wrist displacement revealed a significant main effect of Dimension ($F_{(2, 18)}$ = 8.803, p = .002) but non-significant main effects of Shape ($F_{(1, 9)}$ = 2.903, p = .123) and Size ($F_{(2, 8)}$ = 0.815, p = .458) and non-significant interactions (p > .05 for all interactions). The group means and standard errors are shown in Table 6.5 and Figure 6.7.

Table 6.5. Mean maximum wrist displacement (mm) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	310.10 (3.89)		302.26 (4.17)		304.38 (4.60)	
Square 50	307.90 (4.87)		304.81 (3.56)		299.45 (4.84)	
Square 60	309.34 (4.19)		305.00 (3.91)		302.55 (4.38)	
Notched Circle 40	313.39 (4.41)		305.30 (3.80)		304.83 (4.47)	
Notched Circle 50	308.66 (3.58)		307.32 (3.66)		303.67 (3.71)	
Notched Circle 60	313.39 (4.41)		303.23 (4.25)		304.28 (4.22)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	309.11	310.68	304.02	305.28	302.12	304.26
	(3.94)	(3.80)	(3.09)	(3.76)	(4.21)	(4.01)

Planned comparisons revealed that significantly greater wrist displacements were made with 3D targets relative to the 2D condition ($t_{(9)}$ = 3.987, p = .003). The wrist displacements used in the 2D-enhanced condition were between the 2D and 3D conditions and did not significantly vary from them ($t_{(9)}$ = 1.101, p = .300 and $t_{(9)}$ = 2.661, p = .026, respectively; α = .0167).

6.3.3.4. Maximum Wrist Height

Similar results were obtained for maximum wrist height. The analysis revealed a significant main effects of Dimension ($F_{(2, 18)}$ = 5.295, p = .016) but non-significant effects of Shape ($F_{(1, 9)}$ = 0.578, p = .467) and Size ($F_{(2, 8)}$ = 0.163, p = .851) and non-significant interactions (p > .05 for all interactions). The group means are shown in Table 6.6 and Figure 6.7.

Table 6.6. Mean maximum wrist height (mm) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	266.64 (2.99)		259.39 (2.98)		260.58 (2.80)	
Square 50	265.22 (2.52)		261.14 (3.18)		260.85 (2.49)	
Square 60	266.43 (3.34)		258.84 (2.89)		261.39 (2.48)	
Notched Circle 40	266.38 (3.12)		259.10 (3.19)		261.90 (2.89)	
Notched Circle 50	266.68 (3.08)		258.96 (2.70)		259.96 (2.48)	
Notched Circle 60	265.60 (2.98)		259.89 (2.29)		259.92 (3.06)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	266.10	266.50	259.79	259.32	260.94	260.59
	(2.88)	(2.93)	(2.95)	(2.63)	(2.55)	(2.79)

Planned comparisons revealed that wrist height was greater in the 3D condition relative to both the 2D ($t_{(9)}$ = 2.264, p = .050) and the 2D-enhanced ($t_{(9)}$ = 2.558, p = .031) conditions. However, neither of these comparisons was significant after the Bonferroni

correction (α = .0167). The wrist reached very similar heights in the 2D and 2D-enhaced conditions ($t_{(15)}$ = 0.937, p = .373).

6.3.3.5. Movement Duration

Movement duration also did not vary as a function of target dimensionality, shape or size. The analysis revealed that none of the main effects of Dimension ($F_{(2, 18)}$ = 0.956, p = .403), Shape ($F_{(1, 9)}$ = 1.034, p = .336) or Size ($F_{(2, 8)}$ = 0.308, p = .739) and none of the interactions were significant (p > .05 for all interactions). The group means are shown in Table 6.7 and Figure 6.7. It should be noted that there was a trend for longer durations in the 3D condition.

Table 6.7. Mean movement duration (msec) for each stimulus size in each condition. Standard errors are in brackets.

	3D		2D-enhanced		2D	
Square 40	873.25 (45.30)		829.69 (30.43)		833.07 (33.00)	
Square 50	861.95 (40.71)		856.80 (24.32)		859.69 (30.12)	
Square 60	859.90 (33.34)		836.64 (24.25)		841.94 (33.89)	
Notched Circle 40	871.62 (32.89)		859.68 (24.93)		838.22 (28.22)	
Notched Circle 50	860.57 (30.77)		857.10 (23.13)		835.57 (28.33)	
Notched Circle 60	873.42 (38.47)		868.35 (31.21)		851.38 (31.37)	
	Square	**N. Circ.**	**Square**	**N. Circ.**	**Square**	**N. Circ.**
Mean (s.e.)	865.03	868.54	841.04	861.71	844.90	841.83
	(37.16)	(33.31)	(22.56)	(25.17)	(31.20)	(27.93)

Experiment 6 - Grasping 3D, 2D and 2D-enhanced Targets

(a) Maximum Grip Aperture (mm)

(b) Percent Time to MGA

(c) Maximum Wrist Velocity (mm/sec)

(d) Percent Time to MWV

(e) Maximum Wrist Displacement (mm)

(f) Maximum Wrist Height (mm)

Square
Notched Circle
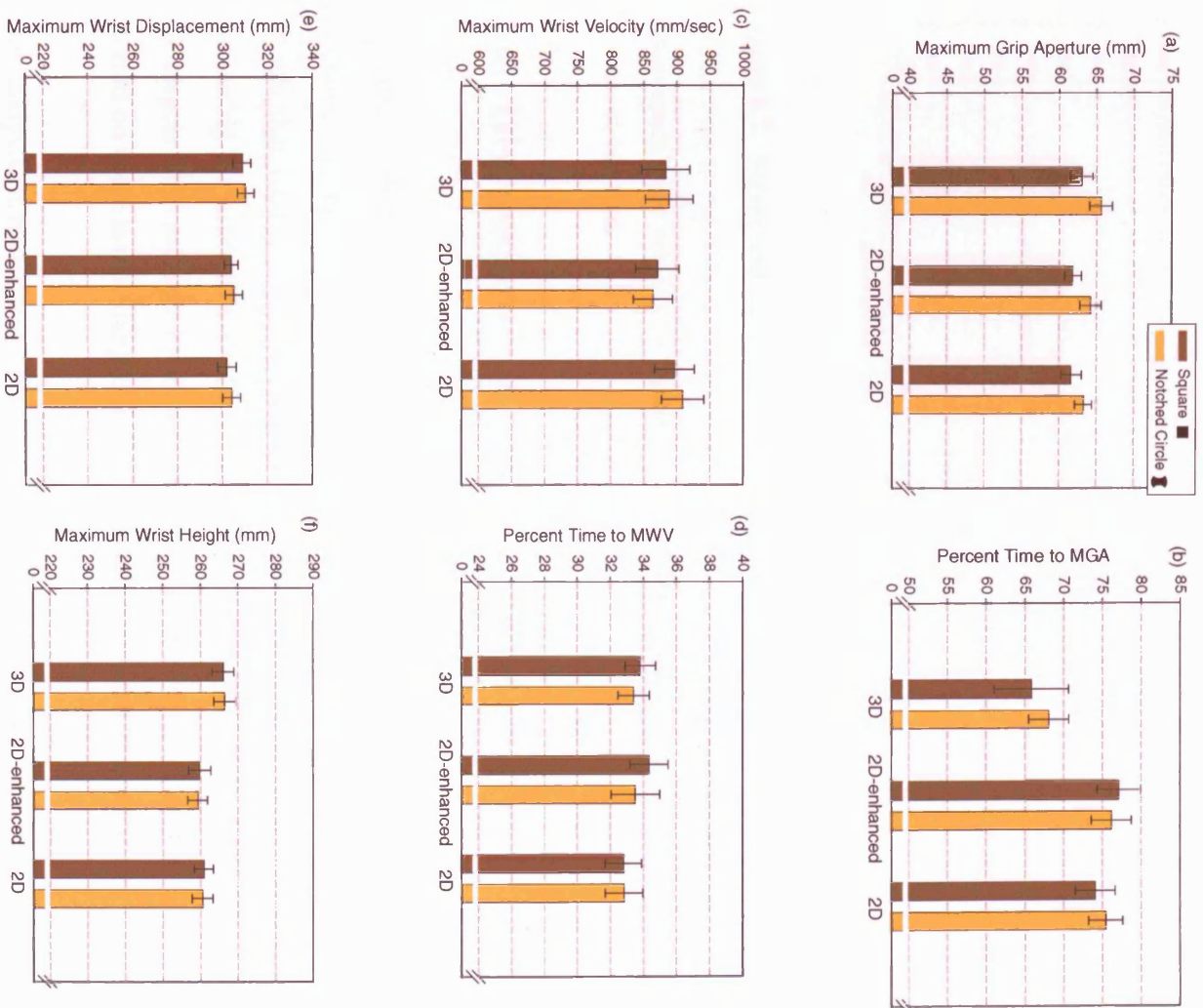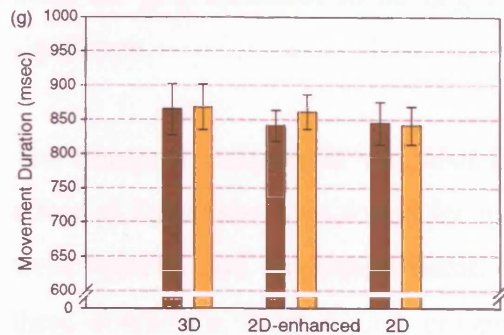
Figure 6.7. Means and standard errors (error bars) for: (a) maximum grip aperture (MGA), (b) percent time to maximum grip aperture, (c) maximum wrist velocity (MWV), (d) percent time to maximum wrist velocity, (e) maximum wrist displacement, (f) maximum wrist height and (g) movement duration.

6.4. Discussion

The aim of this experiment was to establish whether grasps towards 2D targets are mediated by the dorsal visual system or whether this system is engaged solely by stimuli that have a 3D structure. This question was explored in two ways. First, by comparing the kinematic profiles resulting from grasps aimed at 3D, 2D-enhanced and 2D targets and second, by measuring whether the effect that the Diagonal illusion exerted on these tasks changed as a function of target dimensionality.

The analysis of maximum grip aperture clearly shows that similar apertures were used in grasps with the three types of targets suggesting that this variable was not affected by target dimensionality. These results are in agreement with Westwood et al. (2002) who also found no significant differences in the maximum grip apertures from grasps with 3D, 2D and 2D-enahnced targets for a subset of the participants. By contrast, the results do not fully replicate Kwok and Braddick's (2003) study where larger grip apertures were found for grasps aimed at 3D targets. Although in the present study there was a

trend for grip apertures to be larger in the 3D condition, these differences were not significant.

The transport component was also largely unaffected by target dimensionality as no effect of Dimension was found for maximum wrist velocity, percent time to maximum wrist velocity and movement duration. The similar kinematic profiles obtained in the three conditions suggest that grasping with all three targets involved very similar visuomotor mechanisms, and by implication, that the dorsal visual system mediates grasps aimed at targets that lack a 3D structure.

These conclusions are further supported by the typical kinematic profiles observed in the 2D and 2D-enhanced conditions. Maximum grip aperture increased as a function of target size with both targets and it occurred within the range typically observed in manual prehension (Jeannerod, 1984; Smeets & Brenner, 1999). Moreover, the typical coupling between the transport and grasp components was maintained in both conditions. These findings suggest that the typical kinematic parameters of manual prehension were used with these targets.

Finally, the above conclusions are also supported by the similar illusion effects observed in the three conditions. If grasping in the 2D and 2D-enhanced conditions was mediated by the ventral visual system, a greater illusion effect should have been observed with these targets. Contrary to this prediction, the illusion effect did not significantly differ in the three tasks suggesting that the 2D and 2D-enhanced targets did not recruit greater modulation by ventral visual mechanisms. These results are in agreement with the findings from the comparison between Experiments 4 and 5, which also showed that the introduction of 2D elements in the illusion display (in Experiment 5) did not increase the magnitude of the illusion effect.

In contrast to the above findings, the timing of maximum grip aperture and wrist displacement were affected by target dimensionality. Specifically, grip apertures

occurred proportionally earlier in the 3D condition relative to both the 2D and 2D-enhanced conditions and maximum wrist displacement was greater for the 3D condition relative to the 2D condition. A strong trend for greater wrist height in the 3D condition was also observed, but this did not reach significance after the conservative Bonferroni correction was applied to the significance level. These results are not comparable to previous published findings as neither Westwood et al. (2002) nor Kwok and Braddick (2003) analysed kinematic variables other than maximum grip aperture. However, they are partly in agreement with previous investigations in our laboratory (Kwok, 2003; unpublished thesis) which also found that maximum grip aperture occurred earlier in grasps with 3D targets relative to 2D targets. The lack of haptic feedback in the 2D and 2D-enhanced conditions is unlikely to account for these results. Although the effect of adding haptic feedback to a grasping task with 2D stimuli has not been directly investigated, Experiment 7 presented in this thesis clearly suggests that adding regular haptic feedback to an open loop grasping tasks does not affect several of the kinematic parameters, including the timing of maximum grip aperture and wrist displacement.

Slower movements and larger apertures that occur proportionally earlier have been suggested as indices of the accuracy demands of a task (Connolly & Goodale, 1999; Smeets & Brenner, 1999). Specifically, several studies have reported larger and earlier grip apertures for tasks where increased difficulty resulted from reduced visual information. For instance, Berthier, Clifton, Gullipalli, McCall, and Robin (1994) reported larger and earlier apertures for grasps aimed at an object glowing in the dark. Similar findings were reported by Sivak and MacKenzie (1990) for grasps based exclusively on peripheral vision. Finally, Wing, Turton and Fraser (1986) and Jakobson and Goodale (1991) found larger and earlier apertures for grasping under open loop conditions, relative to closed loop conditions. All the above studies, except for Wing et al. (1986), also reported longer durations under reduced visual feedback and Jakobson and Goodale (1991) reported an increase in maximum wrist height under these conditions. Moreover, in agreement with the above claim, slower velocities and larger grip apertures occurring earlier in the movement have been reported for tasks where

increased accuracy demands resulted from a reduction of the contact surface on the target object (Zaal & Bootsma, 1993).

In manual prehension, larger grip apertures would allow for a greater margin of error in the computation of target size and earlier maximum apertures would lengthen the "grip-closure" phase, therefore providing longer time for the adjustment of grip aperture according to target size. Similarly, slower velocities would also result in longer time for finer movement control and the processing of visual (and perhaps proprioceptive) feedback. Finally, as suggested by Hu, Eagleson and Goodale (1999), greater wrist height, and probably wrist displacement, could indicate that greater clearances are required in the grasping task. In this study, maximum grip aperture and maximum velocity were not found to differ in the 3D and 2D conditions, however, earlier grip apertures, greater wrist displacement and a strong trend for greater wrist height were observed with the 3D targets. Thus, these kinematic parameters could be interpreted to suggest that grasping the 3D targets was construed as requiring more accuracy than grasping the 2D and 2D-enhanced targets. This interpretation is to some extent supported by the trend for larger grip apertures, lower velocities and longer movement durations found in the 3D condition.

A model of grasping recently proposed by Smeets and Brenner (1999) could explain how grasping 3D targets could be construed as a more difficult task (Figure 6.8). These authors abandoned Jeannerod's (1981, 1984) notion of a transport and grasp component and the concept that grip aperture is a variable of the latter. Instead, they proposed that, during grasping, the fingers and thumb move more or less independently and orthogonally towards suitable positions on the target. Smeets and Brenner (1999) point out that orthogonal trajectories are generally used in motor control and would result in two advantages. First, a perpendicular approach would reduce errors in the selection of the contact points that could result from the spatial variability inherent to human motor control. Second, it would apply a perpendicular force to the target surface that would improve grip stability. Accordingly, Smeets and Brenner (1999) further proposed that

visuomotor responses requiring more accuracy are more likely to use orthogonal trajectories.

(a): 2D target   (b): 3D target
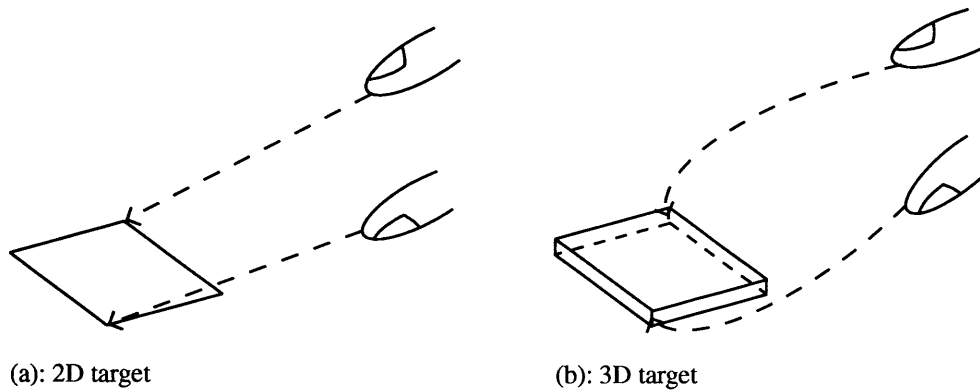
Figure 6.8. Thumb and index finger trajectories in a grasping task orthogonally approaching the suitable positions on the target with 2D (a) and 3D (b) targets.

These authors tested this claim with an artificial network and found that greater orthogonality in the trajectory (in their model a measure of task difficulty) resulted in slower velocities and in larger grip apertures that occurred proportionally earlier in the movement. These results are in agreement with the empirical findings reported above where increased difficulty resulted from either reduced visual information or reduced target surface. Figure 6.8 illustrates how this model could account for the effect of target dimensionality found in this study. First, it clearly shows how maximum grip aperture could have increased with 3D targets if the perpendicular approach was used. Whereas when grasping the 2D stimuli the digits must move perpendicularly to the flat surface of the square, grasping the 3D targets requires approaching perpendicularly the smaller vertical sides. Thus, the different contact points alone in these two conditions would predict larger grip apertures. Moreover, the figure also shows that the contact surface in the 3D target are substantially smaller than the surface available in the 2D target. Thus, Smeets and Brenner's (1999) model would predict that grasping the 3D targets would require greater accuracy of the approach and result in larger grip apertures occurring proportionally earlier in the movement. Indeed, the model's prediction for the timing of

maximum grip aperture was supported in this experiment and a trend for larger apertures in the 3D condition was also observed. Thus, Smeets and Brenner's (1999) model can to some extent explain these latter results. The lack of a significant difference in the maximum grip aperture used with 2D and 3D targets could be due to the location of the contact points on the shapes and is further discussed in the General Discussion.

Taken together, the results from this study suggest that no differences were found between grasps aimed at 3D, 2D-enhanced and 2D targets in several of the kinematic parameters, most notably in maximum grip aperture and maximum wrist velocity. Moreover, the Diagonal illusion exerted equivalent effects irrespective of target dimensionality. These findings suggest that the three tasks engaged very similar visuomotor mechanisms, and by implication, that grasping 2D targets is mediated by the dorsal visual system. Nevertheless, the earlier apertures and larger wrist heights and displacements observed in the 3D condition could be interpreted to suggest that the visuomotor system treated the 3D targets as having a greater level of difficulty. Of course, such an account would strongly suggest that the extension in depth of the 3D targets was computed by the visuomotor system and, by implication, that the full geometry of these objects was represented in the dorsal system. These conclusions would be in agreement with the findings of Hu et al. (1999) who also claimed that a volumetric representation of the target object is computed in this system.

Although this latter account is to some extent speculative and more research is needed, it is not in disagreement with the former conclusion that the dorsal visual system mediates actions aimed at both 3D and 2D targets. It is certainly possible that both instances are true: That the dorsal system is engaged by both 3D and 2D targets *and* that it fully represents their 3D structure. However, it remains to be established whether this system is *equally* engaged by 3D and 2D objects. The present results suggest that grasps aimed at these targets may be treated as having different degrees of difficulty.

At *prima facie*, the finding that movements aimed at both functionally relevant (3D) and irrelevant (2D) stimuli are mediated by the dorsal visual system could suggest that reducing computational load is not a significant factor in the visual system. In reality, indiscriminate dorsal activation as observed in this study could be the most efficient solution for at least two reasons. First, the model proposed in Section 6.1 rests on the assumption that dorsal representations are computationally more expensive than ventral representations. If this is incorrect, no computational advantage would result from the mediation of actions aimed at functionally irrelevant stimuli by the ventral system. Second, determining "functional relevance" according to target dimensionality as postulated by the model could entail substantial additional processing. Thus, it is possible that, in agreement with the claim that the visual system favours computational efficiency (Rueckl et al., 1989), indiscriminate dorsal mediation of action irrespective of target functional relevance could be the most efficient strategy after all. It may well be the case that, due to computational requirements or some other factor still unknown, the dorsal system passively processes all the visual information that its neural architecture can support and that decisions on functional relevance and target dimensionality are based only on processing carried out within the ventral system.

7. Experiment 7 – The Effect of Haptic Feedback on Manual Estimation and Prehension

7.1. Introduction

This experiment examined two methodological questions still unaddressed in this area of research, namely whether differences in haptic feedback in manual estimation and open loop grasping could account for some of the characteristics of the kinematic profiles observed in these tasks.

As discussed above, psychophysical evidence for the existence of a dorsal and ventral visual system in neurologically intact individuals is largely based on illusion studies that reported a differential illusion effect on perception and action. Although some of these studies used visuomotor responses for which haptic information could make a lesser contribution, for example posting (Dyde & Milner, 2002) and pointing (Post & Welch, 1996), the majority of these studies quantified the illusion effect by comparing differences in hand aperture in manual estimation and grasping tasks (Daprati & Gentilucci, 1997; Franz et al., 2000; Haffenden & Goodale, 1998; Haffenden & Goodale, 2000; Kwok & Braddick, 2003; Westwood et al., 2000). Given the direct comparison between these two tasks, it is of primary importance to rule out the possibility that somatosensory differences in the two conditions could account for some of these results.

A major difference between grasping and manual estimation is that haptic feedback is present after each grasp but it is absent from manual estimations. If haptic information contributed in some way to the computation of hand aperture in these two tasks, it could

be possible that differences in hand aperture between these two conditions could be due, at least partly, to differences in haptic feedback.

7.1.1. Processing of Haptic Information in Manual Estimation and Prehension

The contribution of haptic information in manual prehension in neurologically intact individuals has been investigated by Gentilucci, Toni, Daprati and Gangitano (1997). Gentilucci et al. (1997) compared the kinematic profiles obtained under normal open loop grasping conditions and in an open loop task where the distant phalanges of the participants' index finger and thumb were anaesthetised. Tactile anaesthesia of the fingers removed haptic feedback but left proprioception unaffected, therefore it allowed an examination of haptic information in isolation. Gentilucci et al. (1997) found that anaesthesia affected both the grasp and transport components of prehension. More specifically, maximum grip aperture and time to maximum grip aperture significantly increased in the anaesthesia condition suggesting that the finger opening phase was affected. Moreover, the removal of haptic information resulted in an increase in trajectory variability, mostly in the deceleration phase, a decrease in movement velocity and an increase in movement duration. Gentilucci et al.'s (1997) concluded that tactile signals are used by the visuomotor system to control manual prehension.

The evidence from interference studies is, however, not so conclusive. Gentilucci, Daprati and Gangitano (1998) used an interference paradigm to examine the integration of somatosensory and visual information in manual prehension and manual estimation. These authors found that when participants were required to grasp a sphere with the left hand while manipulating a smaller or bigger sphere with the right hand, the hand aperture in the grasping task was affected in the direction of the size of the manipulated sphere. For example, if the larger sphere was manipulated by the left hand, larger apertures were recorded in the grasping task. This effect was not found when the same procedure was carried out with a manual estimation task. Gentilucci et al. (1998) concluded that irrelevant haptic information can interfere with the guidance of object-

directed action in the sensorimotor system but not with the execution of manual estimation. More specifically, that haptic information is readily integrated with visual information for the guidance of sensorimotor responses but not for manual estimation.

An opposite pattern of results has been recently reported by Westwood and Goodale (2003) who used a similar interference paradigm, but performed entirely without visual information. Westwood and Goodale (2003) examined whether the size-contrast effect previously reported in the visual modality (e.g., Hu & Goodale, 2000) was also present in a purely haptic task. The size-contrast effect consists of a perceived increase or decrease of an object's size (target object) when this is presented adjacent to, and in conjunction with, a larger or smaller object (comparison object), respectively. Hu and Goodale (2000) examined this effect with visually presented stimuli and found that, as expected, manual estimation, but not grasping, was affected by the size-contrast display.

Westwood and Goodale (2003) tested this effect in the haptic modality. In a 2-step manipulation procedure participants were first asked to manipulate the flanker (comparison) object and then to manipulate the target object. Both objects were placed under the table and manipulated with the left hand. After this, participants had to grasp or manually estimate another identical target that was placed above the table. In agreement with the results from the visual modality, Westwood and Goodale (2003) found that the size of the manipulated comparison object affected hand aperture in the manual estimation task but not in the grasping task. Moreover, the effect was in the same direction as predicted, specifically larger apertures were found when a smaller comparison object was manipulated, and *viceversa*.

At present it remains unclear why Gentilucci et al. (1998) and Westwood and Goodale's (2003) studies produced discrepant results. It is important to note that Gentilucci et al.'s (1998) interference model can not account for the effect observed on manual estimation in Westwood and Goodale (2003) as this was in the opposite direction to that predicted by the model. For example, manipulating the smaller comparison objects resulted in

larger and not smaller hand apertures. The discrepancy could be perhaps accounted for by differences in the type of sensory information. In Gentilucci et al. (1998) both visual and haptic information were present whereas only the latter was available in Westwood and Goodale (2003). Another possible explanation is that whereas in Gentilucci et al. (1998) participants were asked to manipulate only the comparison object before executing the task, in Westwood and Goodale (2003) the target object placed under the table was always the last to be manipulated. Thus, in this study at task initiation there was no discrepancy between haptic feedback (or most recent haptic memory trace) and actual target size.

7.1.2. Haptic Information and Manual Estimation

Although at present no clear conclusions can be drawn for the exact role of haptic information on grasping and manual estimation, the above studies clearly suggest that this type of sensory information could affect performance on both tasks. These results have strong implications for illusion (and other) studies that directly compared manual estimation with manual prehension as they suggest that the differences in hand aperture observed in these studies could be due, at least partly, to differences in haptic feedback in these two conditions.

Indeed this problem has been recognised by some authors (Ganel & Goodale, 2003; Haffenden & Goodale, 2000, Haffenden Schiff & Goodale, 2001; Hu, & Goodale, 2000; Hu, Goodale & Eagleson, 1999) who have controlled for these potential differences by asking participants to reach out and grasp the target after each manual estimation. However, these studies adopted this control measure without directly examining whether adding haptic feedback to the manual estimation task actually affected hand aperture. Therefore, at present it still remains unclear whether the absence of this type of sensory feedback in manual estimation could account, at least partly, for the hand aperture profile observed in this task. By implication, it remains unclear whether this control measure, that is grasping the target after manual estimations, should be

universally adopted. This is a methodological question of interest, in particular considering that the large majority of studies that used manual estimation did not control for potential differences in haptic feedback (e.g., Hu et al, 1999; Kwok & Braddick, 2003).

7.1.3. Haptic Information and Open Loop Grasping

Gentilucci and colleagues' (Gentilucci et al., 1997; Gentilucci et al., 1998) findings that haptic feedback is used by the visuomotor system to control manual prehension have clear implications for studies that used open loop grasping tasks, in particular for studies that compared grasping under full lighting conditions (closed loop) with grasping in the dark (open loop). In open loop grasping, due to a lack of visual feedback, there is the possibility that participants could misreach the target, and therefore introduce a difference in haptic feedback relative to closed loop grasping. Although not entirely, this potential difference has been controlled for in procedures where the target was lifted from the experimental surface after each grasp (Aglioti et al., 1995; Connolly & Goodale, 1999; Goodale et al., 1991; Haffenden & Goodale, 2000; Hu et al, 1999). Lifting the target can not ensure that participants place the fingers at the "correct" locations, that is, at locations specified in the instructions and used under full lighting conditions, however, it is reasonable to assume that positioning the fingers at "incorrect" locations on the target is likely to result in unstable grasps, and ultimately in dropping the target. Therefore, the open loop grasp-and-lift procedure provides a way to identify, and discard, some of the trials in which the fingers could be positioned at "incorrect" locations on the target. In other words, this procedure could help to reduce possible differences in haptic feedback between open loop and closed loop grasping.

Several studies, however, including the experiments presented in this thesis, have used open loop grasping procedure that, for reasons often imposed by the experimental set-up, did not include lifting the target after each grasp (Culham, Danckert, DeSouxa, Gati, Menon & Goodale, 2003; Dijkerman, Milner & Carey, 1996; Dijkerman, Milner &

Carey, 1999; James, Culham, Humphrey, Milner & Goodale, 2003; Kwok & Braddick, 2003; McIntosh, Dijkerman, Mon-Williams & Milner, 2004). In this procedure, misreaching can not be easily identified by a drop of the target, therefore there is the possibility that this type of open loop grasping could result in different haptic feedback relative to closed loop grasping. This possibility is strengthened by the observation that, in agreement with the kinematic changes observed by Gentilucci et al. (1997) in grasps without haptic information, grasping under open loop conditions produces greater maximum grip apertures, lower peak velocities and longer durations (Jakobson & Goodale, 1991; Berthier, Clifton, Gullapalli, McCall & Robin, 1996) than closed loop grasping. In light of these arguments, it is a question of methodological interest to establish whether differences in haptic feedback potentially generated in open loop grasping procedures that do not include lifting the target could affect any of the kinematic parameters.

7.1.4. The Present Study

The aim of this study was twofold. First, it examined whether adding regular haptic feedback after each manual estimation affected hand aperture. This would have helped to establish whether differences in hand aperture between grasping and manual estimation tasks could be due to differences in haptic information in the two conditions. This was measured by comparing manual estimations performed with and without having to grasp the target after each trial. It was predicted that, if haptic feedback does not affect hand aperture in manual estimation then no differences should have been observed in this comparison.

The second aim of the study was to examine whether differences in the kinematic profiles obtained in open loop and closed loop grasping, when the former is performed without lifting the target, could be due to differences in haptic feedback in the two conditions. This was measured by comparing performance in a normal open loop grasping task with an identical condition in which regular haptic feedback was

introduced by grasping the target under full vision after each open loop trial. It was predicted that, if some of the characteristics of the kinematic profile obtained in the normal open loop grasping condition were due to a reduction in haptic feedback resulting from misreaches, then differences should have been observed between this condition and the open loop task where regular feedback was introduced.

Grasping was also recorded under closed loop conditions and then compared with both the manual estimation and the open loop grasping tasks, with and without regular haptic feedback. It was predicted that if differences in haptic feedback do not affect any of the kinematic parameters in these tasks, then the same pattern of results should have been observed when comparing closed loop grasping with the two haptic feedback conditions, in either manual estimation or open loop grasping.

7.2. Method

7.2.1. Design

This study used a Repeated Measures design as all participants took part in all 5 conditions, grasping in closed loop (CL), grasping in open loop without regular feedback (OL), grasping in open loop with regular haptic feedback (OLHF), manual estimation without feedback (ME) and manual estimation with haptic feedback (MEHF). Conditions were individually presented in blocks of 24 trials (8 trials for each of the 3 sizes) and order of presentation was counterbalanced across subjects according to a Latin Square arrangement. Stimulus presentation followed a different pseudorandom order for each block with the restrain that any given size could not be repeated for more than 3 consecutive trials.

7.2.2. Participants

Nineteen participants took part in the study. Of these, one was discarded due to loss of markers and two due to unstable apertures in the manual estimation tasks. The data analysis was carried out on 16 participants (9 females and 7 males, mean age 21.7 years). They all had normal or corrected-to-normal self-reported visual acuity, stereo vision ≤ 120 min arc (TNO, Laméris, Utrecht) and were right handed as assessed by the modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). All participants gave informed consent, were paid to participate and were debriefed at the end of the study.

7.2.3. Apparatus and Materials

7.2.3.1. Stimuli

The squares used in Experiment 5 were obtained with a computer numerically controlled (CNC) machine and, given their high degree of precision, it was decided to use them in this study as well. Thus, the stimuli consisted of squares made of 3-mm thick Perspex with a side of side of 28.3, 35.4 and 42.4 mm (diagonals of 40, 50 and 60 mm, respectively). In this study, participants were asked to grasp the squares along the front-to-back axis, however, for simplicity, throughout the report the length of the diagonals is used to indicate the size of the stimuli (i.e., 40, 50 and 60 mm).

Each square was attached to paper cards (29.7 x 42 cm) and centred along the vertical midline. The distance between the bottom edge of the stimuli and the bottom edge of the card was kept constant at 12 cm.

7.2.3.2. Apparatus and Set-up

Unless otherwise stated, the apparatus was as in Experiment 5. A lamp (60 Watts) was placed on a corner of the experimental table and its switch, interposed between stimuli and participant, was used as the Start button. This latter was raised 10.5 cm above the experimental table and was coplanar with the experimental surface (34.7 x 76.2 cm). The distance between the centre of the start button and the bottom edge of the stimuli was maintained constant at 18 cm.

7.2.4. General Procedure

Unless otherwise stated, the procedure was as in Experiment 5.

At the beginning of each condition, participants performed a minimum of 3 practice trials, one for each of the three sizes. More trials were performed if needed to learn the task. Participants sat in front of the table, with the stimuli centred along their midsagittal plane. The height of the chair was adjusted to allow a comfortable position as well as a "bird's eye view" of the stimuli. Movements were recorded for 2 seconds and analysed off-line.

7.2.4.1. Closed Loop Grasping (CL)

At the start of each trial, the participant pressed down the Start button with the index finger and thumb close together and kept his/he eyes closed. At the verbal cue "open", the participant was instructed to open the eyes and to look at the stimuli. After a 3-sec delay, the verbal cue "go" was given and the participant's task was to reach out and grasp the square front-to-back, using a precision grip. The participant was instructed to maintain the index finger and thumb on the target until the verbal instruction "ok" signalled the end of the trial and that (s)he could return to the Start position. In this condition, the lamp, which provided the only source of light in the room, was not

operated by the Start button and was kept switched on for the whole duration. Thus, participants had full vision of the stimuli and of their hand during movement execution.

7.2.4.2. Open Loop Grasping (OL)

This condition was identical to the closed loop grasping condition except that the lamp was now operated by the Start button. Thus, as soon as the hand was lifted to initiate the movement, the switch was released and the lamp was turned off. This ensured that participant did not see their hand or the target during movement execution.

7.2.4.3. Open Loop with Haptic Feedback Grasping (OLHF)

This condition was identical to the open loop grasping condition except that after each open loop trial the participant was instructed to grasp the target with the lamp switched on. More specifically, each open loop grasp was repeated under closed loop conditions. This procedure ensured that if participants misreached the target during open loop grasping, in the second phase of each trial they had the opportunity to receive the same haptic feedback as in the closed loop grasping condition. Grasps performed under full lighting conditions were not recorded, however, participants were not informed of this fact.

7.2.4.4. Manual Estimation (ME)

This condition was identical to the open loop grasping condition except that at the verbal cue "go", the participant was instructed to lift the hand above the Start button and to manually estimate the width of the square along the front-to-back axis. Participants were not allowed to move towards the target and were informed that the manual estimation had to be completed within 2 seconds.

7.2.4.5. Manual Estimation with Haptic Feedback (MEHF)

This condition was identical to the manual estimation condition except that, immediately after each manual estimation, the participant was required to grasp the target with the lamp switched on. More specifically, every manual estimation was followed by a closed loop grasp. This procedure ensured that the haptic feedback received in this condition was the same as in closed loop grasping. As before, the grasps following each manual estimation were not recorded, however, participants were not informed of this fact.

7.2.5. Data Collection and Variables

Data collection and variables were as described in Experiment 1.

7.3. Results

Participants performed 8 trials for each of the 3 sizes in each of the 5 conditions. A small number of trials were not included in the analysis due to the loss of marker values. The means entered in the analysis were computed from a minimum of 3 trials. Where not otherwise specified, an alpha level of 0.05 was used for the tests of significance and where necessary, Geisser-Greenhouse adjustments were made to the degrees of freedom. Simple comparisons were analysed with repeated measures t-tests and Bonferroni correction.

7.3.1. Maximum Grip Aperture

The mean maximum grip apertures were analysed in a 5×3 repeated measures ANOVA with Task (CL/OL/OLHF/ME/MEHF) and Size (40/50/60 mm) as factors. This revealed a significant main effect of Task ($F_{(4, 60)} = 14.540$, p < .001), a significant main effect of Size ($F_{(2, 30)} = 443.411$, p < .001) and a significant Task x Size interaction

$(F_{(3.70, 55.56)} = 3.049$, p = .027). The group means and standard errors are shown in Table 7.1 and Figure 7.2.

Table 7.1. Mean maximum grip aperture (mm) for each stimulus size in each condition. Standard errors are in brackets. ME = manual estimation; HF = haptic feedback.

	40 mm	50 mm	60 mm	Mean (s.e.)
Closed Loop	43.87 (1.06)	50.09 (1.21)	55.79 (1.39)	49.92 (1.16)
Open Loop	44.44 (1.27)	51.17 (1.56)	56.83 (1.38)	50.81 (1.34)
Open Loop with HF	46.05 (1.50)	51.84 (1.23)	56.94 (1.45)	51.61 (1.29)
Manual Estimation	36.47 (1.37)	44.24 (1.66)	52.08 (1.86)	44.26 (1.53)
ME with HF	37.16 (1.21)	44.82 (1.20)	52.39 (1.64)	44.79 (1.25)
Mean (s.e.)	41.60 (1.02)	48.43 (1.06)	54.81 (1.13)	

Figure 7.1 shows the Task × Size interaction. It can be seen that the difference between the apertures used in the manual estimation and grasping tasks decreased proportionally with increase in target size. This interaction was further explored by analysing the effect of Task at each level of Size. The results revealed that the critical comparison between open loop grasping with and without regular haptic feedback was not significant for any of the target sizes (for all comparisons p > .05, see Table 7.2). Similarly, no significant differences were found between the two manual estimation tasks for any of the target sizes (for all comparisons p > .05, see Table 7.2). These results clearly suggest that adding haptic feedback after each manual estimation or open loop grasp did not affect maximum grip aperture.
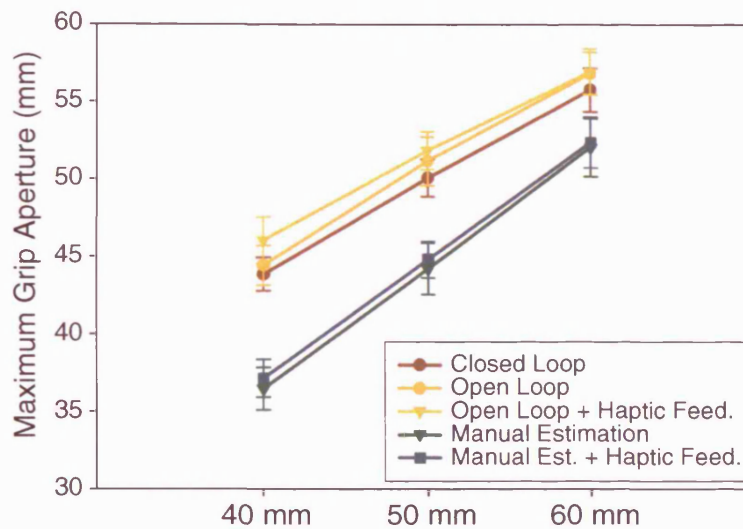
Figure 7.1. Maximum grip aperture in the 5 conditions plotted as a function of target size.

Table 7.2 shows the results from the comparisons between the two open loop tasks and closed loop grasping. Both comparisons were non-significant (p > .05) and further strengthen the conclusions that adding haptic feedback to the open loop task did not affect maximum grip aperture. Similarly, the two manual estimation tasks produced equal results when compared with either closed or open loop grasping. As shown in Table 7.2, for the 40 and 50 mm targets the hand apertures from both manual estimation tasks were significantly smaller than either closed or open loop grasping, whereas for the 60 mm targets these comparisons were not significant. However, what is of interest here is that the same pattern of results was obtained for the two manual estimation conditions, regardless of haptic feedback.

Table 7.2. Planned comparisons ($\alpha = .002$) for maximum grip aperture.

Comparison	40 mm targets	50 mm targets	60 mm targets
OL – OLH	$t_{(15)} = 1.367$; p = .192	$t_{(15)} = 0.680$; p = .507	$t_{(15)} = 0.097$; p = .924
CL – OL	$t_{(15)} = 0.624$; p = .542	$t_{(15)} = 0.818$; p = .426	$t_{(15)} = 0.897$; p = .384
CL – OLH	$t_{(15)} = 1.460$; p = .165	$t_{(15)} = 1.335$; p = .202	$t_{(15)} = 0.704$; p = .492
ME - MEH	$t_{(15)} = 0.869$; p = .399	$t_{(15)} = 0.497$; p = .639	$t_{(15)} = 0.230$; p = .821
CL – ME	$t_{(15)} = 6.083$; p < .001	$t_{(15)} = 3.778$; p = .002	$t_{(15)} = 1.988$; p = .065
CL – MEH	$t_{(15)} = 5.529$; p < .001	$t_{(15)} = 3.700$; p = .002	$t_{(15)} = 1.959$; p = .069
OL – ME	$t_{(15)} = 5.981$; p < .001	$t_{(15)} = 3.927$; p = .001	$t_{(15)} = 2.253$; p = .040
OL – MEH	$t_{(15)} = 5.354$; p < .001	$t_{(15)} = 3.785$; p = .002	$t_{(15)} = 2.610$; p = .020

Figures 7.1 and 7.2 also show that maximum grip aperture was scaled according to the target size in all conditions. Planned comparisons confirmed that grip aperture significantly increased from the 40 mm to the 50 mm targets and from the 50 mm to the 60 mm targets in all five conditions (for all comparisons, p < .001).

7.3.2. Further Comparisons for the Grasping tasks

For the three grasping conditions, six additional kinematic variables were further analysed with a series of 3 × 3 repeated measures ANOVA with Task (CL/OL/OLHF) and Size (40/50/60 mm) as factors.

7.3.2.1. Percent Time to Maximum Grip Aperture

The analysis of percent time to maximum grip aperture revealed a significant main effect of Size ($F_{(2, 30)} = 4.862$, p = .015) but a non-significant main effect of Task ($F_{(2, 30)} = 0.942$, p = .401) and a non-significant interaction ($F_{(4, 60)} = 0.580$, p = .678). The group means are shown in Table 7.3 and Figure 7.2. It can be clearly seen that maximum grip aperture occurred within the expected range, between 70% and 80% of movement execution (Jeannerod, 1984), in all conditions.

Table 7.3. Mean percent time to maximum grip aperture (%) for each stimulus size in each condition. Standard errors are in brackets. HF = haptic feedback.

	40 mm	50 mm	60 mm	Mean (s.e.)
Closed Loop	70.10 (2.42)	71.22 (1.36)	74.01 (1.62)	71.78 (1.59)
Open Loop	71.94 (2.01)	72.92 (1.64)	74.40 (1.71)	73.09 (1.68)
Open Loop with HF	73.64 (1.63)	73.40 (1.76)	74.89 (1.16)	73.98 (1.37)
Mean (s.e.)	71.90 (1.64)	72.51 (1.31)	74.43 (0.96)	

The effect of Size was further explored with repeated measures t-tests. These revealed that whereas maximum grip aperture occurred at very similar times for the 40 and 50 mm targets ($t_{(15)}$ = 0.811, p = .430), the significant comparison between the 50 and 60 mm targets ($t_{(15)}$ = 2.772, p = .014) suggest that apertures occurred later for the larger targets.

7.3.2.2. Maximum Wrist Velocity

Similar results were obtained for maximum wrist velocity. The analysis of this variable revealed a significant main effect of Size ($F_{(2, 30)}$ = 30.100, p < .001) but a non-significant main effect of Task ($F_{(2, 30)}$ = 2.514, p = .098) and a non-significant interaction ($F_{(4, 60)}$ = 2.123, p = .089). The group means are shown in Table 7.4 and Figure 7.2.

In agreement with the finding that hand velocity is inversely related to task difficulty (e.g., lower velocities are used for tasks with smaller targets; Castiello, 1996), further analysis revealed that wrist velocity significantly increased with target size ($t_{(15)}$ = 3.833, p = .002 and $t_{(15)}$ = 3.903, p = .001 for 40-50 mm and 50-60 mm comparisons, respectively).

Table 7.4. Mean maximum wrist velocity (mm sec^{-1}) for each stimulus size in each condition. Standard errors are in brackets. HF = haptic feedback.

	40 mm	50 mm	60 mm	Mean (s.e.)
Closed Loop	495.86 (15.57)	508.32 (15.89)	526.54 (15.13)	510.24 (15.22)
Open Loop	473.80 (19.00)	485.05 (20.91)	489.07 (21.14)	482.64 (20.23)
Open Loop with HF	474.67 (17.97)	485.65 (18.64)	491.98 (17.41)	484.10 (17.87)
Mean (s.e.)	481.44 (15.60)	493.01 (16.51)	502.53 (16.11)	

7.3.2.3. Percent Time to Maximum Wrist Velocity

Percent time to maximum wrist velocity revealed non-significant main effects of Task ($F_{(2, 30)}$ = 0.471, p = .629) and Size ($F_{(1.44, 21.67)}$ = 0.031, p = .969) and a non-significant interaction ($F_{(4, 60)}$ = 1.315, p = .275). The group means are shown in Table 7.5 and Figure 7.2.

It should be noted that maximum wrist velocity occurred proportionally earlier than maximum grip aperture (see Table 7.3) for all grasp conditions. This indicates that the typical coupling between the transport and grasp components reported in previous studies (e.g., Jeannerod, 1981) was maintained in all tasks.

Table 7.5. Mean percent time to maximum wrist velocity (%) for each stimulus size in each condition. Standard errors are in brackets. HF = haptic feedback.

	40 mm	50 mm	60 mm	Mean (s.e.)
Closed Loop	40.52 (1.06)	40.18 (0.98)	40.36 (1.21)	40.35 (1.04)
Open Loop	41.50 (1.33)	40.59 (1.44)	41.46 (1.47)	41.18 (1.36)
Open Loop with HF	40.67 (1.26)	41.64 (1.24)	40.83 (1.14)	41.05 (1.14)
Mean (s.e.)	40.90 (1.09)	40.80 (1.03)	40.88 (1.13)	

7.3.2.4. Maximum Wrist Displacement

The analysis of maximum wrist displacement revealed a significant main effects of Task ($F_{(2, 30)}$ = 13.676, p < .001) and Size ($F_{(2, 30)}$ = 63.884, p < .001) but a non-significant

interaction ($F_{(4, 60)}$ = 0.472, p = .756). The group means are illustrated in Table 7.6 and Figure 7.2.

Table 7.6. Mean maximum wrist displacement (mm) for each stimulus size in each condition. Standard errors are in brackets. HF = haptic feedback.

	40 mm	50 mm	60 mm	Mean (s.e.)
Closed Loop	201.30 (2.39)	209.10 (3.69)	212.88 (3.55)	207.76 (3.12)
Open Loop	194.24 (2.11)	200.27 (1.81)	204.88 (2.43)	199.80 (2.03)
Open Loop with HF	195.58 (2.65)	201.03 (3.18)	205.70 (3.22)	200.77 (2.91)
Mean (s.e.)	197.04 (2.20)	203.47 (2.72)	207.82 (2.87)	

Planned comparisons further revealed that wrist displacement significantly increased as a function of target size ($t_{(15)}$ = 6.090, p < .001 and $t_{(15)}$ = 5.971, p < .001 for the 40-50 mm and 50-60 mm comparisons, respectively). A significant difference was also found in the comparisons between the closed loop condition and the two open loop grasping tasks ($t_{(15)}$ = 4.486, p < .001 and $t_{(15)}$ = 5.593, p < .001 for OL and OLHF, respectively). However, the comparison of interest between the two open loop conditions was not significant ($t_{(15)}$ = 0.516, p = .613).

7.3.2.5. Maximum Wrist Height

Similarly, the analysis of maximum wrist height revealed a significant main effects of Size ($F_{(2, 30)}$ = 14.446, p < .001) but a non-significant main effect of Task ($F_{(1.43, 21.38)}$ = 0.821, p = .416) and a non-significant interaction ($F_{(4, 60)}$ = 0.934, p = .451). The group means are illustrated in Table 7.7 and Figure 7.2.

Table 7.7. Mean maximum wrist height (mm) for each stimulus size in each condition. Standard errors are in brackets. HF = haptic feedback.

	40 mm	**50 mm**	**60 mm**	**Mean (s.e.)**
Closed Loop	223.33 (2.88)	223.95 (2.97)	224.64 (3.03)	223.97 (2.93)
Open Loop	218.69 (2.91)	221.51 (3.39)	221.65 (3.26)	220.61 (3.13)
Open Loop with HF	220.68 (3.25)	222.22 (3.40)	223.80 (3.65)	222.23 (3.40)
Mean (s.e.)	220.90 (2.69)	222.56 (2.76)	223.36 (2.90)	

The effect of Size was further examined with planned comparisons which revealed that wrist height significantly increased from the 40 mm to the 50 mm targets ($t_{(15)} = 4.071$, p = .001). This suggests that a greater displacement on the vertical axis occurred for the larger targets. A similar trend was observed for the 50-60 mm comparison, however this difference did not reach significance ($t_{(15)} = 1.900$, p = .077).

7.3.2.6. Movement Duration

Similar results were obtained for movement duration as neither the main effects of Task ($F_{(2, 30)} = 0.245$, p = .784), Size ($F_{(2, 30)} = 0.189$, p = .828) nor the interaction ($F_{(2.67, 39.98)} = 0.461$, p = .689) were significant. The group means are illustrated in Table 7.8 and Figure 7.2.

Table 7.8. Mean movement duration (msec) for each stimulus size in each condition. Standard errors are in brackets. HF = haptic feedback.

	40 mm	**50 mm**	**60 mm**	**Mean (s.e.)**
Closed Loop	766 (13.40)	777 (16.83)	765 (16.78)	769 (14.01)
Open Loop	782 (20.38)	779 (24.98)	781 (24.04)	780 (22.77)
Open Loop with HF	763 (15.88)	767 (19.36)	767 (18.23)	766 (17.04)
Mean (s.e.)	770 (11.63)	774 (14.68)	771 (14.24)	

Experiment 7 – The Effect of Haptic Feedback
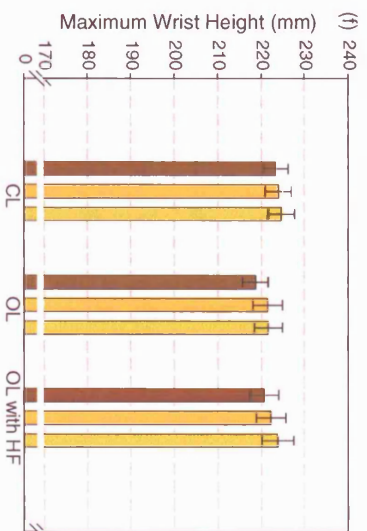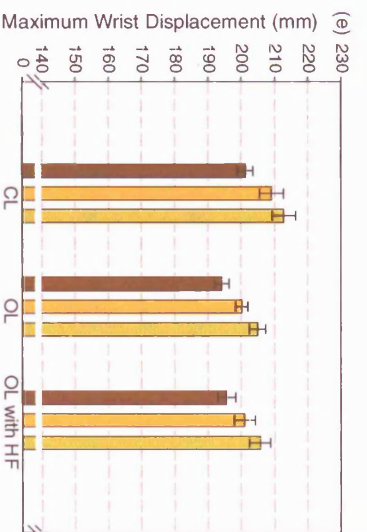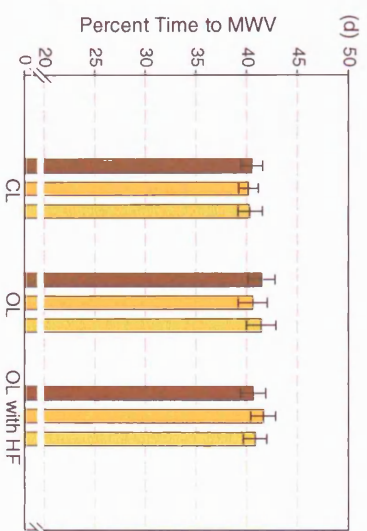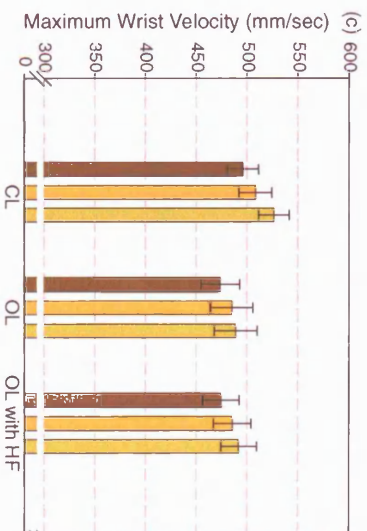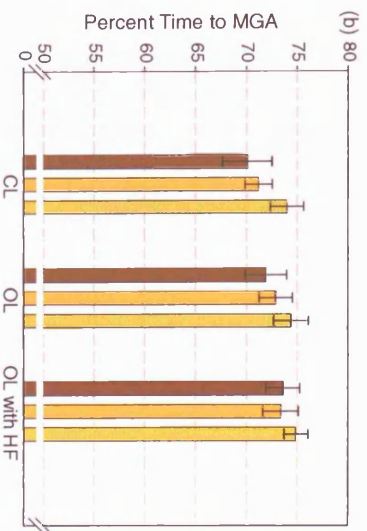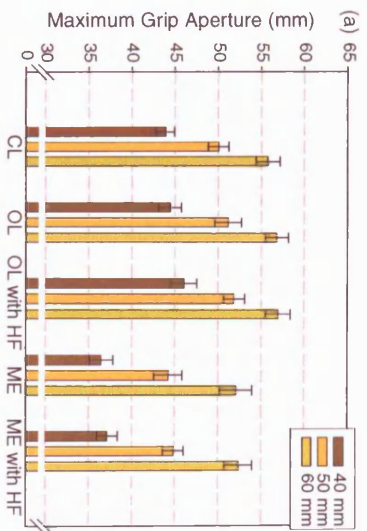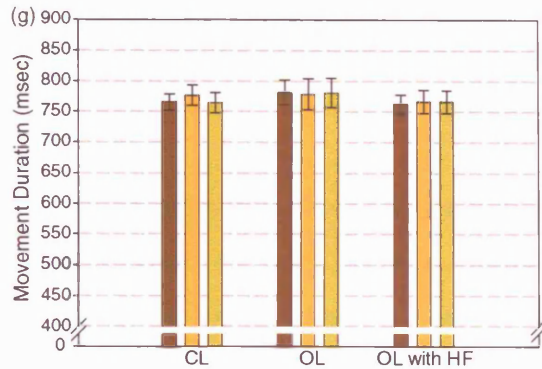
Figure 7.2. Means and standard errors (error bars) for: (a) maximum grip aperture (MGA), (b) percent time to maximum grip aperture, (c) maximum wrist velocity (MWV), (d) percent time to maximum wrist velocity, (e) maximum wrist displacement, (f) maximum wrist height and (g) movement duration.

7.4. Discussion

The first aim of this study was to examine whether adding regular haptic information to a manual estimation task affected hand aperture. The analysis of maximum grip aperture did not reveal a significant difference between manual estimations performed with and without grasping the target after each trial clearly suggesting that the addition of haptic feedback to this task did not have an effect.

These conclusions are further strengthened by the similar pattern of results that was observed when the two manual estimation tasks were compared with closed loop grasping. Although the difference between manual estimation and grasping was significant for the 40 and 50 mm targets but not for the 60 mm targets, the same pattern of results was found for the two estimation tasks. Similar results were obtained when the estimation tasks were compared with open loop grasping. The finding that these comparisons were not significant for the 60 mm targets is in agreement with previous reports that the size-scaling function for manual estimation has a steeper slope than the scaling function for grasping (Westwood & Goodale, 2003). Under these conditions, the

apertures from the two tasks would be expected to convergence at larger targets. Finally, the above conclusions are also strengthened by the finding that hand aperture in both manual estimation tasks similarly increased as a function of target size.

Taken together, the above results strongly suggest that similar processes underpinned the responses in both manual estimation tasks and, by implication, that haptic information is not taken into account for the calibration of hand aperture in manual estimation. They also rule out the possibility that differences in hand aperture between manual estimation and grasping reported in studies that did not control for haptic feedback are due to a discrepancy in this sensory modality. Thus, the methodological implications of these findings are that the version of the manual estimation task that is largely used, that is, manual estimation not followed by grasping, can be used as it is, without having to introduce regular haptic feedback after each trial as implemented by some authors (Ganel & Goodale, 2003; Haffenden & Goodale, 2000, Haffenden Schiff & Goodale, 2001; Hu, & Goodale, 2000; Hu, Goodale & Eagleson, 1999).

With regard to the ongoing debate raised by the discrepant results from the interference studies, the present findings are in agreement with Gentilucci et al. (1998) who also did not find a significant effect of haptic information on manual estimation. By contrast, these results are in disagreement with Westwood and Goodale's (2003) findings that a haptic illusion had an effect on manual estimation. Due to major methodological differences between this study and the interference studies any comparison should be made with caution. Nevertheless, the present results lend some support for Gentilucci et al.'s (1998) account.

The second aim of the study was to examine the possibility that reduced haptic feedback resulting from misreaching the target in open loop procedures where grasping is not followed by lifting could have some effect on the kinematic parameters. In the present study, no significant differences between the two versions of the open loop procedure, with and without regular haptic feedback, were observed in any of the kinematic

variables that were examined. The introduction of regular haptic feedback did not change maximum grip aperture, the time at which it occurred or overall movement duration. The transport component was also unaffected as both maximum wrist velocity and the time at which it occurred remained unvaried. Hand trajectory was not directly examined, however the non-significant differences observed for maximum wrist displacement and maximum wrist height indirectly suggest that this variable remained stable across the two open loop conditions. The only significant effect of Task that was found in this study was for maximum wrist displacement, however, further analysis revealed that this was due to a greater displacement of the wrist in the closed loop task, relative to both open loop procedures.

In addition to the above comparisons, both types of open loop procedures produced typical kinematic profiles. More specifically, they both had a biphasic aperture curve and the expected coupling between the transport and grasp components, with maximum wrist velocity occurring before maximum grip aperture (e.g., Jeannerod, 1981). Moreover, for both open loop conditions maximum grip aperture increased as a function of target size and occurred within the expected range, between 70% and 80% of movement execution (Jeannerod, 1984). Similarly, in agreement with previous reports (e.g., Castiello, 1996), wrist velocity was inversely proportional to task precision as that faster movements were used for larger targets in both conditions. Taken together, the results from this study suggest that adding regular haptic information after each open loop grasp did not affect any of the kinematic parameters that were examined.

These results could be interpreted in two ways. First, they could suggest that the non-significant difference between the two open loop tasks demonstrate that haptic information is not used by the visuomotor system. This account would be in agreement with Westwood and Goodale's (2003) conclusions, but in disagreement with previous reports that haptic feedback affects several of the kinematic parameters of both the transport and grasp components of prehension (Gentilucci et al., 1997; Gentilucci et al., 1998). More importantly however, this account would be largely based on the

assumption that participants misreached the target in open loop grasping and that, as a result, haptic feedback, if not controlled for, was reduced under these conditions. Given that at present it is not possible to ascertain whether misreaches occurred in the open loop task, it would be unwarranted to draw these conclusions from the present results.

A second, more plausible, interpretation would be that no significant differences between the two open loop conditions were found because participants did not misreach the target in open loop and therefore a very similar amount of haptic information was present in the two conditions. Importantly, according to this account the present results could not be used to inform the debate on whether the visuomotor system uses haptic information, as these findings could have been equally obtained if this was the case, but also if it wasn't. Nonetheless, this second account is preferred to the first because it does not need to be in disagreement with Gentilucci and colleagues' findings (Gentilucci et al., 1997; Gentilucci et al., 1998) and it does not rest on an unsupported assumption. In any case, the methodological implications of the present results are clear and the same for both interpretations as they equally suggest that the two open loop procedures currently used in this area of research, grasp-and-lift and grasp only, are equivalent and result in very similar kinematic profiles.

8. Experiment 8 – The Perception of Kanizsa Figures in Rats: Part 1

8.1. Introduction

This last part of the thesis seeks to provide some preliminary evidence for the occurrence of ventral visual processing in rats and to explore some of the properties of the ventral representations in this species.

At present, the question whether the dorsal-ventral cortical parcellation of function has homologues in species other than primates has been surprisingly addressed only sporadically and by a small number of authors (for review see Ellard, 1998, 2002; Kolb, Burhmann, McDonald and Sutherland, 1994). With the exception of these few authors, the general approach to rat vision so far has been to either assume that ventral visual processing occurs in this species (e.g., Murray & Bussey, 1999) or to dismiss the existence of separate cortical visual systems on the bases that rats have afoveate vision and a poorly differentiated visual cortex (Livingstone & Hubel, 1988). As pointed out earlier, there is now evidence that the visual cortex of this species is more heterogeneous than initially proposed (Montero, 1993) therefore opening the possibility that this species might have relatively well developed cortical visual systems.

As discussed in Chapter 1, there is little doubt that vision has evolved to detect stimuli and their motion in the environment for the purpose of prey catching and predator avoidance (Goodale, 1996; Horridge, 1987). In organisms that can move, vision extended to mediating their actions in relation to these two basic functions (Horridge, 1987). In agreement with this view, it has been proposed that vision in rats subserves primarily, and directly, visually guided action (Goodale & Carey, 1990; Goodale,

1996). Findings that both the superior colliculus and visual cortex in rodents mediate head orientation and locomotion towards targets (Goodale & Carey, 1990; Goodale & Milner, 1982) support this view.

Nevertheless, it is often assumed that rodents have visual processing comparable to those subserving object recognition in humans and primates (Kolb, 1990; Murray & Bussey, 1999). This assumption is primarily based on the finding that rat can be trained to solve visual discrimination tasks with a variety of stimuli and that lesions to primary visual cortex impair this ability (see Goodale & Milner, 1982 for review). As pointed out in Goodale's (1996) review of Carey et al.'s (1990) findings (see Chapter 1), the gerbils' ability to solve visual discriminations is likely to be mediated by more cognitive cortical structures that could involve some representation of the world:

> While the representation of objects in the gerbil's brain may not be as complex as that found in higher primates, some sort of representation must be available to the cognitive mechanisms that mediate learning and memory .... In summary, there is evidence for the emergence of representational networks in the gerbil's visual system, networks that access motor outputs via the cognitive machinery mediating the learning of associations between objects and events in the world. (p. 395).

In the two-visual-systems framework, ventral but not dorsal representations are made available to other cognitive networks such as those mediating learning and memory. Thus, the finding that rodents can learn stimulus-response and stimulus-stimulus associations, as in matching-to-sample (MTS) or nonmatching-to-sample (NMTS) tasks (Aggleton, 1985; Nakagawa, 1993), suggest that these animals might possess representational networks comparable to those present in the ventral visual system of humans in primates. A similar argument has been proposed by Milner (1998) who suggested that findings that in monkeys the inferotemporal cortex but not the posterior parietal cortex has reciprocal connection with the amygdala, a structure known to

mediate visual stimulus-reward associations, suggests that the ventral visual system might process visual information for associative learning tasks.

As reviewed in Chapter 1, among the few notable exceptions that looked at cortical visual processing in rodents are studies that have clearly demonstrated that the cortical visual system in these animals can mediate visuomotor behaviour (Goodale & Carey, 1990; Goodale & Milner, 1982). Thus, there seems to be a cortical system comparable to some extent to the dorsal visual system found in humans and primates in this species. Other authors have concentrated on finding evidence of homologues of both cortical systems (Kolb, 1990; Kolb et al., 1994). For instance, Kolb et al. (1994) found that rats with lesions to the posterior parietal cortex (PPC) were impaired at visual spatial tasks such as the Morris water maze or the landmark task but were able to solve visual discriminations in a NMTS or delayed-NMTS (DNMTS) task. The converse pattern was observed in rats with posterior temporal cortex (PTC) lesions. Similar findings have been reviewed by Kolb (1990). Kolb et al. (1994) concluded that these findings provide evidence of an occipitoparietal and an occipitotemporal visual system in rats that mediate the visuospatial guidance of behaviour and object recognition, respectively.

Kolb et al.'s (1994) conclusions are however not universally accepted. For instance, Ellard (1998, 2002) has recently questioned whether there could be a homologue of the ventral visual system in rats, pointing out that in humans and primates this system would involve awareness and viewpoint-independent object recognition. Particularly, Ellard (2002) proposed that it could be possible that if a homologue of the occipitotemporal system exists in rodents, it might still mediate movement and navigation. Thus, at present it is still a matter of debate whether rats posses visual processing comparable to those known to occur in the ventral visual system of humans and primates.

In the present experiment, we started by asking whether rats perceive visual illusions. As seen in Chapter 1, a large body of evidence suggests that whereas the human ventral

visual system is affected by visual illusions the dorsal system is resilient to these effects (e.g., Kwok & Braddick, 2002). An implication of these findings is that the signal giving rise perceptually to the illusion is not processed in the dorsal visual system. Thus, evidence that rats perceive visual illusions would support the claim that visual processing comparable to those found in the human ventral system occurs in this species. Moreover, this evidence would suggest that in rats as in humans, the representational/perceptual system processes visual illusions.

To our knowledge, at the time of this experiment only one previous study explored the perception of visual illusions in rats. Ducharme, Delorme and Boulard (1967) tested whether rats perceive the Oppel-Kundt illusion which refers to the increase in length perceived when a horizontal line (or empty space) is hatched by smaller vertical lines, relative to the same line un-hatched. Albino rats were trained to choose the longest of two horizontal lines, 60 and 30 mm long (ratio 2:1), that were either both hatched or un-hatched. During two sets of test trials the ratio of the length of the two lines was changed to 1.4:1 and 1.3:1 and only one of the two test lines was hatched in any test pair. Ducharme et al. (1967) used Lashley's (1912) finding that rats cannot easily discriminate between size differences of a ratio of, or less than, 4:3 and suggested that if the discrimination was not solved with the test pair with the shortest line hatched, but solved when the longer line was hatched, it would have been evidence that the illusion was perceived. According to this criterion, three subjects overestimated the hatched line and one underestimated it and Ducharme et al. (1967) concluded that these rats perceived the illusion. Although these results provide some preliminary evidence that rats might perceive visual illusions, due to the heterogeneous direction of the effect and the small sample size they are not conclusive.

The present experiment tested whether rats perceive Kanizsa illusory figures. This illusion was chosen for two reasons. First, Kanizsa contours have been extensively studied in other species and there is evidence that monkeys (Peterhans & von der Heydt, 1989) cats (Bravo, Blake & Morrison, 1988), owls (Nieder & Wagner, 1999) and

honeybees (van Hateren, Srinivasan & Wait, 1990) behaviourally respond to these stimuli (for reviews, see Nieder, 2002; Ohzawa, 1999). Thus, it would be reasonable to suggest that rats, a species phylogenetically between monkeys and honeybees, should also perceive Kanizsa illusions. Second, end-stopped neurons have been found in layers 2, 3 and 5 of the rat primary visual cortex (Montero, 1981) suggesting that this species might have the neural structures suggested as a substrate for illusory contour perception (see Chapter 2 for review).

In a transfer procedure eight rats were trained to discriminate between a luminance-defined square and triangle and once at criterion performance, they were tested with Kanizsa corresponding figures. It was predicted that if rats can perceive this illusion, they should be able to solve the discrimination task with the Kanizsa stimuli. A control condition (Rotated) examined the possibility that the discrimination task with the Kanizsa stimuli was solved using a coarse analysis of the spatial layout of the inducers. As the Kanizsa square and triangle differed both in the number of inducers that they contained (4 versus 3), and in their spatial layout, the rats could have used these differences, and their similarity with the number and spatial distribution of corners in the training stimuli, to solve the discrimination. The Rotated condition controlled for both possibilities, as these stimuli were identical to the Kanizsa stimuli, but had a different rotation of the inducers that should have disrupted the formation of the illusory figures. Thus, chance level performance in the Rotated condition would provide evidence that the number and location of inducers was not used to solve the discrimination.

A second control condition (Crosses) controlled for the possibility that subjects used the luminance-defined contours specified by the inducers to solve the task in the Kanizsa trials. The luminance-defined contours inside the inducers were present in both the training and Kanizsa stimuli, making it possible for the rats to use cues from any of these local features to solve the discrimination in the Kanizsa trials. To control for this possibility, we used stimuli that have been previously used for this purpose (Davis &

Driver, 1998) as they have the same amount and distribution of luminance-defined contours inside the inducers as the Kanizsa stimuli, but without generating an illusory figure. Chance level performance in the Crosses condition would therefore be evidence that subjects did not solve the task using these luminance-defined contours.

8.2. Method

8.2.1. Subjects

Eight experimentally naïve male Hooded Lister rats, approximately three months old at the beginning of the experiment, were kept on a 12:12 light cycle and at 90% of their free-feeding weight. All animals had free access to water in the home cages and were housed in groups of four.

8.2.2. Apparatus and Materials

8.2.2.1. Stimuli

All stimuli were created with a vector-based drawing programme and printed on 9 x 9 cm lightweight cards that were covered with a plastic film.

Luminance-defined condition: The luminance-defined stimuli (Figure 8.1a) were used for training and consisted of a 57 x 57 mm white square, and a white isosceles triangle, 57 mm wide and 57 mm high, positioned with its vertex at the bottom. Both shapes were presented on a black background and centred on the cards.

Kanizsa condition: Unless otherwise specified, the white Kanizsa stimuli (Figure 8.1b) were obtained by positioning black inducers on a white background as described in Experiment 1. To match the training stimuli, the illusory shapes had to appear to be white. Thus, black inducers on a white background were used for these stimuli. The

diameter of the notched circles was 33 mm. For the Kanizsa square, the linear distance between the centres of any pair of inducers was 57 mm. The linear distance between the centre of the two inducers at the base and sides of the triangle was 57.0 mm and 63.7 mm, respectively. Thus, the support ratio for the Kanizsa square and triangle was 0.58 and 0.54, respectively. The Kanizsa figures were centred on the cards.

Rotated condition: The Rotated stimuli were identical to the Kanizsa stimuli except that the inducers were rotated as shown in Figure 8.1c in order to disrupt the formation of the Kanizsa figures.

Crosses condition: Unless otherwise specified, the Crosses stimuli (Figure 8.1d) were obtained by forming imaginary shapes with black crosses as described in Experiment 1. The arms of the crosses were 30 mm long and 7.5 mm wide and were positioned so that they resulted in the same support ratio as used in the Kanizsa condition (0.58 and 0.54 for the square and triangle, respectively). The linear distance between the internal edges of the crosses matched the dimensions of the training stimuli. The imaginary square and triangle in these stimuli were centred on the paper cards.
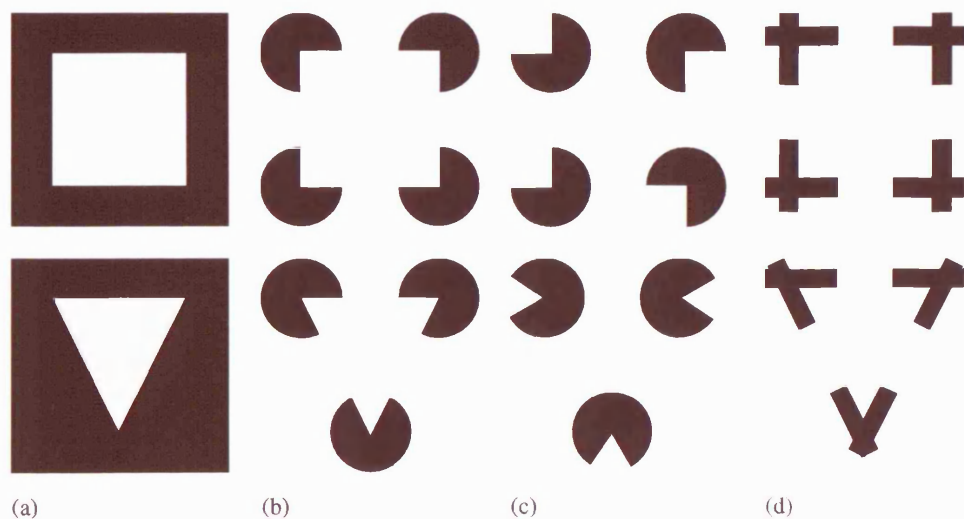

(a)   (b)   (c)   (d)

Figure 8.1. The luminance-defined figures used in training (a) and the Kanizsa (b), Rotated (c) and Crosses (d) stimuli used in the transfer tests.

8.2.2.2. Apparatus and Set-up

The simultaneous discrimination apparatus (Figure 8.2) consisted of three interconnected areas: Namely a Start, a Discrimination and a Goal area, this latter subdivided into two adjacent chambers. The door leading from the Start to the Discrimination area was manually operated through an external lever whereas the doors to the Goal chambers consisted of 9 x 9 cm swing doors. The entire apparatus was made of black Perspex except for the lids which were in transparent Perspex. The internal wall separating the two goal chambers extended 7.5 cm into the Discrimination area and two magazines trays were positioned on the external walls of each goal chamber.

Rats have a tendency to be nocturnal and very bright light can be deleterious for them (Wolfensohn & Lloyd, 1998). In an attempt to create more ecologically valid conditions for this species, the study was conducted in a darkened room in which the only source of light was provided by two halogen spotlights (20W low voltage dichroic lamps, beam angle of 12°) that illuminated the two stimuli directly. The lights were mounted on a track system and positioned 50 cm from the floor of the apparatus and 40 cm from the corresponding swing door, that is, at a linear distance of 64 cm from the stimuli. Moreover, the amount of light entering the discrimination area was reduced by covering one third of the lid with a black plastic sheet, as shown in Figure 8.2.
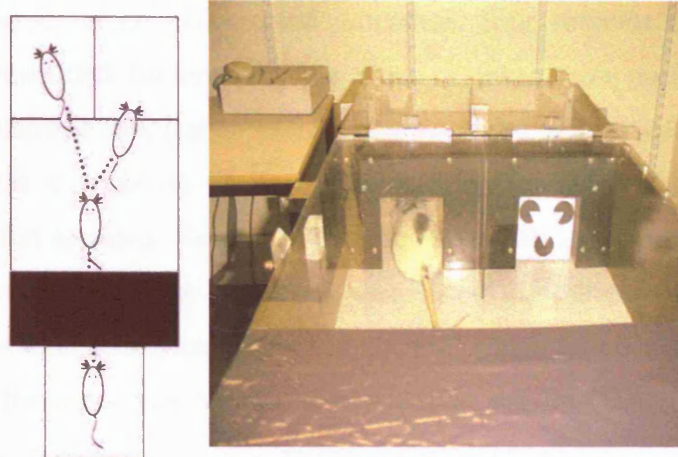
Figure 8.2. Left: Schematic representation of the dual-discrimination apparatus (top view, in scale). The black area indicates the proportion of the lid covered. Right: A subject entering the goal chamber with the Kanizsa square.

8.2.3. Procedure

Pretraining: Rats were first acclimatized to the apparatus through a gradual procedure. On day 1, 2 and 3 they were placed in the maze in groups of four and food pellets (45mg Noyes) were scattered on the floor of the whole maze, the discrimination area and goal chambers or the goal chambers alone, respectively. From day 4 to day 11, individual subjects were place in the maze and the task was to go from the Start area to one of the Goal chambers to retrieve 4 food pellets placed in the magazine trays. Once the subject ate the pellets from one magazine tray it was manually removed and placed in the Start area to start a new trial. The doors leading to the goal chambers were taped open on day 4 and the aperture was gradually decreased until fully closed doors were used on day 11. Thus, at the end of day 11, all rats were able to enter the goal chambers by pushing the swing door.

Training: On day 12, training with the stimuli began. The luminance-defined square and triangle were placed on the swing doors leading to the Goal chambers. Sessions consisted of 26 trials and correct responses were rewarded with 4 food pellets that were

manually delivered. In an uncorrected procedure, four subjects (rats 1 to 4, Group Square) were rewarded for entering the Goal chamber with the square on its door whereas the remaining four (rats 5 to 8, Group Triangle) were rewarded for entering the chamber with the triangle on its door. The left/right position of the two shapes was randomised within sessions. Sequences were created with a random sequence generator with the constraint that pairs or triplets were used (i.e., 2 or 3 trials with stimulus presented on the same side), except for the last trial which was not required to be part of a pair/triplet. This procedure was used in order to counterbalance the test stimuli as described below. A representative sequence, including test trials, is shown in Figure 8.3.

Several studies suggest that rats rely more heavily on visual stimuli presented in the lower hemifield (Lashley, 1938; Sutherland, 1961; Simpson & Gaffan, 1999), therefore, in order to maximise these subjects' ability to discriminate between the training shapes, the triangle was presented with the vertex down. Olfactory cues were removed by regularly cleaning the paper cards, the swing doors and the apparatus. Moreover, the paper stimuli were also regularly replaced with new sets.

<p style="text-align:center">R R L L R R R L L L L R R L L R R L L L L R R L L L L R R</p>

Figure 8.3. A representative test sequence: Test trials are in red. R and L indicate presentation on the left and right doors, respectively.

Testing: As soon as a rat reached a criterion of two successive sessions at, or greater than, 80% accuracy it was exposed to a series of five transfer tests. Each test comprised five sessions, during which the rat received exposure to one of the sets of test stimuli shown in Figure 8.1. In three of the five transfer tests, the rats were exposed to Kanizsa figures, and in the remaining two test sets they were exposed to each of the two control conditions. The control test sessions were interspersed with the Kanizsa test sessions. Specifically, all animals were first exposed to a set of Kanizsa tests, then to the Rotated condition followed by another Kanizsa set and finally to the Crosses condition also

followed by a Kanizsa set. Each set was separated by 2 sessions of the original training in order to maintain the discrimination and, within set, sessions were separated by at least 1 training session with performance on maintenance trials at or above 80% correct. Due to poor health one subject (rat 4) was not tested with the last Kanizsa set.

Each test session comprised 4 nonreinforced trials with 22 reinforced maintenance trials with the original training stimuli. Test trials could not occur in the first five trials in the sequence, were separated by at least one training trial, occurred once at the beginning and once either in the second or in the third trial of a pair/triplet and their side of presentation was randomised within session. A representative test sequence is shown in Figure 8.3.

8.3. Results and Discussion

Correct discrimination performance was calculated by dividing the total number of correct responses by the total number of test trials for each rat for each test condition and was expressed as a percentage. A total number of 20 test trials were collected for each test stimulus except for rat 3 who refused to respond to 5 of the Crosses trials. Accordingly, the mean value for this subject in this condition was calculated out of 15 trials. Test results were not included in the analysis if performance in the maintenance trials of the test session fell below 60% correct. One session was discarded due to this criterion.

Figure 8.4 shows the individual and group learning curves. The mean number of trials (plus standard deviation) that the rats needed to learn the task was 854±157. An independent-samples t-test revealed that there was no statistical difference between the number of trials needed to learn the square versus triangle discrimination ($t_{(6)}$ = 1.833, p = .117).
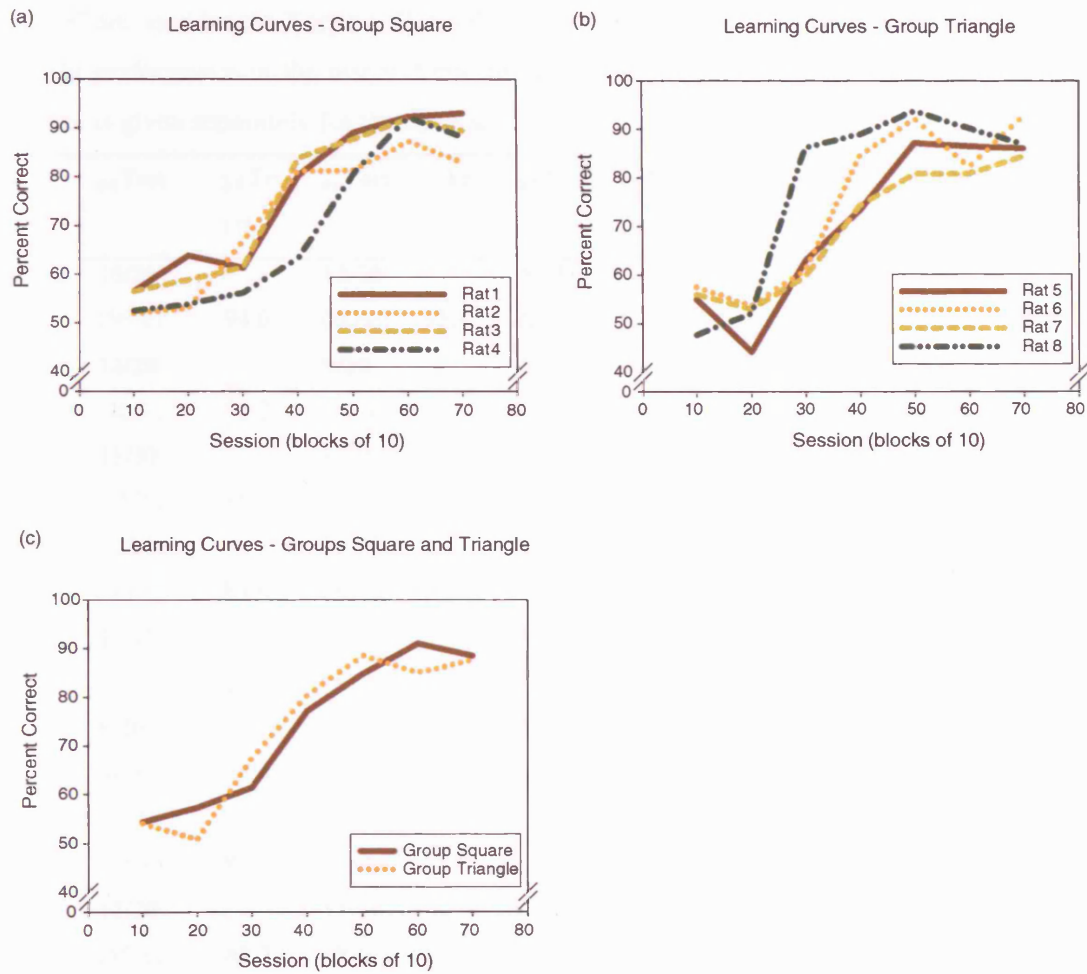
Figure 8.4. Learning curves for individual rats in (a) Group Square and (b) Group Triangle. (c) Mean performance in the two groups.

The mean correct performance for individual rats in the test and training trials of the five transfer tests is shown in Table 8.1.

Table 8.1. Individual discrimination performance during test sessions. The prefixes "k", "ro" and "cr" are used for the Kanizsa, Rotated and Crosses conditions, respectively. "Test" and "Tr" indicate performance in the test and maintenance trials, respectively. The data for the Kanizsa sessions is given separately for the three sets.

	k1Test (%)	k1Tr	roTest (%)	roTr	k2Test (%)	k2Tr	crTest (%)	crTr	k3Test (%)	k3Tr (%)
Rat 1	10/20 (50%)	94.6	12/20 (60%)	95.4	12/20 (60%)	93.4	12/20 (60%)	96.6	12/20 (60%)	97.2
Rat 2	14/20 (70%)	90.2	9/20 (45%)	81	11/20 (55%)	85.4	10/20 (50%)	90	10/20 (50%)	87.2
Rat 3	11/20 (55%)	86.2	9/20 (45%)	93.4	10/20 (50%)	95.2	7/15 (47%)	95.8	8/20 (40%)	98.2
Rat 4	12/20 (60%)	83.6	10/20 (50%)	92.4	12/20 (60%)	88	9/20 (45%)	89	N/A	N/A
Rat 5	11/20 (55%)	80.2	11/20 (55%)	84.4	11/20 (55%)	94.4	12/20 (60%)	93.4	11/20 (55%)	98
Rat 6	9/20 (45%)	76.4	6/20 (30%)	91.8	17/20 (85%)	91.8	12/20 (60%)	93.2	9/20 (45%)	94.4
Rat 7	11/20 (55%)	87.2	11/20 (55%)	81.8	11/20 (55%)	96.2	8/20 (40%)	95.8	11/20 (55%)	92.6
Rat 8	11/20 (55%)	87.2	11/20 (55%)	91.6	11/20 (55%)	94.6	12/20 (60%)	95.8	12/20 (60%)	89.8

The mean performance in the three transfer sets is shown in Figure 8.5. Mean performance during the combined three Kanizsa test conditions was tested with a two-tailed repeated measures t-test conducted against 50% which confirmed that this discrimination was statistically significantly above chance level ($t_{(7)} = 4.681$, p = .002). These results clearly suggest that rats trained to discriminate between a luminance-defined square and triangle were subsequently able to solve a discrimination task with corresponding illusory figures suggesting that these latter were used to solve the discrimination in the Kanizsa condition.

The overall correct level of performance observed with the Kanizsa stimuli was reduced relative to the training phase. However, some generalisation decrement would be expected to follow stimulus changes from training to test. Moreover, performance during these trials was never reinforced introducing the possibility that cues present in the Kanizsa stimuli could have acted as discriminative stimuli for the absence of reinforcement and therefore reduced performance accuracy during test trials. Nevertheless, discrimination performance was above chance level with the Kanizsa stimuli.
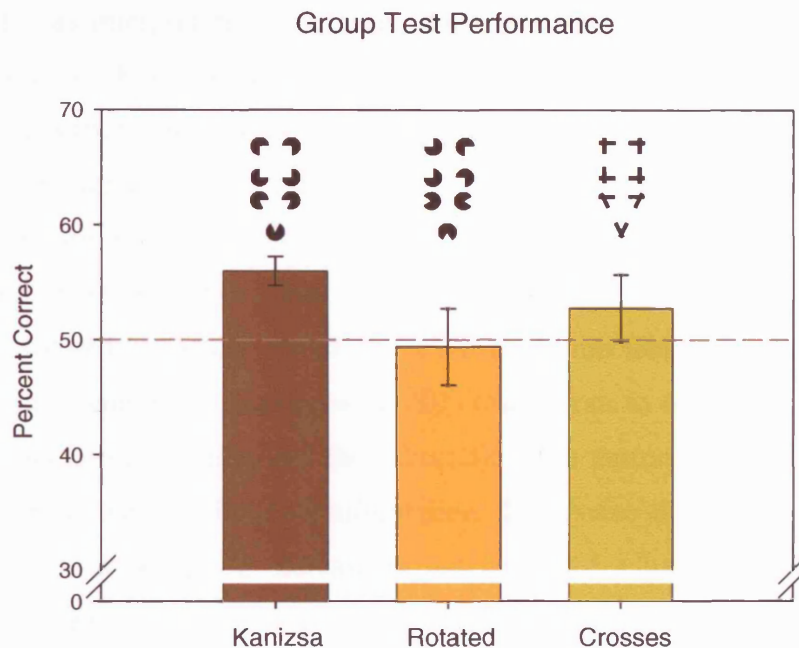
Figure 8.5. Group percent correct performance in the three test conditions.

Performance in the Rotated condition was tested with a two-tailed repeated-measures t-test conducted against 50% correct which confirmed that these results did not significantly differ from chance ($t_{(7)} = -0.188$, p = .857). These results clearly rule out the possibility that the number or location of the inducers were used to solve the discrimination with the Kanizsa stimuli. Similarly, a two-tailed repeated measures t-test conducted on the final transfer test with the Crosses stimuli revealed that performance

did not differ from chance in this condition ($t_{(7)}$ = 0.946, p = .376). These results clearly rule out the possibility that the discrimination with the Kanizsa stimuli was solved using the luminance-defined contours inside the inducers. These results are also in agreement with previous findings that rats trained to respond to whole triangles do not readily transfer to the contours at the vertices when the rest of the figures is removed (Lashley, 1938).

The most likely explanation that could account for the results is that these rats perceived the Kanizsa figures and were therefore able to solve the discrimination with these illusions. If this interpretation is correct, these findings provide preliminary evidence that rats perceive Kanizsa illusions and are in agreement with previous studies that found that a variety of species, including monkeys, cats, owls and honeybees, can discriminate between Kanizsa figures (for reviews, see Nieder, 2002; Ohzawa, 1999). These results are also in agreement with Ducharme et al.'s (1967) findings that rats perceive the Oppel-Kundt illusion. Furthermore, they are in agreement with a second study that explored the perception of visual illusion in rats that was published during the running of this experiment. Nakagawa (2002) trained rats to discriminate between long and short bars and then measured their discrimination performance with bars of equal length but presented in a Ponzo configuration. The Ponzo illusion (see Chapter 1 for figure) refers to a perceived increase in the length of a bar when this is presented between two converging lines and closer to their intersection point, relative to when the same bar is presented either in the middle or closer to the diverging side of the two flanker lines. In agreement with human reports, Nakagawa (2002) found these illusion effects in two groups of 16 and 24 rats and concluded that these animals could perceive the Ponzo illusion.

With regard to the original question addressed in this experiment, given that the human dorsal visual system is known to be resilient to visual illusions, it would be reasonable to conclude that these visual illusions were not processed in the dedicated visuomotor systems that have been well documented in this species (Goodale & Carey, 1990;

Goodale & Milner, 1982). Thus, these results provide empirical support for the claim that rats have visual processing of a representational/perceptual nature, in addition to those mediating visually guided action. Moreover, these findings suggest that the representational/perceptual networks in this species process visual illusions. These results are in agreement with the known properties of the ventral visual system in humans, thus, this study provides preliminary evidence that, at least with respect to processing visual illusions, the representational/perceptual networks in rats and humans are to some extent comparable.

9. Experiment 9 – The Perception of Kanizsa Figures in Rats: Part 2

9.1. Introduction

In the counterbalancing procedure used in Experiment 8, all rats were exposed to two of the three Kanizsa conditions before being exposed to the control trials. Test trials were never reinforced, therefore, there was the possibility that cues specific to the control conditions could have come to serve as discriminative stimuli for the absence of reinforcement to a greater extent than cues specific to the Kanizsa trials. This could have reduced performance accuracy in the control relative to the Kanizsa trials. Although averaging performance in the three Kanizsa conditions, including the third Kanizsa set, controlled for this possibility to some extent, it was decided to replicate Experiment 8 with a more conventional counterbalancing procedure.

The present experiment is a direct replication of Experiment 8 except that stimulus presentation was counterbalanced according to a Latin square arrangement. Moreover, given that the Crosses stimuli could also control for the possibility that the number or spatial arrangement of the inducers in the Kanizsa stimuli could have served as discriminative cues, the Rotated condition was not included. Finally, a new control condition (Contrast) with the figure/ground contrast polarity reversed relative to the training set tested the general ability of these animals to transfer to luminance-defined stimuli.

9.2. Method

9.2.1. Subjects

Eight experimentally naïve male Hooded Lister rats, approximately 22 months old at the beginning of the experiment, were kept on a 12:12 light cycle and at 90% of their free-feeding weight. All animals had free access to water in the home cages and were housed in groups of four.

9.2.2. Apparatus and Materials

Except where otherwise stated, the apparatus and materials were as in Experiment 8.

9.2.2.1. Stimuli

Luminance-defined condition: The luminance-defined stimuli (Figure 9.1a) were used for training and consisted of a 56 x 56 mm white square, and a white equilateral triangle, 56 mm wide and 48.47 mm high, positioned with its vertex at the bottom. Both shapes were presented on a black background and centred on the cards.

Kanizsa condition: The Kanizsa stimuli (Figure 9.1b) were obtained as described in Experiment 8 except that the inducers had a diameter of 34 mm and that for both Kanizsa figures the linear distance between the centres of any pair of inducers was 56 mm. Thus, the support ratio was 0.61 for both Kanizsa figures. The linear distance between the internal edges of the crosses matched the dimensions of the training stimuli.

Crosses condition: The Crosses stimuli (Figure 9.1c) were obtained as described in Experiment 8 except that the arms of the crosses were 34 mm long and 8 mm wide. The

linear distance between the internal edges of the crosses matched the dimensions of the training stimuli.

Contrast condition: The Contrast stimuli (Figure 9.1d) were obtained by reversing the figure/ground contrast polarity of the training stimuli so that black shapes were now presented on a white background.

(a)   (b)   (c)   (d)
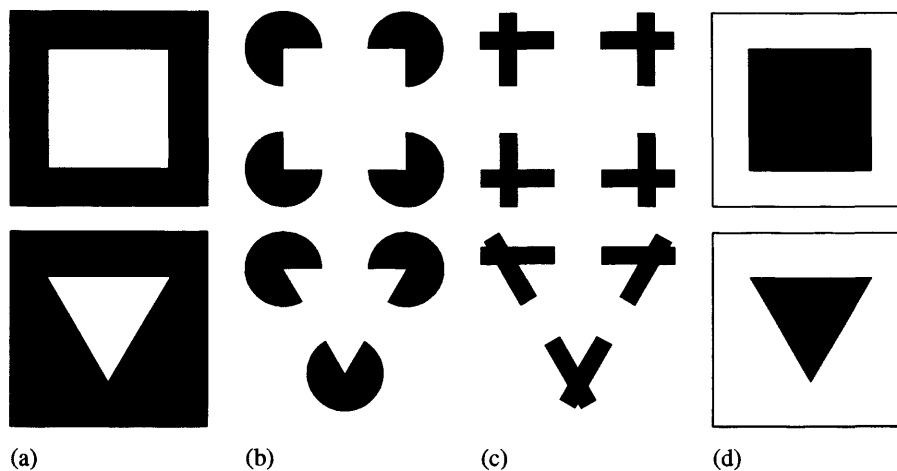
Figure 9.1. The luminance-defined figures used in training (a) and the Kanizsa (b), Crosses (c) and Contrast (d) stimuli used in the transfer tests.

9.2.2.2. Apparatus and Set-up

The apparatus and set-up were as described for Experiment 8.

9.2.3. Procedure

Pretraining: Pretraining was as described for Experiment 8.

Training: Training was also as described for Experiment 8, except for the following changes. All animals were trained with the luminance-defined stimuli for 46 sessions of 16 trials each. Sequences were created with a random sequence generator with the only

constraint that stimuli could not be presented for more than three consecutive times on the same side. From session 47, side of presentation was randomised according to a Gellerman sequence (Gellerman, 1933). This latter controlled for potential inflation of correct performance due to position habits or alternation. A Gellerman protocol requires sessions that are multiples of 10. Accordingly, session duration was increased to 20 trials from this point. A modified correction procedure was used in which the same stimulus configuration was repeated for a maximum of 5 times after an incorrect response. On session 22, rat 6 was discarded from the study as at this point it refused to push the swing doors to enter the Goal chambers.

Testing: As soon as a subject reached a criterion of five successive sessions at, or greater than, 80% accuracy it was exposed to three sets of transfer stimuli: The Kanizsa (A), Crosses (B) and Contrast (C) stimuli. A Latin Square counterbalancing procedure was used that yielded ABC, BCA and CAB combinations and animals were randomly assigned to them within group (Square or Triangle). One combination was used twice in Group Square. Each transfer set consisted of 5 sessions each containing 4 test trials. In test sessions, the 4 nonreinforced test trials were interspersed with 16 maintenance training trials. Test trials were interspersed with maintenance trials as described for Experiment 8 except that they could also occur outside a pair/triplet. For left/right randomisation purposes, these latter were considered equivalent to trials occurring at the beginning of a pair/triplet.

Test sessions were run successively, unless performance in maintenance trials fell below 70% correct in which case training resumed until a performance of at least 80% correct was achieved over three consecutive sessions. No correction procedure was used for test trials. However, in order to shorten the testing phase and to reduce the number of non-responses to the test stimuli, in test instances where the Goal chamber was not entered directly, rats were allowed to make only three turns between the two doors after which they were removed from the Discrimination area and returned to the Start box for a new attempt with the same stimulus configuration. Similarly, rats were removed from the

Discrimination area and returned to the Start box if they remained for more than 1 minute without approaching the Goal chambers. This procedure was repeated for a maximum of 5 times and if a Goal chamber was not entered at this point the test trial was recorded as a "non-response". As shown in Table 9.1, this procedure resulted in only one non-responded test trial (rat 2).

9.3. Results and Discussion

Correct discrimination performance was measured as in Experiment 8 except that correction trials were included in the calculation of the correct responses. Twenty test trials were collected for each of the three test stimuli. Rat 2 refused to respond to one Crosses trials and, accordingly, for this subject the mean value in this condition was calculated out of 19 trials.

Figure 9.2 shows the individual and group learning curves. The mean number of trials (plus standard deviation) that the rats needed to learn the task was 899±94 (162±94 if the first 46 sessions are excluded). A two-tailed independent-samples t-test revealed that there was no statistical difference between the number of trials needed to learn the square versus triangle discrimination ($t_{(5)} = -1.843$, p = .205).
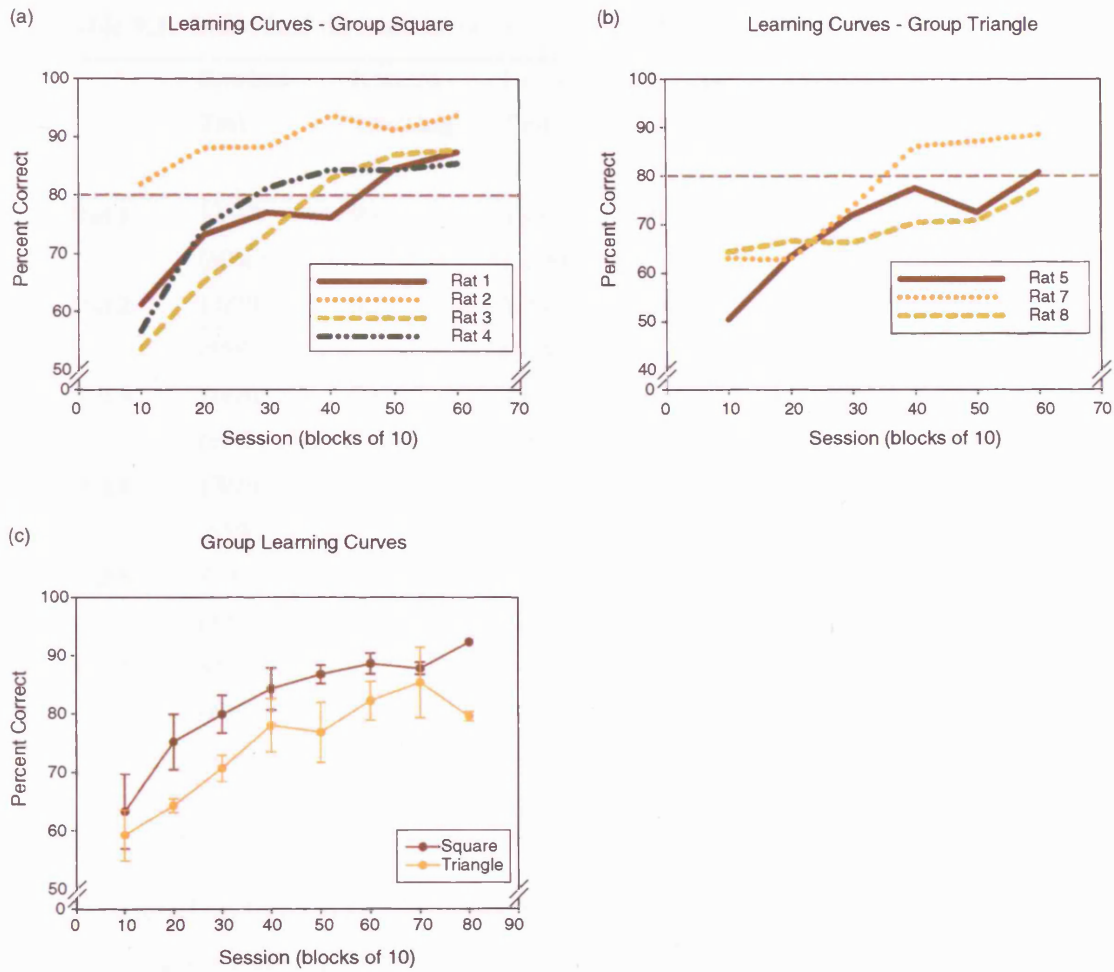
Figure 9.2. Learning curves for individual rats in (a) Group Square and (b) Group Triangle. (c) Mean performance in the two groups.

The mean correct performance for individual rats in the test and training trials of the transfer sets are shown in Table 9.1.

Table 9.1. Individual discrimination performance during test sessions.

	Kanizsa Test	Kanizsa Training (%)	Crosses Test	Crosses Training (%)	Contrast Test	Contrast Training (%)
Rat 1	12/20 (60%)	90	13/20 (65%)	91	5/20 (25%)	87
Rat 2	11/20 (55%)	92	7/19 (37%)	97	12/20 (60%)	87
Rat 3	10/20 (50%)	79	11/20 (55%)	87	7/20 (35%)	90
Rat 4	13/20 (65%)	84	13/20 (65%)	84	8/20 (40%)	89
Rat 5	8/20 (40%)	77	10/20 (50%)	80	9/20 (45%)	79
Rat 7	8/20 (40%)	90	9/20 (45%)	96	5/20 (25%)	93
Rat 8	9/20 (45%)	92	9/20 (45%)	71	9/20 (45%)	91

The individual and group performance in the three transfer sets is shown in Figure 9.3. These data were tested with a series of two-tailed one-sample t-tests conducted against 50% which confirmed that discrimination performance was statistically at chance level in the Kanizsa ($t_{(6)} = 0.194$, p = .853), Crosses ($t_{(6)} = 0.428$, p = .684) and Contrast ($t_{(6)} = -2.287$, p = .062) conditions, although in this latter a preference for the negative shape approaching significance was observed.
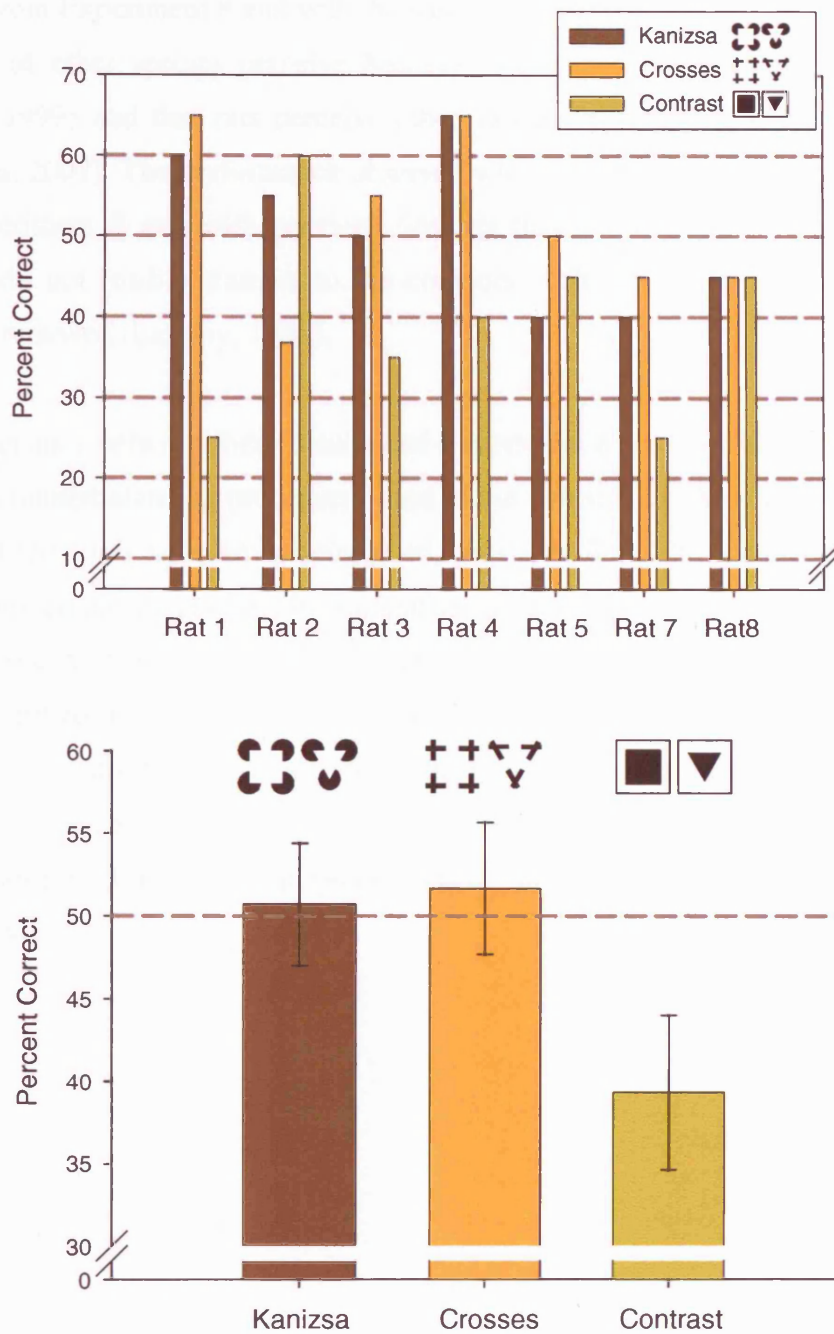
Figure 9.3. Individual (left) and group (right) correct performance in the three test conditions.

The above results clearly suggest that these rats were not able to solve the discrimination with the Kanizsa stimuli. These results are in disagreement with the

findings from Experiment 8 and with the studies reviewed in Chapter 8 that suggest that a variety of other species perceive Kanizsa figures (for reviews, see Nieder, 2002; Ohzawa, 1999) and that rats perceive other visual illusions (Ducharme et al., 1967; Nakagawa, 2002). The performance observed with the Crosses stimuli are in agreement with Experiment 8 and with previous findings that rats trained to respond to whole triangles do not readily transfer to the contours at the vertices when the rest of the figures is removed (Lashley, 1938).

The discrepancy between these results and Experiment 8 could be accounted for by the different counterbalancing procedures used in the two studies. As stated in Section 9.1, given that test trials were never reinforced, cues specific to the test stimuli could have increasingly come to serve as discriminative stimuli for the absence of reinforcement and therefore reduced performance accuracy in test trials. Although this possibility was partly controlled in Experiment 8, it is possible that the Latin Square arrangement used in this study controlled more fully for extinction resulting from order of presentation. However, this account is unlikely. Although not formally tested, visual inspection of the data did not reveal any trends between accuracy in test trials and order of presentation (Figure 9.4).
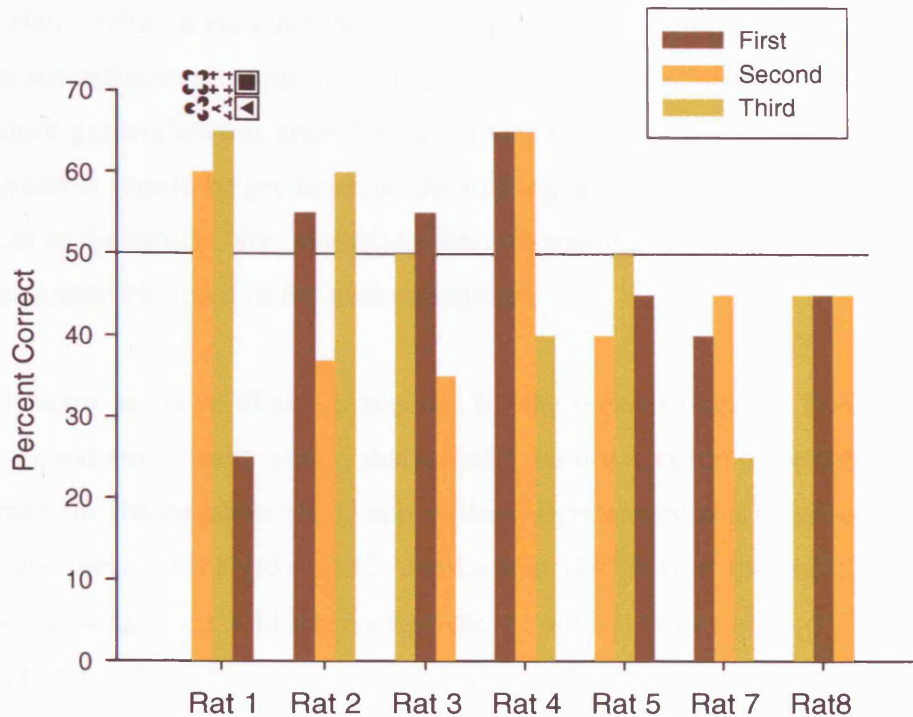
Figure 9.4. The accuracy in test trials is colour coded as a function of order of presentation. The legend indicates which condition was presented first, second and third to individual animals. For all rats, the first, second and third columns represent the data from the Kanizsa, Crosses and Contrast trials, respectively.

There were other procedural differences in overtraining, in the use of a correction procedure and in the support ratio between this experiment and Experiment 8 that should be considered. The latter two are unlikely to have affected the results, in particular, given that larger support ratios, as used in the present study, result in stronger effects of the illusion in humans (Shipley & Kellman, 1992). However, overtraining could have affected generalization. In this study, a longer training procedure and a more stringent correct criterion performance were adopted as it was assumed that repeated exposure to the training stimuli would have strengthened the acquired distinctiveness of the two shapes by strengthening the attention that the animals paid to the relevant features. Although such an effect has been reported by some authors, overtraining has also been reported to have opposite effects on generalization (for review see Hall,

1991). Hall (1991) argues that the effect of prolonged exposure depends on whether the features strengthened by overtraining are present or not in the test stimuli. In the former case, more generalization should follow extended training whereas in the latter, less generalization would be predicted as the training and test stimuli would be more likely to appear as dissimilar. The possibility that overtraining decreased generalization in this study is further explored in the next experiment.

A third factor is more likely to account for the present findings. Performance in the Contrast condition clearly shows that transfer did not occur to these stimuli, although a preference for the negative shape approaching significance was observed. These results are in agreement with Fields (1932) and Lashley (1938) who also failed to find transfer from white shapes on a black background to stimuli with reversed contrast polarity. Although a number of factors could account for this performance, failure to transfer to the Contrast stimuli could be the direct result of introducing a large bright region with the white background. Given that rats are nocturnal animals, it would not be implausible to suggest that, for this species, approaching large bright areas could be an aversive task, in particular in a transfer test. Thus, these results can not conclusively rule out the possibility that the chance level performance observed in the Kanizsa and Crosses conditions was partly due to the presence of the large bright background, which was necessarily also present in those stimuli. The effect of reversing the contrast polarity of the background was further explored in the next experiment.

Finally, in this study the two training shapes differed in area and luminance (3136 mm^2 and 1357 mm^2 for the square and triangle, respectively), thus, there was the possibility that subjects used this low-level cue to solve the discrimination. Specifically, it is possible that rats trained to choose the square learned to choose the brightest stimulus whereas those trained to choose the triangle learned to choose the least bright. This account is somewhat supported by the performance in the Contrast trials as a reversal of the luminance relationship between the two figures was followed by a preference for the negative shape that was approaching significance. Importantly, if rats used this response

strategy they would have not transferred to the Kanizsa figure as the brightness relationship was also reversed in those stimuli. The next experiment controlled for this possibility.

10. Experiment 10a – The Perception of Kanizsa Figures in Rats: Part 3

10.1. Introduction

This preliminary experiment aims to establish whether the poor transfer to Kanizsa figures observed in Experiment 9 could be the result of overtraining or the use of a luminance-based response strategy. This possibility was explored by replicating Experiment 9 without overtraining the animals and with equiluminant shapes as the training stimuli. It was predicted that if overtraining steepened the generalization gradient in Experiment 9, good transfer to the Kanizsa stimuli should be observed in this study. Similarly, good discrimination performance should be observed if in Experiment 9 subjects used a luminance differences to solve the discrimination. In addition, the effect of introducing a large bright region was further assessed by measuring the transfer performance of two animals to stimuli with reversed contrast polarity (Contrast stimuli). Finally, the general ability of these rats to transfer to novel luminance-defined stimuli was assessed with outline versions of the training stimuli as good transfer performance has been reported for these stimuli under comparable conditions (Lashley, 1938).

In order to reduce the laborious and time consuming training procedure necessary with the manual discrimination box used in Experiments 8 and 9, in this experiment we used an automated touchscreen apparatus to present stimuli on a monitor at one end of a rectangular box, and rewarded the animals for correct choices at the other end. A further advantage of this apparatus is that it makes if possible to investigate visual discrimination in rats with more traditional psychophysical techniques, with faster and better controlled presentation rates and larger stimulus sets. In addition, this apparatus

fully controls for the potentially confounding effects of olfactory and haptic cues that could be associated with paper stimulus cards.

This experiment includes a large series of transfer tests that, for clarity, are separated into three parts (a, b and c) and presented over this chapter and Chapters 11 and 12. A summary of the rationale of the entire experiment, including parts b and c, is shown in Figure 10.1.
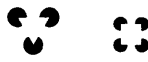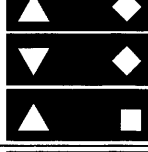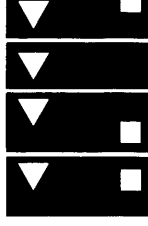
Experiment 10		
Phase	**Purpose**	**Stimuli**
Training	To establish a basic shap e discrimination	Square vs triangle (with shapes on black background)
Probe 1	To test transfer of respondin g to the same shapes defined by illusory contours	Kanizsa shapes
Probe 2	To test transfer of respondin g to luminance edges inside inducers	Crosses shapes
Probe 3	To test transfer of respondin g to altered but luminance-defined (non-illusory) stimuli	Outline shapes / Contrast shapes
Probe 4	To test transfer of respondin g to the training stimuli at altered orientations	Rotated shapes (subset) (bottom but not top shapes elicited reversal of shape preference in one subject)
Probe 5	To test the possibility that rat s used lower hemifield features	Reflected-diamond / Triangle-diamon d / Reflected-square
Probe 6	To test the possibility that rat s used lower hemifield luminance	Displaced-square / Luminance / Displaced-triangle / Displaced-both

Figure 10.1. Summary of the stimuli and rationale of the experiment. For Probe 3, the point at which performance for one rat switched from a preference for the positive shape to a preference for the negative shape is shown.

10.2. Method

10.2.1. Subjects

Five experimentally naïve male Hooded Lister rats, weighing between 510 and 540 grams at the beginning of the experiment, were kept on a 12:12 light cycle and between 85% and 90% of their free-feeding weight. All animals had free access to water in the home cages and were housed in groups of two and three.

10.2.2. Apparatus and Materials

10.2.2.1. Stimuli

Luminance-defined condition: The training stimuli (Figure 10.1) consisted of a white (83 cd/m^2) square and equilateral triangle with the vertex down. The two shapes had equal area and equal local luminance and were presented on a black (0.03 cd/m^2) background. During the automated training procedure, the size of the stimuli systematically decreased from stage 1 to 3 (Figure 10.3). The dimensions of the square and triangle for the three stages were, respectively, 85 × 85 and 119 × 129 mm, 65 × 65 and 86 × 99 mm, 45 × 45 and 59 × 68 mm (height × width).

Kanizsa condition: The Kanizsa stimuli (Figure 10.1) were obtained as described in Experiment 8 except that the inducers had a diameter of 22.5 and 34 mm for the square and triangle, respectively, to maintain the same support ratio (0.5) for both shapes. The linear distance between the centres of any pair of inducers matched the dimensions of the training stimuli.

Crosses condition: The Crosses stimuli (Figure 10.1) were obtained as described in Experiment 8 except that the arms of the crosses were 34 x 7 mm and 22.5 x 5 mm for the triangle and square, respectively, and were positioned to maintain the support ratio

as in the Kanizsa stimuli. The linear distance between the internal edges of the crosses matched the dimensions of the training stimuli.

Contrast condition: The Contrast stimuli (Figure 10.1) were obtained by reversing the figure/ground contrast polarity of the training stimuli so that black shapes were now presented on a white background.

Outline condition: The Outline stimuli (Figure 10.1) were obtained by superimposing (with centres aligned) a black 31 × 31 mm square and a 41 × 47 mm equilateral triangle to the square and triangle of the final training stimuli, respectively. These dimensions ensured that the area of the white region was the same for the two outline shapes.

10.2.2.2. Apparatus and Set-up

The apparatus (Figure 10.2) maintained the dimensions of the discrimination areas of a standard manual discrimination box. It consisted of a rectangular box (height = 30.5 cm; length = 89 cm; width = 45 cm; all internal dimensions) made of aluminium with an openable lid in transparent Perspex and a removable floor. The internal parts in aluminium were painted matt black. One end of the box consisted of a 17" CRT flat screen VGA monitor (Mitsubishi, Diamond Pro 710; resolution 800 × 600) covered with a pressure sensitive glass panel (17" IntelliTouch, Elo TouchSystems) positioned so that the screen started 1 cm above the floor. A standard magazine tray with a hinged Perspex door was positioned 1 cm above the floor along the vertical midline on the opposite side of the box and was attached to a standard pellet dispenser (Campden Instruments Ltd.). A 24 V 2.8 W M.E.S. single filament lamp was placed approximately at the centre of the lid (house light) and a speaker was positioned adjacent to it. Another similar lamp was positioned inside the magazine tray and a third 10 cm above the magazine tray. This latter was not used in any of the procedures reported here. The touchscreen, lights, speaker and pellet dispenser were connected to a standard PC via custom made hardware and were operated with custom made software.

Figure 10.2. The touchscreen apparatus used in Experiments 10 and 11, shown with the stimuli and central partition as used in the latter study. The magazine tray for the delivery of food pellets is located on the side opposite to the screen and is not shown in the picture. Rats had to nose poke the responsive area of the screen corresponding to the positive shape and then collect the reward delivered at the opposite side of the apparatus.

10.2.3. Procedure

A summary of the experimental procedure is shown in Figure 10.3.

Pretraining: Rats were first habituated to the apparatus, with the door of the magazine tray removed. On day 1, all rats from individual cages were left for 20 minutes in the apparatus that had food pellets scattered on the floor and in the magazine tray. On day 2, the same procedure was used but now rats were placed individually in the apparatus. This procedure was repeated on day 3 but food pellets were left only in the magazine tray. Manual shaping started on day 4.

Three of the animals (rats 1, 2 and 3) were assigned the square as the positive shape and two rats (rats 4 and 5) the triangle. On day 4 individual rats were presented with the S^+ positioned along the vertical midline and 20 mm from the bottom edge of the screen. The dimensions of the stimuli were the same as those used for stage 1 of the automated

training. To train the animals to nose poke the S^+, one pellet was attached to the touchscreen with a small piece of double sided tape and positioned approximately at the centre of the stimulus. Eating the pellet was followed by a 1 sec 4 KHz tone, stimulus offset and 2 food pellets. Pellets were manually delivered at this point as the magazine tray was without door and automatic delivery would have scattered the pellets on the floor. As soon as the animal ate the pellet in the magazine tray, the stimulus reappeared and another pellet was manually attached to the touchscreen. Tone onset and stimulus onset/offset were manually controlled with a keyboard.

The same procedure was used on days 5 and 6 except that only 1 food pellet was placed in the magazine tray on these days. On day 7 the same procedure was used, except that no food pellet was placed on the screen and nose pokes to any part of the screen during stimulus presentation were rewarded with 1 food pellet manually delivered to the magazine tray. From day 4 to 7, sessions lasted 30 trials. In day 8, the same procedure as day 7 was repeated except that the door of the magazine tray was on, food pellets were delivered automatically and the stimulus remained on the screen until a response was given. This last session lasted for 30 min with a 10 sec ITI. In all the above sessions, illumination was provided by the room light that was kept to a very low setting. Throughout the whole duration of the study background noise was provided by the fan of the PC. The floor of the apparatus and the touchscreen were cleaned between animals.

Training: The automated training consisted of 5 stages during which the size of both stimuli and responsive area on the touchscreen were systematically reduced. Progression from one stage to the next occurred when the animals reached asymptotic performance. In stages 1 to 3, the positive stimulus (S^+) was presented along the vertical midline of the responsive area and 20-mm from the bottom edge of the screen. The responsive area consisted of a square region (side 140, 120 and 100 mm in stage 1,2 and 3, respectively) centred on the screen along the bottom edge. Correct responses (nose pokes to the responsive area) were followed by stimulus offset, a 1-sec 4 KHz tone, the

onset of the magazine light that remained on until the next stimulus presentation and the delivery of one 45-mg food pellet in the magazine tray. Nose pokes outside the responsive area (incorrect responses) were followed by stimulus offset and a 10 sec black-out period. Stimulus offset was triggered by a response (either correct or incorrect), the ITI was 10-sec and sessions lasted for 30 min.

In stage 4, the same stimuli and responsive area as stage 3 were used, but now the S^+ was presented at the lower right corner in half of the trials and at the lower left corners in the remaining half. In this stage subjects learned to give nose pokes to the two stimulus locations that were subsequently used in the actual dual-discrimination task, but without having to discriminate between the two stimuli as only the positive shape was presented. The left and right presentations were pseudorandomly interleaved and the stimulus was always kept 20 mm from both the bottom and left/right edges of the screen. Stage 5 introduced the dual-discrimination task. This was identical to stage 4 except that the S^+ and the S^- were now presented simultaneously at the two lower corners. Additional changes for these last 2 stages were that sessions had 100 trials in stage 4 and 140 trials in stage 5, stimulus presentation was set at 15 sec and the ITI after correct responses was reduced to 5 sec.

After 15 sessions at stage 5, the ITI was further reduced to 3 sec as it was noted that a proportion of the errors was artificially inflated by the long ITI. Specifically, the 5 sec ITI provided sufficient time for the animals to go to the magazine tray, eat the pellet and return to the screen before the presentation of the next stimulus. Once at the blank screen, rats tended to nose poke randomly. This exploratory behaviour artificially inflated the error rate as nose pokes were recorded as an error if they occurred in the region of the S^- in conjunction with stimulus onset. The reduction of the ITI to 3 sec was effective in eliminating this methodological artefact. At this stage of training, in order to decrease the number of trials without responses, stimulus presentation was also increased to 180 sec. During the 5 stages of training, but except for black-out periods, the house light remained switched on and provided the only source of light in the room.

The fan of the PC provided background noise and the floor of the apparatus and touchscreen were cleaned between animals.

| Habituation	Day 1-3		Food scattered on floor and inside magazine tray, which had door removed.
Manual Shaping	Day 4		Pellet attached to touchscreen. When pellet was eaten: tone + 2 pellets in magazine tray. Pellets manually delivered. Sessions of 30 trials. Room light on.
	Day 5 & 6		As above, except that when rat ate pellet on touchscreen, only 1 pellet was manually delivered to magazine tray.
	Day 7		As above, except no pellet on touchscreen. Nose pokes to any part of touchscren, during stimulus presentation, were rewarded.
	Day 8		As above, except: (1) pellets automatically delivered, (2) door of magazine tray on, (3) stimulus on screen until response given, (4) ITI was 10 sec, (5) session 30 min long.
Automated Training	Stage 1		As above, except: (1) magazine light onset after corret responses, (2) in correct responses, that is nose pokes to non-responsive area, followed by 10 sec black-out, (3) room light switched off.
	Stage 2		As above, except that responsive area and stimulus size were reduced.
	Stage 3		As above, except that responsive area and stimulus size were further reduced.
	Stage 4		As above, except: (1) responsive area moved to bottom right and left corners - only S+ was presented in each trial at one of these 2 possible locations, (2) stimulus presented for 15 sec, (3) ITI reduced to 5 sec, (4) session of 100 trials.
	Stage 5		Introduction of dual-discimination task. As above, except that both positive and negative shapes were presented simultaneously in each trial, one at each corner. Session increased to 140 trials.
	Session 15		As above, except that ITI was reduced to 3 sec and stimulus presentation was increased to 180 sec.

Figure 10.3. Summary of the experimental procedure. The third column contains, in scale, illustrations of the touchscreen, stimuli and their location. The grey squares represent the responsive areas on the touchscreen. The dashed lines indicate when shapes could be presented at either at the two bottom corners. The figure illustrates the set-up for rats with the square as the positive shape. For the other rats, a triangle was used in manual shaping and up to Stage 4 of the automated training.

Testing: Testing with the Kanizsa and Crosses conditions began once performance reached asymptote. In test sessions, 10 test trials were interleaved with 130 training trials. Test trials could not occur in the first 5 trials and were separated by between 5 and 9 training trials. Five Kanizsa and 5 Crosses test sessions were presented in an alternate order and the condition to be presented first was randomly assigned to each

animal. With this procedure, rats 1, 3 and 5 started testing with the Kanizsa stimuli whereas rats 2 and 4 started with the Crosses. None of the contingencies described for the training trials were maintained in the test trials, except for stimulus offset and ITI onset.

After testing with the Kanizsa and Crosses conditions, rats 4 and 5 were presented with training sessions until they reached asymptotic performance. After this, they were presented with sequences in which half of the training trials were pseudorandomly interleaved with the Contrast stimuli. Each shape×contrast-polarity combination occurred at each of the left and right response locations with equal probability (25%). This procedure was carried out for 12 sessions for rat 4 but had to be interrupted after 11 sessions for rat 5 as at this point this subject developed an aversion to the door of the magazine tray.

Rats 1, 2 and 3 were tested with the Outline stimuli directly after the Kanizsa and Crosses trials whereas rats 4 and 5 after the Contrast trials. All 5 animals were presented with training sessions and brought to asymptotic performance before testing began. After a number of attempts to re-train rat 5, it was decided to try the procedure with the magazine door taped open. Performance increased immediately to asymptotic level and this modification was therefore adopted for all the subsequent trials with this animal. All subjects were tested with the Outline stimuli for 5 consecutive sessions.

10.3. Results and Discussion

Correct discrimination performance was calculated as described in Experiment 9 except that performance in the "corrected" trials of the correction procedure was not included in this calculation. Figure 10.4 shows the individual learning curves for stage 5 and performance in the maintenance trials of the Kanizsa and Crosses sessions. It can be clearly seen that good discrimination performance was reached by all subjects and maintained during the test phase. The figure also shows that the two rats with the

triangle as the positive shape reached criterion (85% correct over 2 consecutive sessions) in a relative small number of sessions (25 and 18 for rats 4 and 5, respectively). Subjects with the square as the positive shape also learned the discrimination, however rats 1 and 3 reached asymptotic performance at 80% and rat 2 at 70%. These animals also required a higher number of sessions (52, 61 and 49, respectively) indicating perhaps a greater difficulty to use this shape as the positive stimulus. A two-tailed independent-samples t-test revealed that the number of trials to reach asymptotic performance was significantly smaller for the rats with the triangle as the positive shape relative to the other group ($t_{(3)}$ = 6.091, p = .009).
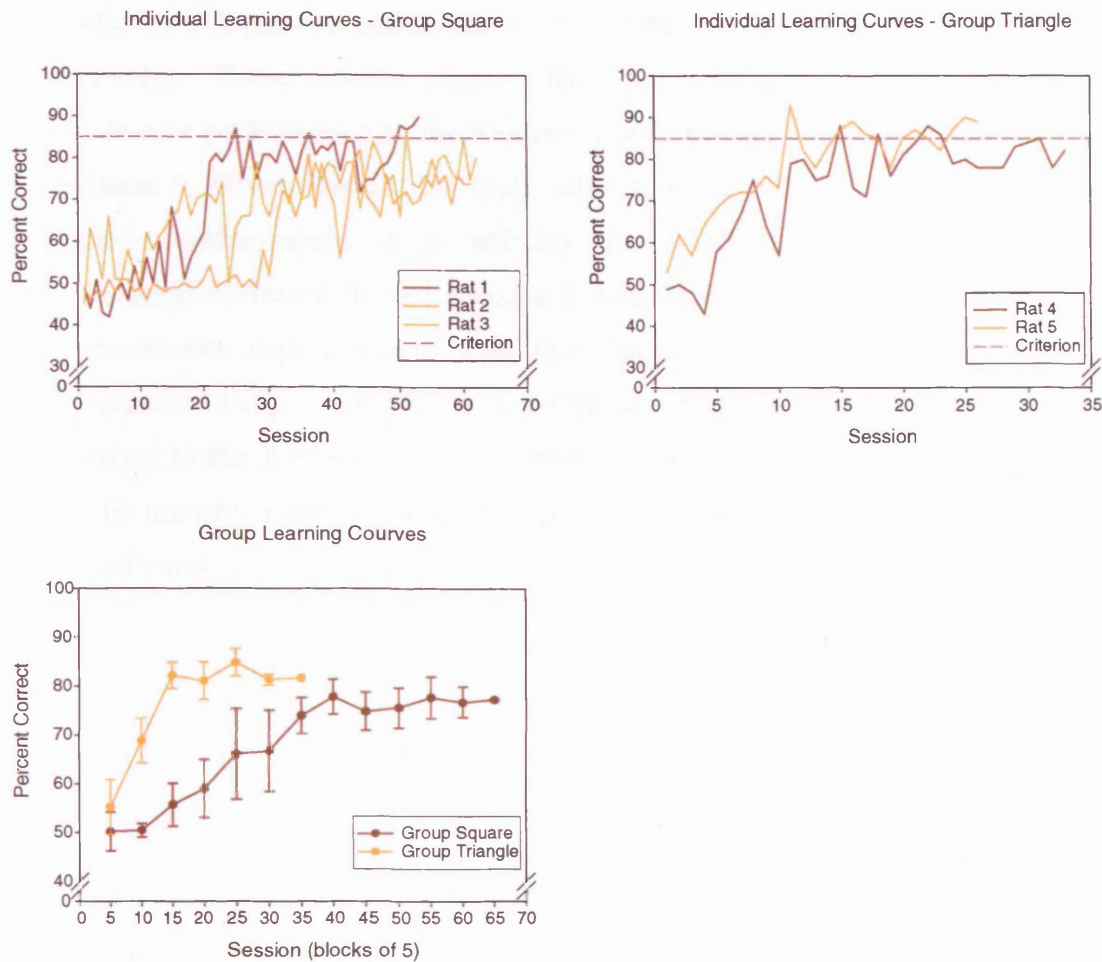
Figure 10.4. Individual and group learning curves for Stage 5 and performance in the maintenance trials of the Kanizsa and Crosses conditions.

A total of 50 test trials were collected for each rat over the five test sessions for each of the two test stimuli. For rats 4 and 5 this number was reduced to 48 and 49 trials for the Crosses and Kanizsa conditions, respectively, as these subjects refused to respond to some of the test stimuli in the first test session. Figure 10.5 shows individual and group test performance in the two test conditions. It can be seen that, performance for all animals was close to chance level with both the Kanizsa and Crosses stimuli, with the exception of rat 1 who seemed to have, if anything, a preference for the negative Kanizsa shape. Two-tailed one-sample t-tests confirmed that performance did not differ

from chance in these two conditions ($t_{(4)}$ = -0.168, p = .875 and $t_{(4)}$ = -1.000, p = .374, respectively). These results suggest that these subjects did not transfer their discriminative performance to the Kanizsa stimuli and are therefore in agreement with Experiment 9. Given that in this study subjects were tested as soon as they reached asymptotic performance, it is unlikely that overtraining can account for the generalization decrement to the Kanizsa stimuli observed in Experiment 9. Moreover, these results also suggest that it is unlikely that in Experiment 9 learning to solve the discrimination using a luminance-based response strategy prevented the rats from transferring to the Kanizsa stimuli. In this study, equiluminant training stimuli did not allow the use of such a response strategy, nevertheless, the rats did not transfer to the Kanizsa figures.
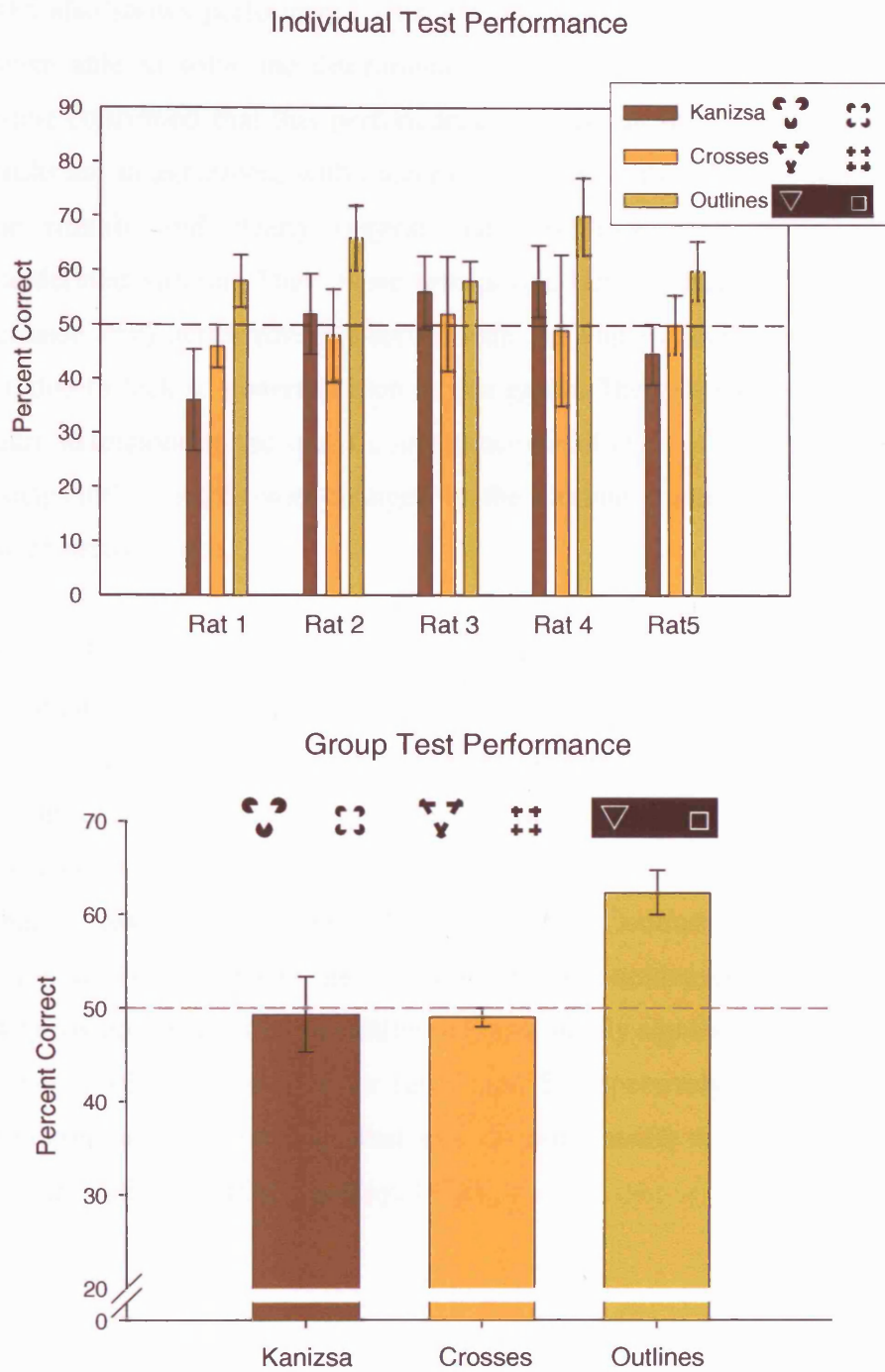
Figure 10.5. Individual and group test performance for the Kanizsa and Crosses conditions. The dashed line marks chance level.

Figure 10.5 also shows performance with the Outline stimuli where it can be seen that all rats were able to solve the discrimination above chance level. A two-tailed one-sample t-test confirmed that this performance was significant ($t_{(4)}$ = 5.167, p = .007). These results are in agreement with Lashley (1938), who also reported positive transfer to outline stimuli, and clearly suggest that these rats could generalize to novel luminance-defined stimuli. Thus, these results rule out to some extent the possibility that the chance level performance observed with the Kanizsa and Crosses stimuli could have been due to lack of generalization in this group. They also suggest that these rats did not learn to respond to the specific luminance distribution of the training stimuli (the "retinal snapshot"), as this was changed in the Outline stimuli without leading to a disruption of performance.

A second possibility explored in this study is that failure to transfer to the Kanizsa and Crosses stimuli could be accounted for by a difficulty to generalize to stimuli with reversed contrast polarity. Figure 10.6 illustrates performance with the training and Contrast stimuli for rats 4 and 5. The difference between the two conditions is substantial and clear. Performance was easily maintained at criterion with the training stimuli but it reverted to chance level with the Contrast stimuli. Notably this performance was observed with the two types of trials interleaved. Two-tailed repeated measures t-tests confirmed that this difference was highly significant ($t_{(11)}$ = 15.383, p < .001 and $t_{(10)}$ = 16.981, p < .001 for rats 4 and 5, respectively). These results are in agreement with previous findings that rats do not transfer to stimuli with reversed contrast polarity (Fields, 1932; Lashley, 1938).
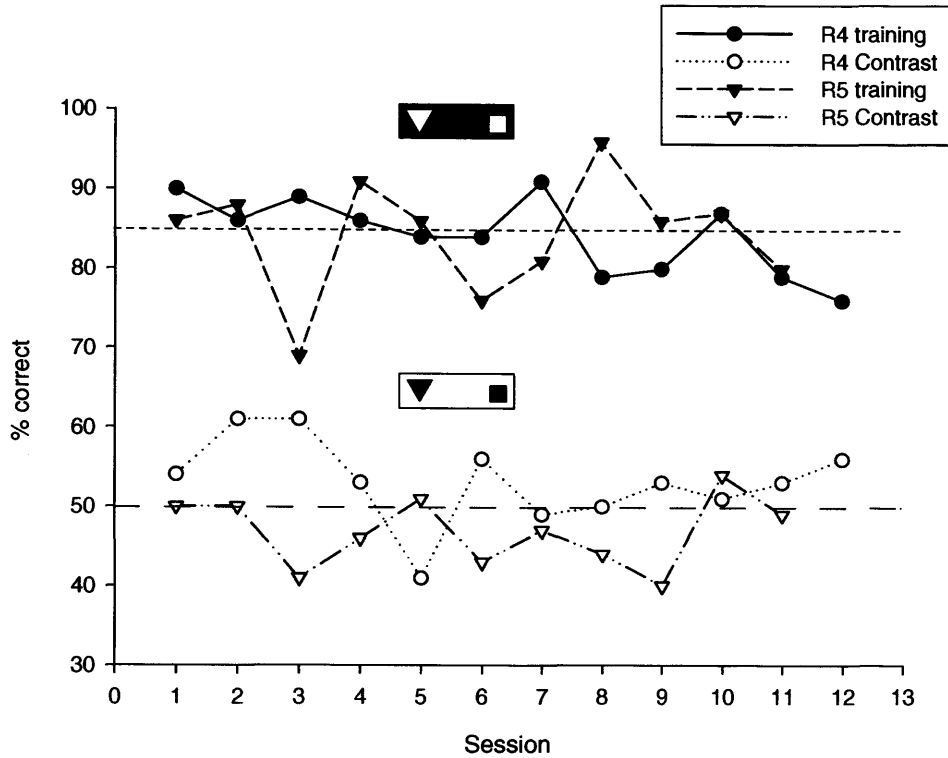
Figure 10.6. Performance in the training and Contrast trials for rats 4 and 5.

Taken together, the present results suggest that although these rats can generalise to novel stimuli, as shown by the Outline results, they seem to be disrupted by the introduction of a large bright region, as shown by the performance with the Contrast stimuli. Thus, these results can not conclusively rule out the possibility that the chance level performance observed in the Kanizsa and Crosses conditions was partly due to the presence of the large bright region background that was present in those stimuli.

Of course, the possibility remains that rats could not generalize to the Kanizsa stimuli because they did not perceive the Kanizsa square and triangle, perhaps because they lack the necessary visual processing capability to extract form from illusory contours, or more generally, to perceive visual illusions. Although, as previously noted, these conclusions would not be in agreement with studies that found that rats perceive visual illusions (Ducharme et al., 1967; Nakagawa, 2002) and with studies that found that

several species can discriminate between Kanizsa figures (for reviews, see Nieder, 2002; Ohzawa, 1999), they can not be ruled out by the present results.

In future research, the disrupting effect of introducing a large bright region could be reduced by using Kanizsa displays with a lower local luminance for the background. However, given that in humans the strength of the illusory figure increases with increased luminance contrast between inducers and background (Shipley & Kellman, 1992), these stimuli with probably not provide a good measure of illusory figures perception in rats.

The use of equiluminant training stimuli in this study ruled out the possibility that global luminance was used as a discriminative cue. However, failure to transfer to the Kanizsa figures could also be accounted for if subjects learned to use some other low-level cues, rather than the *shape* of the stimuli, to solve the discrimination. This possibility is explored in the next experiment. Finally, it should be noted that due to the small number of subjects in the study these results should be interpreted with caution.

11. Experiment 10b – Shape Perception in Rats: Part 1

11.1. Introduction

In Experiments 9 and 10a, it was assumed that the rats would process the shape of the stimuli when making the discrimination with the training set. A shape-based response strategy was a necessary condition for transfer to the Kanizsa figures as shape, or parts of it, was the discriminative cue available in these stimuli. Indeed, that rats do process shape when solving visual discrimination tasks with geometric shapes is an implicit assumption generally made in discrimination studies. This assumption, however, has never been properly verified, is not universally accepted (Ingle, 1978; 1991) and rests mainly on a sparse and relatively old literature (Fields, 1932; Lashley, 1932; Sutherland, 1961).

Although not exclusively so, in nature, ecologically meaningful information is more likely to be stored at the level of objects than of local features. Thus, there could be an evolutionary advantage in having the ability to process the global structure of objects. In agreement with this observation, there is evidence that humans more readily use global structure than local features in discrimination and recognition tasks (Navon, 1977).

The ability to perceive shape in other species has been traditionally investigated with the transfer paradigm where animals are trained to choose between simple geometric shapes and then presented with test stimuli where variations in size or spatial properties such as orientation are introduced. The assumption is that shape recognition is present in a species when there is evidence of shape-recognition invariance, that is, when the

shape is recognised irrespective of its size or spatial properties (Ingle, 1991). This ability is also referred to as shape constancy. Ingle (1978, 1991) has extensively reviewed the discrimination studies in vertebrates and concluded that, except for monkeys and pigeons, no conclusive evidence of shape constancy has been found in any other species.

11.1.1. Shape Perception in Rats: Visual Discrimination Tasks

Early transfer studies that directly addressed shape constancy in rats do not provide clear results. For instance, Fields (1932) and Lashley (1938) found successful transfer to enlarged and reduced stimuli and Lashley (1938) found positive transfer to changes in discontinuity of surface and outlines. These findings suggest that shape and not low-level features such as size, luminance or distance from the outer edges was used to solve these discriminations. However, in disagreement with these findings the same authors failed to find clear transfer to rotated stimuli suggesting that responses were made to a specific retinal luminance distribution rather than to the shape of the stimuli. Fields (1932) found successful transfer only to small rotations (10° to the left) but not to rotations of 20° or more. Even after prolonged training with a larger stimulus set, transfer occurred only to rotations of 55° to the left and up to 30° to the right. Similarly, Lashley (1938) found that transfer failed when a triangle and cross were rotated by 90° and 45°, respectively, although it succeeded when "H" and "X" were rotated by the same amount. However, Ingle (1991) noted that in the "H" vs "X" discrimination Lashley (1938) did not control for the possibility that rats used the difference in the number of lines (3 vs. 2) or intersections (2 vs. 1) to solve the discrimination. Taken together, these results suggest that rats can transfer to some rotated stimuli, but that this ability is largely modulated by the magnitude and side of the rotation and by the type of stimuli used. Thus, these results do not provide conclusive evidence of shape constancy in rats.

Shape perception in rats has been subsequently explored by Sutherland (1961) who, in a partially automated apparatus, found that rats trained to discriminate between 2 identical white rectangles, one oriented horizontally and the other vertically, could transfer to stimuli with larger or smaller sizes, discontinuous surfaces or where the relative height relationship was changed. Sutherland (1961) concluded that "animals had learned something about the shapes as a whole" (p. 117). However, all except one of these tests could have been solved using the relative height between the two discriminanda, if the discontinuous patterns were perceived as a unique shape, as this was maintained as during training. As pointed out by Ingle (1991), the poor acuity of the rat could aid the impression of grouping in simple discontinuous patterns. Moreover, Ingle (1991) suggests that the successful transfer to the discriminanda with the same height could also have been solved by using relative height as the halved positive test shape was still taller than the negative shape used in training. In general, in his review Ingle (1991) concludes that in discrimination studies exploring shape perception in rats the animals seemed to have chosen the easiest solution. Furthermore, because these studies did not control for all the possible alternative response-strategies, they do not provide conclusive evidence that shape constancy occurs in this species.

Simpson and Gaffan (1999) have recently investigated shape perception in rats with an automated Y-maze where stimuli were displayed on a pair of monitors placed at the end of each arm. In a constant-negative paradigm rats were presented with the same "constant" scene (S⁻) in every trial in one arm and with a trial-dependent "variable" scene (S⁺) in the other arm. The third arm was the start point. Each scene consisted of a specific configuration of the stimuli, mirrored in the two monitors at each arm. In a series of experiments, Simpson and Gaffan (1999) systematically manipulated area, local luminance, global luminance, shape and complexity of the scene and measured whether there was any natural preference for any of these variables in scene discrimination. Although the rats seemed to use global luminance, Simpson and Gaffan (1999) found that subjects were able to solve the discrimination when layout, area and local and global luminance were matched in the two scenes suggesting that shape was

processed to some extent. Moreover, differences in shape improved performance even in discriminations that could have been solved using area differences alone. Simpson and Gaffan (1999) concluded that rats spontaneously use shape to solve this type of visual discrimination and that they do not have a strong preference for using low-level features such as area or luminance.

However, although Simpson and Gaffan's (1999) paradigm ensured that individual elements in the constant scene could not be used to solve the discrimination as they could have appeared in the variable scenes too, it did not seem to control for the possibility that rats could have used a *configuration of features* rather than a *configuration of shapes*. This possibility is not implausible given that the constant scene, and therefore the same configuration of features, was present in every trial.

Alternatively, it could be possible that Simpson and Gaffan's (1999) configural learning paradigm discouraged the use of low-level strategies and aided the processing of shape. Configural learning is thought to require a more complex representation of the stimuli (Rudy & Sutherland, 1995) than non-configural $A^+ B^-$ visual discriminations such as those used by Fields (1932), Lashley (1938), Sutherland (1961) and in the studies presented in this thesis. If the processing of shape requires a global representation of the stimulus elements, it could be argued that configural learning tasks could facilitated the use of shape as the discriminative cue. As pointed out by other authors (Healy & Gaffan, 2001; Rudy & Sutherland, 1995), an animal's response strategy can be dependent on a variety of experimental parameters that are not necessarily directly linked with either the logical description of the problem or the stimulus properties. If this analysis is correct, it still remains unclear whether rats use shape to solve simple non-configural discrimination tasks.

11.1.2. Shape Perception in Rats: Spatial Learning Tasks

The question whether rats process shape or not has parallels with the current debate in the spatial learning community about whether animals process environmental shapes globally or locally (Cheng & Newcombe, 2005). In navigation tasks, the finding that disoriented rats are as likely to visit the "correct" corner (i.e., the corner not visited before an interrupted feeding bout) as the rotationally equivalent corner has been interpreted as evidence that these animals use geometric, shape-related, cues in addition to featural cues, even when these latter alone would result in a smaller number of errors (Cheng, 1986). More recently however, this view has been challenged and the "rotational error" has been accounted for by simpler response strategies based on low-level local features (Pearce, Good, Jones & McGregor, 2004) such as learning to navigate to a corner that has a short wall to the left of a long wall or to swim to the end of a long wall. Pearce et al. (2004) tested this claim by training rats in a rectangular pool and by subsequently transferring then to a kite-shaped pool. These authors argued that the lack of correspondence between the global shape of the two pools should have resulted in poor transfer performance. Contrary to this prediction, however, transfer performance was good in the test arena and Pearce et al. (2004) concluded that rats must have used strategies based on local cues to solve the discrimination. Thus, at present it remains unclear whether rats use shape to solve spatial navigation tasks.

11.1.3. The Present Study

Taken together the above results suggest that the evidence that rats process shape to solve visual discrimination tasks and that they are capable of shape constancy is not conclusive. This question is relevant to our understanding of the development of the two-visual-systems model. In this framework, shape constancy is found in the ventral visual system, where object recognition is based on allocentric coordinates and relative metrics. By contrast, shape in the dorsal visual system is processed in egocentric coordinates and in absolute metrics. Thus, evidence of shape constancy in rats would

suggest that the representational/perceptual networks in this species are comparable, in this respect, to those found in the ventral visual system of humans in primates. Moreover, it would provide empirical support for the claim that rats have visual processing of a representational/perceptual nature, in addition to those mediating visually guided action.

In the next part of this preliminary experiment we used a modified staircase procedure to re-explore whether rats can recognize stimuli at different orientations. As outlined above, previous studies that examined this question are not conclusive (Fields, 1932; Lashley, 1938). We reasoned that if the rats were using shape as the discriminative stimulus in Experiment 10a, then they should be able to transfer to the same shapes at altered orientations. Thus, correct discrimination performance for rotated stimuli might provide some evidence that shape, rather than local low-level cues dependent on a specific retinal luminance distribution, was being used to solve the discrimination. Moreover, it would provide evidence of orientation invariance in this species.

11.2. Method

11.2.1. Subjects

The same subjects used in Experiment 10a took part in the study.

11.2.2. Apparatus and Materials

The apparatus and training stimuli were as in Experiments 10a. The Rotated stimuli (Figure 11.1) were obtained by rotating the training stimuli, clockwise and around their centre, by incremental steps of 3.75°. Rotations ranged from 0° to 60°.

0°(training)	0°
	3.75°
15°	
	7.5°
22.5°	
	11.25°
26.25°	
	15°
	18.75°
30° (start)	
	22.5°
33.75°	
	26.25°
	30° (start)
37.5°	
	33.75°
45°	
	37.5°
48.75°	41.25°
	45°
52.5°	
	48.75°
56.25°	52.5°
60°	56.25°
	60°
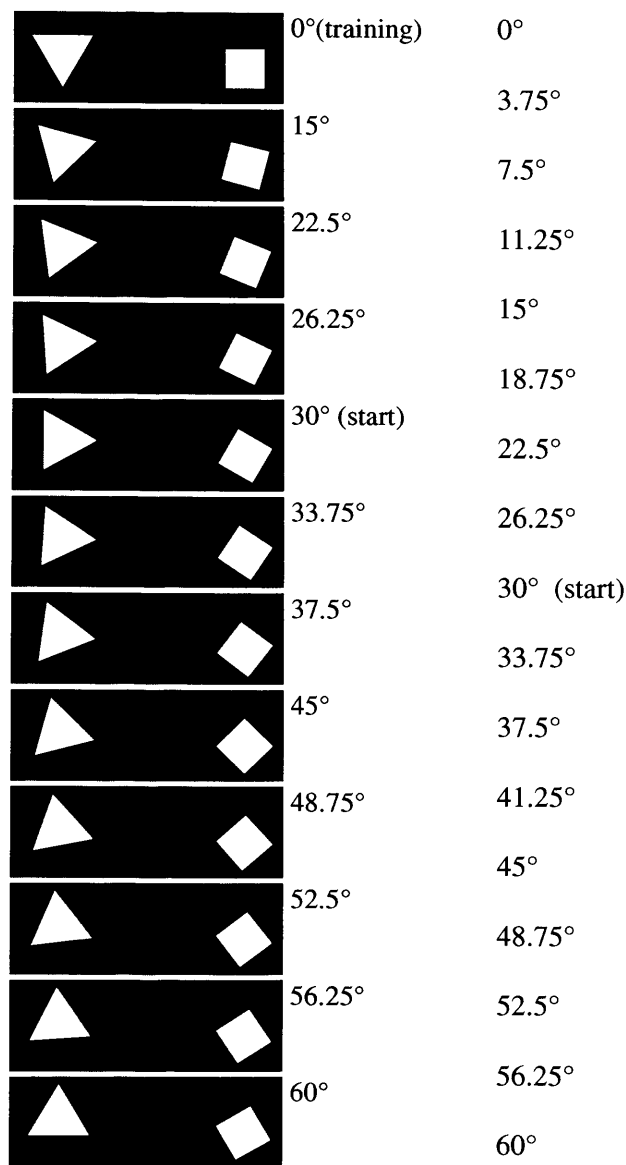
Figure 11.1. Left: the steps in the staircase actually "visited" by the rats. Some steps were never visited (see Procedure and right of figure). Note that the figure only shows the stimuli with the triangle on the left. These were used in conjunction with an identical set with the triangle on the right. Right: the entire range of rotations available in the staircase.

11.2.3. Procedure

Unless otherwise stated the procedure was as in Experiment 10a. After the Outlines trials, all rats were presented with training sessions until they reached asymptotic

performance and then were tested with the Rotated stimuli. Responses to the Rotated stimuli were never reinforced. The modifications to the staircase procedure were introduced to maintain exposure to non-reinforced test stimuli to a minimum in order to delay the onset of extinction. The staircase procedure was applied iteratively until a threshold level was confirmed over two phases, and it allowed a quick determination of rotation thresholds (within 3-6 phases) for all subjects except for rat 3, who was withdrawn from the study due to deteriorating health. For this subject, the threshold was based on the measurement obtained from a single phase. The staircase started with a 30° rotation and the angle of rotation was increased if a 70% correct or above performance was achieved over 2 consecutive sessions for the same level. The angle of rotation was decreased if this criterion was not reached. Movements up and down the staircase were always of 2 steps unless this led to a previously visited level, in which case increments and decrements of 1 step were used. Phase 1 ended when movements of 1 step led to a previously visited level. An identical procedure was used for successive phases except that the start point was determined by the performance in the previous phase. Specifically, the new phase would start 1 level up or at the same level if the last level of the previous phase was passed of failed, respectively. If the same level was failed twice over two consecutive phases the new phase would start one level down. For all phases, increments and decrements from the start point (30°) were always of 4 steps. Individual phases were separated by 3 training sessions.

11.3. Results and Discussion

On average, threshold performance was reached in 9 transfer sessions with the Rotated stimuli. With the exception of rat 4, high rotation thresholds were obtained for all subjects, clearly indicating that these rats were able to solve the discrimination when even quite substantial changes to the orientation of the stimuli were introduced. Rats 1, 2 and 3 were able to solve the discrimination with stimuli rotated by 60° (which maps the triangle onto itself). The threshold was similarly high for rat 5, who passed the 56.25° rotation level. Rat 4 was much lower at 26.25°. It should be noted that the 60°

rotation was the upper boundary of the rotation range used in this study and that rats 1, 2 and 3 might therefore have reached a higher rotation threshold if further tested.

Taken together, these results seem to suggest that rats have some degree of orientation invariance and that their ability to discriminate between the two stimuli was largely independent of the specific orientation of the training set. It should also be noted that rotating the stimuli around their centre changed, to some extent, their spatial location. Thus, correct discrimination with these stimuli also provides some evidence that rats have some degree of translational invariance, that is, that they can recognize objects irrespective of location. Evidence of orientation and translational invariance could have been interpreted as evidence of shape discrimination in this species. However, as explored in the next part of the study, a low-level explanation in fact more fully accounts for these results. Finally, as noted above, due to the small number of subjects that took part in the study these results should be interpreted with caution.

12. Experiment 10c – Shape Perception in Rats: Part 2

12.1. Introduction to Part (i)

In the Rotation trials of Experiment 10b, it was noted that rat 4 had a slight preference for the negative shape when the shapes were sufficiently rotated that the triangle approached a base down orientation and the square a vertex-down one. Notably, in these configurations, two of the salient features that could have been used to identify the two shapes, that is, the horizontal edge for the square and the vertex for the triangle in the lower part of the shapes (hereafter "lower hemifield"), were reversed.

Although in the Rotation trials the other subjects did not seem to be disrupted by the reversal of these salient features, we decided to further test the effect of this manipulation on the entire group. Specifically, we tested the possibility that this rat, and by implication perhaps the others, might be using features in the lower hemifield to make a judgement. This would be in accord with finding that rats prefer to use the lower parts of the shapes when solving visual discriminations (Lashley, 1938; Simpson & Gaffan, 1999; Sutherland, 1961).

We tested this claim with Reflected-diamond stimuli (RD), in which the triangle was reflected on the *x*-axis to become base-down, and the square was presented in a diamond configuration, and with the Triangle-diamond (TD) and Reflected-square (RS) stimuli, where the square and triangle, respectively, were reflected on the *x*-axis and presented in pairing with the corresponding unrotated training shape (Figure 12.1). If, as speculated, the animals were in fact using the lower hemifield, in which the triangle had a vertex down and the square a base down, then reversing this relationship should have resulted in a preference for the negative shape. Moreover, if these features played a role, performance should have been at chance level in the Triangle-diamond (TD) and Reflected-square (RS) conditions, as the two vertices and horizontal edges that these stimuli contained, respectively, in the lower hemifield would have not allowed to solve the discrimination with these cues. Conversely, if, as suggested by the relative good performance in the Rotated trials of Experiment 10b, subjects were using the shape, then no disruption in correct performance should have been observed with any of these test stimuli.

12.2. Method

12.2.1. Subjects

The same subjects used in Experiment 10b took part in the study.

12.2.2. Apparatus and Materials

The apparatus and training stimuli were as in Experiments 10b. The RD stimuli (Figure 12.1) were obtained by rotating the training triangle and square by 60° and 45°, respectively. The TD and RS stimuli (Figure 12.1) were identical to the RD stimuli except that the square and triangle were left as in training, respectively. In these three conditions, the stimuli were rotated around their centre, but their position along the

vertical axis was adjusted to maintain a 20-mm distance from the bottom edge of the screen as during training.

12.2.3. Procedure

Unless otherwise stated the procedure was as in Experiment 10b. After the staircase procedure, all rats were presented with training sessions until they reached asymptotic performance. After this, they were presented with three sessions for each of the RD, TD and RS stimuli, respectively. All test sessions were alternated with training sessions. Given the large number of non-reinforced test trials that had been presented to the animals at this point of the study, the same contingencies used in training were adopted for these and all the subsequent test trials.

12.3. Results and Discussion

As shown in Figure 12.1, in the Reflected-diamond trials all subjects showed a strong preference for the negative shape, which was confirmed to be significant by a two-tailed one-sample t-test ($t_{(3)}$ = -4.847, p = .017). Thus, during these test trials, subjects that had been previously trained to choose the square now chose the base-down triangle, possibly because this now provided a horizontal edge in the lower hemifield. Similarly, subjects that had been previously trained to choose the triangle now chose the diamond-rotated square in these test trials, possibly as this shape now provided a vertex in the lower hemifield. Remarkably, this behavior was clearly observed for all animals. It thus seems that they were ignoring the shape of the stimuli and using a local feature in the lower hemifield to make the discrimination. These conclusions were further supported by the level of performance observed in the Triangle-diamond condition, which was not significantly different from chance level ($t_{(3)}$ = 1.906, p = .153). This suggests that subjects were no longer able to solve the discrimination when they were presented with two vertices in the lower hemifield, even though the stimuli still consisted of a triangle and a square.

Test stimuli	RD ▲ ◆	TD ▼ ◆	RS ▲ ▢
Rat 1	7	50	47
Rat 2	30	70	43
Rat 4	27	90	43
Rat 5	3	57	43
Mean (s.e.)	16.67 (6.80)	66.67 (8.82)	44.17 (0.83)
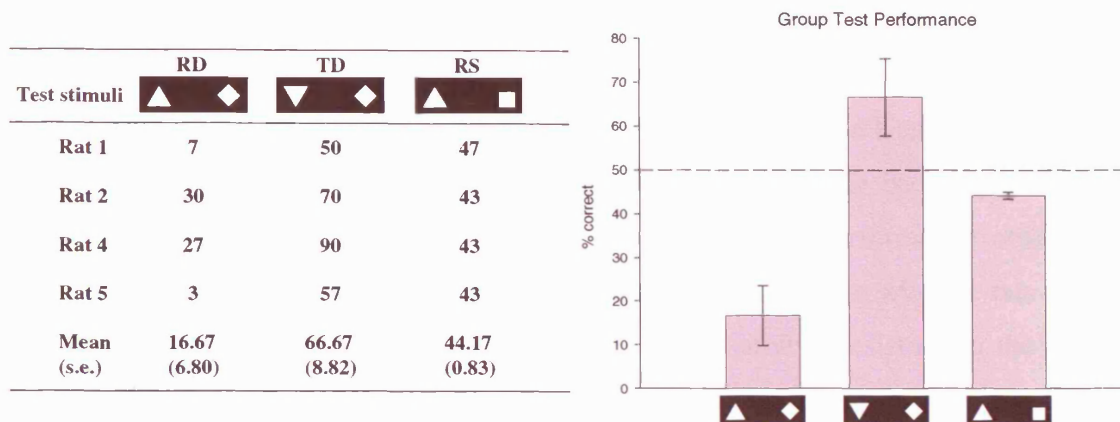
Figure 12.1. Individual (left) and group (right) percent correct performance with the stimuli testing the use of lower hemifield features. Error bars indicate the standard errors. The preference for the negative shape is clearly seen in the RD trials.

The ability to solve the discrimination was also disrupted in the Reflected-square trials, where two horizontal edges were presented in the lower hemifield. Interestingly, however, performance in this condition, instead of being at chance level was significantly *below* chance ($t_{(3)}$ = -6.000, p = .009). Thus, in these trials, as in the Reflected-diamond trials, rats had a preference for the negative shape. As shown in Figure 12.1, this preference was small, but consistent for all animals. These results cannot be entirely accounted for by the presence of two horizontal edges in the lower hemifield as this would have predicted chance level performance in these trials.

After some consideration, it was realised that this behaviour might be explained if subjects had used, as the discriminative cue, not just the configuration of edges, but differences in the luminance of the two shapes in the lower region of the visual field. The two training shapes had been matched in terms of area and local and global luminance. However, the luminance in the lower hemifield was always greater for the square, and this relationship was reversed in the Reflected-diamond and Reflected-square stimuli, where performance was also reversed. Such a response strategy would have been in agreement with the well known finding that rats rely more heavily on

features presented in the lower part of the shape (Lashley, 1938; Simpson & Gaffan, 1999; Sutherland, 1961). Crucially, such a strategy could have accounted for all the results obtained so far for these animals, with the exception of the Kanizsa and Contrast trials. However, as previously noted, the introduction of a white background in these two conditions could have accounted for the disruption in performance observed in these trials. In fact, the use of a luminance strategy might explain why the rats were so badly affected by the Contrast transformation, but relatively resistant to the Outline transformation.

The above interpretation of the results, that luminance differences in the lower hemifield, rather than salient features, were used as the discriminative cue, is further supported by the observation that changes to the salient features did not disrupt performance in the Rotation trials. In those trials, three subjects were able to solve the task with the 60° rotation, where the reversal of salient features was very similar to that of the Reflected-diamond stimuli. However, one important difference in the two studies is that in the Rotation trials, after rotation, the stimuli were not realigned to maintain the 20-mm distance from the bottom edge of the screen as in training (see Method). As a result, in the Rotated trials, configurations that had the triangle with its base down and the square in a diamond-like configuration maintained the luminance relationship between the two shapes in the lower hemifield as in training, that is, the square had a greater luminance than the triangle. Thus, correct discrimination in these Rotated trials, where salient features were also reversed but where the luminance relationship in the lower hemifield was maintained as in training, further strengthen the conclusion that luminance differences in the lower region of the visual field, and not salient features, may have been used to solve the discrimination. This possibility was further explored in the next part of the experiment.

12.4. Introduction to Part (ii)

This part of the study tests the claim that subjects used differences in the global luminance of the two shapes in the lower region of the visual field to solve the discrimination. In order to test the luminance hypothesis, the vertical extent of the animals' processing, that is, the upper boundary of the "lower hemifield", first had to be determined. The Reflected-square stimuli proved to be suitable for this task and allowed us to estimate the location of this threshold to be at approximately a 40-mm vertical distance from the bottom edge of the two shapes. As illustrated on the left panel of Figure 12.2, at this level, the area of the triangle (1812 mm^2) was greater than the area of the square (1800 mm^2) but this relationship was reversed, that is, it returned as in training, at a height of 41 mm (area of triangle and square 1833 and 1845 mm^2, respectively). Given that subjects in the Reflected-square stimuli had a preference for the negative shape, the above calculations suggest that these rats may have computed the luminance of the two shapes below or at the 40-mm threshold, as above this level the luminance relationship returned as in training and should have resulted in a preference for the positive shape.
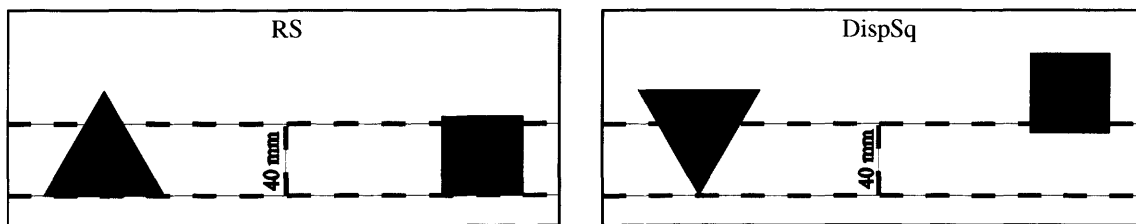
Figure 12.2. Left: The Reflected-square stimuli showing the position of the estimated 40-mm threshold for the upper boundary of the "lower hemifield". Right: the DispSq stimuli showing the area of the square falling in this region. For illustrative purposes the contrast polarity of the stimuli is reversed.

The 40-mm threshold was thus used for the construction of the stimuli in this part of the experiment. In the first set, the Displaced-square stimuli (DispSq, Figure 12.3), the

luminance relationship of the two shapes below the 40-mm threshold was reversed by vertically displacing the square by 35 mm, as illustrated in the right panel of Figure 12.2. Under these conditions, the area of this shape below the 40-mm threshold was smaller than the area of the triangle. That is, the luminance relationship between the two shapes was reversed relative to training. A displacement of 35 mm was chosen as it reversed the luminance difference below the 40-mm threshold, but it also maintained the square largely within the 100 × 100 mm responsive area of the touchscreen. It was predicted that if subjects used luminance differences in the lower hemifield as the discriminative cue, reversed performance, that is a preference for the negative shape, should have been observed in these trials.

A second set of stimuli, Displaced-both (DispBoth, Figure 12.3), examined whether the two shapes were processed relative to their position on the screen (allocentric coding) or relative to their position in the visual field (egocentric coding). Both shapes were vertically displaced by 35 mm. It was predicted that if the stimuli were processed relative to their position in the visual field, no disruption in performance should have been observed in these trials as the relative position of the two shapes was maintained as in training. Albeit vertically displaced, a movement of the head would have been sufficient to reposition both stimuli in the visual field as in training in this condition. However, if rats encoded the stimuli allocentrically, a disruption in performance should have been observed in this condition as the position of the stimuli relative to the screen was changed with respect to training. In humans, allocentric coding is a property of ventral representations, thus correct performance with these stimuli could provide some preliminary evidence that visual processing comparable to those found in the human ventral visual system occurs in this species.

A third set of stimuli, Displaced-triangle (DispTr, Figure 12.3), controlled for the possibility that displacement alone could have been sufficient to disrupt performance in the DispSq condition. In the DispTr stimuli, the triangle was vertically displaced by 35 mm, however, because the luminance relationship between the two shapes below the

40-mm threshold was not changed relative to training, no disruption in performance should have been observed in these trials. By contrast, if the effect observed in the DispSq condition was the result of displacement alone, a similar effect should have been observed in the DispTr condition.

A final condition, Luminance (Lum, Figure 12.3), further tested the use of luminance differences in the lower hemifield with a square and triangle that were equiluminant below the threshold corresponding to the height of the square (45 mm). Given that in training the square was shorter than the triangle, it could have been possible that subjects stopped processing luminance differences between the two shapes at this level. It was predicted that if subjects processed luminance differences below this 45-mm threshold, performance should have been at chance in this condition. Importantly, if the 40-mm threshold calculated earlier was considered as a more accurate estimate of the upper boundary of the lower hemifield, a preference for the positive shape should have been observed in this condition as the global luminance would have been greater for the square than for the triangle at this threshold level.

12.5. Method

12.5.1. Subjects

The same subjects used in Part (i) of this Experiment took part in the study.

12.5.2. Apparatus and Materials

The apparatus and training stimuli were as in Experiments 10b. The DispSq, DispBoth and DispTr stimuli were constructed by vertically displacing by 35 mm the square, both shapes, and the triangle, respectively (Figure 12.3). The Lum stimuli were obtain by reducing the local luminance of the square to 47.25 cd/m^2 so that its global luminance matched the global luminance of the triangle (local luminance 81.84 cd/m^2) below the

45-mm threshold. In a CRT monitor, luminance levels can vary according to several factors (Harris, Makepeace & Troscianko, 1987), therefore luminance values were calculated as the average of 3 measurements.

12.5.3. Procedure

Unless otherwise stated, the procedure was as described in Experiment 10b. After the RD, TD and RS test trials, subjects were presented with training sessions until they reached asymptotic performance. Subjects were then tested with the DispSq, DispBoth, Lum and DispTr stimuli, respectively. Each set of stimuli was presented for 3 sessions that were alternated with training sessions. For health reasons, rat 5 was withdrawn from the study after the DispBoth condition.

12.6. Results and Discussion

Figure 12.3 shows the percent correct performance for individual rats in the test conditions. It can be seen that, as predicted, in the DispSq condition there was a general preference for the negative shape. If luminance differences between the two shapes below the 40-mm threshold were used as a discriminative cue, this preference for the negative shape should have resulted in performance significantly below chance level. However, a two-tailed one-sample t-test revealed that performance in this condition was at chance ($t_{(3)}$ = -1.920, p = .151). Albeit not entirely in agreement with the directional prediction initially suggested, these results show that changing the luminance relationship below the 40-mm threshold was sufficient to reverse choice performance. Thus, overall, these results are in agreement with the suggestion that subjects used luminance differences in the lower hemifield to solve the discrimination task.
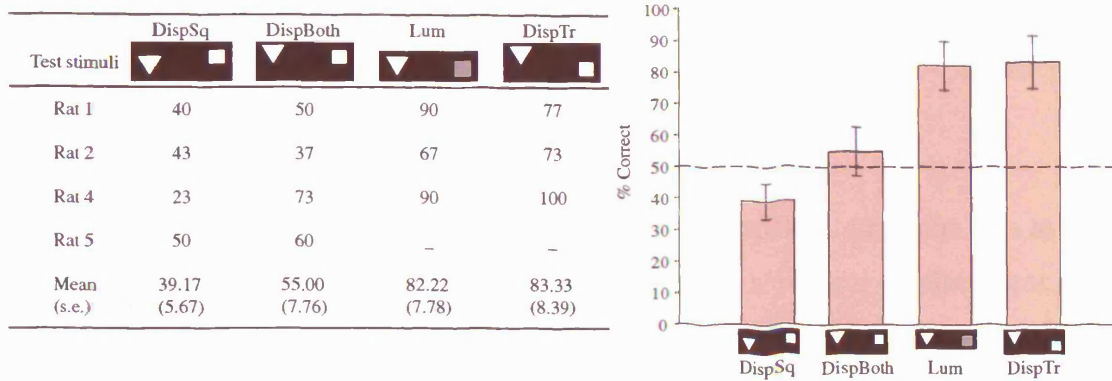
Test stimuli	DispSq	DispBoth	Lum	DispTr
Rat 1	40	50	90	77
Rat 2	43	37	67	73
Rat 4	23	73	90	100
Rat 5	50	60	–	–
Mean	39.17	55.00	82.22	83.33
(s.e.)	(5.67)	(7.76)	(7.78)	(8.39)

Figure 12.3. Individual (left) and group (right) percent correct performance with the stimuli testing the use of luminance differences in the lower hemifield. Error bars indicate the standard errors.

These conclusions are further supported by the results from the DispTr condition, where it was found that when the displacement of the triangle alone did not change the luminance differences in the lower hemifield, performance was maintained above chance level (Figure 12.3). Although these results did not reach statistical significance ($t_{(2)} = 3.962$, p = .058, two-tailed), it can be seen that in this condition, unlike in the DispSq condition, there was a preference for the positive shape. Thus, these results suggest that the pattern of performance observed in the DispSq condition was not the result of displacement alone.

The above conclusions are however not entirely supported by the results from the Lum condition, in which the local luminance of the square was reduced to make the two shapes equiluminant below the 45-mm threshold, that corresponded to the height of the square. Although in this case performance was statistically at chance ($t_{(2)} = 4.217$, p = .052, two-tailed), contrary to our prediction, it was maintained at relatively good levels. Thus, these results do not entirely support the claim that luminance differences below this threshold were used as the discriminative cue. Notably, this performance could be accounted for if these animals processed the stimuli below the 40-mm threshold, and

not the 45-mm threshold used in this condition. At the 40-mm threshold, as in training, the global luminance would have been greater for the square than for the triangle (.085 and .075 cd, respectively) and this should have resulted in a preference for the positive shape.

Finally, as shown in Figure 12.3, performance in the DispBoth condition was at chance level ($t_{(3)}$ = 0.656, p = .559, two-tailed) suggesting that a vertical displacement of both stimuli substantially disrupted performance. These results suggest that the two stimuli were encoded allocentrically, taking into consideration their position within the screen. Given that in humans allocentric coding is a property of ventral representations only, these results could be interpreted as some preliminary evidence that ventrally mediated visual processing occurs in this species. However, further research is needed to draw firmer conclusions. In particular, it should be ruled out that the chance level performance observed in these trials was not due to a failure of the animals to move their head to reposition the stimuli in the visual field as in training. Moreover, the displacement used in this condition assumed that egocentric coding in rats is retinally-centred. It is important to note that the displacement used would not have distinguished between allocentric and egocentric coding in this species if this latter is based on a head- or body-centred coordinate system in these animals. To our knowledge, which part of the body is used by this species to code for egocentric representations is a question that at present remains unanswered.

Taken together, this series of tests suggests that these animals used luminance differences between the two shapes in the lower hemifield to solve the discrimination. Thus, the results from this preliminary experiment do not provide evidence that rats can process shape. However, as noted before, due to the small sample size used in this study these results should be interpreted with caution.

13. Experiment 11a – Shape Perception in Rats: Part 3

13.1. Introduction

The results from Experiments 8, 9 and 10 suggest that not only did rats not discriminate illusory shapes of the Kanizsa type, but they did not use shape *at all* to solve the basic square-triangle discrimination, even though this cue was a readily available predictor of reward. Thus, the next experiment explores in more detail the question of whether rats do process shape at all when solving visual discrimination tasks.

In Experiment 10, the use of luminance differences in the lower hemifield as a response strategy was made possible, and perhaps encouraged, by at least four methodological parameters. First, except for the right/left shift, the location of the stimuli on the screen was maintained the same throughout the study. Fixed stimulus locations made it possible to determine the region that could have been reliably used for the computation of local luminance differences. Second, fixed stimulus sizes could have also encouraged the use of such a strategy. Third, the fact that the 2 stimuli differed in height could have encouraged only a partial portion of the stimuli. Finally, the dimensions of the two shapes resulted in a luminance difference in the lower hemifield.

In this experiment, we explored whether rats can use aspect ratio to solve a square vs rectangle discrimination. Reasoning that the core of the concept of "shape" must necessarily involve some kind of metric processing in two dimensions, we devised a set of stimuli in which information from both dimensions simultaneously, in other words, the aspect ratio, was as far as we could determine the only relevant discriminand. Moreover, aspect ratio was judged to be a suitable measure of shape in rats as it is

entirely derivable from the visual array without requiring previous knowledge (Zanker & Quenzer, 1999). Thus, four rats were trained to distinguish between squares (aspect ratio of 1) and rectangles (aspect ratio of 2 or 0.5), with shapes that varied in absolute size, relative size, luminance and allocentric position, to thwart any attempts to use local features. A control group of four rats, trained to solve simpler square-rectangle discriminations that required relative size judgements only in the horizontal (n = 2) or vertical (n = 2) dimensions, were used to confirm that rats can make each of the relevant unidimensional judgements, and to ascertain the learning curve thereof. Because in all groups the size and location of the stimuli was repeatedly changed during training, correct discrimination performance in any of these groups would also provide evidence of size and translational invariance in this species.

13.2. Method

13.2.1. Participants

Dark Agouti rats were used in this experiment because of their superior performance, relative to Lister Hooded, in concurrent visual tasks (Gaffan & Eacott, 1995; Gaffan & Woolmore, 1996). Eight experimentally naïve males, weighing between 215 and 255 grams at the beginning of the experiment, were kept on a 12:12 light cycle and at 85% of their free-feeding weight. All animals had free access to water in the home cages and were housed in groups of four.

13.2.2. Apparatus and Materials

13.2.2.1. Stimuli

Images of the complete stimulus set are provided in Appendix A.

Bidimensional Discrimination (BD) group: for this group, every display (hereafter 'permutation', Appendix A) consisted of a white square and a white (83 cd/m²) vertically oriented rectangle presented on a black (0.03 cd/m²) background. Two sets of stimuli were used, one was used from the start of the study and the other was introduced after 18 sessions.

For the initial set (Appendix A, Figure A.1), squares with a side of 15, 25, 85 or 90 mm were paired with 50 x 25, 60 x 30, 70 x 35 or 80 x 40 mm rectangles. The screen was subdivided into 2 halves containing 4 identical quadrants and within the set each of the 8 shapes was presented once in every quadrant. Stimuli were positioned at the centre of the quadrants, however, when due to their large size this central alignment resulted in encroachment into the opposite hemiscreen or outside the screen, the stimulus was moved towards the centre of the hemiscreen until a distance of 10 mm from the central partition and the edges of the screen was obtained. This procedure resulted in 32 permutations. For each permutation, the size, side (right or left side of screen) and quadrant (within hemiscreen) of the square were chosen from a list of all the possible options. The side of the matching rectangle was necessarily determined by the side of the square, but its size and quadrant were also selected from a list of the possible options. The dimensions of the squares and rectangles ensured that the relative height, width and area of the two shapes were fully controlled within stimulus set. More specifically, the square was higher, wider and had a greater area than the rectangle in half of the permutations obtained and it was shorter, narrower and smaller than the rectangle in the other half. This ensured that these low-level properties could not be used to solve the discrimination. For the first 18 sessions, each of the 32 permutations was presented 4 times in a training sequence of 128 trials, these 128 trials constituting a session. The position of the permutations in the training sequence was determined by a random function.

After 18 sessions, we discovered that to maintain the relative size constraints outlined above, permutations always contained average-sized rectangles paired with large or

small squares (Appendix A, Figure A.2), and that rats might have used this unintended regularity to solve the discrimination on the basis of the rule "avoid/choose medium-sized/large shapes". To control for this possibility, a new set of average-sized squares (side of 30, 40, 50 and 60 mm) and very large (170 x 85 and 180 x 90 mm) and very small (15 x 7.5 and 25 x 10 mm) rectangles was introduced. These stimuli were constructed as described above and yielded 32 new permutations that, together with the initial set, were now presented twice in each training sequence.

Unidimensional Discrimination (UD) control groups: The Unidimensional Discrimination control groups were subdivided into a Unidimensional Discrimination Horizontal (UDH) group (n=2) and a Unidimensional Discrimination Vertical (UDV) group (n=2). For the UDH group, a square with a side of 30, 40, 50 or 60 mm was always paired with a rectangle that had twice its width whereas for the UDV group these squares were paired with rectangles that had twice their height (Appendix A, Figures A.3 and A.6).

For both groups, the background was maintained black, however, in order to prevent the use of either local or global luminance as a discriminative cue, the luminance of the square and rectangle varied between three possible luminance levels. The first luminance set was presented from the start of training and contained white squares and rectangles (83 cd/m^2). However, because for the two UD groups the rectangle had always twice the area of the square, after 13 sessions it was realised that subjects could have used this systematic difference in global luminance to solve the discrimination. This possibility was controlled by introducing two additional luminance levels. In the second set (Appendix A, Figures A.4 and A.7), white squares were paired with equiluminant rectangles whose local luminance was halved (41.5 cd/m^2). The third set (Appendix A, Figures A.5 and A.8) controlled for the possibility that the lower local luminance of the rectangle in the second luminance set could have been used as a discriminative cue. Thus, in this final set white rectangles were paired with squares that had their local luminance halved (41.5 cd/m^2), to match the local luminance of the

rectangles in the second set. As in previous experiments, luminance levels were calculated as the average of 3 measurements.

Each luminance set resulted in 32 permutations. Permutations were obtained by matching the square and rectangle with a procedure similar to that described for the BD group, except that for the UD groups, due to the nature of the discrimination, the size of the rectangle, in addition to its side, was also determined by the dimensions of the chosen square. The size and location of the stimuli for each permutation were determined once, and maintained the same for the three luminance sets. The 96 permutations that resulted from the three luminance sets were presented once in a 128-trial training sequence. For the remaining 32 trials, 11 permutations were randomly taken from the first luminance set, 11 from the second and 10 from the third. The position of the permutations in the training sequence was determined by a random function.

13.2.2.2. Apparatus and Set-up

The apparatus used in this experiment was the same as in Experiment 10, except that a partition (30 cm high × 15 cm wide) divided the screen in two halves. This was introduced to force animals to make a choice before reaching the touchscreen, and therefore prevented side-switching at the response location.

13.2.3. Procedure

Training: Rats were first habituated to the apparatus for three days. On day 1, the four rats in each cage were left for 20 minutes in the apparatus and food pellets (45mg Noyes) were scattered on the floor and placed in the magazine tray. The same procedure was used for individual rats on day 2. On day 3 the procedure was repeated with food pellets only in the magazine tray. Training with the stimuli and touchscreen started on day 4.

Unless otherwise stated, the same procedure was used for all groups. In the BD group, half of the subjects were randomly assigned the rectangle as the positive stimulus (rats 1 and 2) and the other half the square (rats 3 and 4). Similarly, for the UDH group, rat 5 was assigned the rectangle as the S^+ and rat 7 the square. For the UDV group, rat 6 was assigned the rectangle as the S^+ and rat 8 the square. The stimuli remained on the screen until the animal nose poked the touchscreen. Nose pokes to the hemiscreen with the S^+ were coded as correct responses and were followed by stimulus offset, onset of the light inside the magazine tray and delivery of one 45-mg food pellet. Stimulus offset resulted in a black screen. Nose pokes to the hemiscreen with the S^- were coded as incorrect responses and were followed by stimulus offset, a 2-sec burst of white noise and a 10-sec black-out period. Except during black-out periods, the house light remained on throughout the study and provided the only source of light in the room. For correct responses, the ITI was started when the rat pushed the door of the magazine tray. For the initial 30 sessions the ITI was set at 3 sec but this was reduced to 1 sec thereafter (see Experiment 10 for an explanation of the rationale). A modified correction procedure was used whereby the same permutation was repeated up to two times after an incorrect response. Responses from correction trials were not included in the calculation of the percent correct performance. Training sessions lasted for 128 trials. Background noise was provided by the fan of the PC and the floor of the apparatus and touchscreen were cleaned between animals.

13.3. Results and Discussion

Figure 13.1 shows the learning curves for the BD and UD groups where it can be seen that difference learning rates were produced by the two groups. Firstly, whereas the UD group reached criterion performance (80% correct or above over 3 consecutive sessions) in a relatively small number of trials performance in the BD group remained below this level even after prolonged training. Secondly, learning was much faster for the UD

group as indicated by the steeper gradient. These results clearly suggest that the two discriminations entailed different levels of complexity for these animals.

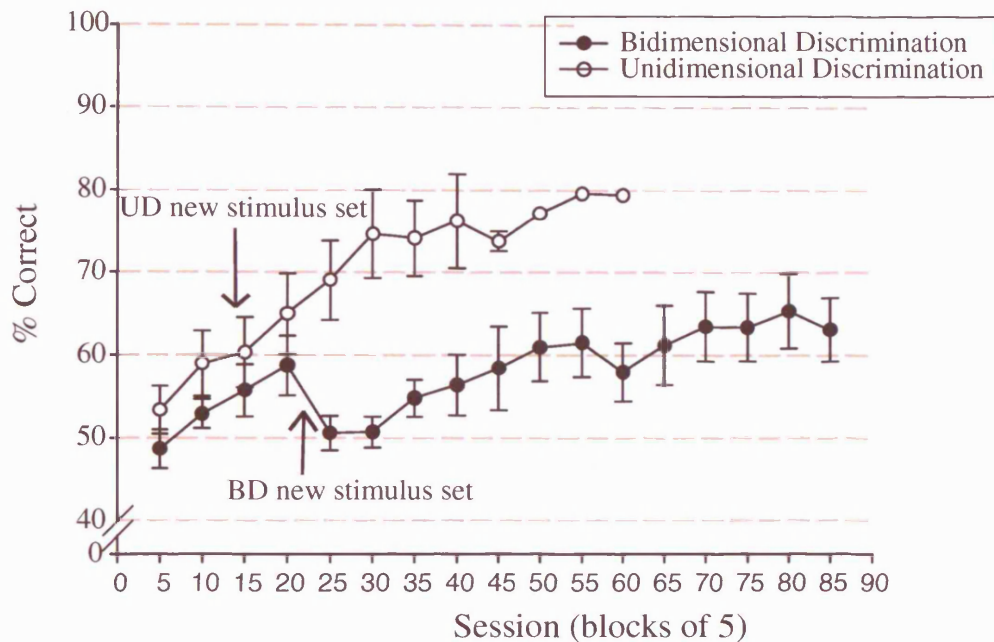## Group Discrimination Performance

Figure 13.1. Learning curves for the BD and UD groups. The graph illustrates performance up to criterion for the UD group and just before the testing phase for the BD group. Error bars indicate the standard errors.

Figure 13.1 also shows a steep gradient for the BD curve in the first 18 sessions and a sharp decrement in performance when the new stimulus set was introduced for this group at session 19. Although performance in the UD group was significantly better than performance in the BD group in these sessions ($t_{(34)}$ = -2.368, p = .024, two-tailed), a two-tailed one-sample t-test confirmed that for the BD group performance was significantly above chance ($t_{(17)}$ = 3.391, p = .003). Thus, these results support the observation that rats in the BD group might have initially used the "avoid/choose extreme shapes" rule that might have required only a luminance or unidimensional size

judgement. A two-tailed one-sample t-tests further confirmed that when new stimuli were added to foil this strategy, the performance of the Bidimensional Discrimination rats fell to chance ($t_{(9)}$ = 0.490, p = .636, for sessions 19 to 29). By contrast, a two-tailed one-sample t-tests confirmed that no such decrement in performance was observed for the UD group when the two new luminance sets were introduced ($t_{(9)}$ = 11.784, p < .001, for sessions 14 to 23). These results suggest that the UD animals did not try to exploit global luminance differences to solve the discrimination at the start of training and that a clear difference in strategy use between the two groups had already developed by this stage.

Training lasted until criterion performance for the control rats (on average for 39 sessions) and for 85 sessions (67 if the first 18 sessions are not considered) for the Bidimensional Discrimination rats. Given that each session comprised 128 trials, this resulted in 4992 (average) and 10710 trials (8576 if only trials from session 19 are considered) for the control and Bidimensional Discrimination rats, respectively. Within-group analysis of performance for rats trained to choose the squares vs. rectangles revealed no difference dependent on which was the positive shape ($t_{(2)}$ = 0.632, p = .592, two-tailed), so these data were combined. Similarly, in the Unidimensional Discrimination group there was no difference dependent on whether the relevant dimension was horizontal or vertical ($t_{(2)}$ = -2.163, p = .163, two-tailed), so these data were also combined.

To control for the possibility that the false start experienced by the Bidimensional Discrimination rats slowed their ability to learn the discrimination, we compared the training curves for 40 sessions starting from session 1 for the control rats and from session 25 for the Bidimensional Discrimination rats. Even with this allowance, it can be clearly seen that there is a marked difference in the learning rate of the BD and UD groups, and statistical analysis confirmed that the control rats learned their discrimination significantly faster ($t_{(78)}$ = -5.992, p < .001, two-tailed). A two-tailed independent-samples t-test comparing asymptotic performance (last 15 sessions for the

controls and 70-85 for the Bidimensional Discrimination rats) confirmed that maximal performance was significantly worse for the rats in which aspect ratio was the only predictor of reward ($t_{(28)}$ = -9.249, p < .001), being only 64% at asymptote. Thus, rats seemed to be quite poor at using the rule "choose the rectangle" or "choose the square", whereas they were relatively quite good at using "choose the wider figure" or "choose the taller figure".

Despite the above, by the end of prolonged training performance for the Bidimensional Discrimination rats was significantly above chance level, indicating that subjects were able to solve the discrimination to *some* extent. This was confirmed with a two-tailed one-sample t-test carried out on the average of the last 10 training sessions ($t_{(3)}$ = 3.775; p < .05). These results suggest that rats might be capable to some extent of using aspect ratio, and by implication shape, to solve visual discriminations. Importantly, the finding that these rats were able to use shape across different sizes and locations indicate that size- and translation-invariant object recognition might occur in this species. However, the large number of trials needed to achieve levels of performance well below criterion also suggests that aspect ratio is not naturally used by this species to solve this type of task. These findings, together with the decrement in performance of the BD rats when the new squares and rectangles were added to the stimulus set, further corroborate the conclusions from Experiment 10 (and suggested by Ingle, 1978) that rats will try to solve shape discriminations using low-level cues, such as luminance differences, whenever possible.

14. Experiment 11b – Shape Perception in Rats: Part 4

14.1. Introduction to Part (i)

The stimuli for the Bidimensional Discrimination rats controlled, as far as we could determine, for all possible discriminating features other than aspect ratio. In this part of the experiment we tested the ability of this group to generalize to novel dimensions and provide preliminary evidence that rules out the possibility that these rats might have used low-level response strategies. The rationale of these tests is summarised in Figure 14.1. For clarity, the figure also includes the rationale of the entire experiment.

Probe 1: A Test for the Hypothesis that Rats Used Large Bright Areas

This series of probes (Probe 1, Figure 14.1) tested the possibility that very large bright areas were used as the discriminative cue during training. In the training stimuli, 16 of the 64 permutations contained very large rectangles. Visual inspection of the number of errors made for individual permutations in the last 20 training sessions revealed that, overall, three of the four rats made fewer errors when permutations contained the 2 largest rectangles (170 x 85 and 180 x 90 mm) of the added BD stimulus set. Correct performance was not always observed with permutations that contained large rectangles and very few errors were observed with some of the permutations not containing these large stimuli. Nevertheless, there was the possibility that rats might have chosen/avoided large bright areas in these 16 permutations and performed at chance level with the remaining 75% of the training stimuli. Notably, such response strategy would have resulted in a correct percent performance of 62.5% (0.50 x 0.75 + 1 x 0.25),

a level very similar to that achieved by this group at the end of training (Figure 13.2). This possibility was directly tested with permutations containing a very large square paired with a medium-sized rectangle. It was predicted that, if during training rats learned to approach/avoid large areas, a preference for the negative shape should have been observed with these stimuli.

Probe 2: A test for the Hypothesis that Rats Used the Height Relationship

In the second series of probes (Probe 2, Figure 14.1) we tested the possibility that aspect ratio was indeed used to solve the discrimination by presenting the animals with a rectangle and a square of equal height. These stimuli maintained the aspect ratio as the training set but introduced a new relationship between the two shapes that subjects had never experienced before. It was predicted that if rats had learned to use aspect ratio during training, this manipulation should not have affected their ability to solve the discrimination.

Probe 3: A test for the Hypothesis that Rats Used Area or Alignment

In the training stimuli, area and luminance were fully controlled and this should have discouraged subjects from using these features to solve the discrimination. This claim was tested with stimuli with the rectangle and square with equal areas (Probe 3, Figure 14.1). These trials also explored the role of alignment by using pairs of shapes that were aligned either along the lower edge, the centre or the top edge. It was predicted that, if rats learned to use aspect ratio as intended, none of these manipulations should have affected their ability to discriminate between the two shapes.

All probe stimuli were made with shapes with dimensions never presented before. Thus, correct performance in these trials would also provide evidence of generalization in this group and rule out the possibility that these subjects learned to respond to the specific dimensions of the training set (i.e., by using a 'retinal snapshot').
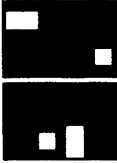
Experiment 11				
Phase	**Purpose**	**Stimuli**	**Group**	
Training	To establish shape discrimination based on aspect ratio	Square vs rectangle (aspect ratio only discriminand)	BD	
	To establish shape discrimination based on the *horizonal* (UDH) or *vertical* (UDV) dimension	Square vs rectangle (relative height.luminance and position controlled)	UDH — UDV	
Probe 1	To test the possibility that rats used large bright areas. Also tested transfer to novel dimensions	Stimuli with very large squares and medium-sized rectangles	BD	
Probe 2	To test the possibility that rats used height relationship. Also tested transfer to novel dimensions	Stimuli with squares and rectangles of equal height	BD	
Probe 3	To test the possibility that rats used area or alignment. Also tested trasnfer to novel dimensions	Stimuli with equal area and alignment of either centre. top edge or bottom edge	BD	
Probe 4	To test transfer of responding to stimuli with novel dimensions	Stimuli with novel dimensions	UDH — UDV	
Probe 5	To test the possibility that rats used aspect ratio	Stimuli with no discrepancy in the trained dimension	UDH — UDV	
Probe 6	To test the possibility that rats used area	Stimuli with equal area	UDH — UDV	
Probe 7	To test the possibility that rats used a size discrepancy in the untrained dimension	Stimuli with discrepancy only in untrained dimension	UDH — UDV	
Probe 8	To test the possibility that rats had a preference for using the size discrepancy in the trained dimension	Identical stimuli with discrepancy in both trained and untrained dimensions	UDH UDV	

Figure 14.1. Summary of the stimuli and rationale of the experiment.

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14.2. Method

14.2.1. Subjects

The same subjects used in the BD group in Experiment 11a took part in the study.

14.2.2. Apparatus and Materials

The apparatus and training stimuli were as in Experiment 11a. The Probe 1 stimuli (Figure 14.2) consisted of 12 permutations with a 140 x 140 mm square paired with a 80 x 40 mm rectangle. Both shapes were presented at least once at each of the 8 quadrants and this resulted in 8 permutations. The location of the stimuli for the remaining four permutations was randomly chosen. The Probe 2 stimuli (Figure 14.2) consisted of a 120 x 120 mm square paired with a 120 x 60 mm rectangle. To remove the potential confounding effect of position, both shapes were presented at the centre of the hemiscreen, once in each side. Thus, only 2 permutations were obtained for this series. Finally, the Probe 3 stimuli (Figure 14.2) consisted of a 120 x 60 mm rectangle and a square of equal area (side of 84.85 mm). The square was aligned with either the top edge, the centre or the bottom edge of the rectangle for each of the two hemiscreens giving a total of 6 permutations.

Images of the complete sets of probes are provided in Appendix A.

14.2.3. Procedure

Testing Procedure: The BD group did not reach criterion ($\geq$ 80% correct over 3 consecutive sessions) so testing started after 85 training sessions, when they appeared to have reached asymptotic performance. Unless otherwise stated, the same procedure was used for all test conditions. In test sessions, the 128-trial sequence contained 12 probe permutations pseudorandomly interleaved with 116 training trials. Test trials could not

occur in the first 5 trials of the sequence and were separated by between 5 and 9 training trials. In Probe 1 sessions, each of the 12 probe permutations was presented once. In Probe 2 sessions, each of the 2 permutations was presented 6 times and in Probe 3 sessions each of the 6 permutations was presented twice. The contingencies after correct and incorrect responses for test trials were maintained as in the training trials, with the exception that the modified correction procedure was not used for incorrect responses to test stimuli. Each set of probes was presented for 3 consecutive sessions and testing progressed from Probe 1 to Probe 2 to Probe 3.

14.3. Results and Discussion

The mean correct performance for individual rats is shown in Figure 14.2. It can be seen that all rats in this group correctly solved the discrimination with all three sets of probes, although performance was more accurate in Probe 3. A series of two-tailed one-sample t-tests confirmed that this performance was significantly above chance level for Probe 1 ($t_{(3)} = 4.371$, p = .022), Probe 2 ($t_{(3)} = 5.093$, p = .015) and Probe 3 ($t_{(3)} = 4.151$, p = .025).

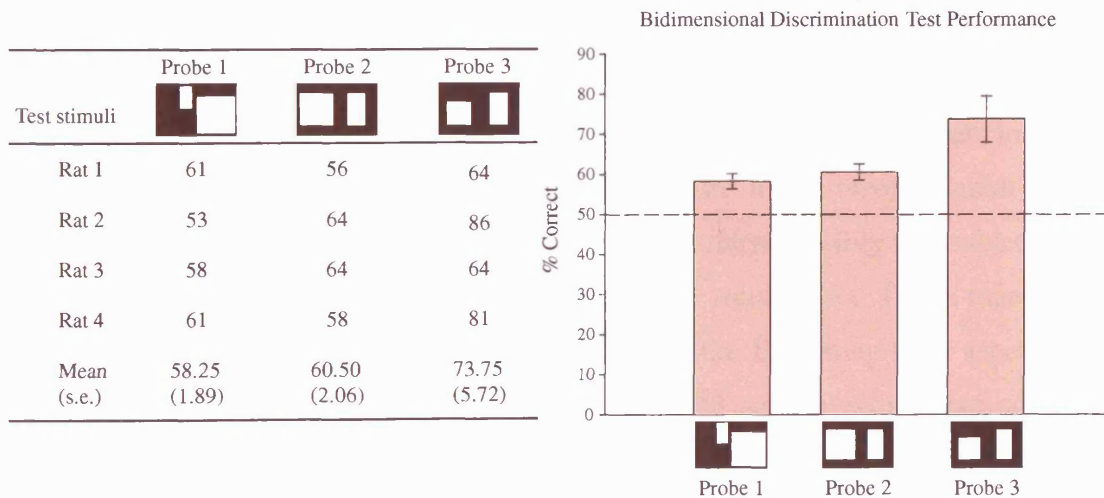| Test stimuli	Probe 1	Probe 2	Probe 3
Rat 1	61	56	64
Rat 2	53	64	86
Rat 3	58	64	64
Rat 4	61	58	81
Mean (s.e.)	58.25 (1.89)	60.50 (2.06)	73.75 (5.72)

Figure 14.2. Individual (left) and group (right) percent correct performance with the Probe 1, Probe 2 and Probe 3 stimuli. Error bars indicate the standard errors. The permutations shown are examples taken from the test sets.

The results from Probe 1 suggest that subjects chose the positive shape independently of relative luminance and rule out the possibility that rats in this group used large bright rectangles as the discriminative cue in a subset of the permutations. Thus, these results rule out the possibility that the correct discrimination performance observed for this group in Experiment 11a was artificially inflated by the use of this luminance-based response strategy.

This conclusion is further supported by the good performance observed in the Probe 3 trials which suggests that neither area, luminance nor the alignment of the two shapes were used to make the discrimination. The effect of alignment was further examined with a 3-way repeated measures ANOVA with Alignment as factor. This analysis revealed no significant differences in the number of errors made with the three different alignments ($F_{(2,6)}$ = 3.167; p = .115) confirming that alignment was not a cue used by these animals. These results are in agreement with Kurylo, Van Nest and Knepper (1997) who also found that rats do not use alignment as a cue for perceptual grouping when having to judge the orientation of an arrays of disjoint dots (see General Discussion for a fuller description of the study).

The results from the Probe 2 trials revealed that performance was not disrupted by changing the height relationship between the discriminanda therefore providing further support for the early conclusion that aspect ratio was used by the BD rats to solve the discrimination. Finally, correct discrimination with these novel stimuli provides evidence of generalization in this group and rules out the possibility that subjects merely learned to respond to the specific dimensions of the training set. Taken together these results further strengthen the claim that subjects in the BD group used aspect ratio to solve the discrimination. However, due to the small sample size, these conclusions should be treated with caution.

14.4. Introduction to Part (ii)

The stimuli for the Unidimensional Discrimination rats were not fully controlled. These rats had, in addition to aspect ratio, other discriminating features: Particularly horizontal or vertical extent, and area. Specifically, the rectangle had always twice the area of the square and the aspect ratio was always 1:1 for the square and 1:2 or 2:1 for the rectangle, depending on orientation. Therefore, subjects could have used any of these systematic differences between the two shapes to solve the discrimination. The next series of probes tested whether these animals had learned anything about the shapes of the stimuli (i.e., the aspect ratio) or whether they were solving the discrimination using features alone.

Probe 4: A Test Measuring Generalization to Novel Dimensions

The first series of probes (Probe 4, Figure 14.3) for the UD animals tested their general ability to transfer to novel stimuli. Correct discrimination in this condition would have ruled out the possibility that these subjects learned to respond to the specific dimensions of the training set (i.e., by using a 'retinal snapshot').

Probe 5: A test for the Hypothesis that Rats Used Aspect Ratio

The use of aspect ratio as a discriminative cue was tested with the Probe 5 stimuli (Figure 14.3) consisting of squares and rectangles that no longer differed in the trained dimension (i.e., horizontal for the UDH group and vertical for the UDV group) but that maintained the same aspect ratio as in training. Good discrimination performance, or at least above-chance performance, should have been observed if aspect ratio was used as a discriminative cue.

Probe 6: A test for the Hypothesis that Rats Used Area

The third series of tests (Probe 6, Figure 14.3) explored whether area may have formed the basis of successful discrimination for these animals. Subjects were presented with permutations containing squares and rectangles of equal areas but which, again, maintained the same aspect ratio as during training. It was predicted that if area had been used to solve the discrimination then performance should have been at chance level with these stimuli. By contrast, if aspect ratio had been learned, then positive discrimination should persist.

14.5. Method

14.5.1. Subjects

The same subjects used in the UD group in Experiment 11a took part in the study.

14.5.2. Apparatus and Materials

The apparatus and training stimuli were as in Experiment 11a. The Probe 4 stimuli (Figure 14.3) were obtained by pairing 4 squares with a side of 15, 20, 25 and 70 mm with matching rectangles of equal height and double width for the UDH group and of equal width and double height for the UDV group. A total of 12 permutations, 4 for each of the 3 luminance levels used in training, were constructed for this set of probes. Permutations were formed with a procedure similar to that used for the training set. For each luminance level, the side and quadrant of the square and the quadrant of the rectangle were randomly assigned, with the only constraint that for any given stimulus quadrants could not be repeated across the 3 luminance levels. This ensured that location was sufficiently varied for the test stimuli. Side of presentation was randomised within luminance set.

For the UDH group, the Probe 5 stimuli (Figure 14.3) were obtained by pairing 4 squares with a side of 50, 60, 70 and 80 mm with rectangles of the same width and half the height. Thus, for these animals the square and rectangle did not differ in the trained dimension (horizontal) but maintained the same aspect ratio as in training. For the UDV group the same squares were paired with rectangles of the same height and half the width, resulting in pairs that did not differ in the vertical dimension. The rest of the procedure was as for the Probe 4 stimuli.

Finally, for the UDH group the Probe 6 stimuli (Figure 14.3) were obtained by pairing 4 squares with a side of 40, 50, 60 and 70 mm with rectangles of the same area, and of the same aspect ratio used in training (i.e., 56.6×28.3, 70.7×35.4, 84.9×42.4 and 99.0×49.5 mm rectangles). For the UDV group the same permutations were used except that the rectangles were rotated by $90°$. The rest of the procedure was as for the Probe 4 stimuli.

Images of the complete sets of probes are provided in Appendix A.

14.5.3. Procedure

Testing Procedure: Testing started immediately after the animals reached criterion performance. Test and training trials were interleaved as described in Section 14.2. For all series of probes, each of the 12 test permutations was presented once in the test session. Each set of probes was presented for 3 consecutive sessions and testing progressed from Probe 4 to Probe 5 to Probe 6.

14.6. Results and Discussion

Figure 14.3 shows the mean correct percent discrimination performance for the three sets of probes. A series of two-tailed one-sample *t*-tests revealed that correct responses

in Probe 4 were significantly above chance level ($t_{(3)}$ = 4.824, p = .017) but that they were at chance in Probe 5 ($t_{(3)}$ = -2.023, p = .136) and Probe 6 ($t_{(3)}$ = 2.324, p = .103).

The results from the Probe 4 trials, which tested for generalization, suggest that subjects were able to solve the discrimination with novel stimuli and provide evidence for generalization in this group. Thus, during training subjects did not merely learn to respond to the specific dimensions of the training stimuli.

Test stimuli	Probe 4	Probe 5	Probe 6
Rat 5	61	33	69
Rat 6	75	47	50
Rat 7	67	31	67
Rat 8	61	50	56
Mean	66.00	40.25	60.50
(s.e.)	(3.32)	(4.82)	(4.52)
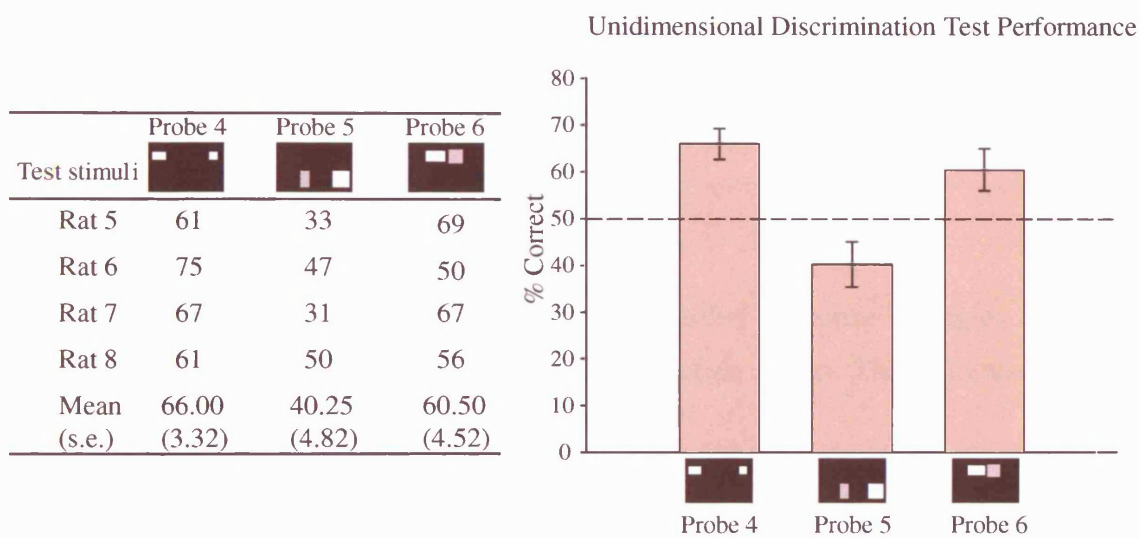
Figure 14.3. Individual (left) and group (right) percent correct performance with the Probe 4, Probe 5 and Probe 6 stimuli. Error bars indicate the standard errors. The permutations shown are examples taken from the test sets.

The chance level performance observed with the Probe 5 trials, with stimuli with aspect ratio as in training but with the discrepancy in the trained dimension removed, suggest that these rats had not spontaneously learned that aspect ratio (squareness or rectangleness) predicted reward. This conclusion is further strengthened by the chance level performance observed in Probe 6, where aspect ratio was also maintained as in training but not used by the animals. These results support the conclusions made earlier

that this measure of shape is not naturally used by this species to solve visual discriminations.

In addition, the chance level performance observed in Probe 6, where squares and rectangles had equal areas, suggests that this low-level stimulus property could have played a role in solving the discrimination. This would not be surprising considering that the area of the rectangle was always twice the area of the square during training. This possibility was further tested in the next series of trials. Finally, as noted above, due to the small sample size the conclusions from this part of the study should be treated with caution.

14.7. Introduction to Part (iii)

This final part of the experiment explores two further response-strategies that could have been used by the Unidimensional Discrimination group. The rationale for these trials is summarised in Figure 14.4.

Probe 7: A Test for the Hypothesis that Rats Learned to Use a Size Discrepancy in the Untrained Dimension

As shown in Figure 14.3, although performance in the Probe 5 trials was statistically at chance, there was a preference for the negative shape in three subjects. In these trials, the size discrepancy was present in the untrained dimension, but crucially, the patter of performance observed could have been explained if subjects used a rule such as "choose/avoid the shape that exceeds the other shape *in any dimension*". Moreover, the use of such a strategy would have provided an alternative account for the chance level performance observed in the Probe 6 stimuli. In these trials, uniquely, there was a size discrepancy in both the trained and untrained dimensions. Thus, if animals learned to make a size judgment in both the trained and untrained dimensions, it is possible that the size discrepancy in both dimensions impaired their ability to solve the

discrimination in these trials. Importantly, such a strategy could have accounted for all the performance observed in this group in both training and testing up to this point.

This possibility was tested with test stimuli (Probe 7) that consisted of pairs of rectangles that differed in the trained dimension in half of the trials and in the untrained dimension in the other half (Figure 14.5). Thus, these stimuli allowed to compare performance with shape that differed in the trained and untrained dimensions and that did not entailed the original square-rectangle discrimination. If during training subjects learned to make relative size judgements in both dimensions, then clear predictions could have been made for these trials. Specifically, the two rats (rats 7 and 8) that had the square as the positive stimulus, that is rats that learned to choose the smallest shape in training, should now always choose the smallest rectangle of the pair. By contrast, the two rats (rats 5 and 6) that learned to choose the largest shape in training (i.e., rectangle) should now always choose the largest rectangle of the pair. Aspect ratio was also controlled in these stimuli as only half of the permutations, in both the trained and untrained discrepancy sets, had the "correct" rectangle with the aspect ratio used in training (1:2 and 2:1 for the UDH and UDV groups, respectively).

Probe 8: A Test for the Hypothesis that Rats Had a Preference for Using the Size Discrepancy in the Trained Dimension

Although performance in the Probe 6 trials was statistically at chance level, Figure 14.3 clearly shows that there was a trend for choosing the correct shape, in particular for rats 5 and 7. This trend suggests that the dimension taken into consideration when making the relative size judgement was not chosen completely at random, but that subjects had a preference for using the dimension relevant for training. Thus, taken together the results from P5 and P6 could suggest that rats were capable of using differences in the untrained dimension to solve the discrimination but that they preferred to use a discrepancy in the trained dimension when this was available.

We tested this claim with permutations with two identical rectangles, one oriented vertically and the other horizontally (Probe 8, Figure 14.5). We predicted that, if the above analysis is correct, rat 6, who was rewarded for choosing the rectangle in the UDV group, should now choose the rectangle oriented vertically in these trials as this was the bigger shape in the trained vertical dimension for this subject. By contrast, rat 8, who was rewarded for choosing the square in the UDV group, should now choose the rectangle oriented horizontally as this was the smaller shape in the trained vertical dimension. Reversed predictions can be made for the UDH group. Rat 5, who had the rectangle as the positive stimulus, should now choose the horizontally oriented rectangle as this was the larger in the trained horizontal dimension. By contrast, rat 7, who had the square as the positive stimulus, should now choose the vertically oriented rectangle as this was the smaller in the trained horizontal dimension for this animal.

14.8. Method

14.8.1. Subjects

The same subjects used in the UD group in Experiment 11a took part in the study.

14.8.2. Apparatus, Materials and Procedure

Unless otherwise stated, the apparatus, training stimuli and procedure were as described in Section 14.5. The Probe 7 stimuli (Figure 14.5) for the UDV group were made with the following pairs of rectangles: 40 × 25 and 40 × 30 mm, 40 × 25 and 40 × 10 mm, 60 × 25 and 40 × 25 mm or 40 × 30 and 60 × 30 mm. The same stimuli were rotated by 90° for the UDH group. Four permutations were obtained for each of the 3 luminance levels for each group.

The stimuli for the Probe 8 trials (Figure 14.5) were identical for both groups. Permutations consisted of pairs of identical rectangles, one oriented horizontally and the

other vertically, that cold have one of the following dimensions: 25 × 50 mm, 35 × 70 mm, 45 × 90 mm and 55 × 110 mm.

Rat	Training		Probe 7		Probe 8	
	S+	Group	Rule	S+ (●)	Rule	S+ (●)
Rat 5	▬	Horizontal	"choose shape that exceeds other in *any* dimension"	● ▌ ▬	"choose shape that exceeds other in *trained* dimension"	▌ ● ▬
Rat 6	▌	Vertical		● ▬ ▬		● ▌ ▬
Rat 7	▪	Horizontal	"choose shape that is exceeded by other in *any* dimension"	▌ ● ▌	"choose shape that is exceeded by other in *trained* dimension"	● ▌ ▬
Rat 8	▪	Vertical		● ▬ ▬		▌ ● ▬

Figure 14.4. Schematic representation of the rationale and coding system used for probes 7 and 8. The positive shapes (S+) predicted by the rule are marked with ●.

Because the Probe 7 and Probe 8 permutations contained pairs of rectangles and not rectangle-square pairs as the previous stimuli, they required a different coding system for the correct and incorrect responses (Figure 14.4). For both sets of probes, responses were coded as predicted by the hypotheses being tested. Specifically, in the Probe 7 trials nose pokes to the hemiscreen with the largest rectangle of the pair were coded as correct responses for rats 5 and 6 (in UDH and UDV, respectively; both with rectangle as S$^+$) but as incorrect responses for rats 7 and 8 (in UDH and UDV, respectively; both with square as S$^+$). In the Probe 8 trials, nose pokes to the hemiscreen with the vertically oriented rectangle were coded as correct responses for rats 6 (in UDV group with rectangle as S$^+$) and 7 (in UDH group with square as S$^+$). As noted above, it was argued that if rats 6 and 7 had learned to respond to the largest shape in the vertical dimension and to the smallest shape in the horizontal dimension, respectively, they should have now shown a preference for the vertically oriented rectangle as this shape satisfied both conditions. Similarly, nose pokes to the hemiscreen with the horizontally oriented

rectangle were coded as correct responses for rats 5 (in UDH group with rectangle as S$^+$) and 8 (in UDV group with square as S$^+$). If these subjects had learned to respond to the largest shape in the horizontal dimension and to the smallest shape in the vertical dimension, respectively, they should have now shown a preference for the horizontally oriented rectangle in the Probe 8 trials as this shape satisfied both conditions.

Images of the complete sets of probes are provided in Appendix A.

14.9. Results and Discussion

Figure 14.5 shows the mean percent correct discrimination performance in the two probes. For Probe 7, the results from the trials with the size discrepancy in the trained and untrained dimensions are illustrated separately. It can be clearly seen that, although performance was more accurate when the discrepancy was in the trained dimension, all except one of the subjects were able to solve the discrimination with the discrepancy in the untrained dimension. A two-tailed repeated-measures t-test confirmed that correct discrimination performance was similarly accurate when the size discrepancy was in the trained and untrained dimension ($t_{(3)}$ = 2.640, p = .078) suggesting that subjects were able to solve the task with these latter stimuli. However, when performance in the two sets of probes was tested with two two-tailed one-sample t-tests against chance level, it was found that performance was significantly above chance when the discrepancy was in the trained dimension ($t_{(3)}$ = 7.086, p = .006) but that it remained at chance with the discrepancy in the untrained dimension ($t_{(3)}$ = 2.368, p = .099). Thus, although these results provide some preliminary evidence that subjects learned to make the size discrepancy judgement in the dimension not relevant in training, they are not conclusive. Further research in needed to draw any firmer conclusions. Nevertheless, it is of interest to note that the clear ability of these subjects to solve the task with the two rectangles differing in the trained dimension confirms our previous conclusions that these animals made unidimensional judgements and that were not using shape to solve the discrimination.

	Probe 7		Probe 8
Test stimuli			
	Trained	Untrained	
Rat 5	78	56	53
Rat 6	67	67	58
Rat 7	67	50	75
Rat 8	78	67	72
Mean	72.50	60.00	64.50
(s.e.)	(3.18)	(4.22)	(5.33)
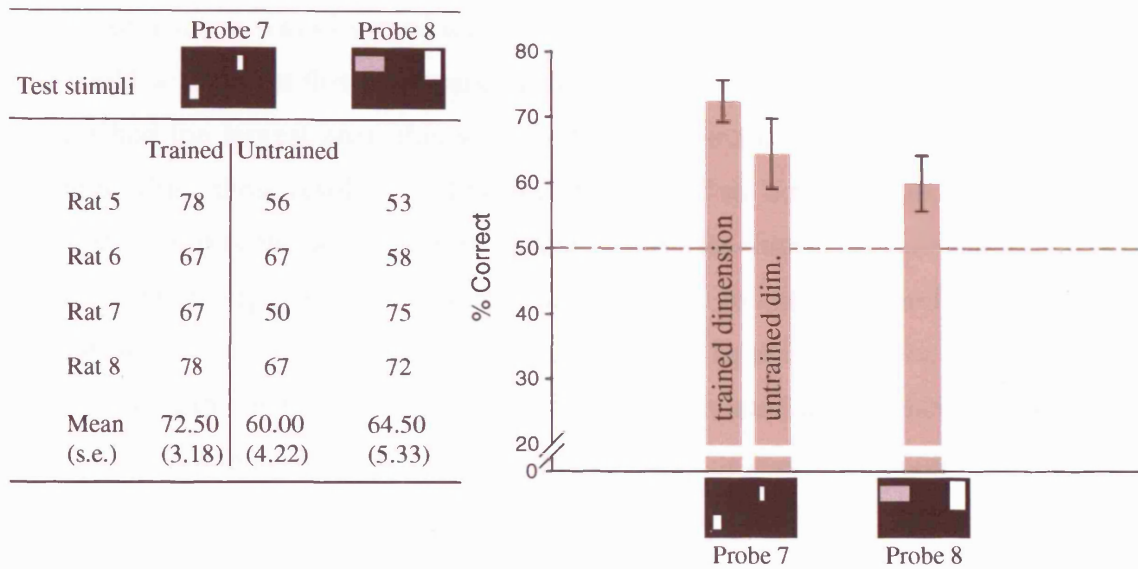
Figure 14.5. Individual (left) and group (right) percent correct performance with the Probe 7 and Probe 8 stimuli. The Trained and Untrained columns contain the results from trials with the size discrepancy in the trained and untrained dimensions, respectively. Error bars indicate the standard errors. The permutations shown are examples taken from the test sets.

Figure 14.5 shows the results from the Probe 8 trials. Although correct performance was in the predicted direction, in particular for rats 7 and 8, the trend was weaker for the two animals with the rectangle as the positive stimulus. In agreement with this observation, a two-tailed one-sample t-test revealed that group performance was at chance level with these stimuli ($t_{(3)} = 2.720$, p = .073). These results could be interpreted to suggest that these animals did not have a preference for using the size discrepancy in the trained dimension. However, the clear difference between subjects with the rectangle (rats 5 and 6) and the square (rats 7 and 8) as the positive stimulus warrant further analysis and investigation.

The performance of rat 6 in these trials is in agreement with its performance in Probe 7, where it performed equally well when the size discrepancy was in the trained and untrained dimensions. However the performance of rat 5 stands in contrast with its performance in Probe 7, where a clear preference for using the discrepancy in the

trained dimension was observed for this animal. One difference between Probe 7 and 8 that could account for this discrepancy is that whereas in the former the largest rectangle always had the largest area, this was not the case for the identical rectangles used in Probe 8. Thus, these results could be accounted for if rat 5 relied more heavily on area than the other rats and was therefore unable to solve the discrimination with the Probe 8 stimuli. This interpretation is however not supported by the good performance of this animal in Probe 6. Alternatively, these results could be accounted for by the different orientation of the rectangle in the two probes as both stimuli had the same orientation in Probe 7 but not in Probe 8. Thus, it is possible that rat 5 was more disturbed by changes in orientation than the other subjects. However, the above accounts are speculative and further research is needed to draw any firmer conclusions.

The good discrimination performance observed for rats 7 and 8 indicates that these animals had a clear preference for using the size discrepancy in the trained dimension. Moreover, because the two rectangles in these stimuli had identical areas, these results rule out the possibility that these subjects used area to make the discrimination. However, as noted before, this study used a small number of subjects. Accordingly, caution should be used when considering these conclusions.

15. General Discussion

This thesis had three main aims. First, it explored whether information about interpolated contours can be used for the calibration of the kinematic parameters in manual prehension. The second aim was to establish whether grasping 2D targets, or visual arrays containing 2D information, engages additional participation from the ventral visual system. The third part of the thesis intended to provide preliminary evidence of representational/perceptual visual processing in rats that could be comparable to those found in the ventral visual system of primates and humans. These points are individually discussed.

15.1. Part 1: Contour Interpolation in Manual Prehension

The first part of the thesis explored whether the dorsal visual system is limited to processing the physically specified properties of the target, that is information explicitly represented on the retina, or whether it can process other signals when these are generated in early visual cortex.

In Experiment 1 this possibility was explored by comparing grasps aimed at 3D, 2D luminance-defined, Kanizsa and Crosses stimuli. The similar kinematic profiles obtained in the 2D luminance-defined, Kanizsa and Crosses conditions suggest that the dorsal visual system had access to the interpolated contours and that this information was used for the calibration of the kinematic parameters. Similar findings were obtained in Experiment 3 where it was found that grasps aimed at partially occluded targets were as accurate as grasps aimed at comparable but fully visible targets. These results clearly suggest that the occluded region was interpolated and made available for the

computation of the kinematic parameters. These findings, if taken together with Experiment 1 and interpreted within the modal/amodal dichotomy that has been proposed for ventral visual processing, suggest that interpolated regions that give rise to both modal and amodal perceptual completion are available to the dorsal visual system for the computation of the kinematic parameters in manual prehension. These results are in agreement with Kellman et al.'s (2001) claim that both types of interpolation are mediated by the same early visual mechanisms.

As noted earlier, an increasing body of evidence suggests that the perception of both modally and amodally completed regions is likely the result of neural interpolation mechanisms in early visual cortex that occur at a single cell level (e.g., Peterhans & von der Heydt, 1989 and Fiorani et al., 1992, 2003; respectively). Moreover, for amodally completed surfaces there is evidence that a good level of accuracy is retained by these interpolation processes (Fiorani et al., 1992, 2003). These conclusions are further supported by psychophysical studies (Dresp & Bonnet, 1995; Rensink & Enns, 1998) and comparative evidence that several species are capable of both modal and amodal completion (e.g., Bravo et al., 1988; Kanizsa et al., 1993, respectively). Taken together, this converging evidence suggests that the interpolated signals giving rise to both types of perceptual completion are present in early visual areas, that is in areas that precede the anatomical separation between the two visual systems. Thus, the most likely explanation for the findings of Experiments 1 and 3 is that the interpolated signals were fed to both visual systems and that this information was therefore directly available to the dorsal system for the control of the movement. These results are therefore in agreement with Dyde and Milner's (2002; also Milner and Dyde, 2003) proposal that this latter can process non-physically specified signals when these are the product of areas common to both systems.

The finding that neural interpolation occurs in the dorsal visual system is plausible and in agreement with the observation that visuomotor performance is not impaired by the lack of visual signals at the blind spot. As noted earlier, the most striking example of

modal perceptual completion occurs at the blind spot. The blind spot corresponds to the optic nerve at the retina and in humans it extends approximately 7.5° in height and 5.0° in width and is located about 15° from the fovea (Fiorani et al., 2003). Remarkably, both contour and surface interpolation occur at this site and as a result we are not normally aware of the discontinuity in the retinal signal at this location (for review, see Pessoa & De Weerd, 2003). Although at present no study has directly investigated how neural interpolation at the blind spot is processed in the dorsal visual system, the observation that visuomotor performance is not impaired by the lack of processing at this retinal location strongly suggests that these interpolated signals are likely processed by this system. Thus, Experiments 1 and 3 suggest that, in addition to processing interpolated signals covering the region of the blind spot, the dorsal visual system also processes the other two known types of neural interpolation: Those known to give rise to modal and amodal perceptual completion. These findings are in agreement with the claim that these three types of neural interpolation are likely to result from the same general visual mechanisms as it is improbable that the visual system developed dedicated neural circuits for each of these interpolation processes (Ramachandran, 2003).

From an evolutionary perspective, the findings presented in this thesis are also plausible. Perceptual completion fulfils a valuable biological function as collinear oriented edges on the retina often reflect actual occlusion in the natural scene. Accordingly, neural/perceptual interpolation often results in an accurate interpretation of the scene (Mendola, 2003). As noted earlier, partially occluded objects are ubiquitous in nature and are likely to act not only as targets but also as obstacles in several visuomotor responses (Fiorani et al., 2003). Thus, interaction with, and navigation among, partially occluded objects would be substantially improved in organisms with a dorsal visual system capable of using the interpolated regions of these objects in its computations.

The above interpretation is based on the assumption that the interpolated signal was processed in the dorsal visual system and that it was therefore available throughout movement execution. However, an alternative account that cannot be ruled out by the present studies is that the interpolated signal was exclusively processed in the ventral visual system and that this participated in the selection of the grasp points in the grasping task. As previously discussed, this phase of the movement can be modulated by the ventral visual system under certain conditions, specifically, when previous knowledge about the target is required for the computation of movement parameters such as weight and affordances that are not directly derivable from the visual array (Goodale & Haffenden, 2003).

It could be argued that it is unlikely that the Kanizsa and Crosses stimuli of Experiment 1 and the Occluded condition of Experiment 3 recruited participation from the ventral visual system as it is unclear how previous knowledge about the target would be required for grasping these stimuli. However, a recent study by McIntosh, Dijkerman, Mon-Williams and Milner (2004) suggests that greater ventral stream participation might also be required for selecting the grasp points on targets that are visually complex. McIntosh et al. (2004) tested DF with a hole-grasping task where the objects had to be grasped by inserting the thumb and index finger into two large holes in its surface. The target was made to appear as if it was of three different shapes by painting some regions of its transparent top surface in black. McIntosh et al. (2004) found that, unlike controls, DF was unable to grasp these targets. The possibility that this impairment was due to an inability to encode spatial separation for visuomotor control was ruled out by DF's normal grasping responses with pairs of spatially separated rectangles that had to be grasped as a single object. McIntosh et al. (2004) concluded that DF's poor performance might have resulted from an inability to visually process the relatively complex stimuli, in particular the transparent regions, and that the dorsal system might not have the capacity for processing the fine details of the target object.

McIntosh et al.'s (2004) findings are significant as they suggest that the dorsal visual system does not only require ventral stream participation for the use of properties, such as weight and affordances, that are not fully specified in the visual array and therefore need the mediation of cognitive systems. Instead, they suggest that ventral participation might also be necessary for the use of properties that are entirely available in the visual array. This account has direct implications for the interpretation of Experiments 1 and 3 as it opens the possibility that the visual complexity of the Kanizsa, Crosses and Occluded stimuli might have engaged additional ventral stream participation for the computation of the grasp points. This possibility is made more plausible if it is considered that both modal and amodal completion are likely to entail a detailed analysis of surface properties as the occluding and occluded regions in the target array must be identified. Thus, according to this latter interpretation, the interpolated signal in the ventral and not in the dorsal visual system would have been used for the selection of the grasp points in the Kanizsa, Crosses and Occluded conditions. Notably, this account could also explain the lack of differences found in Experiment 1 between the 2D luminance-defined and the Kanizsa and Crosses conditions. Although the luminance defined border in the former stimuli would have been sufficiently simple to allow the selection of the grasp points based on dorsal processing alone, the presence of the inducers could have added visual complexity to the display. Similarly, McIntosh et al.'s (2004) account could explain the lack of differences between the Clear and Occluded conditions in Experiment 3 as the transparent occluding circle in the former could also have added visual complexity to the display.

It is important to note that McIntosh et al.'s (2004) findings and conclusions are not in disagreement with the initial dual-systems model proposed by Milner and Goodale (1995) as this has always maintained that, despite their functional specialization, there is intense collaboration between the two systems. In particular, as discussed previously, Milner and Goodale (1995; also Goodale, 1998; Goodale & Haffenden, 2003) have proposed that one of the roles of the ventral system is to provide information about the relative location of target objects and their properties such as weight and affordances

that is likely used in the initial planning of the movement. However, it is important to distinguish this ventrally mediated action planning phase from the action selection which depends on dorsal visual processing (Goodale & Milner, 2004). Goodale (1998) illustrates this distinction with a good example. He points out that when we pick up a cup of coffea it is the ventral system that provides information about whether the cup is full of coffea, its weight, and its relative location on the table. However, this information is not sufficient for guiding the action. Once the cup has been 'flagged' by the ventral system, the initial movement parameters are determined by processes in the dorsal system. These latter will compute the target size, shape, location and orientation in egocentric coordinates that will be used for the calibration of the kinematic parameters of the action.

Of course, in such a framework, the degree of ventral stream participation required in action planning cannot be fixed but it is more likely to depend on factors such as the visual and functional complexity of the target. Thus, McIntosh et al.'s (2004) findings can be easily accounted for by the existing framework as processing the transparent regions of the target, or other fine details, is likely to require a greater degree of ventral stream participation than for visually simpler targets. Indeed, this point was explicitly made by McIntosh et al. (2004) who claimed that whereas some simple objects may require little ventral stream participation in the planning phase, more complex targets may require more. Thus, McIntosh et al.'s (2004) findings do not substantially change the dual-systems model initially proposed by Milner and Goodale (1995) but they highlight the possibility that the dorsal visual system may require ventral stream participation for the mediation of a greater number of visuomotor tasks than initially suggested.

Experiment 2 explored the localization accuracy of luminance-defined contours, Kanizsa contours and interpolated gaps in the ventral visual system with a three-line Vernier acuity task. It was predicted that if the ventral visual system had access to the Kanizsa contours, localization with these stimuli should have been more accurate than

localization of the interpolated gaps in the crosses. The Vernier task revealed no significant difference in the localization threshold of these two conditions suggesting that the illusory contour did not improve localization accuracy. As noted above, in Experiment 1 it was found that Kanizsa contours and interpolated gaps were localized with similar accuracy in a visuomotor task. Similarly, in this experiment the localization of these stimuli was found to be equally accurate in a ventrally mediated task. Given the correspondence between these findings, the results from Experiment 2 cannot rule out the possibility that the accurate performance observed in Experiment 1 with the interpolated contours was due to the participation of ventral visual processing. Ventral stream participation could also account for the use of interpolated information in Experiment 3. These possibilities cannot be entirely ruled out by the present investigations, however, as noted earlier, replicating these experiments with visual agnosic patients such as DF would provide a clear way to disentangle the two accounts. Specifically, if the use of the modal or amodal interpolated signals in the visuomotor task was due ventral stream participation, these patients should not be able to adjust their grip aperture according to the size of the interpolated region.

In any case, even if future investigations will show that this latter account is more plausible, the results from Experiments 1 and 3 clearly suggest that non-physically specified interpolated signals *are used* for the computation of the kinematic parameters of manual prehension. Thus, they would provide new evidence about the type of visual information that can be used in the mediation of visually guided action.

Lastly, it should be noted that the equivalent performance in the 2D-luminance and Crosses conditions is in agreement with Kellman et al.'s (2001) claim that contour interpolation occurs when appropriately oriented edges are present in the visual array and that this process in independent of whether the contour is perceptually experienced or not. According to these authors, the quality of the perceptual experience generated by neural interpolation is likely to depend on subsequent processes occurring at higher levels in the visual hierarchy, such as depth ordering, that could modulate the boundary

interpolation mechanism. Although not formally tested in this thesis, the patterns used in the Crosses condition generally do not result in the perception of illusory contours (Davis & Driver, 1998). Therefore, it is reasonable to assume that the higher level mechanisms postulated by Kellman et al. (2001) to follow neural interpolation and nullify the perception of the interpolated contour were fully operating in the ventral visual system when participants were presented with these stimuli. By contrast, the accurate visuomotor performance observed with these stimuli in Experiment 1 suggests that these higher level mechanisms were not operating in the dorsal visual system. Thus, these results could provide some preliminary evidence of a further dissociation between ventral and dorsal visual processing that has never been addressed before in this area of research.

This latter account is plausible at an anatomical level as one would expect these higher level mechanisms to be located well within the ventral visual system. However, it is less clear whether it would be evolutionary advantageous for organisms to have a dorsal visual system that processes interpolated contours even when these do not give rise to a perceptual experience. Particularly, if it is considered that the higher level "vetoing" mechanisms postulated by Kellman et al. (2001) are not arbitrary and often result in a correct interpretation of the scene. More studies are needed to further address the exact advantages of having such a distribution of visual processing. However, one possibility is that the dorsal visual system does not rely on the higher level "vetoing" mechanisms as these could occasionally result in an inaccurate interpretation of the scene. This account would be in agreement with the dorsal visual system's requirements for accuracy originally postulated by Milner and Goodale (1995).

Alternatively, it could also be possible that the task used in Experiments 1 and 3 (i.e., forced grasping aimed at interpolated gaps) revealed a property of the dorsal system that has little applications in nature. That is, it is possible that, as suggested by the present results, the dorsal system has access to accurate interpolated information, and that this is revealed under the experimental paradigm used in the thesis, but that these conditions

rarely occur in nature. Indeed it is unlikely that under natural conditions an observer would initiate a visuomotor response towards a region of the display that is not perceived. In particular, if it is considered that the action planning phase that identifies the object to be grasped is largely mediated by ventral visual processing. Future research will perhaps provide answers for some of these questions.

15.2. Part 2: The Effect of Target Dimensionality on Manual Prehension

The second part of the thesis explored the effect of target dimensionality on visually guided manual prehension. Particularly, whether grasping 2D targets, or target arrays containing 2D information, could recruit additional participation from the ventral visual system for the mediation of a visuomotor task. In nature, except for pointing, which can occur towards 2D stimuli (e.g., a spot on a leopard), visually guided responses such as grasping and posting require three-dimensional objects. Thus, it was of interest to establish whether the dorsal visual system mediates visually guided action aimed at 2D targets, that is targets that are likely to have little functional relevance for visuomotor behaviour.

Experiment 4 explored the possibility that 2D elements in an illusion display could recruit additional ventral stream participation and could therefore account for the illusion effects on action reported in previous studies (e.g., Daprati & Gentilucci, 1997). This hypothesis was tested by measuring whether the Diagonal illusion, a phenomenon never investigated before and entirely produced by 3D objects, exerted an effect on action. It was argued that because such an effect could not have been due to the presence of 2D elements in the display, it would have conclusively ruled out that such cues could have accounted for the illusion effects on action previously reported. The results from Experiment 4 are quite clear as it was found that maximum grip aperture was affected by the Diagonal illusion, although to a smaller extent than the perceptual

task. Thus, these results rule out the possibility that the illusion effect on action reported in previous studies could have been due to the presence of 2D elements in the illusion display. By implication, these results suggest that 2D elements in the target array do not recruit additional participation from the ventral visual system and that dorsal mechanisms mediate action towards these targets.

Experiment 5 confirmed that the greater maximum grip aperture observed in Experiment 4 for the notched circle was due to the effect of the illusion and not to potentially confounding variables that could have arisen from physical differences between the two target shapes in the display. Specifically, in Experiment 5 an illusion effect on action was found when the curvatures of the notched circle and differences in the degree of complexity and extension on the non-grip axes of the two shapes had been fully controlled.

The conclusion that 2D information in the visual display does not recruit additional participation from ventral visual processing is also supported by the results from Experiment 6, where it was found that changes to target dimensionality only affected two kinematic parameters. Specifically, grasping 3D targets resulted in earlier maximum grip apertures and greater wrist displacements relative to grasping both 2D-enhanced and 2D targets, however it did not significantly affect any of the other parameters. Moreover, similar effects of the Diagonal illusion were observed with all target dimensionalities. Taken together, these results suggest that the dorsal visual system mediates grasping aimed at targets that lack a 3D structure. These conclusions are in agreement with Westwood et al. (2002) who found comparable results with normal subjects and that DF, the visual form agnosic, was able to adjust her grip aperture according to the size of 2D and 2D-enhanced targets.

The finding that action aimed at 2D objects is mediated by the dorsal visual system has substantial implications for further research as it suggests that the functional properties of this system could be investigated with traditional computer displays and virtual

reality environments. The applications of 2D displays to visuomotor research could be numerous and make a valuable contribution to our understanding of the dorsal visual system. Particularly, if it is considered that a large portion of what is currently known about the "visual system" has been investigated with perceptual responses and therefore is likely to reflect properties of ventral rather than dorsal visual mechanisms. It can therefore be argued that comparatively less information is known about the properties of these latter. For instance, it would be of interest to explore whether this system can extract shape from texture and motion.

Nevertheless, in Experiment 6 some differences were found between grasping 2D and 3D objects and it was suggested that these findings could have reflected a greater demand for accuracy in the grasping task with the 3D targets. Smeets and Brenner's (1999) model of grasping was used to illustrate how the surface selected for the contact points, the size of this surface and the requirement for an orthogonal approach could have accounted for this claim. Moreover, it was noted how Smeets and Brenner's (1999) model could also account for the lack of differences in maximum grip aperture observed between the 2D and 3D targets in Experiment 6. Notably, this model could explain why a similar comparison resulted in larger grip apertures for the 3D condition in Experiment 1. Although Experiment 1 did not directly address the effect of target dimensionality on manual prehension, grasping 3D and 2D luminance-defined squares were compared in that study and the former resulted in greater and earlier maximum grip apertures.

Figure 15.1 illustrates the model applied to the stimuli used in Experiment 1 (a and b) and Experiment 6 (c and d). A claim of Smeets and Brenner's (1999) model is that the demand for accuracy increased as an inverse function of contact surface size. Thus, smaller surfaces should be approached more orthogonally and should result in larger and earlier grip apertures. As shown in the figure, whereas the squares in Experiment 1 were grasped front-to-back, in Experiment 6 they were grasped along their diagonal. Thus, due to a reduction in contact surface size in this latter experiment, grasping along

the diagonal *per se* could have increased the demand for greater accuracy in the 2D task. If this increased grip aperture in the 2D condition it could have attenuated the difference with the 3D condition in this study. Alternatively, it could be possible that vertically positioning the stimuli, as it was used in Experiment 6, affected the results either by changing the demand for accuracy or in some other way. Future studies could test this possibility by replicating Experiment 6 with horizontally placed stimuli.

(a): 2D target in Experiment 1   (b): 3D target in Experiment 1

(c): 2D target in Experiment 6   (d): 3D target in Experiment 6
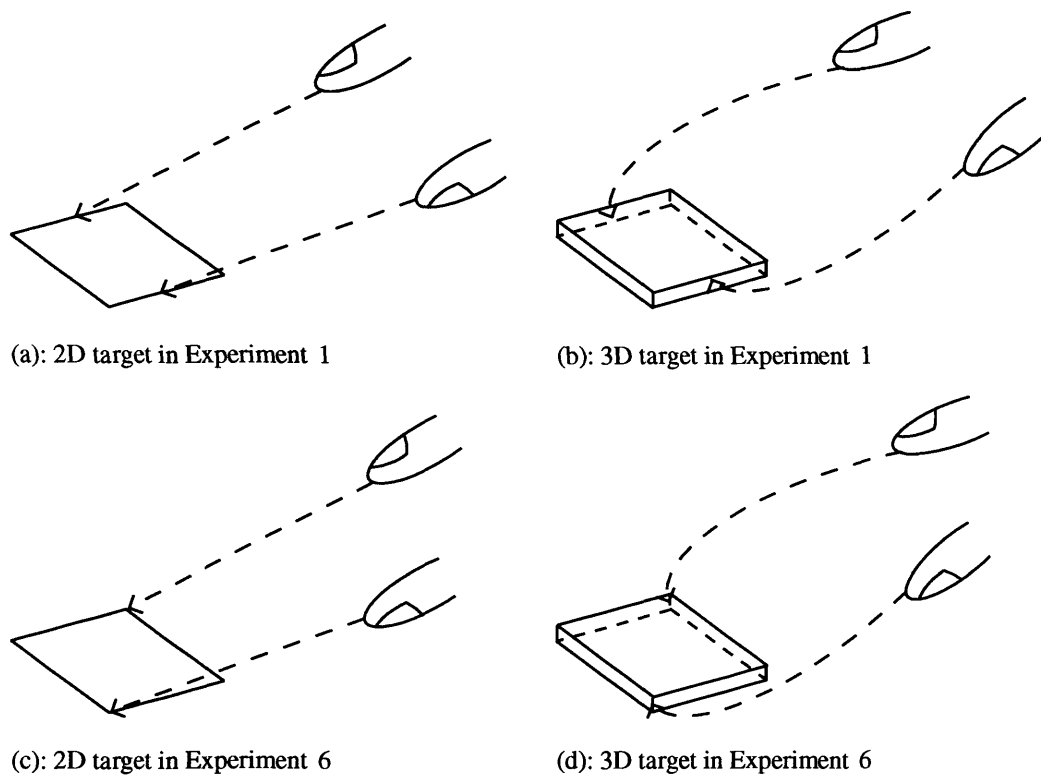
Figure 15.1. Trajectories of the thumb and index finger orthogonally approaching the suitable positions on 2D and 3D targets in Experiments 1 (a and b, respectively) and 6 (c and d, respectively).

It is of interest to note that Smeets and Brenner's (1999) claim that increased accuracy demands rather than the introduction of 2D elements in the display would result in larger and earlier grip apertures is also supported by the comparison between Experiments 4 and 5. Larger grip apertures were observed in Experiment 5, where participants had to grasp metal bars superimposed to 2D renditions of the target shapes.

Thus, unlike Experiments 1 and 6, in this comparison the version with the 2D elements resulted in larger grip apertures. As discussed in Chapter 5, due to their small size and a low luminance contrast with the background the metal bars in Experiment 5 could have been construed as a target requiring greater accuracy. Thus, as predicted by Smeets and Brenner's (1999) model the more difficult task resulted in larger grip apertures in this comparison. Finally, it is of interest to note that this model could also explain the larger and earlier grip apertures observed in the Whole condition of Experiment 3 as this was the only condition involving grasping the 3D target along its thin sides. The remaining three conditions in this study provided a larger contact surface size for the index finger.

Smeets and Brenner's (1999) model suggests that grasping tasks might differ in their level of difficulty and that this could affect the approach parameter and ultimately how the movement kinematics are computed by the visuomotor system. In the first part of this discussion it was noted that the dorsal visual system might not be capable of processing the fine details of visually complex stimuli and that, under these instances, the selection of the contact points might be carried out by ventral visual mechanisms (McIntosh et al., 2004). Thus McIntosh et al.'s (2004) findings suggest that increased task difficulty due to visual complexity may recruit additional participation from the ventral visual system for the mediation of visuomotor responses. By contrast, the evidence from the experiments presented in this thesis and from other studies that compared grasping 2D and 3D targets (Kwok & Braddick, 2003; Westwood et al., 2002) suggests that, although the latter might be construed as a more difficult task, these responses seem to be mediated by the dorsal visual system. It is therefore a challenge for future research to explore how exactly task difficulty can affect the kinematic parameters of manual prehension with particular attention to the factors that determine which visual system will mediate the task. Of course, in order to pursue such investigations task difficulty must be quantified. Task difficulty is likely to depend on a confluence of factors, including contact surface size, shape symmetry and whether the target is grasped along the natural grasp-axis. As discussed earlier, task difficulty is likely to be inversely related to these factors: Grasps aimed at small contact surfaces,

asymmetrical objects and along orientations that deviate from the natural grasp-axis should be more difficult. More generally, factors that facilitate holding the object in place and its manipulation are likely to contribute to task difficulty. It is a challenge for future research to fully identify these factors and to establish their relative contribution to task difficulty.

15.3. Methodology: The Effect of Haptic Feedback

Experiment 7 explored two methodological questions still unaddressed in this area of research. The first examined whether the differences in maximum grip apertures generally observed between manual estimation and grasping tasks could be accounted for by differences in haptic feedback in these conditions. This could be a possibility given that haptic feedback is available after each grasping trial but absent in manual estimation. Some authors have controlled for this potential confounding factor by asking participants to reach out and grasp the target after each manual estimation (Ganel & Goodale, 2003; Haffenden & Goodale, 2000, Haffenden Schiff & Goodale, 2001; Hu, & Goodale, 2000; Hu, Goodale & Eagleson, 1999). However, this control measure is not universally used and the changes resulting from introducing haptic feedback have not been directly and formally assessed. Thus, at present it still remains unclear whether this control measure should be universally adopted.

This experiment explored the above question by comparing the maximum grip apertures from a manual estimation task with the apertures from a task where participants were asked to grasp the target after each manual estimation trial. No significant differences were found in this comparison clearly suggesting that adding haptic feedback to manual estimation did not have an effect. Thus, these results suggest that the differences in maximum grip aperture observed between manual estimation and grasping tasks are not attributable to differences in haptic feedback. The methodological implication of these findings is that manual estimation tasks can be performed without having to control for the lack of haptic feedback.

The second methodological question explored whether irregular haptic feedback potentially generated by misreaching in open loop grasping tasks that do not require lifting the target could account for differences in the kinematic profiles of closed and open loop grasping. Although grasp-and-lift open loop procedures can prevent to a large extent the occurrence of misreaching, open loop tasks that do not require lifting the target cannot control for this possibility. Importantly, this latter version of the open loop procedures has been used in several studies (Culham et al., 2003; Dijkerman et al., 1996; Dijkerman et al., 1999; James et al., 2003; Kwok & Braddick, 2003; McIntosh et al., 2004) and in the experiments presented in this thesis. The above question was explored by measuring whether adding regular haptic feedback to this second version of the open loop procedure affected the kinematic profile. No significant differences were found clearly suggesting that both versions of the open loop procedure, grasp-and-lift and grasp only, result in similar kinematic profiles and can be equally used.

Finally, it should be noted that the finding that changes to haptic feedback did not affect grasping has implications for the interpretation of some of the results in Experiments 1, 3 and 6. Specifically, the present finding suggests that differences in haptic feedback in the stimuli of Experiments 1, 3 and 6 are unlikely to account for the differences in the kinematic profiles observed in those studies.

15.4. Part 3: Representational Networks in Rats

The third part of the thesis sought to provide preliminary evidence for the existence of representational/perceptual networks in rats and to explore some of the properties of ventral visual representations in this species.

Experiments 8, 9 and preliminary experiment 10a began by asking whether rats perceive Kanizsa illusory shape and the remainder of Experiment 10 and Experiment 11 focussed on whether rats use shape *at all* to solve visual discriminations. In Experiment 8 it was

found that subjects were able to solve the discrimination with Kanizsa figures. However, these results were not replicated when the study was repeated with a more stringent counterbalancing procedure in Experiment 9 and preliminary experiment 10b suggesting that rats do not perceive Kanizsa illusory figures. The positive transfer obtained with the outline stimuli in preliminary experiment 10b confirmed that these animals did not fail to transfer to the Kanizsa stimuli due to poor generalization abilities. More surprising, however, was the finding that these animals did not use luminance-defined shape to solve the discrimination but that they relied on a more low-level cue, namely luminance differences in the lower hemifield. When these differences were reversed a significant preference for the negative shape was observed. Although the small number of subjects used in some of these experiments does not allow strong conclusions to be drawn, taken together these results suggest that subjects did not use "squareness" or "triangleness" to solve the task but that instead responded to the shape with the smallest/largest luminance in the lower portion of the visual field. The preference for processing visual stimuli in the lower hemifield observed in this study has been also reported by other authors (Lashley, 1938, Simpson & Gaffan, 1999; Sutherland, 1961).

The above conclusions are further strengthened by the findings from Experiment 11 where it was found that rats could use shape (aspect ratio) to discriminate between squares and rectangles when they were prevented from using luminance differences in the lower hemifield. However, a very large number of trials was needed to reach levels of performance well below criterion and a big decrement was observed relative to subjects presented with the unidimensional discrimination. Although these results clearly show that the former animals were able to use aspect ratio, and by implication shape, to solve the task they also suggest that this stimulus property is not naturally used by this species to solve visual discriminations of this type. This conclusion is further supported by the observation that subjects presented with the unidimensional discrimination did not learn to use aspect ratio when this was readily available and that the rats forced to use aspect ratio adopted a luminance-based response strategy when

luminance differences were inadvertently introduced at the beginning of training. Taken together, these results suggest that rats can use aspect ratio, and by implication shape, to solve visual discriminations *when no other constant discriminative cue is available*, however, that whenever possible, these animals will try to use a simpler response strategy that could be based on either local or global luminance differences.

Nevertheless, the subject presented with the aspect ratio discrimination were successfully trained with a complex training procedure and stimuli varying in size and location providing evidence of size and translational invariances in this species. This conclusion is further supported by these animals' ability to successfully transfer to stimuli with novel sizes and presented at novel locations. Rotation invariance was not explicitly tested in this group, however, the finding that some of the rats presented with the unidimensional discrimination were able to make the size relative judgement in the untrained dimension in some of the probe trials provides some evidence of rotation-independent recognition in this species. Thus, the results from this experiment also provide evidence of size and translational invariance in rats.

Taken together, the results from Experiment 11 provide preliminary evidence that rats have representational/perceptual visual mechanisms comparable to some extent to those found in the ventral visual system of humans and primates. Specifically, the first part of the study provides evidence that rats can use shape to solve visual discrimination tasks. Importantly, this ability was assessed with a highly variable and large stimulus set where both local and global luminance were, as far as it could be determined, fully controlled. The transfer tests in the second part of the study provide preliminary evidence that this species is capable of shape constancy. In the two-visual-systems model (Milner & Goodale, 1995), visual processing in the ventral but not the dorsal visual system depends on representations that are viewpoint-independent and based on relative metrics. By contrast, the representations in the dorsal system that mediate the guidance of object-directed action are based on stimulus-specific metrics that are egocentrically coded. The ability to use shape irrespective of size and location, that is

shape constancy, requires viewpoint-independent processing based on relative metrics. Thus, the finding that rats are capable of shape constancy provides evidence of ventral visual processing in this species and suggests that these animals might have object recognition mechanisms comparable to that of humans and primates.

Of course, there are substantial neurophysiological and behavioural differences between humans, primates and rodents that need to be addressed before extending the two-visual-systems model to rats. For instance, manual prehension in humans cannot be easily compared with the use of paws in rats. Nevertheless, whereas it is probably correct to say that the main function of vision in rats is to mediate visuomotor behaviour (Goodale & Carey, 1990), the present findings suggest that rats have additional visual processing that are viewpoint-independent and use relative metrics. Thus, these findings are in agreement with the small number of studies that support the existence of two modes of visual processing in rodents (Kolb, 1990; Kolb et al., 1994).

The present findings have significant implications as they suggest that rats can provide a suitable model for investigating the cortical visual parcellation of function in lower mammals. This would be useful for several reasons. First, rodent neurobiological studies could further our understanding of the neurobiology of the two visual systems, especially with newly emerging transgenic models and lesion and single cells studies that could be performed with this species. Second, further research could explore whether, as proposed by Ellard (2002), the homologue of the occipitotemporal system in rodents also mediates movement and navigation. Such findings could be used to establish whether the evolution of the representational/perceptual visual system preceded the anatomical parcellation in phylogeny (Ellard, 2002). Finally, evidence of a real homologue of the ventral visual system in rodents might lead to a conceptualization of ventral visual processing that does not require association with conscious experience.

It is also of interest to note that the present results have clear implications for studies that use visual discrimination in this species. The ability to use local luminance

differences observed in Experiment 10 clearly suggests that equiluminant stimuli, a control strategy often adopted in visual discriminations studies, are not sufficient to rule out the use of luminance as a discriminative cue. Moreover, the sharp decrement observed for the rats forced to use aspect ratio in Experiment 11, when new shapes were introduced to foil a "choose/avoid extreme sized shapes" strategy, suggests that rats will try to use simple luminance-based strategies even when presented with more complex learning tasks. Thus, these results suggest that both local and global luminance differences should be fully controlled in visual discrimination studies with this species.

However, more interestingly perhaps, such a readiness to use luminance differences could underline some fundamental aspect of visual processing in this species. Specifically, these results could be due to a limited capacity for processing the global shape of the stimuli or to an inability to discover shape as the discriminative cue. There is little doubt that the visual discrimination tasks and geometric shapes used in this thesis were not naturalistic and were unlikely to have had any ecological significance for these animals. Thus, if rats have some innate preference for processing stimuli with ecological significance as suggested by some authors (Ingle, 1978), it is possible that the lack of ecological relevance in the response mode, apparatus and stimuli of these studies lead to a failure to discover shape as the discriminative cue. Future studies exploring visual function in rats should try to create more natural settings and use more relevant stimuli. However, some sparse but converging evidence also supports the view that rats might have limited visual abilities for processing global shape. First, rats have been found to have a diminished capacity, relative to humans, to use proximity and alignment cues for perceptual grouping (Kurylo, Van Nest & Knepper, 1997). Kurylo et al. (1997) found that rats trained to discriminate horizontal from vertical solid luminance-defined lines did not readily transfer to arrays of similar orientations that consisted of disjoint elements (dots) varying in proximity and alignment. Specifically, Kurylo et al. (1997) found that proximity was used as a cue for perceptual grouping, however, its effectiveness was diminished relative to humans. Moreover, alignment was not used by rats as a grouping cue when tested in isolation. A diminished ability to use

proximity and alignment cues for perceptual grouping would likely result in poorer object recognition in this species, in particular it would diminish these animals' ability to use shape as a discriminative cue. Thus, such diminished ability could provide an explanation for the reluctance of rats to use shape to solve visual discriminations.

The above account is further supported by antipredator behaviour studies in gerbils that found that these animals exhibit avoidance behaviour in the presence of an overhead object regardless of its shape, size, speed or trajectory (Ellard, 1998). Rather, gerbils seem to base their fleeing response on contextual factors such as the familiarity of the spatial context, that is, they seem to use *where* an object is rather than *what* it is (Ellard, 1998). These studies suggest that shape is not used by these animals to identify overhead objects as potential treats and, taken together with the present and Kurylo et al.'s (1997) findings, might underline a more general inability of rodents to use shape to solve a variety of visual tasks.

More studies are needed to draw any firmer conclusions on the rat's ability to process visual stimuli. However, despite the potential limitations of the rat's visual system, the present findings provide evidence that rats are capable of using shape and shape constancy to solve visual discrimination tasks and that therefore these animals are likely to have visual processing other than those mediating visuomotor behaviour. Due to a faster learning rate and flexibility and control over stimulus presentation, the automated touchscreen developed in this study provides a valuable apparatus to further investigate the exact nature of the different modes of visual processing in rats. Future investigations could combine training in this apparatus with psychophysical, lesion and single cells recording techniques.

15.4.1. The Touchscreen Apparatus

The final part of this chapter discusses the contribution made by the touchscreen apparatus developed in this thesis to the methods currently available for the study of

visual processing in rats. To our knowledge, there are only a very small number of published reports that have used touchscreen apparatuses to test visual discrimination in this species (Bussey et al., 1994; Cook et al., 2004; Keller et al., 2000; Markham, et al., 1996; Sahgal & Stickler, 1994). However, as already pointed out by other authors (Gaffan & Woolmore, 1996), in these studies good levels of learning were achieved generally after unique modifications to the apparatuses and/or after laborious shaping techniques. For instance, in the apparatus used by Bussey et al. (1994) the stimuli had to be displayed above a shelf placed approximately 15 cm from the floor so that the animals had to stop, rear up and lean towards the stimuli before nose poking the screen. It could be argued that rats do not naturally interact with visual stimuli in this way and that this procedure could have added complexity to the discrimination task. Similarly, Markham et al. (1996) did not obtain good levels of learning until the touchscreen was made slightly movable. The authors themselves admitted that it was unclear why this modification improved learning. Except for the introduction of the touchscreen, and therefore of nose pokes as the response mode, in the apparatus developed for this thesis good levels of learning were obtained without introducing any major modifications to the procedure traditionally used in dual discrimination boxes. Although it could be argued that manual shaping in Experiment 10 was slightly complex, Experiment 11 clearly demonstrates that this pretraining phase was not necessary to obtain good levels of learning in this apparatus.

An additional advantage of this apparatus is that nose pokes could be recorded directly from pressure changes on the screen. Previously used comparable apparatuses used either infrared (Bussey et al., 1994; Keller et al., 2000) or resistive (Markham et al., 1996; Sahgal & Steckler, 1994) touchscreens. The former introduce a distance, albeit small, between the screen and the point at which the response is recorded and the latter have a water-sensitive membrane that has to be protected. The touchscreen used in this study is free from these shortcomings and it could therefore provide a more suitable tool for investigating visual processing in rodents. Finally, whereas other trouchscreens have modified standard operant conditioning chambers with a relatively short discrimination

area, this apparatus combined in a unique way a long discrimination area with the reward site placed at the opposite side of the screen. These features could be suitable for investigating a variety of visually guided behaviour in rats.

15.5. Conclusions

This thesis explored two original questions related to the two-visual-systems model in humans. First, it explored whether interpolated information is available to the dorsal visual system for the mediation of visually guided manual prehension. The findings reported make a significant contribution to what is currently known about the properties of the two visual systems. Experiments 1 and 3 clearly suggest that interpolated information is used in the mediation of manual prehension. Both studies have raised the question of whether the interpolated information is processed in the dorsal or ventral visual system and suggestions for further research that could help to clarify this point were proposed. It is hoped that future studies will explore these possibilities.

The second question explored whether manual prehension is mediated by the dorsal visual system when aimed at targets that lack, either partly or entirely, a 3D structure. The effect found on action with the Diagonal illusion, a phenomenon never investigated before in this area of research and entirely the product of three-dimensional objects, conclusively ruled out that the effect on action reported in previous studies might have been due to the presence of 2D elements in the illusion displays. Experiment 6 confirmed that actions aimed at 2D objects are mediated by the dorsal visual system, although as suggested by Smeets and Brenner's (1999) new model of grasping these movements might be construed as requiring less accuracy than actions aimed at 3D targets. These findings have substantial implications for the methodologies that might be used in future explorations of the two-visual-systems model (Milner & Goodale, 1995) as they suggest that dorsal visual mechanisms could be explored with traditional computer displays and virtual reality settings.

Finally, the third part of the thesis attempted to provide preliminary evidence that rats have representational/perceptual visual processing comparable to those found in the ventral visual system of humans and primates. Although the illusion studies are not conclusive, Experiment 11 found evidence of shape constancy in this species. Taken together, these results are significant as they provide preliminary evidence for the existence of visual processing of a representational/perceptual nature in rats and are encouraging in suggesting that further investigations of the two-visual-systems model could be pursued in this species. The automated touchscreen apparatus developed in the thesis would provide a valuable tool to further explore the nature of the different modes of visual processing in rodents.

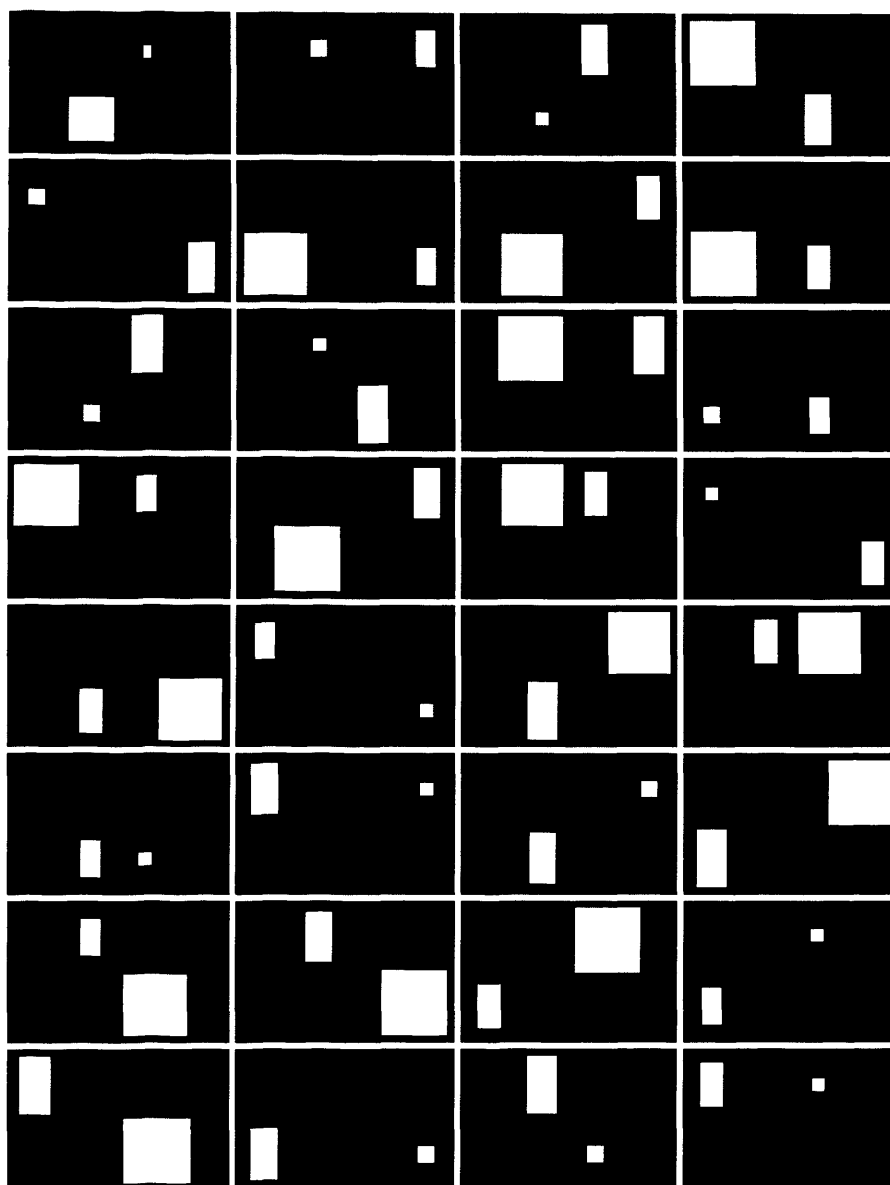# Appendix A. Stimuli relating to Experiment 11

Figure A.1. The complete set of stimuli (32 permutations) used for the Bidimensional Discrimination group introduced at the start of the study. This consisted of medium-sized rectangles paired with very large or very small squares.
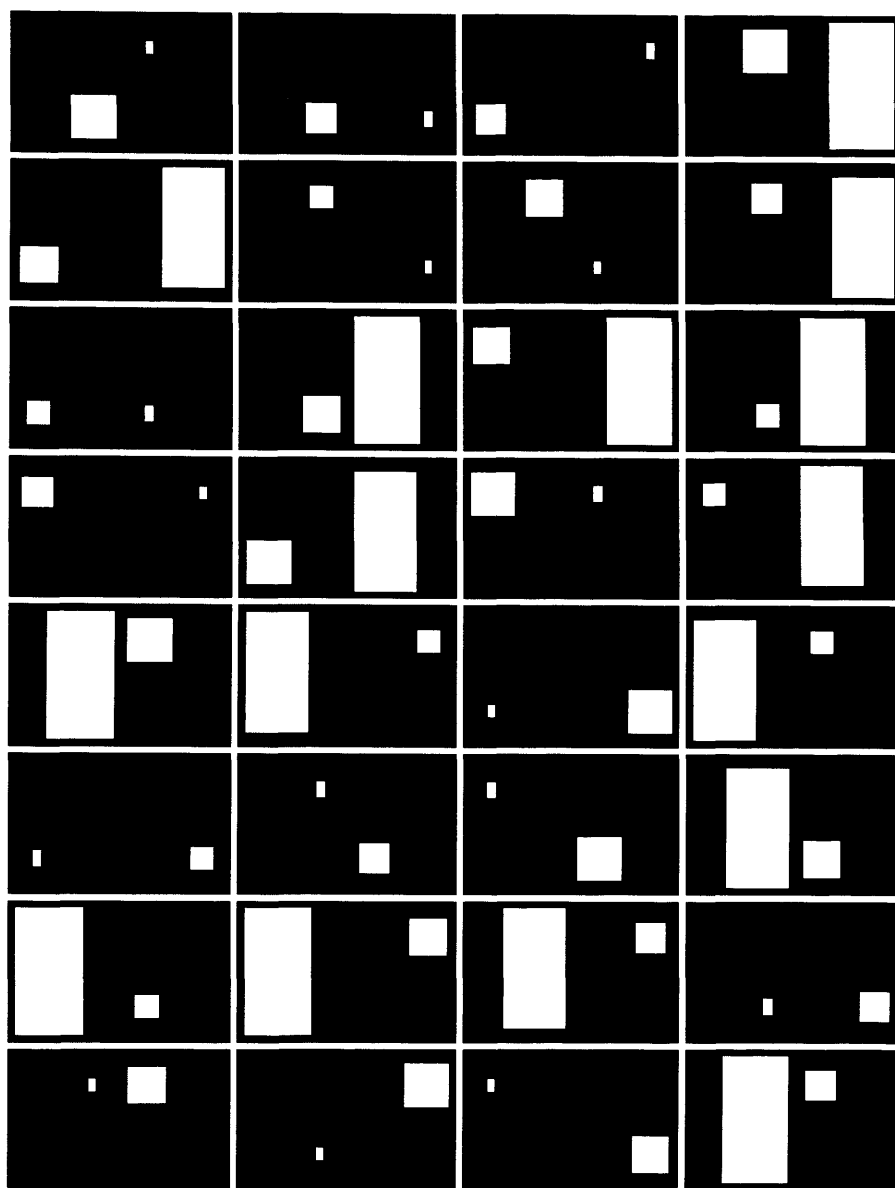
Figure A.2. The complete set of stimuli (32 permutations) used for the Bidimensional Discrimination (BD) group introduced at session 19. This consisted of medium-sized squares paired with very large or very small rectangles.
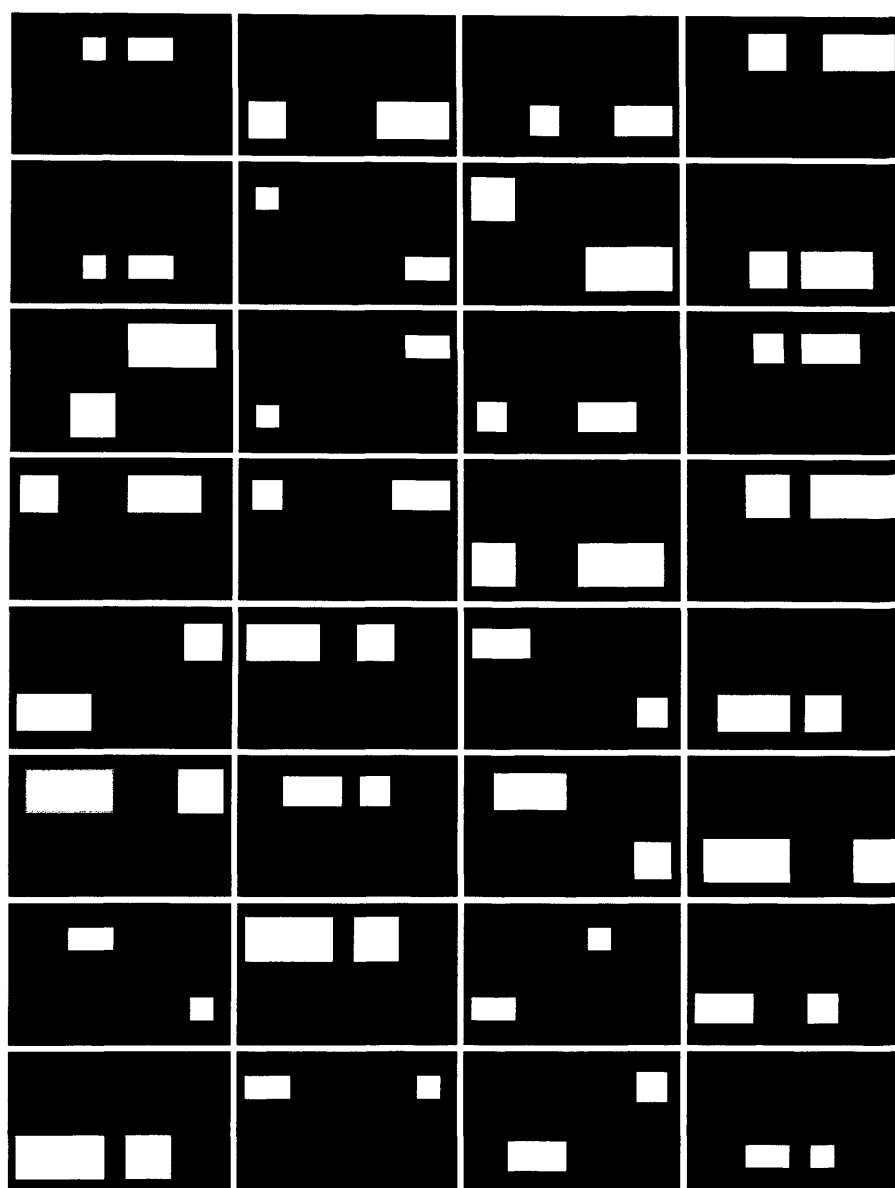
Figure A.3. The complete set of stimuli (32 permutations) used for the Unidimensional Discrimination Horizontal (UDH) group from the start of the study. The luminance of both stimuli and background were 83 and 0.03 cd/m^2, respectively. These stimuli constituted the first luminance set for this group.

Figure A.4. The complete set of stimuli (32 permutations) introduced for the Unidimensional Discrimination Horizontal (UDH) group at session 14. These permutations were identical to those presented in Figure A.3 except that, in order to prevent the use of global luminance as a discriminative cue, the local luminance of the rectangle was halved (41.5 cd/m^2). Thus, in these sets the white squares were paired with equiluminant rectangles. These stimuli constituted the second luminance set for this group.
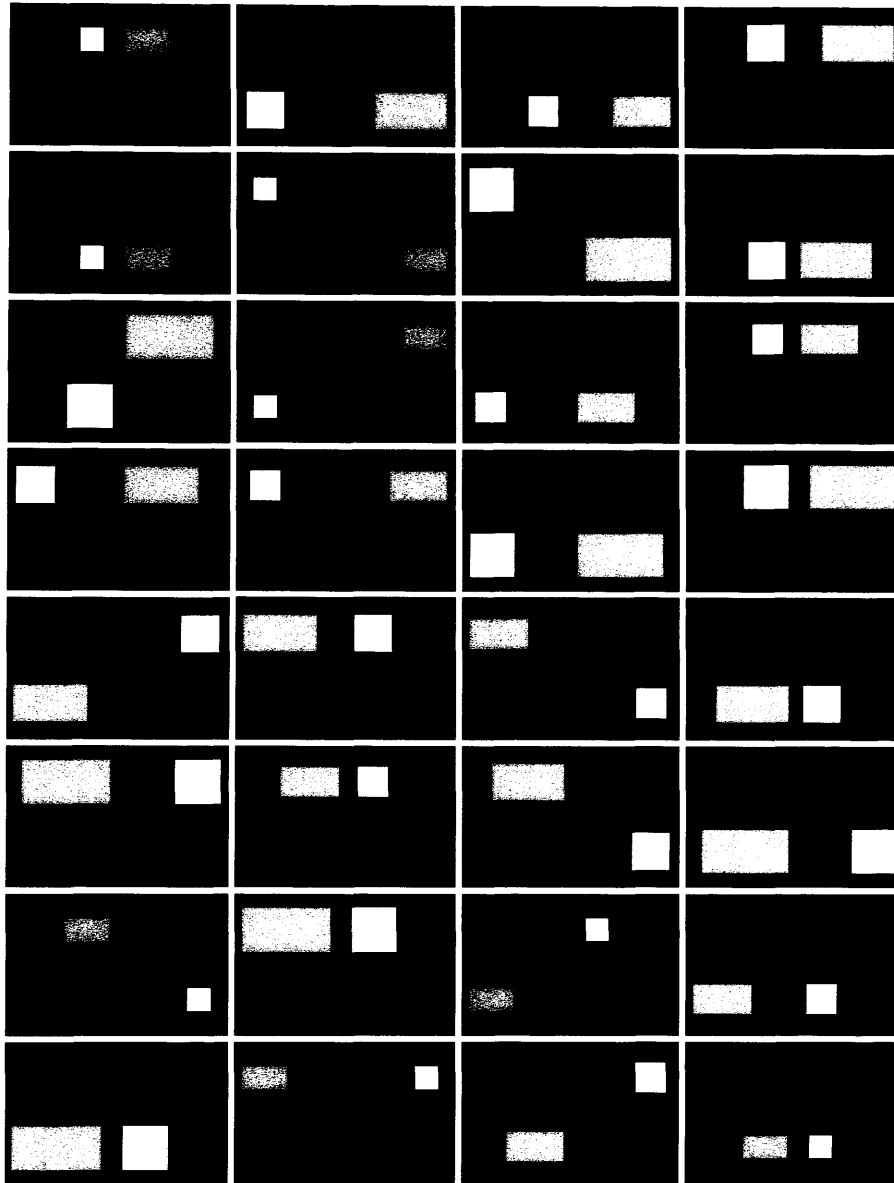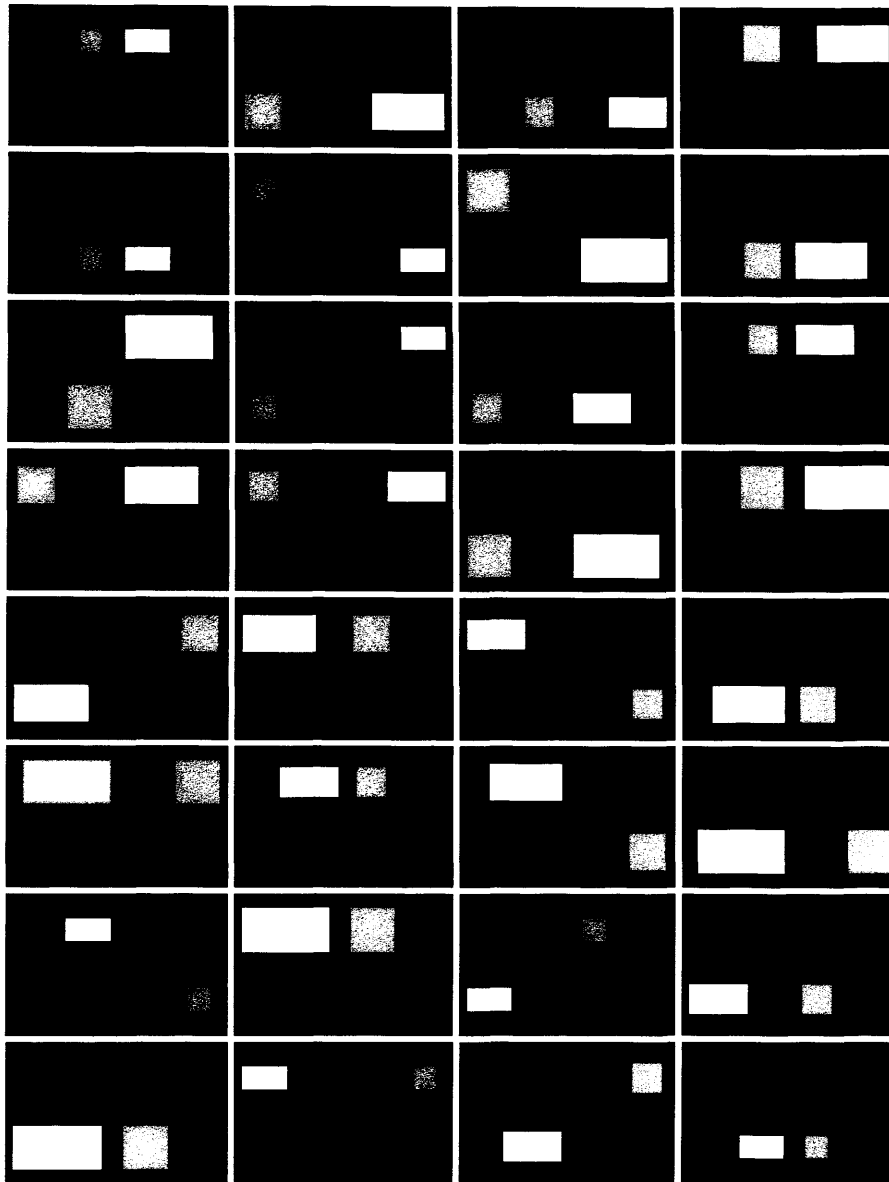
Figure A.5. The complete set of stimuli (32 permutations) introduced for the Unidimensional Discrimination Horizontal (UDH) group at session 14. These permutations were identical to those presented in Figure A.3 except that, in order to controlled for the possibility that the lower local luminance of the rectangle in the second luminance set could have been used as a discriminative cue, the local luminance of the square was also halved (41.5 cd/m^2) to match the local luminance of the rectangles in that set. These stimuli constituted the third luminance set for this group.
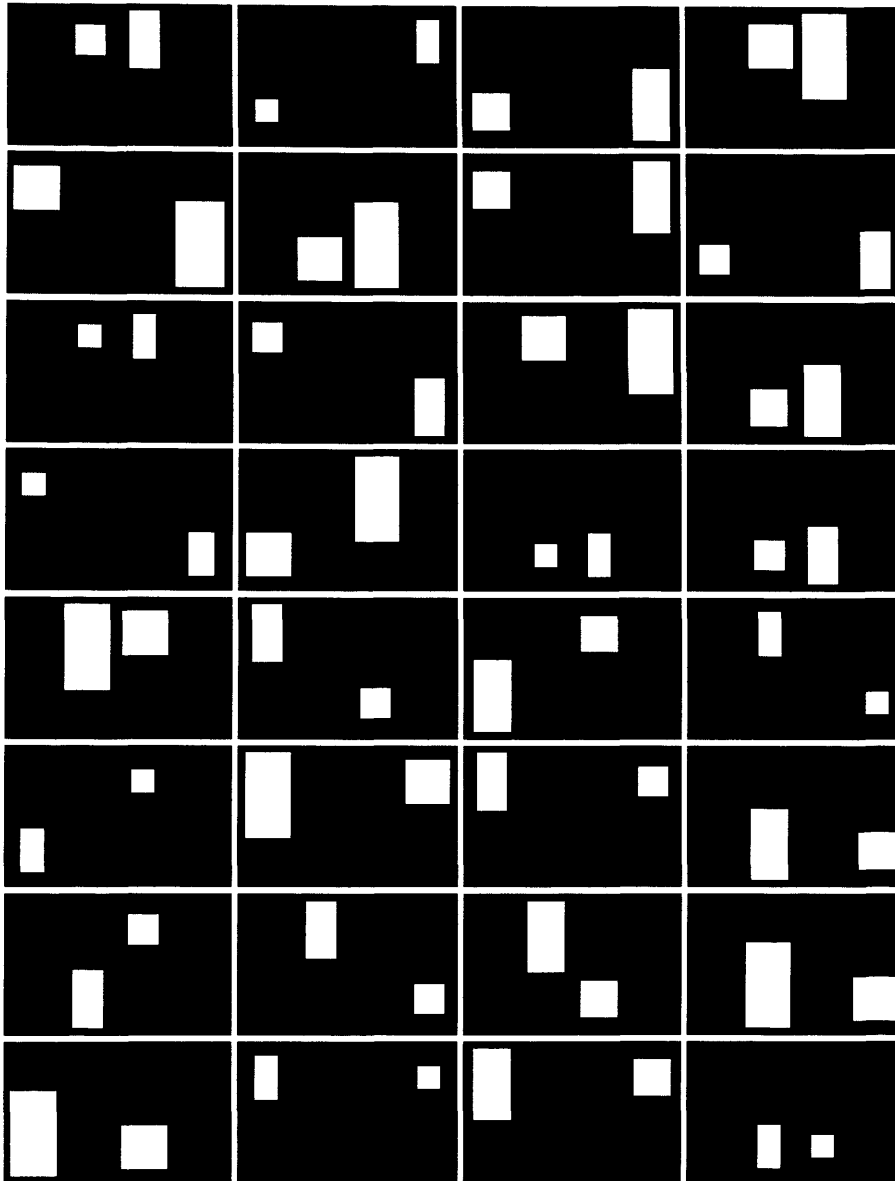
Figure A.6. The complete set of stimuli (32 permutations) used for the Unidimensional Discrimination Vertical (UDV) group from the start of the study. The luminance of both stimuli and background were 83 and 0.03 cd/m^2, respectively. These stimuli constituted the first luminance set for this group.

Figure A.7. The complete set of stimuli (32 permutations) introduced for the Unidimensional Discrimination Vertical (UDV) group at session 14. These permutations were identical to those presented in Figure A.6 except that, in order to prevent the use of global luminance as a discriminative cue, the local luminance of the rectangle was halved (41.5 cd/m^2). Thus, in these sets the white squares were paired with equiluminant rectangles. These stimuli constituted the second luminance set for this group.
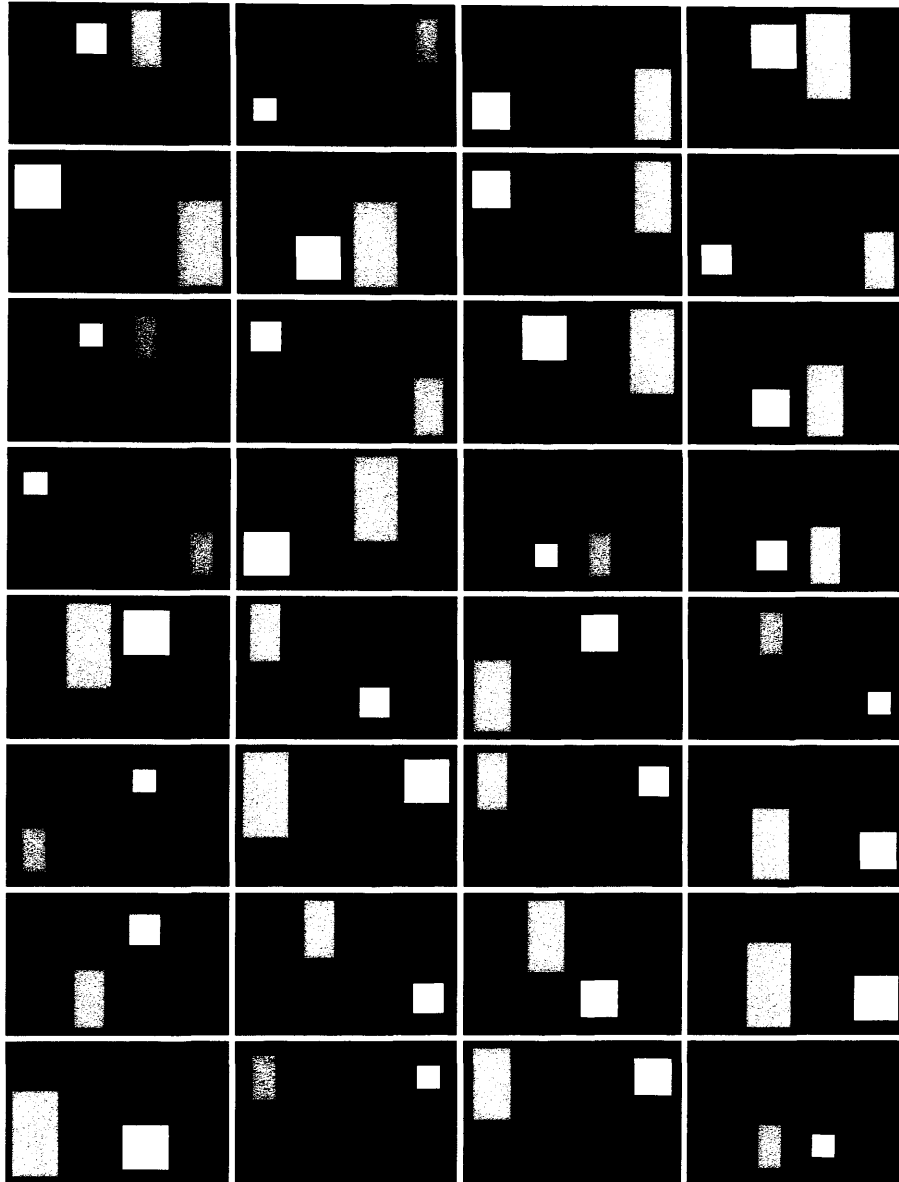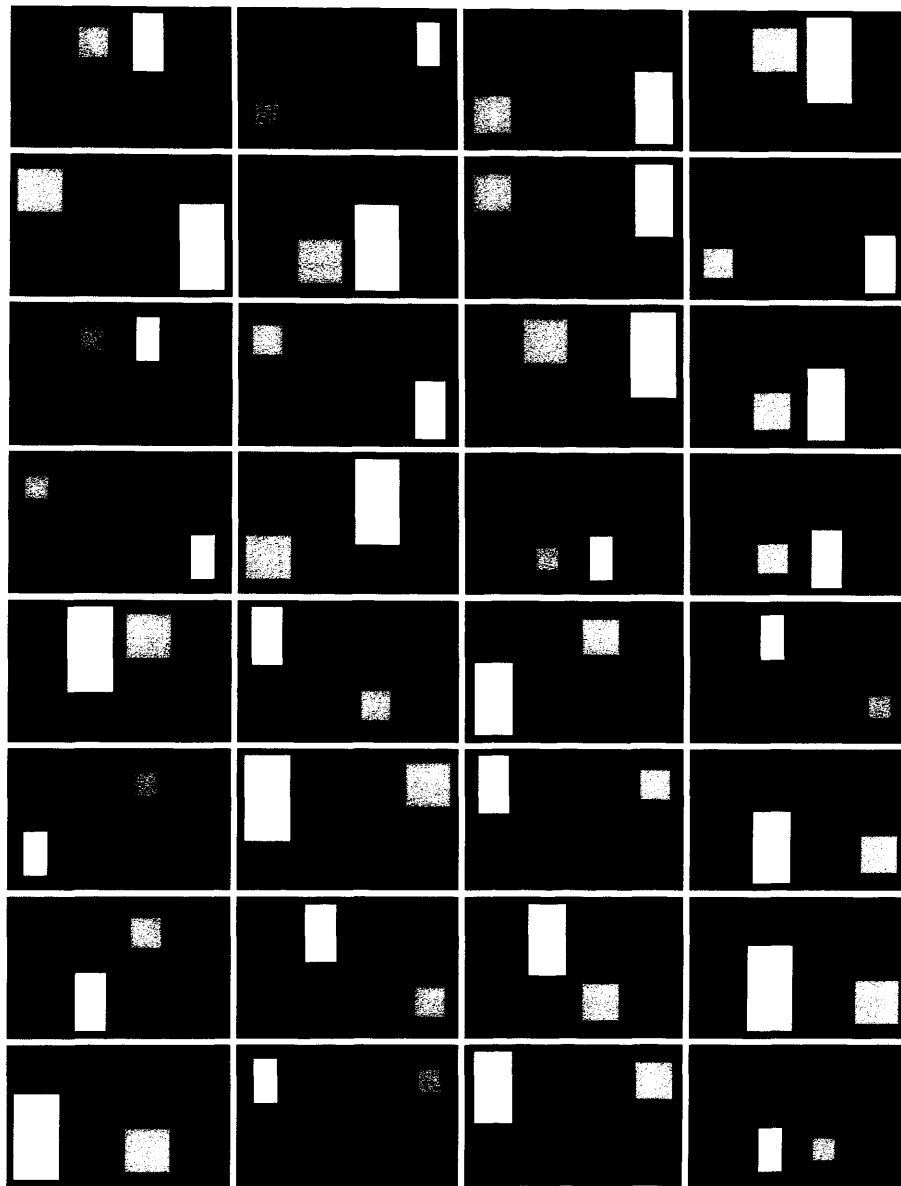
Figure A.8. The complete set of stimuli (32 permutations) introduced for the Unidimensional Discrimination Vertical (UDV) group at session 14. These permutations were identical to those presented in Figure A.6 except that, in order to controlled for the possibility that the lower local luminance of the rectangle in the second luminance set could have been used as a discriminative cue, the local luminance of the square was also halved (41.5 cd/m^2) to match the local luminance of the rectangles in that set. These stimuli constituted the third luminance set for this group.
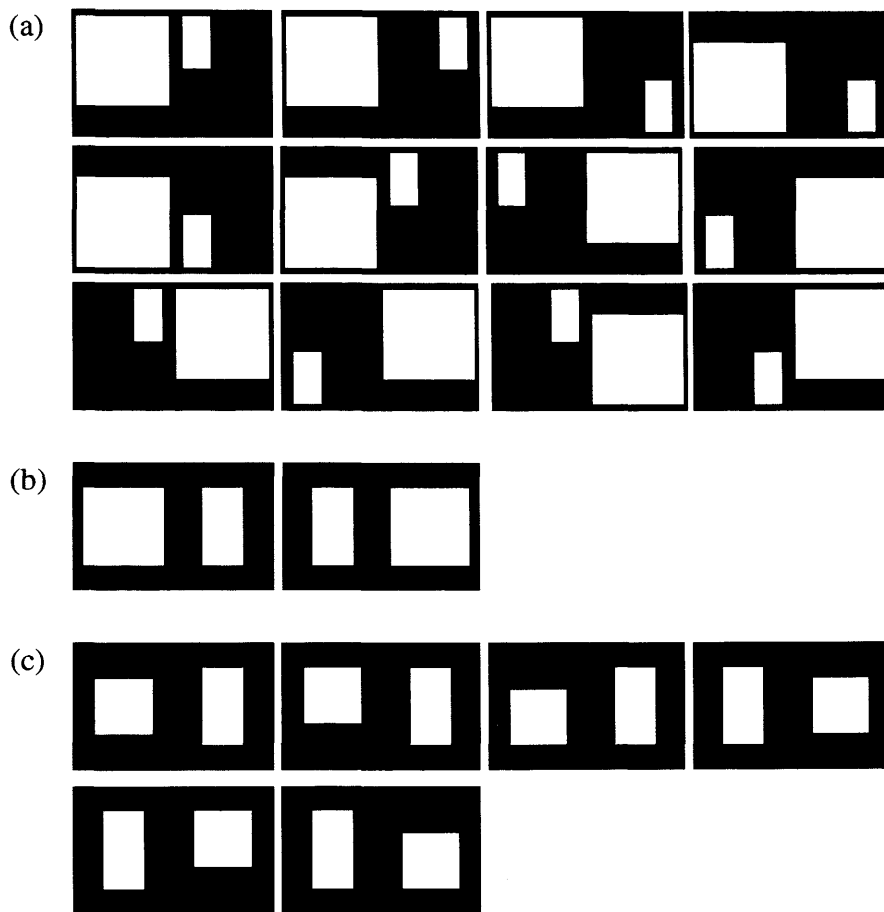
Figure A.9. The complete set of probe stimuli that tested for (a) the use of large bright areas (Probe 1), (b) the height relationship (Probe 2) and (c) area and alignment (Probe 3) by the Bidimensional Discrimination (BD) rats. All probes also tested for generalization to novel dimensions.
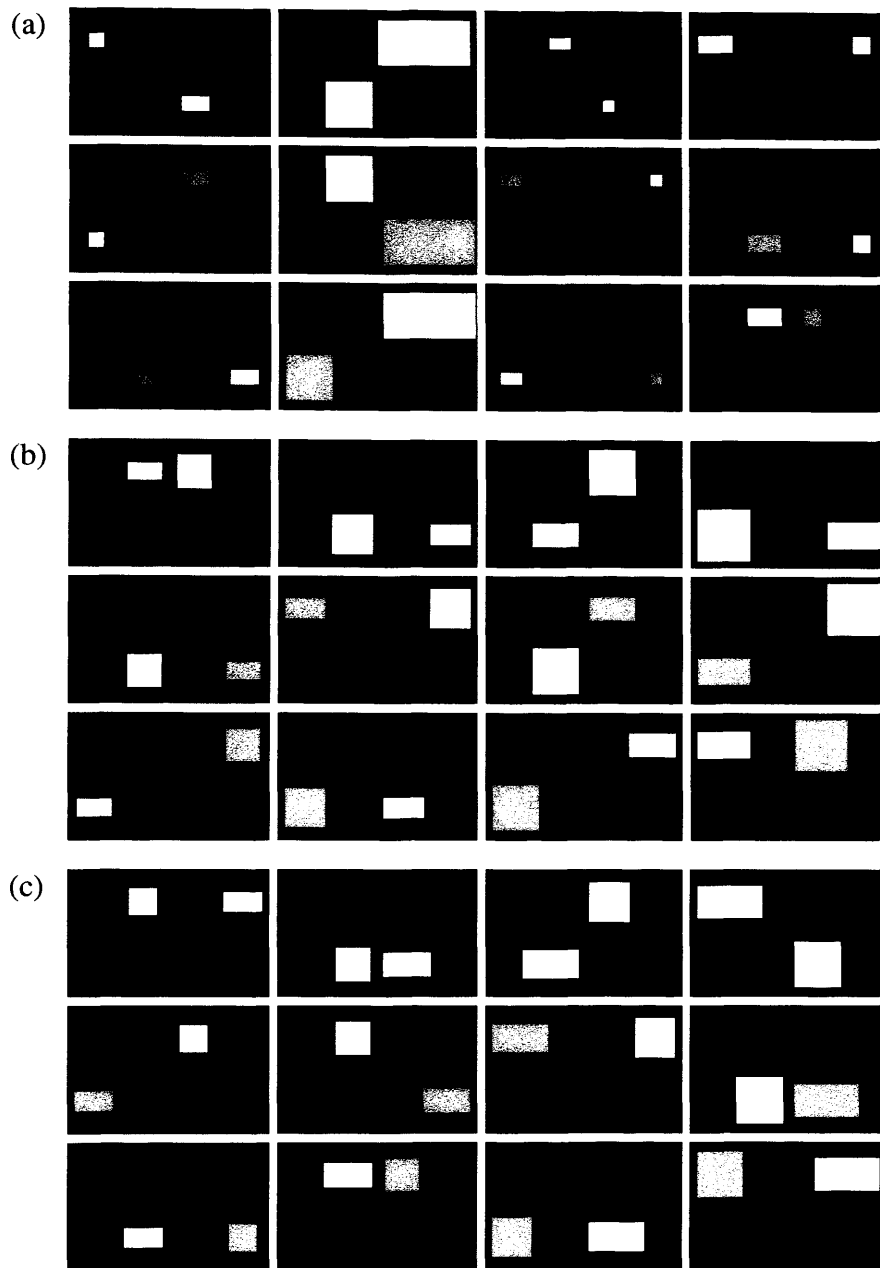
Figure A.10. The complete set of probe stimuli that tested for (a) generalization to novel dimensions (Probe 4), (b) the use of aspect ratio (Probe 5) and (c) the use of area (Probe 6) by the Unidimensional Discrimination Horizontal (UDH) rats. Each probe consisted of 12 permutations, four for each of the three luminance sets.
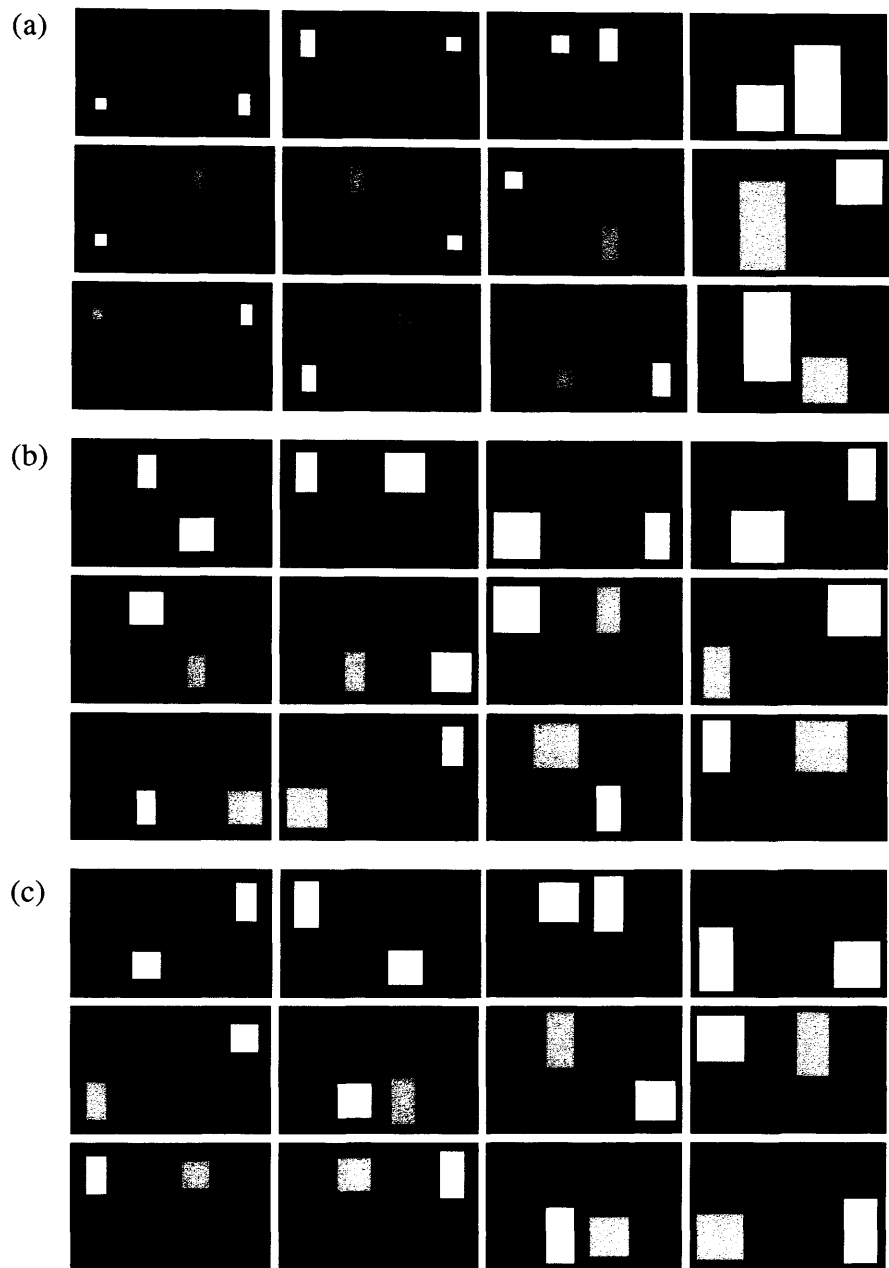
Figure A.11. The complete set of probe stimuli that tested for (a) generalization to novel dimensions (Probe 4), (b) the use of aspect ratio (Probe 5) and (c) the use of area (Probe 6) by the Unidimensional Discrimination Vertical (UDV) rats. Each probe consisted of 12 permutations, four for each of the three luminance sets.

Figure A.12. The complete set of probe stimuli that tested for the use of a size discrepancy in the non-relevant dimension (Probe 7) by (a) the UDH and (b) UDV rats. Each probe consisted of four permutations for each of the three luminance sets. (c) The complete set of the Probe 8 stimuli, used for both the UDV and UDH groups, that tested whether rats had a preference for using a discrepancy in the relevant dimension.

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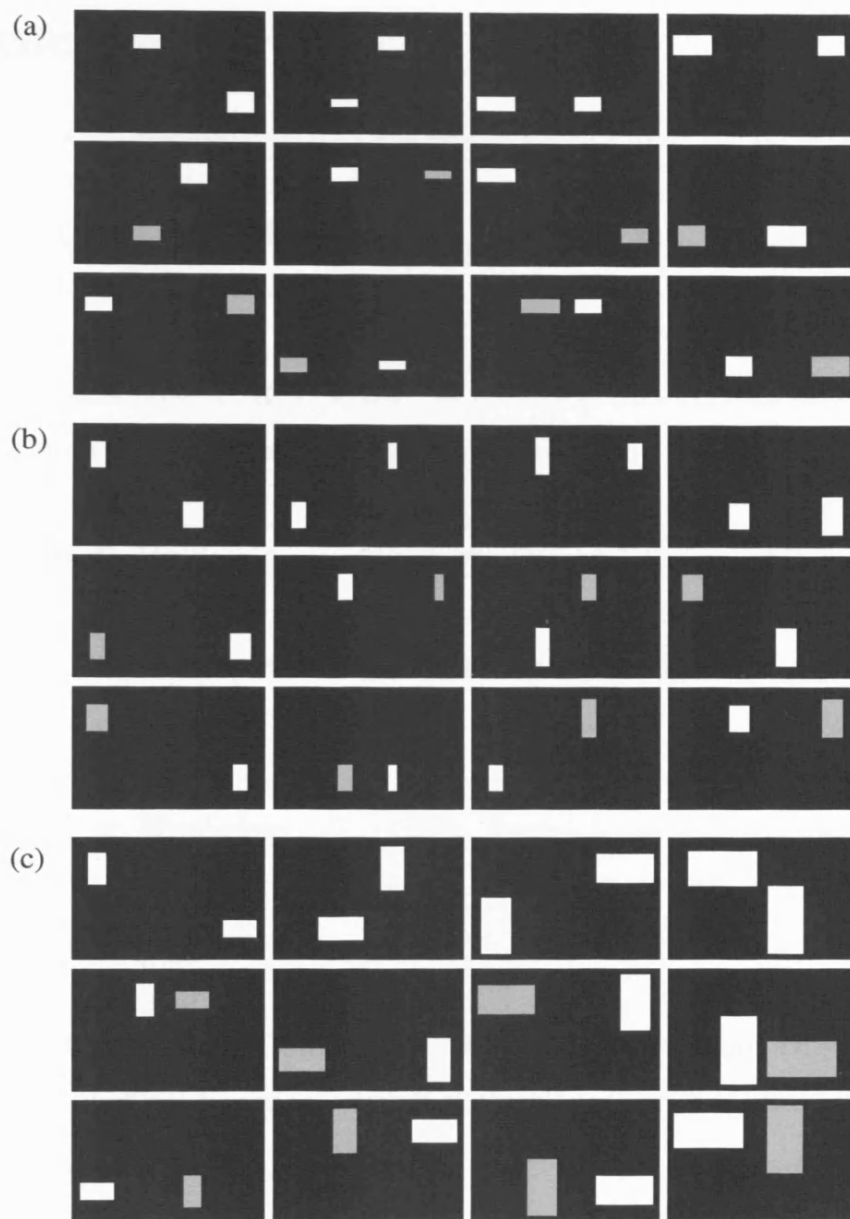
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