Functional Aspects of Colour Processing within the Human Brain

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Abstract

In a seminal work, Ungerleider and Mishkin (1982) offered substantial evidence that two separate visual pathways – coding what/where-- exist within the primate brain. Recently, human evidence has resulted in the "what/where" pathways being reconsidered in terms of ventral stream (vision for perception) and dorsal stream (vision for action; Goodale & Milner, 1992). Consistently, many studies have demonstrated that there is an overrepresentation of magnocellular (luminance) information within the dorsal stream; parvocellular input (colour, shape, consistancy) represents the primary source of information for the ventral stream. Although luminance contrast is important in perceiving moving objects, colour discrepancies help the visual system to identify the detailed characteristics of the environment and, subsequently, to prepare the motor system for action. This thesis endeavors to determine the role played by colour, in contrast with luminance, in influencing the programming and control movement production. Using a grasping paradigm and two different luminance conditions (iso-luminance vs. heteroluminance) within two separate experiments (experiment 1 – programming; experiment 2 – online control), we show that chromatic information can be successfully be used by motor circuits to complete the grasping task faultlessly. Although significant temporal delays in terms of reaction time and movement time between colour and luminance processing are identified, the human visual system seems able to fully integrate colour features for action with no significant spatial error cost.

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Chapter I

Thesis introduction

Colour is our perceptual response to a very narrow span of the total electromagnetic radiation available with light. From the retina to the superior command centres, the chromatic information has to travel through several nervous structures that amplify and modulate the nervous impulse.

Ungerleider and Mishkin, (1982) first formulated the hypothesis that objects are represented differently during action than they are for a purely perceptual task. In brief, they argued that the brain's visual pathways split into two main streams: the dorsal "where" pathway and the ventral "what" pathway. The "where" pathway runs dorsally from primary visual cortex into posterior parietal cortex, and the "what" pathway runs ventrally from primary visual cortex into inferotemporal cortex. The dorsal stream deals with the information required for object location and the other is concerned with object identification by analyzing its shape, texture or colour. In the recent years, a new approach has been offered for reconsidering these two pathways in terms of vision for perception and vision for action instead of "what" and "where". (perception - action model; Goodale & Milner, 1992). Another model that has been proposed (Glover, 2004) is the planning-control model. This approach, is not significantly different from the model proposed by Goodale and Milner,

but introduces a new perspective on how the two streams process visual information during planning and action, independently. Although many studies have been performed to investigate how the dorsal and the ventral pathways process information (e.g., Milner & Goodale, 1995; Rizzolatti, Fogassi, & Gallese, 1997; Jeannerod, 1988), there have been few projects examining the chromatic properties of neurons in cortical areas belonging to the dorsal and/or the ventral stream, and fewer still focusing on the use of colour in controlling the motor system.

The present thesis consists of four chapters; the first chapter contains a broad review of the previous literature regarding the two major visual streams and colour processing mechanisms. The second chapter encloses a pilot study examining the use of colour for preparing/performing a movement. Specifically, we examined the precision of manual grasping towards a colour object displayed on an isoluminant background. In general, even though colour signals take slightly longer to be processed (Nowak & Bullier, 1997; Tanaka & Shimojo, 1996; Tanne, Boussaoud, Boyer-Zeller, & Rouiller, 1995), they appear to be efficiently used by the motor system for a variety of functions. The third part of this thesis contains two experiments which have been written in a format suitable for publication and undertake to precisely examine colour utilization for action. These experiments aimed to determine the role of chromatic information for the real time modulation of action. In particular, we examined the impact of chromatic information towards the

planning and the online control of the motor task within both heteroluminant (different luminance) and isoluminant (same luminance) conditions. The last section presents general conclusions of the thesis, future direction and inherent limitations of the present studies.

Literature review

General context

A key feature of the primate visual system is the separation of visual areas into two major cortico-cortical processing pathways: The dorsal and the ventral streams. Ungerleider and Mishkin (1982) first proposed an anatomical distinction between the ventral pathway and the dorsal pathway in the primate visual system. The ventral stream projects from the primary visual cortex toward infero-temporal cortex whereas the dorsal stream projects dorso-laterally from the primary visual cortex to parietal areas. Ungerleider and Mishkin based their anatomical distinction on neurophysiological and behavioural evidence collected from the study of macaque monkeys. They performed intrusive lesions in the ventral and in the dorsal pathway of the visual system of macaque monkeys and found a double dissociation. Animals with a lesion in the ventral pathway were impaired in the identification of objects but they were relatively unimpaired in tasks of spatial orientation. Conversely, animals with lesions of the dorsal areas showed deficits in locating the target but their identification capacity was preserved. On this basis, Ungerleider and Mishkin concluded that the ventral pathway of the primate visual system is the *What* system and the dorsal pathway of the primate visual system is the *Where* system.

Dorsal/Ventral dissociation; Psycho-behavioural models

Over a decade after the initial observation of Ungerleider and Mishkin, Goodale and Milner (1992) provided a new conceptual account of how the brain processes visual information. They proposed the perception - action (PA) model and made two major assumptions: (1) The ventral stream processes visual information for perception purposes; (2) perception and action are two separate domains, the latter being an exclusive property of the dorsal stream. According to Goodale and Milner, the ventral stream has its main role in object recognition and preparing the first stage of information processing (object identification), while the dorsal stream analyzes an object's spatial location and coordinate movement. To support this notion they stress the dissociation between the behaviour of the agnosic patient D.F. and that of the ataxic patient A.T. (Perenin & Vighetto, 1988*).* A.T., suffering from optic ataxia manifests a profound inability in reaching to targets under visual guidance but no difficulty in observing and recognizing them whereas the visual form agnosic patient D.F., has problems in recognizing objects visually, but can still use visual information to guide her movements. Although the PA model has been widely accepted as a pertinent explanation of the dual system theory (humans included), some authors questioned its

validity and wonder if the strict dichotomy this model advances is perhaps too inflexible.

The PA model point of view was in accordance with the classical notion of the parietal cortex as the place for unitary space perception. The posterior parietal cortex consists of a mixture of areas, each receiving specific efferent information. These different types of sensory information are transformed into information appropriate for action. Space perception appears to derive from the joint activity of a series of sensorimotor fronto-parietal circuits which encode the spatial location of an object and prepare it to be used for a future action (Rizzolatti et al., 1997, Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino, & Matelli, 1998). Taken together, within the dorsal stream, there are parallel cortico-cortical circuits, each of which elaborates a specific type of visual information in order to guide different types of action.

In opposition with the PA model, Glover (2004) explored the evidence for a distinction in human performance between the planning and on-line control of actions. This new approach establishes an anatomical substrate of the ideas offered previously by Woodworth (1899). Yet, the planning - control (PC) model that he proposed facilitates a new distinction between the visual and cognitive processes involved in planning and control. Brain imaging studies support the dichotomy, in that planning in humans is linked with activity in a distributed network including a visual representation in the inferior parietal lobe, whereas control is associated with activity in a separate

network including a visual representation in the superior parietal lobe (SPL) (Deiber, Ibanez, Sadato, & Hallett, 1996; Desmurget, Grea, Grethe, Prablanc, Alexander, & Grafton, 2001; Grafton, Fagg, & Arbib, 1998; Grafton, Mazziotta, Woods, & Phelps, 1992; Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998). The inferior parietal lobe receives inputs from two major sources: firstly, the visual information from the visual cortex is carried out to the IPL via the temporal lobe or by a third stream directly from primary visual cortex (V1) to IPL (Boussaoud, Ungerleider, & Desimone, 1990). However, the temporal lobe inputs include the non-spatial (i.e., function, fragility, weight, and colour) spatial (i.e., orientation, size, and shape) features as well as information in the vicinity of the target (e.g., background, other objects). Proprioceptive information from somatosensory association areas is also integrated in the IPL together with information from frontal lobe (i.e., memories and past experiences). Once a motor act is planned, a copy of the motor schema is sent over to SPL and cerebellum. These efferences are to be used by the SPL once the movement is initiated. If needed, the whole motor plan can be adjusted online using this efference copy.

There are few main distinctions that differentiate the PC model from other models (including PA model) (Glover, 2004). The planning-control model proposes separate visual representations underlying the two stages of action by assigning the inferior and superior areas of the parietal lobes to their specific roles in computing these visual representations. Furthermore, in

opposition with Jeannerod (1988), the PC model makes no specific distinction between the information used during reaching versus grasping. It also takes into consideration a gradual rather than discrete transition between the two stages of action. Thus, the PC model differs from some models of motor control that assume that control can only begin when feedback loops have had time to close (Crossman & Goodeve 1983; Posner & Keele, 1968; Woodworth 1899). Similarly to Wolpert, Ghahramani, and Jordan (1995), the PC model suggests that an efference copy may be used to adjust movements from any time after initiation.

There are two major features that differentiate the PC model from PA model. Specifically, the first distinction resides in the fact that in the PC model, the two stages of action utilize distinct visual representations in the IPL and SPL, and those distinct representations result in interactions between cognitive and visual information in planning but not in control. Conversely, in the PA model (Goodale & Milner, 1992; Milner & Goodale, 1995), both planning and control primarily utilize representations in the SPL with some exceptions (e.g., pieces of perceptual information that may be imported from the ventral stream; Haffenden & Goodale, 2000; Milner & Goodale, 1995). In particular, the PA model suggests that parameters of movement dependent on the spatial characteristics of the target will be both planned and controlled independently of cognitive and perceptual influences. Second, while the planning–control model assumes that the IPL is involved in the kinematic

computation of all movements, the perception-action model states that IPL requires information regarding only the nonspatial target characteristics.

With deference to all these approaches, the question that has been raised still encounters some difficulties. Are ventral features available to the dorsal stream? Specifically, the point of interest to this study is that of colour as a putative ventral attribute used to program and guide a motor schema in real time.

Vision - Physiological and anatomical aspects

The capability of primates to see colour rises from the existence of two chromatic channels (Derrington, Krauskopf, & Lennie, 1984) which correspond to modulation of the response of the short wavelength (S) cones and the difference between large wavelength (L) and middle wavelength (M) cone activation; the achromatic (luminance) channel is derived from additive combination of cone signals. Kaiser and Boynton, (1996) advanced the idea of three colour channels. One channel carries out signals the sum of L and M cone excitations and can be selectively activated by light/dark (e.g., white/black) grating stimuli. This channel is sometimes referred to as the "luminance" channel. The two other channels, which are constant in luminance, are referred to as "chromatic" channels.

Luminance, as a physical feature, is defined as "*the integral over wavelength of the radiance of a source, weighted by the spectral luminosity V(λ)* " (Gegenfurtner & Hawken, 1996, p. 395). Having said that, if the

quantity of light of a stimulus is attuned by modifying only the wavelength and keeping constant the amount of light, the new stimulus will likely have a different colour but the luminance will stay the same. The two stimuli will be therefore *isoluminant* (See Fig. 1). If an organism uses a stimuli identifying system based only on luminance discrepancies, then the two stimuli will appear alike to that identifying system. Conversely, if the quantity of wavelength of stimuli is modified and tuned to grayscale (e.g., achromatic environment) without paying attention to luminance gradients, the new stimuli will be easy to identify based on amount of light that reflects from its surface (i.e. luminance; see Fig. 2).

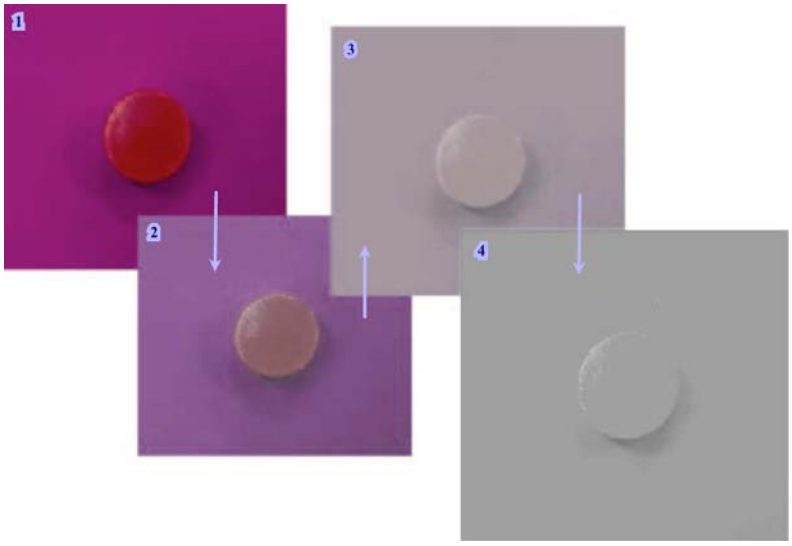

Fig. 1. Iso-luminant variance. By attuning the colour of an isoluminant scene to a neutral achromatic value, the chromatic contrast disappears and the components of the scene will appear alike.

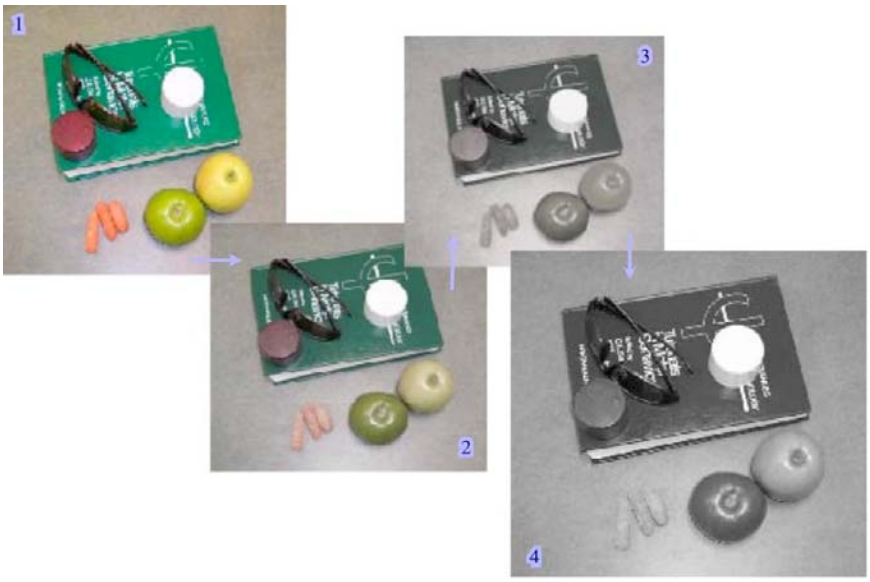

Fig. 2. Hetero-luminant variance. If the quantity of wavelength of a different scene is modified and attuned to grayscale, the object forming the scene will still be easily identified due to the luminance discrepancies.

Parvo(P) and Magno (M) pathways

Significant anatomical and electrophysiological evidence suggests that chromatic and achromatic signals are carried in separate ways from the retina to the primary visual cortex (V1) (Hubel & Wiesel, 1966; De Valois, Abramov, & Jacobs, 1966; Derrington et al., 1984; Hendry & Yoshioka, 1994; Martin, White, Goodchild, Wilder, & Sefton, 1997; De Valois, Cottaris, Elfar, Mahon, & Wilson, 2000). Investigations of the neural origin for separated colour channels have focused largely on the cells within the parvocellular (P) and magnocellular (M) subcortical separations of the macaque visual system. These pathways were named based on their

anatomical distinction in the lateral geniculate nucleus (LGN) of the thalamus; four LGN layers contain densely crowded, “parvo” small cells, and two contain more sparsely placed, “magno” large cells, (Merigan & Maunsell, 1993; Dobkins & Albright, 1998). The P cells are involved in object vision, colour, shape, and texture. They have low contrast sensitivity and are sensitive only to large differences in brightness. The P cells are also slower but have higher acuity and are embryological younger than the M cells. Conversely, the M cells carry information regarding the spatial features such as depth, motion and location of stimuli. They are more sensitive than the P cells to differences in brightness and have high contrast sensitivity. Further M cells are faster and serve both central and peripheral vision, but they are colour blind. Livingstone and Hubel (1982; 1987) were the first to connect this early segregation between the P and M pathways to neurochemical compartmentalization of primate primary visual cortex (V1). By staining the visual cortex with cytochrome oxidase (a large trans-membrane protein found in the mitochondrion) Livingstone and Hubel found that cytochrome oxidase-rich regions of striate cortex called *blobs* are specialized for colour processing while the regions surrounding them (*interblobs*) are dominated by neurons with high orientation selectivity but poor colour specificity. Livingstone and Hubel proposed that the chromatic channels (P) supply the inputs to mechanisms for colour perception, but have a modest contribution to early processes for spatial orientation integration. Livingstone and Hubel further

made the assumption that there are two pathways that connect the LGN to V1 (i.e., P & M). They also proposed the idea that P and M channels remain segregated well beyond the primary cortex. More recently, it has been suggested that the ventral and dorsal projection streams identified by Mishkin and Ungerleider (1982) might represent the continuations of the P and M systems, respectively (Livingstone & Hubel, 1988).

Nevertheless, recent physiological evidence shows that in macaque V1 a significant proportion of cells respond intensely to combined modulation of colour and luminance (Thorell, De Valois, & Albrecht 1984; Lennie, Krauskopf, & Sclar, 1990; Leventhal, Thompson, Liu, Zhou, & Ault, 1995; De Valois et al., 2000), including cells showing a high degree of orientation-selectivity (Johnson, Hawken, & Shapley, 2001). Xiao and Felleman (2004) studied the degree of the segregation between the two streams by anatomical tracing and demonstrated that both blobs and interblob project to the thin stripes of V2. They debated the hypothesis due to V1 and V2 are connected in parallel to form highly segregated functional streams. Moreover, recorded data from a single neuron within area V2 did not confirmed the total compartmentalization within V2 (Kiper, Fenstemaker, & Gegenfurtner, 1997). Although cells demonstrate colour specificity, the receptive-field properties of cells located in V2 were generally similar for luminance and chromatically defined stimuli. Studies in monkeys with discrete lesions of the P and M layers of LGN also revealed a pattern of deficits that do not conform

to the distinction pointed out previously (Merigan & Maunsell, 1993; Schiller & Logothesis, 1990). Lesions of the M pathway cause a decrease in contrast sensitivity for stimuli of high temporal but low spatial frequency whereas lesions of the P pathway results in a complementary pattern of deficits. These results suggest that the specialization of the P and M cells, at least at the level of the retina and LGN are best understood in terms of an exchange between the different requirements of spatial wavelength and temporal processing (Schiller & Logothesis, 1990). The additional processing at the level of V1 and V2 modifies the response characteristics of the magno and parvo inputs enormously.

Konio pathway - a possible explanation?

Much more recently, long after parvo-cellular and magno-cellular pathways in colour-motion processing were in unanimity accepted, a third pathway, referred to as *koniocellular* (K) pathway has been proposed (Hendry & Yoshioka 1994; Hendry & Reid, 2000). This pathway, first described in primates (macaque; Casagrande, 1994) is thought now to process colour along a dimension that activates the short-wavelength-selective S cones from the retina. This geniculo-cortical stream selectively modulates the blue/yellow dimension. The K pathway is anatomically distinct from the M and P pathways and projects directly to the colour-selective blobs in area V1. The K pathway therefore may offer another explanation by which colour information could influences motion processing.

One important region for examining K pathway is the middle temporal area (Dobkins, 2000). This region belonging to extrastriate visual cortex receives an important input from V1 (Merigan & Maunsell, 1993). Until recently, investigations of colour influences on motion responses in area MT have focused exclusively on red/green input derived from signals in the L and M cones (Gegenfurtner et al., 1994; Pisella, Arzi, & Rossetti, 1998). Wandell, et al., (1999) used functional magnetic resonance imaging (fMRI) to demonstrate S cone input to the motion-responsive region of human visual cortex (referred to as MT1). These experiments were followed by single cell recordings in macaque area MT, demonstrating a clear S cone contribution to directionally selective responses (Seideman & Newsome, 1999).

Regardless the methodology or species, the S cone input to motion was found to be significantly less powerful than light/dark input. The contrast sensitivity of the neurons belonging to MT was significantly lower for blue/yellow as compared to light/dark gradings. These results obtained for stimuli modulated along the blue/yellow dimension are consistent with previous results in MT obtained using red/green gratings (Dobkins & Albright, 1994; Gegenfurtner et al., 1994). One explanation is that the observed S cone influences on MT responses may reflect the functional input from this third visual pathway to motion processing. Thus signals from the K pathway could potentially reach area MT from the V1 blobs via V2 (Merigan & Maunsell, 1993) or directly from K layers in the LGN to MT area (Hendry

& Reid, 2000). As a result the K pathway input to MT might advocate that the S cone signals carried by this pathway could be used to identify the chromatic features of an object as well as to help in motion detection. Another possibility, however, is that the S cone signals might reach area MT by interfering within the M pathway (Calkins, 2000, 2001). Although Calkins provided evidence from retinal anatomy to support this possibility, other neurophysiological studies argued against this hypothesis (Lee, Martin, & Valberg, 1998; Dacey & Lee, 1994). Lee and colleagues, (1998) found that S cone input to M pathway responses is insignificant if not absent.

The blindsight condition

The K pathway's role in modulation of chromatic perception is not the only account of colour processing within the dorsal/ventral dissociation physiology. Weiskrantz (1986; 1997) brought into discussion a relatively new neuropsychological condition called "blindsight". Blindsight can occur due to a lesion in the primary visual cortex. The lesion is located prior to the bifurcation of the ventral and the dorsal streams. Blindsight is astonishing because of the contrast between the incapacity in providing information about the stimuli presented within the blind area, and the high rate of 80 to 90 % (Marcel, 1983; Weiskrantz, 1997) of correct answers to questions concerning those stimuli. A blindsighted person will report no visual experiences of objects presented within the blind field (Marcel, 1983). Conversely, they are able to give correct answers regarding optical stimuli presented in the blind

area when they are asked (forced choice) to decide between given alternatives.

The extant neuropsychological literature suggests that, in blindsighted patients the visual information is processed by subcortical pathways that bypass the visual cortex and relay visual information to the motor cortex (Schoenfeld, Heinze, & Woldorff, 2001; Parkin, 1996; Weiskrantz, 1998). Indeed there are projections that connect LGN to non-striate visual cortex (Schoenfeld et al., 2001). There are also many fibers (about 150,000 from each eye) that do not project through the geniculo-striate pathway at all (Weiskrantz, 1998). Of special interest are the approximately 100,000 fibers that travel from the retina to the superior colliculus (SC) (Parkin, 1996). Many of these fibers subsequently go through the pulvinar and onto the posterior parietal cortex, which functions in visuomotor abilities. However, although the existence of these neuronal circuits has been acknowledged (Weiskrantz, 1998) no evidence regarding the processing of colour has been forwarded within these pathways.

Present research

Although there is a growing consensus that visual processing occurs in parallel streams which eventually interact at different levels (Hubel & Livingstone, 1987; Zeki, 1993; Milner & Goodale, 1995), the debate regarding colour processing within the two visual streams (i.e. ventral, dorsal) has not produced an unanimous accepted position. Specifically, there is not much experimental research investigating a colour processing mechanism for spatial motor action. However, recent studies have investigated the direct impact of colour towards performing a motor task (Pisella, Arzi, & Rossetti, 1998; Schmidt, 2002; Brenner & Smeets, 2004) and demonstrated inconclusive findings.

Schmidt (2002), using a pointing prime-masking paradigm found that coloured primes evidently altered the pointing responses. Chromatic influences were observed in the first stages of the movement. Similarly, Brenner and Smeets (2004) found that fast on-line adjustments during pointing movements are possible based solely on chromatic information. They showed that people are able to respond to colour almost as quickly as to luminance contrast. Their obtained latency (120 ms) is consistent with the previously reported latency of about 110 ms for responding to displacements of luminance defined targets (Brenner & Smeets 1997; Prablanc & Martin 1992). Still, their findings are consistent with Schmidt (2002) and allude the

ability of the dorsal stream to use chromatic information. Brenner and Smeets countered the results of Pisella, Arzi, and Rossetti, (1998) who proposed that people cannot respond quickly to colour stimuli due to a slower processing within the ventral streams. To address this point, Pisella et al., (1998) used a pointing target perturbation paradigm (go/no go tasks) and found that colour processing is slower than location processing. Further the earliest corrective reactions to the perturbation target occurred sooner in the location-go than in the location-no go condition. The roots of this debate seem therefore to have a more semantic than concrete substrate since both studies (i.e. Brenner & Smeets, 2004; Pisella et al., 1998) showed that colour processing requires more time than location features during reaching tasks. The average latency difference between location and colour processing is consistent with previous research data (Nowak & Bullier, 1997) that confirmed that visual latency in area V4 which send significant input to the ventral stream is 12 ms slower than in area MT which in turn project major inputs to parietal areas from the dorsal stream. Their findings are also consistent with visual latencies reviewed by Nowak and Bullier, (1997). They defined the parietal areas as a "fast brain" (having conduction latencies about 40 - 80 ms) and temporal areas as the "slow brain" (temporal latencies of 100 - 150 ms). Although it appears that colour is processed more slowly within the ventral pathway, (Nowak et al., 1997; Tanaka & Shimojo, 1996; Tanne et al., 1995) the

discussion regarding the efficacy for the preparation and execution of a motor task is still open.

Objectives and Hypotheses

The extent to which the primate motion system makes use of object colour has been an issue of long debate in vision science. The largely accepted view is that colour information should exert little or no influence on motion detection, a notion arising from evidence for discrete processing in the primate visual system (Ungerleider & Mishkin, 1982; Livingstone & Hubel, 1984; Milner & Goodale, 1995). However, several new lines of evidence suggest the contrary: The motion system may be able to use colour information in substantial ways (Merigan & Maunsell, 1993; Wandell et al., 1999; Schmidt, 2002; Brenner & Smeets, 2004).

Although the existence of the two visual streams is largely accepted, some problems regarding aspects of their interaction still exist. Are humans able to clearly program an outgoing grasping movement based only on colour attributes? Specifically, can colour be extracted from the various defining attributes of an object and used by the dorsal stream in real time to modulate a motor act? Our hypothesis underlies these questions. We suggest that colour in isolation is able to offer sufficient information for planning and correcting (if needed) an outgoing grasping movement. Our suggestion is that the chromatic information can be used proficiently by the ventral and within the latter regions by the dorsal stream to accomplish the planning phase of the

motor act. Once the movement is planned, we propose that the posterior parietal areas are able to successfully: (1) integrate colour; (2) initiate; (3) produce; and (4) complete the movement, even though significant temporal delay of the chromatic corrections should occur due to the extensively reported transmission latencies that characterize the colour system.

Chapter II

Pilot Study

Introduction

The visual system has two main pathways for processing visual information; the ventral and the dorsal. Colour, texture and shape are primarily analyzed in the ventral pathway, while motion and egocentric position are analyzed in the dorsal pathway (Ungerleider & Mishkin, 1982). Many neuropsychological studies on brain damaged human patients have confirmed the significance of the anatomical duality between the ventral and the dorsal pathways in the primate visual system. Relying on such neuropsychological evidence, Milner and Goodale (1995) offered a reinterpretation of the psychological and functional significance of the anatomical segregation between the ventral and the dorsal streams within the primate visual system. The PA model poses that the role of the ventral stream is to allow object recognition and conscious visual perception, whereas the dorsal stream is to provide the basis for the visual guidance of actions under no conscious state. Another action-based model that has been proposed is the PC model (Glover, 2004). Although this new approach reflects much of the ideas proposed by Woodworth (1899), it offers a different approach of the relationship between cognition and action. In particular, while the PC model

assumes that the Inferior Parietal Lobe (IPL) is involved in the kinematic parametrization of all movements, the perception-action model states that IPL requires information regarding only the non-spatial target characteristics.

As discussed before (see General Context), previous research using pointing tasks pointed out that colour, although requiring more time than the dorsal features to be processed (e.g., location), can influence human movement to a certain degree (Schmidt, 2002; Brenner & Smeets, 2004). The present experiment was designed to address the degree of association between colour and luminance pathways and the dichotomy of the two parallel streams. Are humans able to accurately program and execute an outgoing movement based only on colour attributes? Specifically, we tested the precision of manual grasping towards objects defined by colour, location and/or size. Although neither the PC model nor the PA model make a distinction between grasping and reaching (Glover, 2004), single cell recordings (Rizzolatti et al., 1988; Gallese et al., 1996) have shown that different neurons from the premotor area F 5 are involved in grasping and in tasks associated with this act (i.e. holding, tearing, lifting). Grasping neurons discharge in a different way as dependent on the type of grasping or the temporal characteristics of the act. Some grasping neurons fire at the beginning of the movement, others fire at the end or when the hand has already pre-shaped the object (Rizzolatti et al., 1988). Some grasping neurons discharge impulses during flexion of the fingers and still others when the

fingers are extended. Culham, Danckert, and Goodale, (2002) reported that the anterior intraparietal (AIP) region of humans shows a larger response for visually grasping tasks than for reaching tasks. Using functional magnetic resonance imaging (fMRI) to separate the visual response and somatomotor responses during delayed grasping and reaching tasks Culham et al., (2002) found that the posterior subregion located at the junction of the intraparietal sulcus and postcentral sulcus showed both visual and somatomotor responses. Conversely, the anterior subregion in the PCS has been suggested to have a large somatomotor response but modest visual reaction (Culham et al., 2002).

This segregation between the neural activation during reaching and grasping within the dorsal areas was initiated by Jeannerod, (1981; 1988; 1995). He proposed dividing of the motor act into two schemas: The first moment is *transport* (the hand makes the reaching movement towards the target) and second is *manipulation* (grasping the object). Arbib, (1981), also divided the motor act into two schemas: One for the slow phase of the reach and the second for the enclose phase of the hand movement. Yet, subsequent experiments showed this model to be inadequate. Paulignan et al., (1991) found that when moving the target object at the beginning of a reach-to-grasp movement to another place the participant was able to correct for this visual perturbation and grasp accurately the displaced object. Although the task was completed, this correction resulted in lengthening the duration of the reach by about 100 ms. Hoff and Arbib, (1993), corrected their two schemas model and

proposed a new approach that postulated a two-way interaction between the transport and grasp schemas. A third coordinating schema was therefore introduced. This third element modulates the other two by estimating the time needed to move the hand from its current location to the desired final one. The schema hypothesis provides therefore a stronger framework for segmenting grasping into elementary action units, and for relating these units to the neural substrate (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995).

Relying on this framework, a grasping paradigm was thereby utilized. The luminance was controlled within all the trials. The participants had to grasp a coloured object presented on the background. The size and the location of the object were manipulated in order to observe the pattern of the grasping movement. A 2000 ms preview of the initial location/ size of the target was utilized to avoid conservative adaptive strategies by the participants (e.g., a pop-up and search response) and to clearly examine the planning of the motor act. If participants demonstrate a smooth transition between the initial and perturbed target locations one can infer that the dorsal stream is able to adapt and integrate ventral features during programming and execution of an outgoing movement.

Methods

Participants

Eleven healthy participants (Range = 19-30 years old, mean = 24.5, SD = 3.5, five females and six males) took part in this study. All were naive to the

experimental question and were right hand dominant by self report. All participants had normal or corrected to normal vision including normal colour perception. Because the experiment required subjects to make a judgment regarding the colour of the object displayed and to grasp it based on its chromatic characteristics, all the participants were administrated the Ishihara colour blindness test (Salvia & Ysseldyk, 1972) prior being admitted in the study (See Fig. 1). The elements of the protocol have been previously forwarded and approved by the University of Saskatchewan Behavioural Science Research Ethics Board for ethical consideration in Human Experimentation in accordance with Declaration of Helsinki (1964).

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Task

The experiment consisted of 80 trials. Within every trial the participant was to grasp a target cylindrical object as accurately as possible using a precision grip (i.e., thumb and index).

Stimuli

Stimuli consisted of two plastic cylindrical objects, one large (radius = 2.2 cm, height = 3.5 cm) and second small (radius = 1.6 cm, height = 2.6 cm). Both were painted using acrylic paint in *red* (R = 252, G = 68, B = 35). The target object was presented on a *purple* cardboard background (R = 194, G =

58, B = 172). Both the background and the objects had the same luminance (1.00 x 100 cd/m^2). The luminance of both the objects and the background was evaluated using TEKTRONIX Narrow Angle Inc. luminance meter. The background was divided into two sections, one (80 cm x 91 cm) being positioned horizontally on a table, and the other one (72 cm x 91 cm) being placed vertically on the far side of the table from the participant in order to ensure a homogenous "purple environment" as the research design required. The distance between the floor and the near edge of the horizontal plane surface was 80 cm (See Fig. 2)

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Apparatus

The goal of this pilot study was to understand the modulation of motor outputs during grasping movements; therefore, equipment for monitoring and recording hand movements was used.

1. Motion Tracking. The movements were recorded by tracking infrared-emitting diode (IREDs). Three markers were used, one placed on the distal phalanx of the right thumb, the second on the distal phalanx of the right index finger and the third on the region of the trapezium-metacarpal joint of the right thumb (Jeannerod & Biguer, 1982). This allowed recording both grasp and transport components of reaching. The position of the IREDs were

sampled for 3 s at 200 Hz following the auditory initiation cue using a Visualeyez 3000 system (Phoenix Technologies Inc., Burnaby, BC, Canada).

2. Liquid Crystal Goggles. To achieve visual occlusion, Liquid Crystal Goggles (Translucent Technologies Inc. Plato Model: P1) were utilized. The motion tracking data was collected using a personal computer BOXX Technologies Inc. running Visualeyez Soft 2.70. Randomized trials were triggered by a second computer (IBM ThinkCentre) running E-Prime Studio soft Version 1.1. The second computer triggered both the experiment and the goggles.

Procedure

Participants were comfortably seated on a stationary chair located in front of the horizontally positioned background in an illuminated room. The light sources were placed above the experimental settings in order to avoid shadows on the testing surface. At the beginning of the trials, the experimental protocols were explained. In order to avoid particular strategies from the participants, a randomization of trials occurred.

The experiment required participants to move “as rapidly and accurately as possible” in response to a start tone. The participants were asked to grasp the red object presented to them using a precision grip (i.e., thumb and index), (Jeannerod, 1982). Participants had to perform 80 trials, starting at home position and traveling 30 cm to the presented red target.

At the beginning of each trial, the participants were asked to put their right hand on the home position. Following this step, the goggles closed for 5000 ms, during which the experimenter positioned the target object on the background surface in concordance with the randomized order. After that interval, the goggles opened for 2000 ms, allowing the participant to become aware of the initial location or size of the object. The goggles were closed again after this interval for another 5000 ms, time wherein the experimenter repositioned the object on the background surface in concordance with the randomized order. After this period the goggles opened concomitant with the tone that indicated the participant to make the grasping movement. (Fig. 3).

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Measurement began at the start tone and was terminated by the experimenter only after the fingers securely grasped the target object. The experiment consisted of eight conditions that were obtained by taking all possible combinations regarding: (1) the target initial size (ISIZ; large, small); (2) the target final size (FSIZ; large small); and (3) change or no change in final location [SLOC (same location - right), DLOC (different location - left)]. In 37.5 % of the trials (30 trials), the red targets randomly changed either location (right to left) or size (large to small or small to large) or both, the rest of 62.5 % being unperturbed targets (50 trials).

Data Reduction and Analysis

An average of 5% (4 trials, Range = 0 - 10) of the total number of trials per participant were eliminated from the analysis due to missed performance of the experimental task (i.e., fail to grasp the object). Position data were filtered off-line using a second-order dual-pass Butterworth filter (low-pass, 15 Hz). Instantaneous velocities were calculated by differentiating displacement data using a five-point central finite difference algorithm. Movement initiation was defined as the first sample where the instantaneous velocity exceeded 50 mm/s for more than 20 samples (Binsted & Elliott, 2001; Elliott, Heath, Binsted, Ricker, Roy, & Chua, 1999); reaction time was the time that elapsed from the collection start to movement start. The end of movement was defined as the first point below the absolute value of 50 mm/s, where the following five points remained below this cut-off value.

A series of dependent variables were examined: reaction time (RT), movement time (MT), peak acceleration, time to peak acceleration, peak velocity, time to peak velocity, peak grip aperture (the maximal opening of the precision grip), time to peak grip aperture.

All hand dependent measures were analyzed using a 2 initial sizes (ISIZ; small, large) x 2 final sizes (FSIZ; small, large) x 2 final locations (SLOC - right; DLOC - left) repeated measures ANOVA, with each score based on the median of 5 trials for perturbed trials and 25 trials for control trials. Where appropriate, *F* statistics were corrected for violations of the sphericity

assumption using the Huynh-Feldt correction. Simple effect analysis and Bonferroni correction for multiple analyses were used when necessary to specify the nature of any significant effect. Alpha was set at $p = .05$ for all statistical analyses.

Results

A significant main effect of final location (FLOC) was observed for RT, F (1, 10) = 6.18, $p < .036$. Movement time also showed a significant effect for FLOC, [F (1, 10) = 6.08, $p < .033$.Together, these effects demonstrate that when target location changed participants took significantly more time to react and reach the new location. FLOC also showed a significant effect on peak grip aperture [F (1, 10) = 5.82, $p < .032$; see Fig. 7] and time to peak grip aperture, F (1, 10) = 7.39, $p < .022$. (See Table 1). Furthermore, a main effect of location was also observed when accounting for the movement path length F (1, 10) = 26.36, $p < .000$.

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Final Size (FSIZ) manifest significant effects on MT, [F (1, 10) = 5.9, $p <$ .09; mean MT large FSIZ = 516 ms, mean MT small FSIZ = 499 ms]. FSIZ also demonstrated a strong effect on movement path length, [F (1, 10) = 13.55, $p < .004$, mean path length large FSIZ = 344mm, mean path length small FSIZ = 337 ms].

Discussion

The debate regarding the speed of colour processing within the human visuo-motor system has a long history; psychophysical experiments have shown that discrimination of colour is about 100 ms longer than discrimination of location (Tanaka & Shimojo, 1996). A feature that indeed needs more clarification is not the absolute speed of chromatic neuronal transmission but the capacity of our primary motor system to utilize colour information in time to accomplish a movement task.

This experiment was designed to investigate the effect of one coloured stimulus and the motor response in a perturbation paradigm. Our results show a powerful effect of final location, although the participants were faultlessly able to use chromatic discrepancies to control an ongoing motor action. Changing of target location influenced the reaction time as well as the movement time, showing that when the participants had to compute the new coordinates of the target based on colour, supplementary time was needed. Nevertheless, they *did* adjust their movement based only on the information received after the hand left the home position. Additionally, changes in location produced a significant perturbation in the travel distance; a mean difference of 14 mm was observed between the trials where the object kept its position (SLOC) as compared with trials where it jumped, (the hand sketched a circle arch in its trajectory to the target when the object appeared in the other location; see Fig. 5). Again, identifying the new location based on

chromatic attributes showed a significant temporal cost in the absence of a spatial error.

The size of the target also influenced the grasping parameters in a similar manner (i.e., reduced efficiency but retained performance). Although the initial size presentation did not disturb the kinematics of the movement, when the target changed size from small to large (or vice-versa) an additional processing of the stimulus was necessary; participants had to (1) locate the object and then (2) compute its size based on its non spatial characteristics (i.e., colour). Although our results revealed significant differences for the trials where changing in size occurred, the task was completed faultlessly but with significant temporal cost.

Overall, our data suggest that the participants were able to program their dynamic parameters and use colour for controlling their movements towards objects defined by location and/or size although significant delays in processing the chromatic information were present. Pisella et al., (1998), Schmidt (2002), Brenner and Smeets (2004) reached similar conclusions in pointing studies in which they showed that even though coloured targets influence movements to a certain point, participants were able to correct on line the reaching parameters based only on chromatic information. Further, although colour manipulation proved to have a significant effect on RT and MT, our participants showed a more rapid adaptation as compared with the results reported by Brenner and Smeets (2004). One possible explanation

could reside in the fact that it is almost impossible to control for a perfect iso-luminance a real 3-dimensional paradigm. Given the real life environment, even within a rigorous experimental design, a large variety of perturbing factors might interfere with our sensory system (i.e., shadows, noise, depth of the field). Still, our findings are consistent with the P/M visual pathways and support the location/colour dissociation. Moreover, these findings suggest that although a strong segregation between the P and M stream exists, these two cortical streams may influence each other through the dense network of cortico-cortical interconnections between different visual areas. The human motor system appears to be almost wholly able to manage colour for programming a grasping task.

Table 1

Summary of Median Values for Final Location (SLOC - same location; DLOC - different location). Significant differences are reported, ($p < .05$).

Median	SLOC	DLOC
RT (ms)	278	292
MT (ms)	494	521
Movement Path Length (mm)	333	347
Time to Peak Grip Aperture (ms)	307	321

Figure Caption

Fig. 1. Ishihara colour blindness test. The test consisted of a series of coloured cards; on each card is printed a circle made of many dots having different sizes and different colours, spread randomly. Within the dot pattern, and differentiated only by colour, is a number. A person having normal vision is able to distinguish the number within the dot pattern.

Fig. 2. Experimental settings. Stimulus consisted of one red plastic cylindrical object. The target was presented on a horizontally placed *purple* cardboard background. In 50 % of the trials the target was large, (radius = 2.2 cm, height = 3.5 cm) and in half the target was small (radius = 1.6 cm, height = 2.6 cm). The task required participant to grasp as accurately and quick as possible the target object using the precision grip (i.e., thumb and index).

Fig. 3 Experimental design. At the beginning of each trial, the goggles closed for 5000 ms, during which the target object was positioned on the background surface in concordance with the randomized order. After this period the goggles opened for 2000 ms, allowing the participant to observe the initial location or size of the target object. The goggles were closed again after this interval for another 5000 ms, time wherein the experimenter repositioned the target object on the background surface in concordance with the randomized order. After this period the goggles opened concomitant with the tone that indicated the participant to make the grasping movement.

Fig. 4. Grip aperture across percents of movement, (SLOC = same location; DLOC = different location).

Fig. 5. Movement pattern for the trials where the target changed location. DLOC = different location. SLOC = same location. Plain circle represents the initial target location (right); dot circle represents the position of the switched location (left). Black lines represent the movement path towards the object located in right; blue lines represent the movement path towards target located in left.

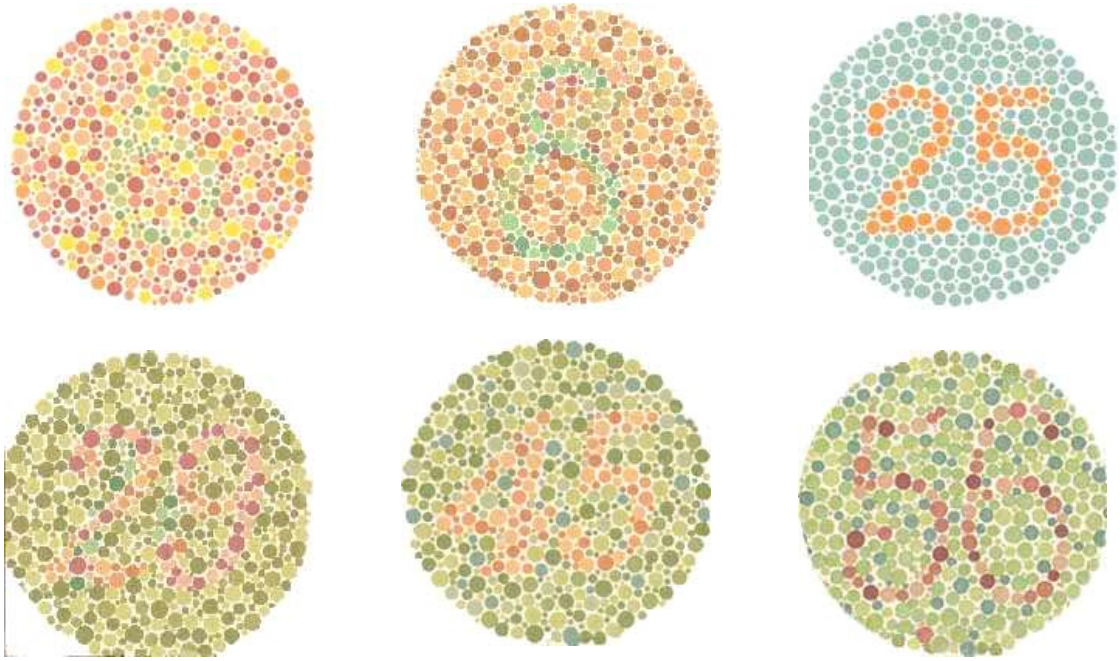

Fig. 1.

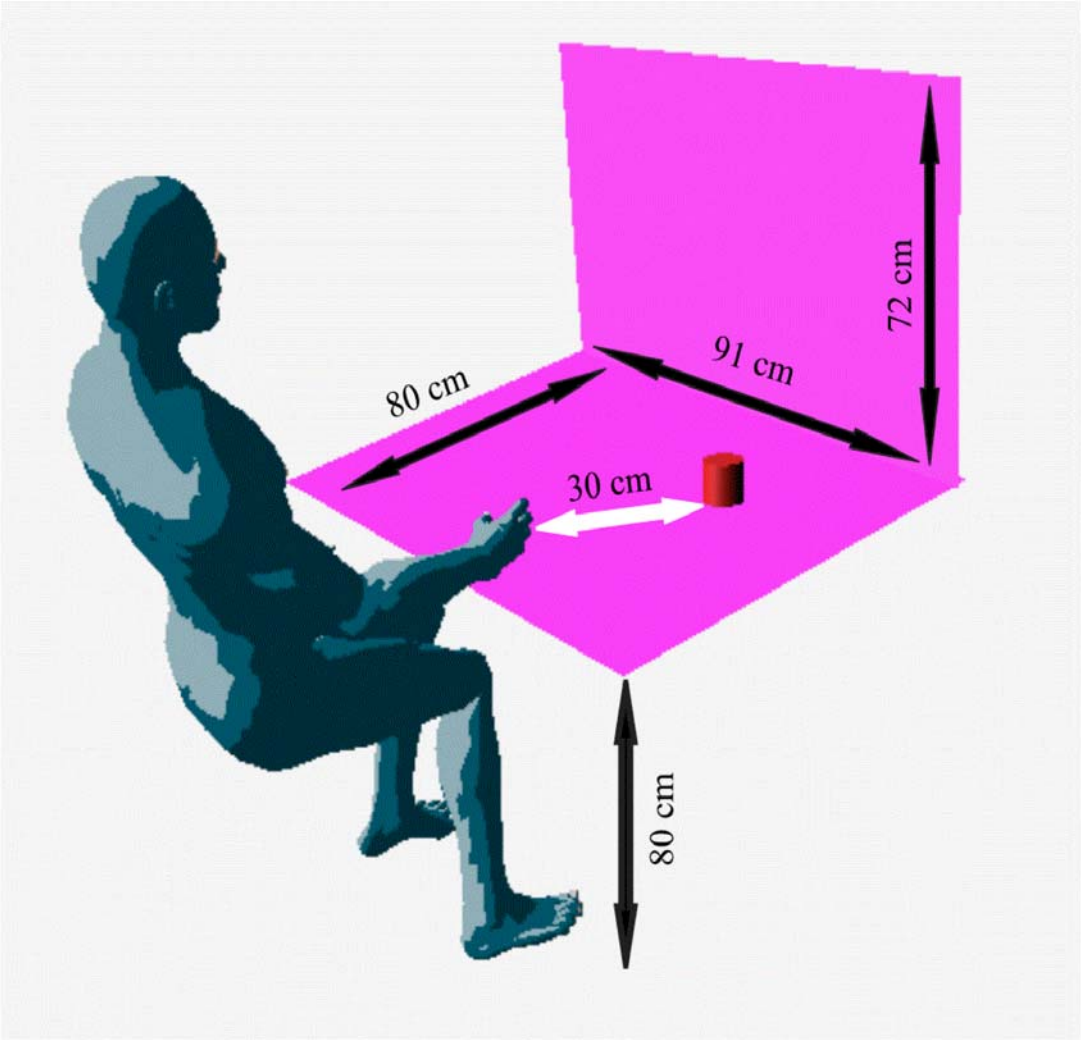

Fig. 2.

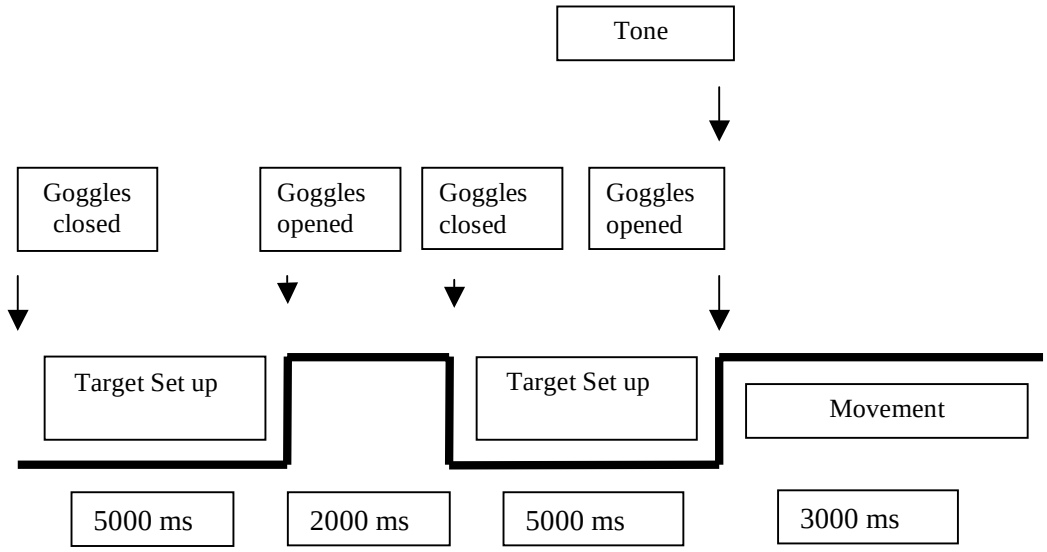
Tone
Goggles closed
Goggles opened
Goggles closed
Goggles opened
Target Set up
Target Set up
Movement
5000 ms
2000 ms
5000 ms
3000 ms

Fig. 3.

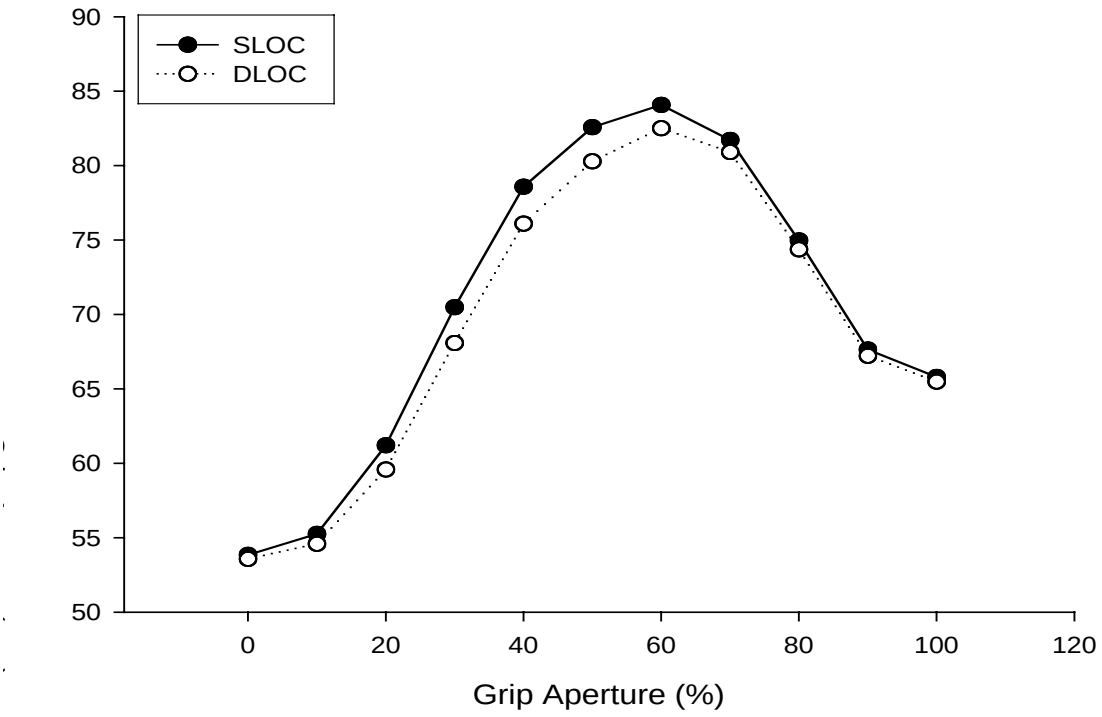
SLOC
DLOC
90
85
80
75
70
65
60
55
50
0
20
40
60
80
100
120
Grip Aperture (%)

Fig. 4.

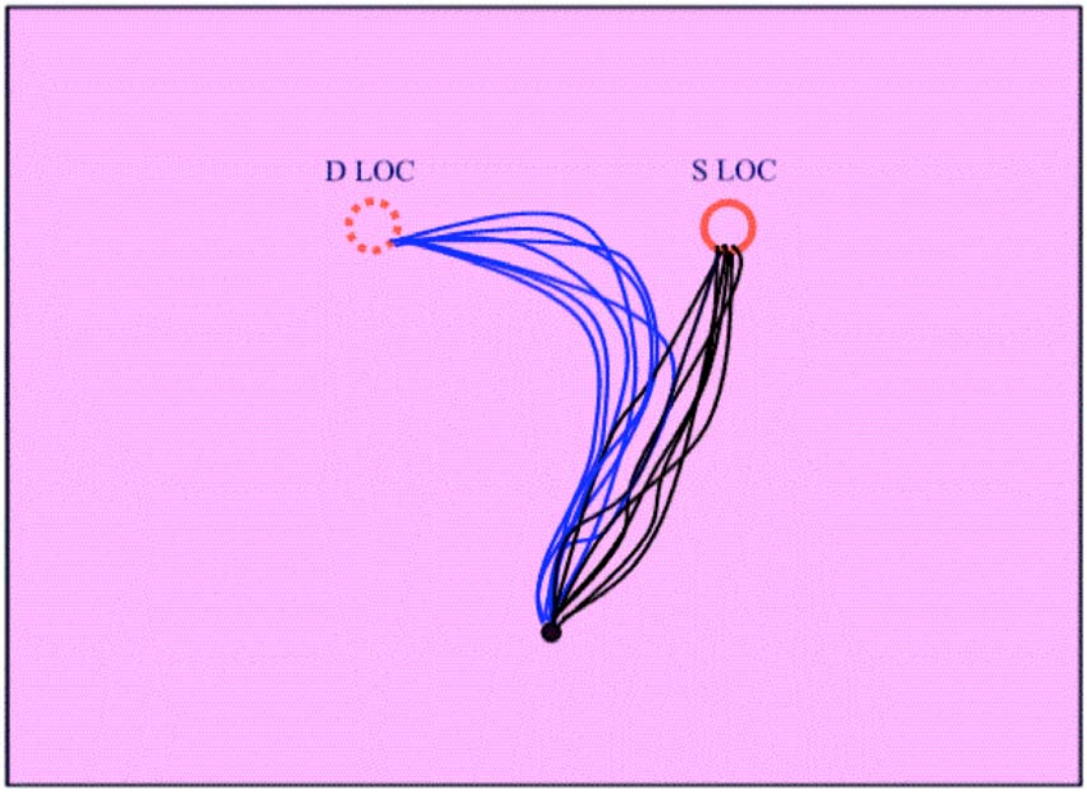

Fig. 5.

Chapter III

Manuscript introduction

The pilot study emphasized the hypothesis that people are able to program and execute a motor task (e.g., grasping) based on chromatic information. Specifically, we showed that colour attributes can be successfully used by the dorsal pathway for adjusting the motor programming schema. Although the grasping task was completed successfully, a temporal dissociation occurred when perturbation of final location/ size took place. This is consistent with previous research (Nowak & Bullier, 1997; Tanaka & Shimojo, 1996; Tanne et al., 1995) which proposed different latencies for dorsal vs. temporal areas. Moreover, our results are consistent with previous researchers (Schmidt, 2002; Brenner & Smeets, 2004), showing that colour input is made available to the dorsal stream during performance of an action at least at a satisfactory level that allows movement to be corrected.

This first experiment was entirely controlled for luminance in order to examine the impact of colour detection and correcting for changes in location. We continue this line of inquiry by performing two experiments in which the luminance is manipulated in half of the trials and the other half remains isoluminent but vary in chromaticity (as in the Pilot Study). This manipulation permits the examination of the relative contributions of M and P systems to movement production. Moreover, in the first experiment, participants are provided vision of the aiming environment only following the start tone and

prior to movement initiation, permitting the examination the relative roles of luminance and chromaticity in movement planning. Based on the PC model (Glover, 2004) one would expect that planning should be able to fully integrate colour, but perhaps less so luminance. Conversely, the PA model (Milner & Goodale, 1992) would predict the opposite. During experiment 2, an open loop condition was introduced in order to observe how colour/ luminance modulates the on-line control of the movement. The goal here was to identify the role played by the ventral stream during the execution of the grasping task. Vision was only present during execution; no vision was available prior to movement initiation. Contrary to experiment 1, both the PA model and PC model would both predict preferential utilization of luminance information.

Functional aspects of colour processing within the human brain

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Introduction

Dual vision system theories

Ungerleider and Mishkin (1982) first proposed that our visual system has a dual organization by advancing the anatomical distinction between the ventral and the dorsal pathway within the primate visual system. The brain's visual pathways were therefore divided into two main pathways: The dorsal stream, referred as the "where" pathway and the ventral stream known as the "what" pathway: The "where" pathway projects from primary visual cortex to posterior parietal cortex, while the "what" pathway connects to inferotemporal cortex. Predominantly, the signals used for *object localization* seem to be generated mainly by the dorsal system whereas the ventral stream is specialized for object *recognition* (Ungerleider & Mishkin, 1982).

A decade later, Goodale and Milner (1992), Milner and Goodale (1995) provided a new conceptual account of how the brain processes visual information. They proposed the perception-action (PA) model and made two major assumptions: (1) The dorsal stream processes visual information for motor purposes, the dorsal path being engaged in guiding the body movements under non-consciousness control (2) The ventral stream is involved in the object perception by assembling the visual elements into a real, aware image. The visual input is made available to the dorsal stream quickly for fast on-line adjustments whereas the ventral stream activity is dominated by continuous interactions with memory areas. In supporting these concepts, Milner and Goodale emphasize the

dissociation between the behaviour of the agnosic patient D.F. and that of the ataxic patient A.T. (Perenin & Vighetto, 1988). A.T., suffers from optic ataxia (consequence of a lesion of dorsal stream), manifests a profound incapability in reaching and grasping targets under visual guidance but having no difficulty in observing and recognizing them whereas the visual form agnosic patient D.F. which has a lesion of the ventral structures shows difficulty in recognizing objects visually, but can still use visual information to guide her movements.

Another pertinent approach of how the two streams process information was proposed by Glover (2004). He explored the evidence for a distinction in human performance between the planning and on-line control of action. The proposed planning–control (PC) model offers a different approach with respect to the visual and cognitive processes involved in movement production. This new model establishes an anatomical substrate of the ideas offered previously by Woodworth (1899), yet, it offers an inclusive analysis of the relationship between cognition and action. The PC model takes for granted a *gradual* rather than *discrete* transition between the two stages of action. Thus, planning in humans is linked with activity in a dispersed network including a visual representation in the inferior parietal lobe (IPL), whereas control is associated with activity in a separate network including a visual representation in the superior parietal lobe (SPL). During planning, information regarding the object's shape, size, orientation, texture, fragility and colour is sent out from the V1 to IPL via

temporal lobe. Once the motor act is planned, a blue-print copy is forwarded to the SPL to be used in real time once the movement is initiated.

Whatever the approach, information regarding stimuli properties first reaches V1 through separate neural pathways (Livingstone & Hubel, 1987, Merigan & Maunsell, 1993). Anatomical studies have revealed that cells within the visual system have different specializations, this being observed even from the retinal level (Hubel & Wiesel, 1966; De Valois, Abramov, & Jacobs, 1966; Hendry & Yoshioka, 1994; Martin, White, Goodchild, Wilder, & Sefton, 1997). Two types of ganglion cells encode visual information; luminance and spatial location are carried out through the philogenetically older Magno-pathway (M) having faster neural conduction speed whereas the chromatic input is transported by the Parvo-pathway (P). A discrete anatomical segregation between these projections can be traced up to V1 (Livingstone, & Hubel, 1987). Although a complete mapping of the M/P or luminance/colour onto the Dorsal/Ventral should seem plausible, there is not enough evidence to support the total separation (for review see Gegenfurtner, 2003).

Colour processing

The cortical processing of colour begins in the striate and extra-striate areas by disassembling and analyzing of perceived image wave length components (Van Essen & Zeki, 1978; Zeki & Marini, 1998). From V1 and V2 the information is sent out to V4 (in primates; Zeki, 1978**;** Zeki & Shipp, 1989), and from V4 the information is forwarded to inferio-temporal cortex. Zeki and Marini (1998)

proposed that colour processing occurs in three stages: (1) recording the colour signal of every point on the visual field; (2) evaluation of the colour from one area with the colour of surrounding area; (3) linking abstract colours to objects and surfaces in the visual field. The first two stages represent the processing of the impulse in V1 and V2 respectively whereas the last stage is the function of V4. Although V4 has been considered for a long time to be the "colour centre" of the visual brain (macaque; Zeki, 1993), its role in processing colour is not completely understood. For example, V4 has also been proposed as the center which integrates vision and cognition regarding the visual scene (Chelazzi, Miller, Duncan, & Desimone, 2001).

However, even considering the possibility that V4 is not the only cortical area involved in the superior stages of processing colour, chromatic information is a distinctive attribute of the ventral stream. Many previous studies (Lennie, 1998; Lennie, Krauskopf, & Sclar, 1990; Livingstone & Hubel, 1987; Milner & Goodale, 1995; Zeki, 1993) have showed that a large number of cells from the ventral stream are sensitive to colour whereas within the dorsal stream there is a significant proportion of neurons that respond to luminance discrepancies. Nevertheless, extrapolating from neuro-anatomical data to real-time action modulation, one might find this mapping difficult since during real life events these neural circuits act together, synergistically, engaging in continuous interaction and modulation. One question rises here: can colour *only* contribute in controlling object-directed action? If we are to test this hypothesis through the

prism of the Milner and Goodale (1995) PA model, we should encounter significant disruptions of the motor act when chromatic information has to be perceived, integrated and processed during fast movements toward targets defined by colour in absence of luminance discrepancies. Conversely, the PC model (Glover 2004) would predict that the motor system should be able to fully integrate both luminance and colour, as well as other object characteristics (e.g., shape, texture) for both planning and control phases of the movement. The usage of colour seems therefore to encounter different interpretations in terms of productivity for the action output.

Using a pointing paradigm, Brenner and Smeets (2004) tested this hypothesis by asking participants to tap as quickly as possible a red target square which might have inter-changed position with a green target. Luminance of the background was either brighter, the same or darker than the targets. The main conclusion drawn by Brenner and Smeets was that colour can contribute to fast online adjustments in the presence of 120 ms delay, time required for the new location to be processed. Brenner and Smeets countered the results of Pisella, Arzi, and Rossetti (1998) who proposed that people cannot respond quickly to colour stimuli due to a slower processing within the ventral streams. The roots of this debate seem therefore to have a more semantic than concrete substrate since both studies showed that colour processing requires more time than location features during reaching tasks. Indeed, there is large body of literature showing that colour is processed more

slowly within the ventral pathway (Nowak & Bullier, 1997; Tanaka & Shimojo, 1996; Tanne, Boussaoud, Boyer-Zeller, & Rouiller, 1995).

Considering this discrepancy in interpretation we extended the research line proposed by Brenner and Smeets (2004) and performed two experiments using a grasping paradigm within a realistic 3-dimensional experimental design. Single neuron recording studies (Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino, & Matelli, 1988 ; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) have shown that different neurons from the premotor area F 5 are involved in grasping in a different manner. Some grasping neurons fire at the beginning of the movement when the hand just leaves the home position, and others fire at the end or when the hand has already pre-shaped the object. Some grasping neurons discharge impulses during flexion of the fingers and other when the fingers are extended. Culham, Danckert, and Goodale, (2002) reported that the anterior intraparietal (AIP) region of humans shows a larger response for visually grasping tasks than for reaching tasks. The segregation hypothesis between the neural activation during reaching and grasping within the dorsal areas has been intensely supported by Jeannerod (1981; 1988), Jeannerod, Arbib, Rizzolatti, and Sakata (1995). Relying on the hypothesis that reaching to a target is considered just a component of the grasping act we aimed to measure the real-time capacity of our visuo-motor system to perceive, integrate and modulate the chromatic information to (1) plan and (2) perform the grasping movement. Within experiment one, participants were instructed to grasp, using a precision grip, an iso-luminant red target displayed on the background in vicinity

of a green object distracter. By using a secondary condition where both the targets and the background had different luminance gradients (e.g., black, white and grey) we endeavored to determine the modulations that occur during planning and execution of the motor task when colour in comparison with luminance had to be computed.

Experiment 1

The first experiment (E1) was performed in order to investigate how chromatic information in contrast with luminance information is able to manage the *planning* of the grasping movement. Within this experiment vision was present only during reaction time period and it was occluded after the participants started the movement production.

Methods

Participants

Twelve university aged participants (eight males and four females) between the ages of 19 and 30 years old (mean age 24.4 years old, SD = 3.1) volunteered to participate in this study. All participants were right handed, in good health and with normal or corrected to normal vision. Because the experiment required subjects to make a judgment regarding the colour of the object displayed and to grasp it based on its chromatic characteristics, all the participants were administrated Ishihara colour blindness test (Salvia & Ysseldyk, 1972) prior being admitted in the study. This investigation was carried out with the approval of the University of Saskatchewan Behavioural Science Research Ethics Board for

ethical consideration in Human Experimentation in accordance with Declaration of Helsinki (1964).

Task

The experiment consisted of two luminance/chromaticity conditions, each of them having 80 trials (160 trials in total). Within every trial the participant had to grasp a target cylindrical object as accurately as possible using a precision grip (i.e. thumb and index).

Stimuli

Stimuli consisted of 8 plastic cylindrical objects, 4 large (radius = 2.2 cm, height = 3.5 cm) and 4 small (radius = 1.6 cm, height = 2.6 cm). One of each size was painted using oil paint in *red*, (R = 252, G = 68, B = 35), one in *green*, (R = 33, G = 136, B = 23), one in *black*, (R = 0, G = 0, B = 0) and one in *white*, (R = 255, G = 255, B = 255). Following painting, objects were coated with a matt finish layer.

The experiment consisted of two main conditions. In the *isoluminant* condition (RG) the red and the green objects were presented on a *purple* cardboard background (R = 194, G = 58, B = 172). The *heteroluminant* condition (BW) involved black and white objects; they were displayed on a *gray* background (R = 126, G = 126, B = 126).

The settings were similar for both conditions, the only exception being that the luminance among the stimuli and the background varied from one condition to the other (see figure. 1). Specifically, in RG condition the objects and the background

had the same luminance (20 cd/m^2) whereas in the BW condition, the objects and the background had different luminance (white target luminance = 136 cd/m^2; black target object luminance = 4 cd/m^2; grey background luminance = 34 cd/m^2). In both conditions the background (70 cm x 90 cm) was positioned on a 60 degrees inclined in front of the participant. The distance between the floor and the near edge of the horizontal plane surface was 80 cm (see Fig. 1).

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Apparatus

1. Motion Tracking. The movements were recorded by tracking the infrared-emitting diode (IRED). Three markers were used, one being placed on the distal phalanx of the right thumb, the second on the distal phalanx of right index finger and the third on the region of the trapezium-metacarpal joint of the right thumb (Jeannerod, 1981; Jeannerod & Biguer, 1982). This permitted deviation of grasp and transport component of reaching. The position of the IRED was sampled for 3 s at 200 Hz following the auditory initiation cue using Visualeyez 3000 system (Phoenix Technologies Inc., Burnaby, BC, Canada).

2. Liquid Crystal Goggles. To achieve visual occlusion where trials require subjects to grasp the target under no vision interval, Liquid Crystal Goggles (Translucent Technologies Inc. Plato Model: P1) were utilized.

3. The motion tracking data were collected using a personal computer BOXX Technologies Inc. running Visualeyez Soft 2.70 (Phoenix Technologies Inc., Burnaby, BC, Canada). The randomization was determined by the second computer (IBM ThinkCentre) running E-Prime Studio Soft Version 1.1

4. The luminance of the objects and the backgrounds was evaluated using TEKTRONIX J-17 luminance meter (Narrow Angle Inc., Beaverton, OR, U.S.).

Procedure

The participants were comfortably seated on an immobile chair in front of the inclined background in an illuminated room (1000 lumen/m^2). The experiment required participants to move "as rapidly and accurately as possible", in response to a start tone to the object presented to them and grasp it using a precision grip (i.e., thumb and index). To avoid adaptive strategies to the targets the participants used a chin rest during all the trials. At the beginning of each trial, the participants were asked to put their right hand on the home position and press the trigger with their index finger. The goggles were then closed for 5000 ms wherein the objects were positioned on the background surface in concordance with the randomized order. Following an additional randomized fore period of 1-3 sec, a starting tone sounded indicating that the participant was to react with a grasping movement. The tone also activated the goggles which opened and stayed open until the finger lifted off. When the finger left the home position the goggles closed and the grasping movement was made under no vision condition.

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Insert Figure 2 about here

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The measurement period was fixed for 3 seconds. After this interval a second tone indicated participants that the measurement ended. Trials were considered valid only if the fingers securely grasp the target object. The distance between the home position and the target was 30 cm; within every trial two objects were displayed on the background, one large and one small (green and red within RG condition and black and white within BW condition). The distance between objects was 14 cm. In each condition there were 4 secondary conditions that were obtained by taking all possible combination regarding: (1) the target object size; and (2) target object location. The experiment consisted of 160 trials, each condition accounting for 80 trials. The conditions were counterbalanced across the participants. The experiment lasted for approximately 60 minutes.

RG condition

The target object within the RG condition was the red object. Both the target and the green distracter were positioned on the purple background. The trials where the target object was located at the *right* were considered control trials and they accounted for 75 % of the total number of trials (60 trials of the total of 80). Before proceeding, the participants were informed that in 75% of the trials the target is located at the right. The other two combinations (i.e., when the target object was located at the left) accounted for 25 % of the total number of trials. In

half of the trials the target object was small and in half the target object was large. In all the trials the distracter object had the opposite dimension (i.e., when the target object was small the distracter object was large). To accomplish the task, participants had to always grasp the red target using the precision grip.

BW condition

The target object for BW condition was the white object. Both the white and the black objects were placed on the grey background. The procedure was identical as for the RG condition.

Data Reduction and Analysis

The initiation of each reaching movement was identified interactively by determining the first sample after which hand velocity attained and maintained a value of 50 mm/s for ten consecutive frames (i.e., 50 ms; Binsted & Elliott, 2001; Elliott, Heath, Binsted, Ricker, Roy, & Chua, 1999); reaction time (RT) was the time that elapsed from the collection start to movement start. Movement offset was the point at which fingers velocities fell below 50 mm/s and remained below this criterion for ten consecutive frames (i.e., 50 ms). IRED position data were filtered off-line using a second-order dual-pass Butterworth filter (low-pass, 15 Hz). Instantaneous velocities were calculated by differentiating displacement data using a five-point central finite difference algorithm.

A series of dependent variables were examined; these included: RT, movement time (MT), the path length, peak acceleration, time to peak acceleration, peak

velocity, time to peak velocity, end wrist position, peak grip aperture, time to peak grip aperture, the proportional grip aperture across the movement.

All hand dependent measures were analyzed using a two luminance conditions [iso-luminance (RG) and hetero-luminance (BW)] x 2 locations (LOC; right, left) x 2 sizes (SIZ; small, large) repeated measures ANOVA, with each score based on the median of 10 trials for perturbed trials and 30 trials for control trials. Where appropriate, F statistics were corrected for violations of the sphericity using Huynh-Feldt correction. Significant effects/interactions were explored using simple effects analyses and a Bonferroni correction for multiple comparisons (alpha = 0.05). Only significant effects are reported ($p < 0.05$).

Results

With the exception of 14 trials (< 2.5 % of total) which were removed from the analysis due to poor marker reading the participants exhibited consistent patterns of movement and performed well across both conditions. Although vision was not available during the movement task, all participants were able to complete the task proficiently and only 4 trials (< 1 %) were missed trials (i.e.; unsuccessful grasping of target object).

As predicted, the luminance/colour treatment demonstrated a significant effect on RT [(BW mean RT = 273 ms, RG mean RT = 289 ms), F (1, 11) = 13.45, $p < .003$]. Moreover, an interaction between the RG/BW variation and change in location occurred, F (1, 11) = 8.25, $p < .014$]. This behaviour was manifest only when target object switched location with the perturbation object

forcing therefore a supplementary processing of target coordinates which turned out to be significantly longer for colour as compared with luminance (See Fig. 3).

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An interesting dynamic evolution occurred after the participants lifted the fingers from the trigger and produced the grasping movement under the no vision condition. A significant interaction was observed between colour/luminance variation and size [F (1, 11) = 125.55, p < .000]. Within the RG condition the participants scaled grip aperture appropriated for target size maximal grip aperture (RG mean peak grip aperture large object = 92.78 mm, RG small object = 82.43 mm), whereas for the BW condition the scaling was insensitive to target size variation (BW mean peak grip aperture for large object = 89.16 mm, BW mean peak grip aperture for small object = 88.67 mm; see Fig. 4).

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A powerful effect of changing location was also manifest for global movement time (F (1, 11) = 25.33, p < .000) with a mean difference of 79 ms between the condition where the target object jumped and those where initial location was preserved (SLOC mean MT = 630 ms, DLOC mean MT = 709 ms). The path length also suffered in similar manner when location was switched having a mean difference of 57 mm, F (1, 11) = 19.80, p < .001. Final location also showed an effect on all dynamic parameters, including peak velocity, time to

peak velocity, peak acceleration and time to peak acceleration [F (1, 11) = 4.78, p < .049, F (1, 11) = 18.34, p < .001, F (1, 11) = 8.42, p < .013, F (1, 11) = 12.77, p < .004 respectively). The participants reached all kinematic markers later and with lower magnitude when the target objects switched location.

The size of the target object influenced the kinematics variables as well. Significant effects of size were found for reaction time [F (1, 11) = 11.72 , p < .005], path length [F (1, 11) = 6.89, p < .022], and peak velocity [F (1, 11) = 5.6 , p < .036]. As expected, participants started moving with increased latency when a small target object was displayed (small size mean RT = 285 ms, large size mean RT = 277 ms). Once the movement was initiated, the participants continued to move more rapidly towards the larger target. The path movement length was shorter for the small object (small target mean path length = 302 mm, large target mean path length = 314 mm).

Discussion

Experiment 1 asked whether colour can be used efficiently for programming a grasping movement. Although the participants successfully completed the task important disruptions occurred. Significant delays in reaction time were encountered when participants had to locate the target within RG settings as compared with the BW condition. Our results are consistent with the dualistic functionality of M/P; luminance are carried out through separate neural pathways at least up to V1 (Hubel & Wiesel, 1966; De Valois et al., 1966; Merigan & Maunsell, 1993; Livingstone & Hubel, 1987; Silveira & Perry, 1991). Specifically,

the observed slower colour processing is consistent with the large body of evidence suggesting that colour information is transported slower through the P pathway (Livingstone & Hubel, 1987; Merigan & Maunsell, 1993). Therefore, even though both signals would eventually contribute to the production of the motor act, the luminance information is made available to the motor areas more quickly via the M pathway. Moreover, the observed latencies in reaction time are consistent with previous findings (Nowak et al., 1997; Tanaka & Shimojo, 1996; Tanne et al, 1995) which proposed different delays for dorsal vs. temporal areas.

Not only was the reaction time influenced by the manipulation of luminance/colour but also the grip aperture. Although vision was not present after the participants lifted their finger off the trigger, the movement was completely performed without visual feed-back, the maximal grip aperture suffered significant effects. Thus, the participants used a correct pre-shaping of the grip to grasp the iso-luminant red target (i.e., RG condition) by adopting a conservative strategy, scaling the grip widely but proportional with the object size. Conversely, within the BW the grip was scaled independent of target size. This proficient grip kinematics behaviour observed for the iso-luminant target during no vision paradigm brings us back to the findings of Jeannerod et al., (1995). It has been suggested that different populations of motor neurons fire differentially in regards to the type of action they are engaged in. If during reaching, programming the motor schema does not necessarily imply any supplementary processing of the 3-dimensional shape of the target, during grasping this processing is mandatory and

it might occur even before the action takes place (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Jeannerod et al., 1995). Secondly, it is known that the control of target-directed movements relies on the visual representations within the posterior parietal areas belonging to the dorsal stream (Milner & Goodale, 1995; Sakata, Taira, Kusunoki, Murata, Tanaka, & Tsutsui, 1998; Goodale & Haffenden, 1998). However, it has also been suggested that perceptual mechanisms stored within the ventral stream may be accessed during movements when the target is not visible during a motor act (Westwood & Goodale, 2003; Glover, 2004). Since the RG dimension proved to elicit correct and accurate motor responses we may assume that scaling of grip aperture is the product of two separate but interconnected processes: (1) it is planned well before the initiation of movement, within specific populations of neurons from IPL which encode the spatial characteristics of the target but do not fire until the movement begins; and (2) it is the product of a ventral stored information which is accessed by the control circuits in the event that vision is not available for guiding the action.

However, our results are consistent with the PA model (Milner & Goodale, 1995) which proposes that the response selection stage of planning is mainly served by the dorsal stream. Indeed, the faster movement initiation reported in the BW condition implies that luminance information is preferentially used by the dorsal stream to perceive the action scene and program the movement. Still, our participants were able to plan their task relying the planning of the movement only

on chromatic information. It is plausible to suggest therefore that both luminance and chromatic information reach the motor cortex; our obtained latencies being the expression of the luminance higher speed processing through the M pathway (Merigan & Maunsell, 1993; Maunsell, Ghose, Assad, Mc Adams, Boudreau, & Noerager, 1999). The temporal dissociation may also reflect the fact that that luminance information may have bypassed V1 through the superior colliculo-thalamic route, thus creating a more efficient pathway to the primary motor cortex (Parkin, 1996).

Our findings are consistent to a certain point with previous research lines (Pisella et al., 1998; Brenner & Smeets, 2004). Participants were able to use colour for programming the motor task, but the entire movement production was delayed when the target changed location. Although colour/luminance variation did influenced the reaction time and peak grip aperture, it did not manifest a significant effect on the other movement parameters. The movement showed strong effects of changing location but no significant disruptions were observed in regard to the colour/luminance manipulation. Participants were able to successfully generate a grip aperture for both conditions with no significant cost (See Fig. 5).

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These few inconsistencies with above mentioned studies can be explained if we are to consider two aspects: firstly, in our experiment a 3-dimensional design was

used, approach more difficult to control and thus more sensitive to external disturbance factors. Secondly, in our study participants performed the movement under no vision condition. This might explain the fact that once the movement was planned and the execution began, the colour/luminance variation stopped influencing on-line movement production.

Summing up, although the participants showed an increased adaptability in processing luminance, the chromatic information was used successfully by the end of the task. This suggests that colour can be used *to plan* the motor task where necessary.

Experiment 2

Within the second experiment we attempted to examine the real time capacity of our visuo-motor system to integrate colour for *real time control* of the grasping task. The luminance variation was manipulated following the same procedure as presented in Experiment 1; the only noticeable change being that the full vision condition was present only during the execution of the movement (i.e., on-line control).

Methods

Participants

Thirteen participants (8 male and 5 female) took part in this study. They were between the ages of 20 and 29 years old (mean age 25.5 years old, SD = 3.2). All participants were strongly right handed, having normal or corrected to normal vision and in good health. All participants were administrated the Ishihara colour

blindness test prior being admitted in the study. This investigation was carried out with the approval of the University of Saskatchewan Behavioural Science Research Ethics Board for ethical consideration in Human Experimentation in accordance with Declaration of Helsinki (1964).

Procedure

The experiment consisted of two luminance/chromaticity conditions, each of them having 80 trials (160 trials in total). The task, the stimuli, the settings and the apparatus were identical with those presented in E1 (See Fig. 1).

As in Experiment 1 participants used a chin rest during all the trials to prevent accommodation to the targets. At the beginning of each trial, the participants put their right hand on the home position and pressed the trigger with their index finger. The goggles were then closed for 5000 ms wherein the objects were placed on the background surface in respecting the randomized order triggered by the computer. Following an additional randomized fore-period of 1-3 sec, a starting tone sounded indicating that the participant was to react with a grasping movement. After the tone the goggles remained closed and stayed closed until the finger lifted off. When the finger left the home position the goggles opened and the grasping movement was made under *full vision conditions* (Fig. 6). The measurement period was fixed for 3 seconds. After this interval a second tone indicated participants that the measurement ended. Again, trials were validated only if the grasping movement was successful.

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Data Reduction and Analysis

Data filtering, reduction and the analysis followed the same schema as presented in experiment 1. Only significant effects are reported ($p < 0.05$).

Results

All thirteen subjects were able to produce grasping movements with surprisingly consistent accuracy for all eight experimental conditions. Although some of the responses showed a small overshoot with respect to the perturbed target, only 4% of the trials were eliminated from the analysis due to total missed performance.

A significant interaction for MT was observed when luminance/colour was manipulated along with location, [F (1, 12) = 7.11, $p < .024$]. Post hoc analysis revealed that participants took more time to correct and complete the task when adjusting their movement parameters based only on colour attributes as compared with luminance features. The effect of colour/luminance was therefore observed only during perturbed trials, when the red object switched position with the green one (See Fig. 7).

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Both size and location also showed also an effect on movement time. Participants moved slowly on average when the size of the objects was smaller compared with the perturbed target, [F (1, 12) = 44.97, p < .000; (mean MT for small object 691 ms; mean MT for large object 657 ms)]. When the target switched location to the left, it forced a delay in processing the new target coordinates. This delay was manifest as a significant effect on the total movement time, F (1, 12) = 93.61, p < .000, (mean MT same location 624 ms; mean MT changed location 724 ms).

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The movement path also suffered significant perturbations (Fig. 8). A significant effect of location was manifest, F (1, 12) = 44.67, p < .000 as well as an effect of size, F (1, 12) = 25.50, p < .000, (large object movement path length 307 mm; small object movement path length 334 mm). When the target kept its initial position (i.e. right) the movement path was almost linear (See Fig 9a). Conversely, in the case of target location perturbation, the hand showed a less efficient trajectory increasing the path length (See Fig. 9 b), (same location movement path length 286 mm; different location movement path length 355 mm).

A similar conclusion holds for the dynamic parameters. Changes in location showed a significant effect on time to peak velocity and time to peak acceleration, respectively, F (1, 12) = 33.70, $p < .000$, F (1, 12) = 9.34, $p < .010$. Location also influenced the kinematic parameters of the grasp, both peak grip aperture and time to peak grip aperture showing significant effects, F (1, 12) = 9.42, $p < .012$; F (1, 12) = 38.06, $p < .000$, (Fig. 9). Furthermore, a significant interaction between changing in location and size occurred [F (1, 12) = 6.39, $p < .030$]. Post hoc analyses suggest that the participants were able to scale their maximal aperture and initialize the final step of the movement faster in the case of small object when this was presented in the same location (Fig. 10).

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Discussion

Our primary goal in E 2 was to test the hypothesis that colour itself can provide enough information to the parietal cortex for controlling a grasping action in real time.

Overall, all thirteen participants were able to clearly complete the task for both conditions. Because vision of the targets was available only after the participants lifted off the finger from the trigger button, no reaction time differences were observed across the trials.

As expected, global movement suffered significant adjustments during completion of the motor task. Although the general impression was that the

participants carried out the task with surprising consistency, the performance was considerably altered within the perturbed trials when we manipulated the location. Changes in location significantly influenced the dynamic parameters by forcing the participant to acknowledge, observe and modify their movement parameters in concordance with a given arrangement. Moreover, the global movement time suffered significant changes across the trials when the iso-luminant (red-green-purple) environment was present as compared with the situation when the experimental settings were not controlled for luminance. These results are consistent with the previous researchers who postulate that colour information is transported by the parvo-cellular pathway whereas the luminance modulation is the function of the mango-cellular path (Livingstone & Hubel, 1987; Merigan & Mausell, 1993). Moreover, significant latencies were observed in terms of movement time, a fact that demonstrates predominant usage of the luminance feature in controlling the outgoing movement.

General Discussion

The present research endeavoured to investigate the functional mechanisms of colour processing for the programming and execution of a motor task. We aimed to identify the particular motor strategies that visual cortex and subsequent pathways adopt when processing colour and luminance. Our two major questions were: (1) Is colour, as a putative ventral attribute, able to be used in identification, selection and programming a motor schema? (2) Can colour solely guide the on-line control of the grasping task?

In respect to both experiments, the main conclusion is that both planning and on-line control can rely on chromatic information. Our results suggest that colour can be used proficiently by the dorsal structures to modulate the grasping task. Using a 3-dimensional grasping task we showed that luminance information is carried out from the retina to the command structures faster than the colour attribute and it is involved as a primary source of information in controlling an outgoing movement.

Further, in this investigation we focused only on red/green modulation and avoided the yellow/blue dimension and konio (K) pathway inputs due to its variable contribution to colour/motion modulation. Although there is evidence to support the possibility that K signals might reach area MT (Wandell, Poirson, Newsome, Baseler, Boynton, Huk, Gandhi, & Sharpe, 1999) and interferes within the M pathway (Calkins, 2000), other neurophysiological studies argued against this hypothesis (Lee, Martin, & Valberg, 1998; Dacey & Lee, 1994). Whether K pathway contribution to colour/motion processing plays a significant role or if it is just a subsidiary path along the P/M pathways, that stands for further examination.

Programming

In accordance with previous research lines (Hubel & Wiesel, 1966; De Valois, Cottaris, Elfar, Mahon, & Wilson, 2000; Derrington et al., 1984; Hendry & Yoshioka, 1994; Martin, White, Goodchild, Wilder, & Sefton, 1997), our results are consistent with the P/M parallel pathways highlighting the idea that there is a constant delay in the transportation, processing and handling of colour as a

defining feature of on target object. Indeed, the parvo-cellular attributes are processed slower on average than the magno-cellular pathway; our participants exhibited constant delays where colour had to be processed. Still, our participants were able to program the task faultlessly, a result consistent with previous findings (Pisella et al., 1998; Brener & Smeets, 2004). Using a more realistic approach (3-dimensional grasping versus pointing and tapping a coloured light array), we showed that colour can solely guide the complete programming schema of the motor act.

More interestingly, our findings highlight the idea that the dorsal stream seems to be involved in the movement programming as early as response selection stage since the luminance manipulation showed faster adaptability to location change. The superior efficacy of the luminance feature in movement production could be the result of two cortical mechanisms. Luminance information may reach first the visual cortex earlier and subsequently be sent to posterior parietal cortex via dorsal connection with higher neural conduction speeds (Nowak & Bullier, 1997; Tanaka & Shimojo, 1996; Tanne et al., 1995). Conversely, luminance feature information might bypass the classical dorsal neural path (LGN - Visual Cortex - Posterior Parietal Cortex) and reach the parietal structures faster through the colicullo-pulvinar pathway (Parkin, 1966; Schoenfeld, Heinze, & Woldorff, 2001). In both cases, the posterior parietal cortex shows that it is able to integrate the luminance information and modulate the response selection stage based on this attribute, a result that is consistent with the PA model (Milner & Goodale, 1995). This finding

is less consistent with the PC model (Glover, 2004) which postulates that the planning of the movement, at least up to the stage of response programming, is the function of the ventral stream.

An alternative account for our findings is that the total segregation between the two main retino-geniculo-visual cortex streams up to V1 reduces after visual striate cortex, (Thorell, De Valois, & Albrecht 1984; Leventhal, Thompson, Liu, Zhou, & Ault, 1995; De Valois et al., 2000; Johnson, Hawken, & Shapley, 2001; Xiao & Felleman, 2004). The corollary of this hypothesis is that both colour and luminance should reach the parietal cortex *and* the ventral cortex. Further, both should be ready to be used for programming the upcoming movement. Thus, latency differences reported between the chromatic and the luminance utilization may be only a matter of the speed of nervous conduction, not efficacy. In this case, it is difficult to assume which stream actually controls the planning stages and to dissociate between the PA model and the PC model since both utilize the same visual representation but within different streams.

However, our results show that once the motor act was planned, the movement did not reveal specific patterns to fully support the second mechanism discussed previously. Although significant differences were present in all kinematics parameters following target perturbation, luminance variation did not influence the precision of the task. Online computation of movement occurred in a similar manner for both BW and RG conditions under no vision circumstance. If

luminance information had been available to the ventral stream, then a powerful effect should have been present during execution of the movement.

Although the luminance feature showed faster processing and superior movement production, scaling the grip aperture based on chromatic attribute demonstrated a surprisingly better performance. One explanation of this effect is offered by the interpretation of Jeannerod et al., (1995). During planning, different populations of grasping neurons from IPL encode the target properties before the movement is initiated. Once the motor act begins, the movement dynamic parameters are modulated by a dense network connection within the dorsal stream; in the event that vision is not available for action, the control mechanisms must access the stored representation of the target from the ventral stream, the same visual representation which was encoded by the grasping neurons before movement production.

Summing up, our results are consistent with the dual system theory. Chromatic information can contribute to planning but its processing is totally dependent on the ventral capacities in modulating the chromatic information. If luminance discrepancies are present (as is likely to occur within a normal environment) then the planning is governed by the luminance attribute. The main finding in this study is therefore consistent with the idea that the dorsal stream is involved in the planning and specifically in the response selection stage of information processing. Moreover, it can program the up-coming actions with a higher degree of spatial resolution than is available to the ventral stream.

Online control

A second question of interest was whether on-line control of grasping a specified target can be completed based on colour attributes solely. Although the task was accomplished, the movements showed significant discrepancies between BW condition and RG condition. This is again consistent with dual visual systems theory, which predicts that visually guided motor actions made directly on an object utilize largely the dorsal stream. Participants showed that the integration of luminance attribute takes less time than chromatic information and result in more efficient execution.

Our results are consistent with previous lines of investigation regarding the usage of chromatic information in controlling an out-going movement. Overall, data suggest that participants were able to modulate the dynamic parameters and use colour for controlling their movements towards objects defined by location and/or size although significant delays in processing the chromatic information were present. Pisella et al., (1998) and Brenner and Smeets (2004) reached similar conclusions in pointing studies where they showed that coloured 2-dimensional targets could influence human movements to a certain point. Our obtained delays for target displacement (mean difference 100 ms) are consistent with their reported value of 120 ms (Brenner & Smeets, 2004). Therefore we may assume that colour features take more time to be integrated whatever the neural path involved.

These finding are again consistent up to a point with Milner and Goodale's (1995) PA model. Obviously, during action participants exhibited faster

movements on average when they could rely on the information received through the magno-occipito-parietal pathway or via colliculo - thalamo - posterior parietal cortex (Parkin, 1966; Schoenfeld et al., 2001). Because vision was available only after the participants initiate the movement (i.e. lifted the finger off the trigger), the coordination of the sequences required only on-line adjustment and the information regarding the colour of the objects, shape and location had to be rapidly forwarded from the visual association areas to the motor cortex. A constant delay between the kinematic parameters was observed across all trials where colour had to be processed to determine object location perturbation. Still, our participants were able to complete the task faultlessly. This fact leads us to the conclusion that colour information might bypass certain ventral processes to be made available to dorsal structures for on line control modulation. Another possibility is that the ventral streams cooperate efficiently with the dorsal streams during online-control. Reconsidering the Milner and Goodale model, we would have expected a larger effect of changing location for luminance processing as compared with chromatic processing since visually guided tasks are largely coordinated by the dorsal stream (Milner & Goodale, 1995).

On the other hand, based on the anatomical predictions of Glover's (2004) PC model, we should not have encountered such a significant interaction between changes in location and luminance manipulation because the chromatic efference copy forwarded from IPL should reach SPL in real time during the control phase of movement (Glover, 2004). Given the fact that IPL information can be used at

any point to adjust and compute on-line a motor schema (Glover, 2004), the movement should have been smooth and the colour information should have not encountered any difficulty in being processed by the SPL during online control.

Our participants showed a considerable temporal delay across trials when colour had to be processed as the only source of information. It is plausible to suggest that during visually guided actions the dorsal stream controls movement relying mainly on the information regarding spatial characteristics of the target (i.e., luminance). If this attribute is carefully attuned to a neutral value for all components of the environmental scene, our results showed that colour is able to offer consistent information for completing the grasping task but with temporal cost in lieu of spatial error.

Figures Caption

Fig. 1. BW and RG Condition; experimental settings. Stimuli consisted of 8 plastic cylindrical objects, 4 large (r = 2.2 cm, h = 3.5 cm) and 4 small (r = 1.6 cm, h = 2.6 cm). One of each size was red, one was green, one black and one white. The experiment consisted of two main conditions. In the *isoluminant* condition (RG) the red and the green objects having different sizes were presented on a *purple* cardboard background. The *heteroluminant* condition (BW) involved black and white objects; they were displayed on a *gray* background.

Fig. 2. Experiment 1. Experimental Design. Within experiment 1 vision was available only during reaction time. At the beginning of each trial, goggles closed for 5000 ms wherein the objects were positioned on the background surface. Following an additional randomized foreperiod of 1-3 sec, a starting tone sounded indicating that the participant was to react. The tone also activated the goggles which opened and stayed open until the finger lifted off. When the finger left the home position the goggles closed and the grasping movement was made under no vision condition.

Fig. 3. Experiment 1. Reaction Time vs. changing in location. BW = hetero-luminant condition; RG = iso-luminant Condition. DLOC = different location. SLOC = dame location. * Indicates significant effect, $p < .05$.

Fig. 4. Experiment 1. Peak grip aperture as a function of target size. BW = hetero-luminant condition; RG = iso-luminant condition. Small = small object size; Large = large object size. * Indicates significant effect, $p < .05$.

Fig. 5. Experiment 1. Peak Grip Aperture in percents of total movement. BW large = Grip aperture for large object within Hetero-luminant condition; BW small = Grip aperture for small object within the hetero-luminant condition; RG large = Grip aperture for large object within the Iso-luminant condition. RG small = Grip aperture for small object within the Iso-luminant condition.

Fig. 6. Experiment 2. Experimental Design. Within experiment 2, vision was available only after participants lifted the finger off the trigger and started the movement. At the beginning of each trial, goggles closed for 5000 ms wherein the objects were positioned on the background surface. Following an additional randomized fore-period of 1-3 sec, a starting tone sounded indicating that the participant was to react. The goggles stayed closed until the finger lifted off. When the finger left the home position the goggles were activated which opened and stayed open until the finger movement was completed.

Fig. 7. Experiment 2. Movement Time vs. changes in location. BW = hetero-luminant condition; RG = iso-luminant condition. DLOC = different location. SLOC = same location. * Indicates significant effect, $p < .05$.

Fig. 8. Experiment 2. Movement path length as a function of size (1) and location (2). Large = large object size. S = small object size. DLOC = different location. SLOC = same location. * Indicates significant effect, $p < .05$.

Fig. 9. Experiment 2. Movement pattern.

a. When target kept its initial position hand movement was linear.

b. The hand corrected its trajectory by sketching an arch in its way to grasps the target when it appeared in left.

Fig. 10. Experiment 2. Peak Grip Aperture in percents of total movement. DLOC large = Grip aperture for large object when located in different location; SLOC large = Grip aperture for large object when located in same location; DLOC small = Grip aperture for small object when located in different location; SLOC large = Grip aperture for large object when located in same location;

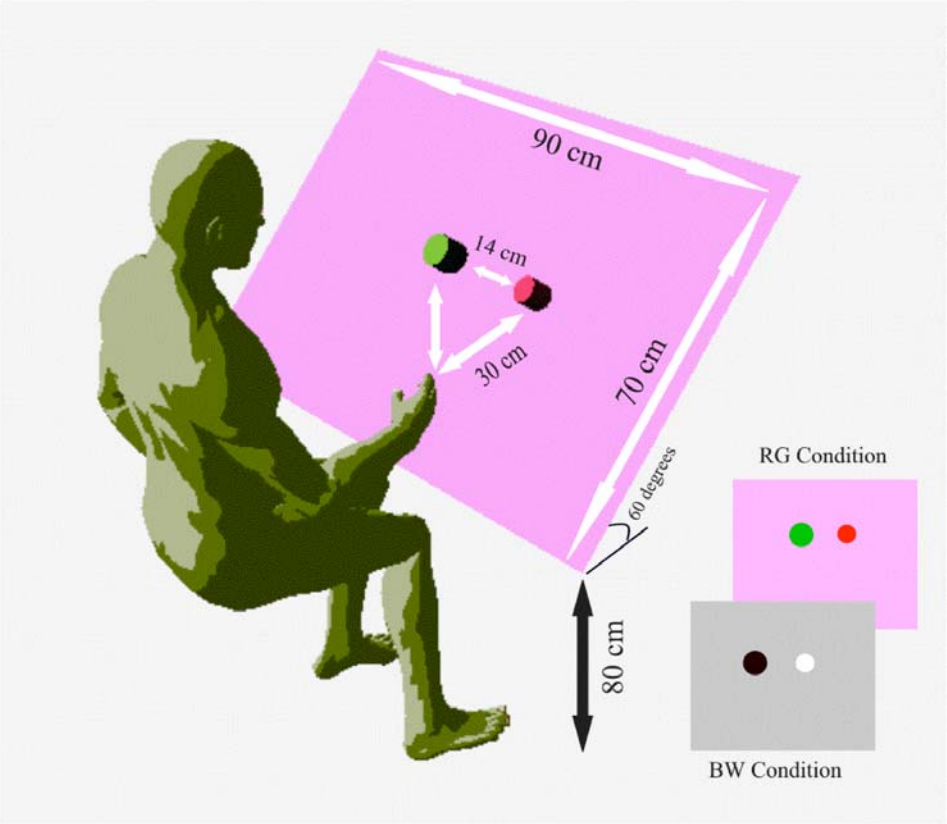

90 cm
14 cm
30 cm
70 cm
60 degrees
80 cm
RG Condition
BW Condition

Fig. 1.

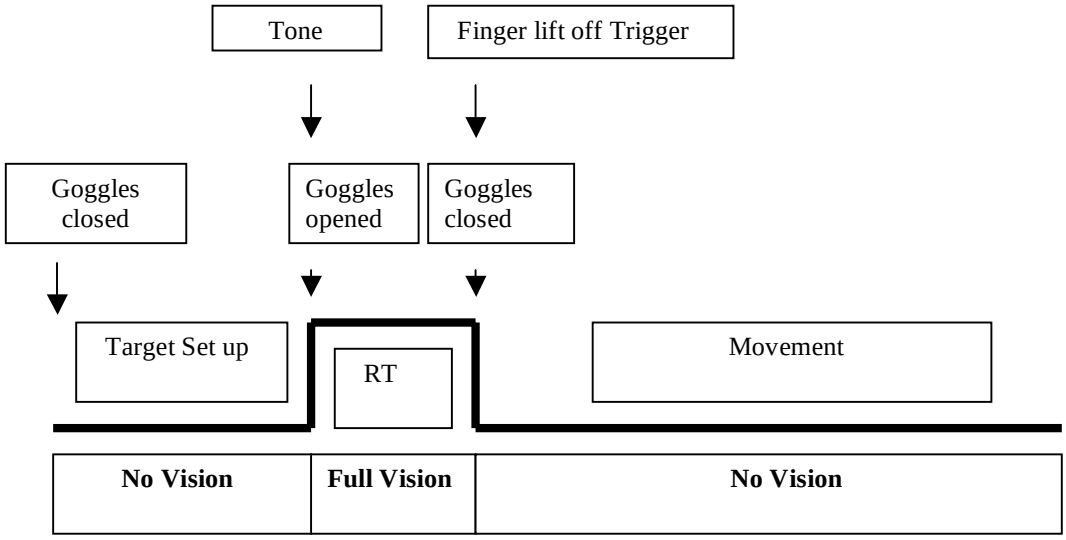
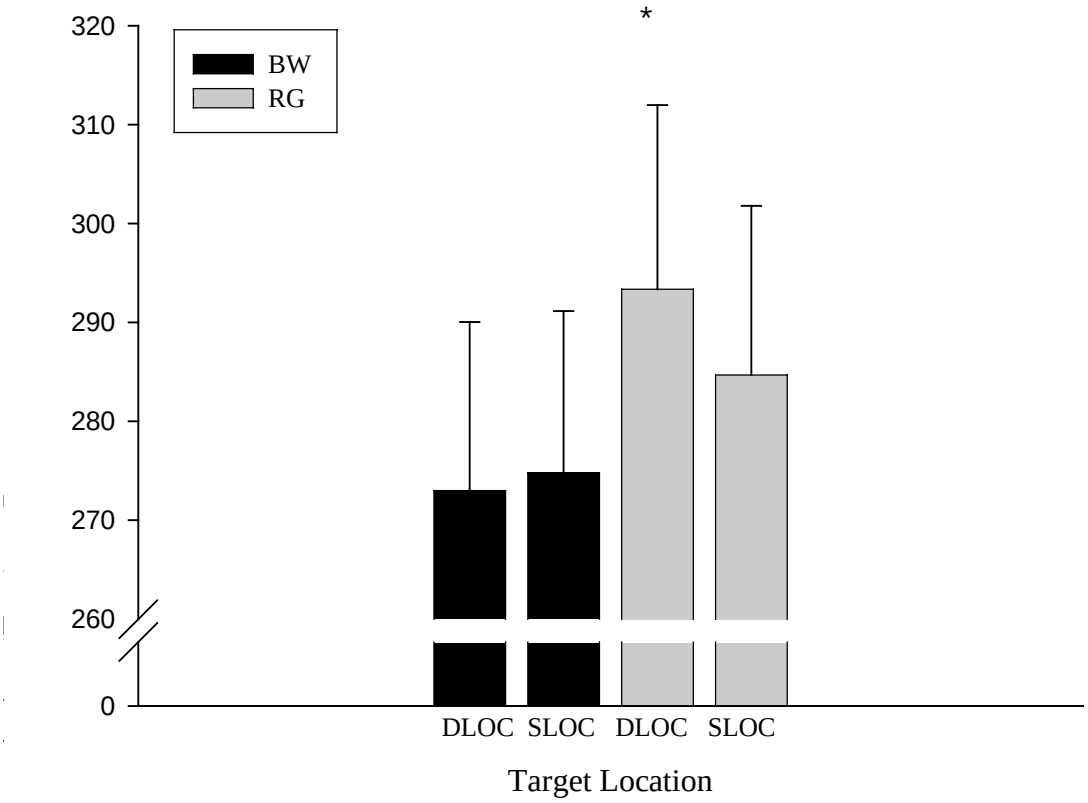

Tone
Finger lift off Trigger
Goggles closed
Goggles opened
Goggles closed
Target Set up
RT
Movement
No Vision
Full Vision
No Vision

Fig. 2.


320
310
300
290
280
270
260
0
BW
RG
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DLOC
SLOC
DLOC
SLOC
Target Location

Fig. 3.

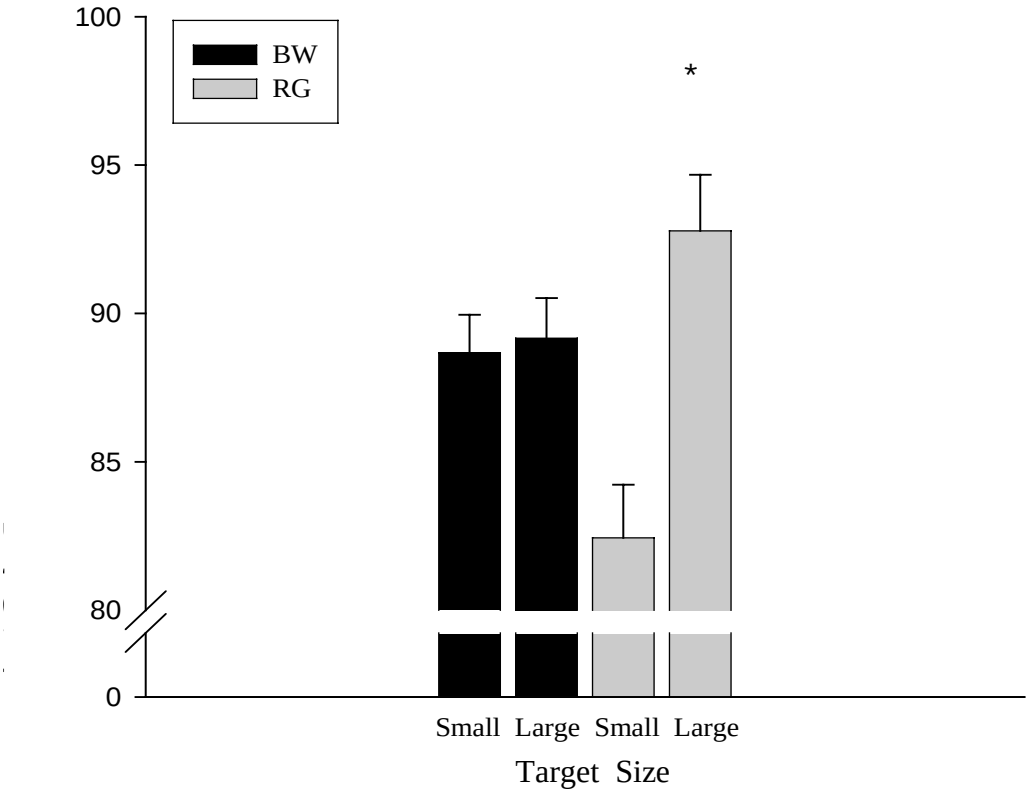

Fig. 4.

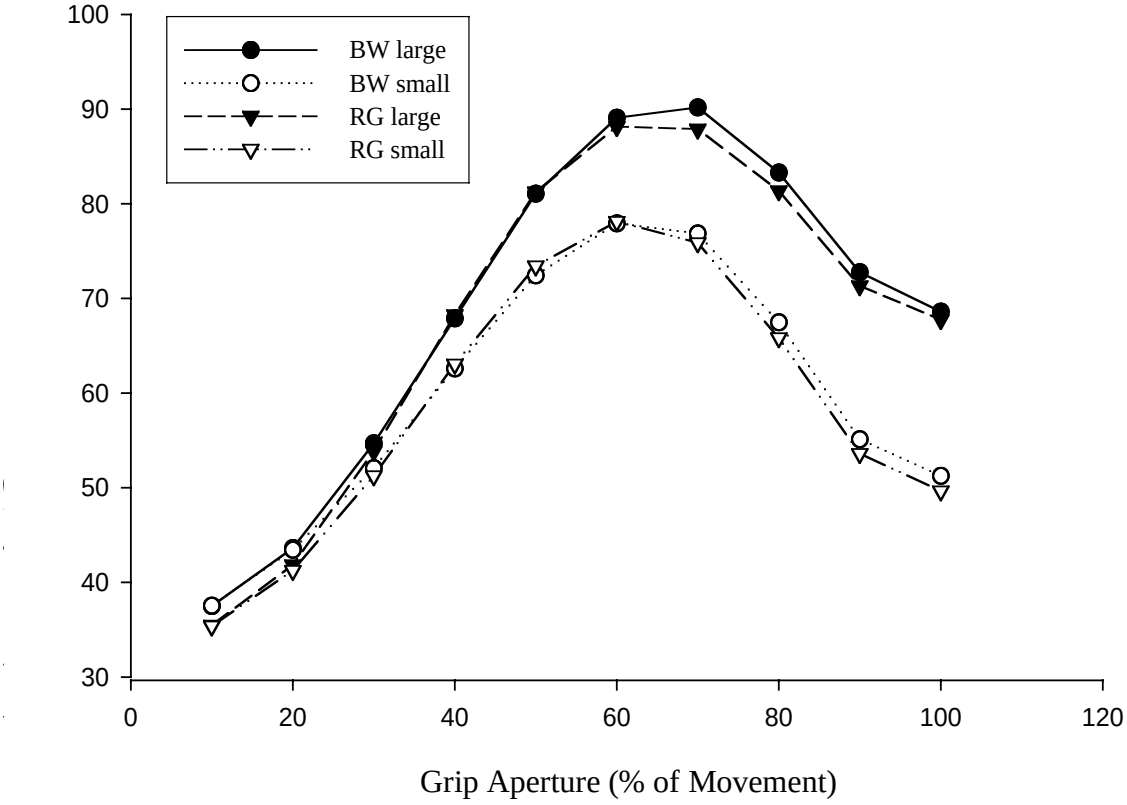
BW large
BW small
RG large
RG small
100
90
80
70
60
50
40
30
0
20
40
60
80
100
120
Grip Aperture (% of Movement)

Fig. 5.

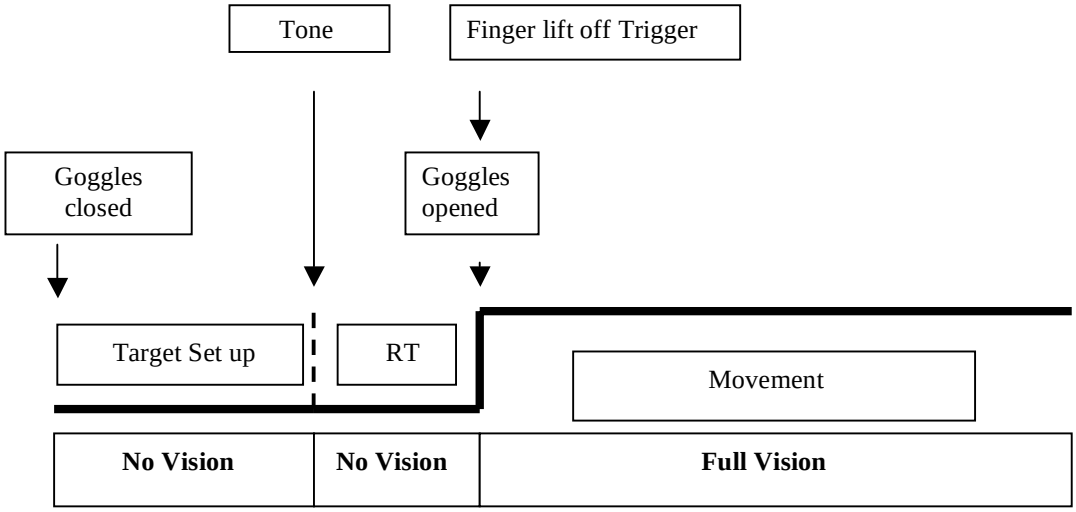
Tone
Finger lift off Trigger
Goggles closed
Goggles opened
Target Set up
RT
Movement
No Vision
No Vision
Full Vision

Fig. 6.

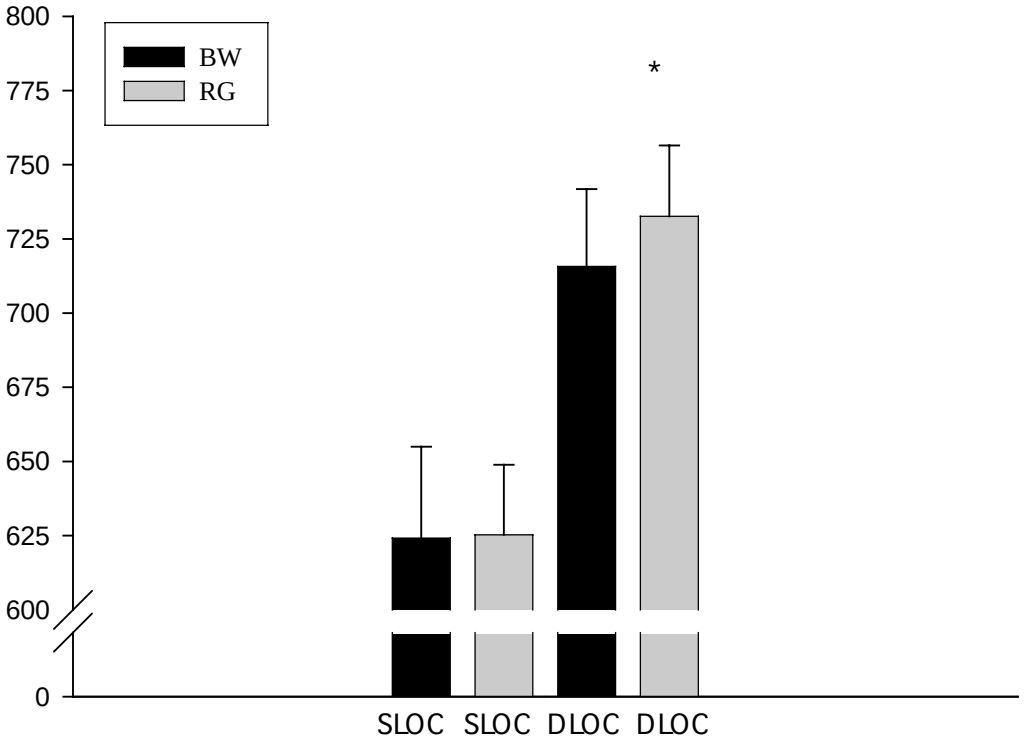
800
775
750
725
700
675
650
625
600
0
BW
RG
*
SLOC
SLOC
DLOC
DLOC
Target Location

Fig. 7.

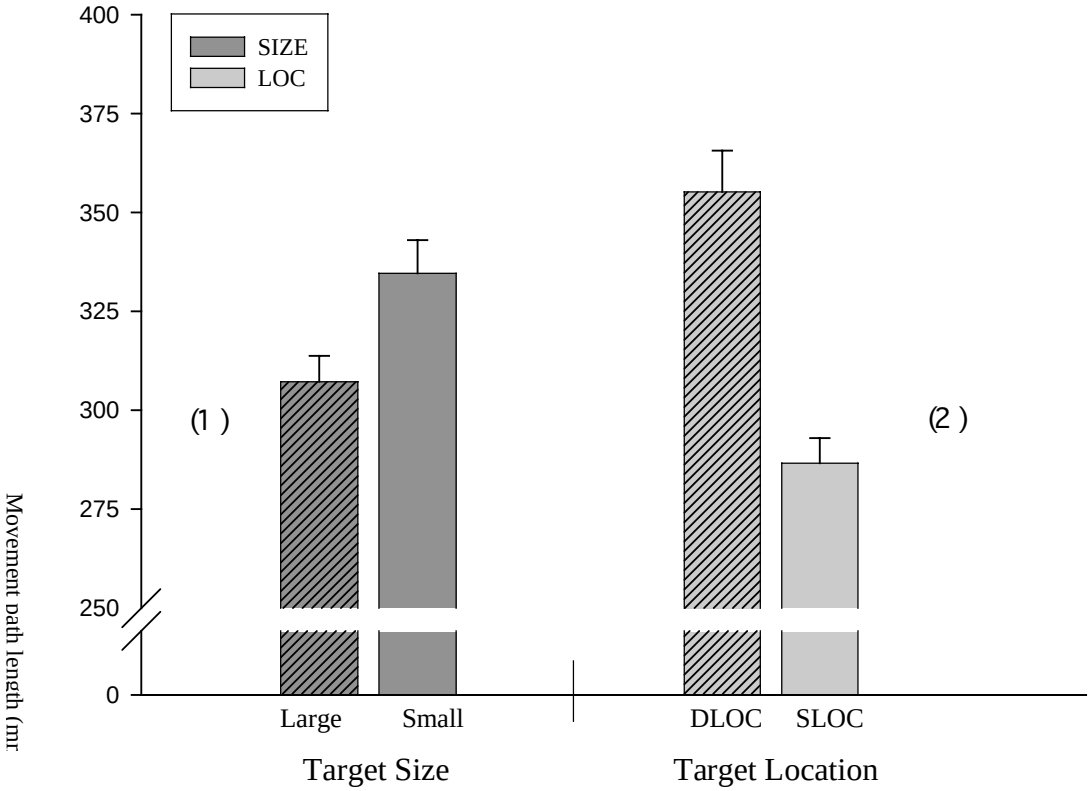
400
375
350
325
300
275
250
0
SIZE
LOC
(1)
(2)
Large
Small
DLOC
SLOC
Target Size
Target Location

Fig. 8.

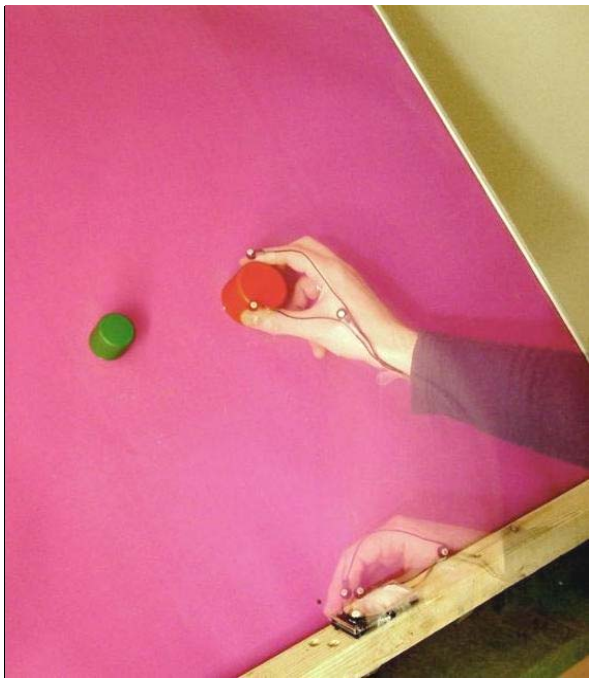

Fig. 9 a.

Fig. 9 b.

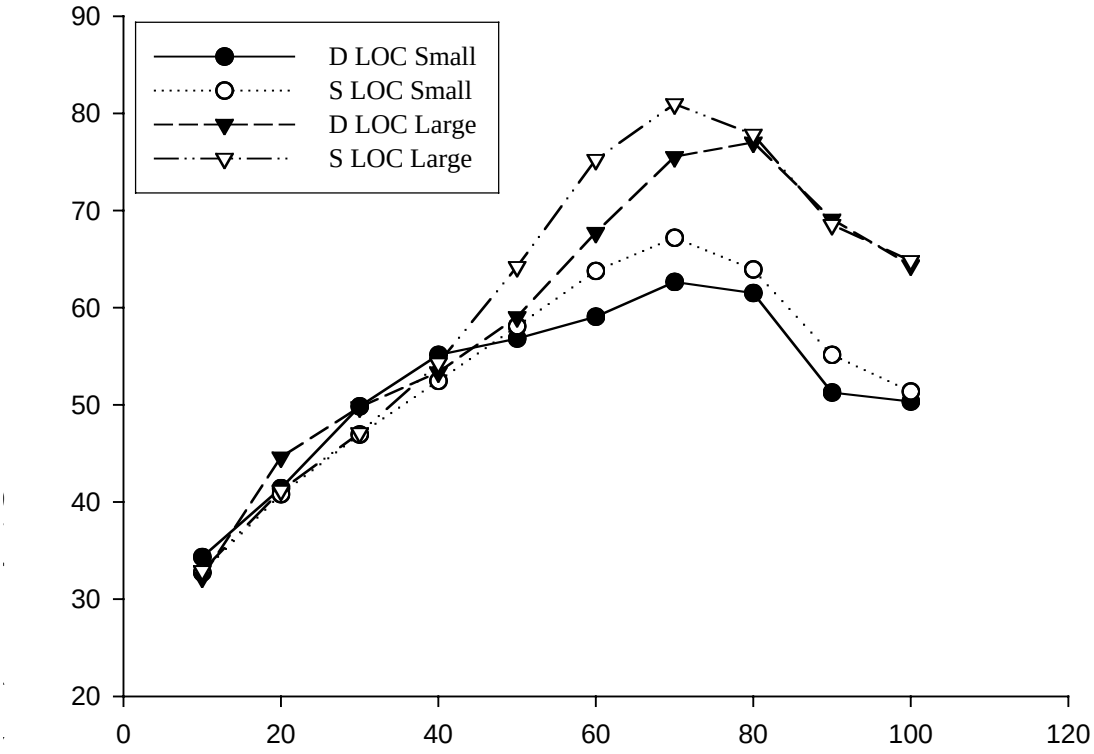
D LOC Small
S LOC Small
D LOC Large
S LOC Large
90
80
70
60
50
40
30
20
0
20
40
60
80
100
120
Grip Aperture (% of Movement)

Fig. 10.

References

Binsted, G., & Elliott, D. (2001). Eye-hand coordination in goal directed aiming. *Human Movement Science, 20,* 563-585.

Brenner, E., & Smeets, J., B., J. (2004) Colour vision can contribute to fast corrections of arm movements. *Experimental brain research, 158,* 302-307.

Chelazzi, L., Miller, E., K., Duncan, J., & Desimone, R. (2001). Responses of neurons in macaque area V4 during memory guided visual search. *Cerebral Cortex, 11,* 761-762

Culham, J., C., Danckert, S., L., & Goodale, M., A. (2002). fMRI reveals a dissociation of visual and somatomotor responses in human AIP during delayed grasping. *Journal of Vision, 2(7),* 701-708.

De Valois, R., Abramov, I., & Jacobs, G. (1966). Analysis of response patterns of LGN cells. *Journal of the Optical Society of America, 56(7),* 966-977.

De Valois, R., L., Cottaris, N., P., Elfar, S., D., Mahon, L., E., & Wilson, J., A. (2000). Some transformations of color information from geniculate nucleus to striate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 97,* 4997-5002.

Derrington, A., M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology (London), 357,* 241-265.

Elliott, D., Heath, M., Binsted, G., Ricker, K., Roy, E., E., & Chua, R. (1999). Goal directed aiming: Correcting force specification error with the right and left hands. *Journal of Motor Behaviour, 31 (4),* 309-324.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119,* 593-609.

Gegenfurtner, K. (2003). Cortical mechanisms of colour vision. *Nature, 4,* 563-572.

Glover, S. (2004). Separate visual representation in the planning and control of action. *Behavioural and Brain Science, 27*, 3-78.

Goodale, M., A., & Haffenden, A., M. (1998). frames of reference for perception and action in human visual system. Neuroscience and Behavioural Reviews, 22, 161-172.

Goodale, M., A., & Milner, A., D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15,* 20-25.

Hendry, S., H., & Yoshioka, T. (1994). A neurochemically distinct third channel in the macaque dorsal lateral geniculate nucleus. *Science, 264,* 575-577.

Hubel, D., H., & Wiesel, T., N. (1966). Effects of varying stimulus size and color on single lateral geniculate cells in Rhesus monkeys. *Proceedings of the National Academy of Sciences of the United States of America, 55*, 1345-1346.

Jeannerod, M., Arbib, M., A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuo-motor transformation. *Trends in Neuroscience, 18,* 314–320.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A (Eds.) *Attention and performance IX* (153–169). Lawrence Erlbaum, Hillsdale.

Jeannerod, M., & Biguer, B. (1982). Visuo-motor mechanisms in reaching within extrapersonal space. In: Ingle D, Goodale MA, and Mansfield R. (Eds.). *Advances in the Analysis of Visual Behavior*, (387-409). Boston, MA: MIT Press.

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements.* Oxford University Press.

Johnson, E., N., Hawken, M., J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience, 4*, 409-416.

Lennie, P. (1998). Single units and visual cortical organization. *Perception, 27*, 889-935.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience, 10*, 649-669.

Leventhal, A., G., Thompson, K., G., Liu, D., Zhou, Y., & Ault, S., J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex. *Journal of Neuroscience, 15*, 1808-1818.

Livingstone, S., M., & Hubel, D., H. (1987a). Psychophysical evidence for separate channels for the perception of form, color, Movement and Depth. *Journal of Neuroscience, 7 (11),* 3416-3468.

Livingstone M., S., & Hubel, D., H. (1987b). Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey. *Journal of Neuroscience, 7,* 3371-3377.

Livingstone M., S., & Hubel, D., H. (1982). Thalamic inputs to cytochrome oxidase-rich regions in monkey visual cortex. *Proceedings of the National Academy of Sciences U S A, 79,* 6098-6101.

Martin, P., R., White, A., J., R., Goodchild, A., K., Wilder, H., D., & Sefton, A., E. (1997). Evidence that blue-on cells are part of the third geniculocortical pathway in primates. *European Journal of Neuroscience, 9,* 1536-1541.

Maunsell, J., H., Ghose, G., M., Assad, J., A, McAdams, C., J., Boudreau, C., E., & Noerager, B., D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience, 16,* 1-14.

Merigan, W., & Maunsell, J., H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience, 16,* 369-402.

Milner, A., D., & Goodale, M., A. (1995). *The visual brain in action.* Oxford, England: Oxford University Press.

Mountcastle, V.,B., Lynch, J., C., Georgopoulos., A., Sakata, H., & Acuna, C, (1975). Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *Journal of Neurophysiology*, 38, 871-908.

Nowak, L., G., & Bullier, J. (1997). The timing of information transfer in the visual system. *Cerebral cortex, 12*, 205-241.

Parkin, A., J. (1996). *Explorations in Cognitive Neuropsychology.* Blackwell Publishers Ltd.: Oxford.

Perenin, M., T., & Vighetto, A. (1988). Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain, 111*, 643–674.

Pisella L., Arzi, M., & Rossetti, Y. (1998). The timing of color and location processing in the motor context. *Experimental Brain Research, 121*, 270-276.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey: II. Area F5 and the control of distal movements. *Experimental Brain Research, 71*, 491-507.

Salvia, J., & Ysseldyk, J. (1972). Criterion validity of 4 tests for green-red color blindness. *American Journal of Mental Deficiency, 76*, 418-430.

Schoenfeld, M., A., Heinze, H., J., & Woldorff, M., G. (2001). Unmasking motion-processing activity in human brain area V5/MT+ mediated by pathways that bypass primary visual cortex. *NeuroImage, 17*, 769-779.

Silveira L., C., & Perry, V., H. (1991). The topography of magnocellular projecting ganglion cells (M-ganglion cells) in the primate retina. *Neuroscience 4,* 217-237.

Tanaka, Y., & Shimojo, S. (1996). Location vs. feature: reaction time reveals dissociation between two visual functions. *Vision Research, 36,* 2125-2140.

Tanne, J., Boussaoud, D., Boyer-Zeller, N., & Rouiller, E. (1995). Direct visual pathways for reaching movements in the macaque monkey. *Neuroreport, 7,* 267-272.

Thorell, L., G., De Valois, R., L., & Albrecht, D., G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research, 24,* 751-769.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, R. J. W. Mansfield, & M. S. Goodale (Eds.), *The Analysis of Visual Behavior* (549-586). Cambridge, Mass: MIT Press.

Van Essen, D., C., & Zeki, S., M. (1978). The topographic organization of rhesus monkey prestriate cortex. *Journal of Physiology, 277,* 193-226.

Westwood, D., & Goodale, M., A. (2003). Perceptual illusion and the real-time control of action, *Spatial Vision, 16,* 243-254.

Woodworth, R., S. (1899). The accuracy of voluntary movements. *Psychological Review Monograph, 3 (13)* , 1-119.

Xiao, Y., & Felleman, D., J. (2004). Projections from primary visual cortex to cytochrome oxidase thin stripes and interstripes of macaque visual area 2.

Proceedings of the National Academy of Sciences U S A 101 (18), 7147-7151.

Zeki, S., M. (1978). Functional specialization in the visual cortex of the rhesus monkey. *Nature, 274,* 423-428.

Zeki, S., M. (1993). *A vision of the brain.* Blackwell: Oxford.

Zeki, S., M., & Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain, 121,* 1669-1685.

Zeki, S. M., & Shipp, S. (1989). Modular connections between areas V2 and V4 of macaque monkey visual cortex. *European Journal of Neuroscience, 1* , 494-506.

Chapter IV

Thesis summary

Conclusions

The present thesis consists of three experiments. Our key question on developing this research line was whether colour can be used to plan and perform a movement as the only source of information for the visual system. We tested our hypotheses by designing and furthermore interpreting the results through the prism of the two psycho-behavioural models, the Perception-Action (PA) model (Milner and Goodale, 1995) and the Planning-Control (PC) model (Glover, 2004). While the PA model postulates a strong dichotomy between the roles played by the two cortical visual streams during perception and action, respectively, the PC model offers a different interpretation of this interaction, yet based on similar neuroanatomical substrates. Whereas the PA model emphasizes the importance of the dorsal stream in perception (perception for action) and in the coordination of the last stage of information processing, the PC model advances the idea of a gradual rather than discrete transition between the stages of action by advancing different concepts in terms of *planning* and *control*. Our aim was to investigate how the two streams manage the performance of a grasping act when colour is offered as the only source of information.

The pilot study was entirely controlled for iso-luminance in order to examine the usage of colour for guiding a motor schema. Our experiment consisted of manipulation of one target object which changed or did not change its location or

its size. This manipulation allowed us to make participants judge targets' coordinates by computing only the chromatic information. The results revealed that colour can contribute to adjusting the movement parameters during *grasping*, although a constant temporal delay was observed across trials where colour had to be used for reprogramming and adjusting the kinematic parameters. Our results are consistent with previous lines of investigation (Pisella et al., 1998; Schmidt, 2002; Brenner & Smeets, 2004). Using pointing/reaching tasks they showed that people are able to faultlessly use chromatic information although temporal delays were manifest. Our findings are also consistent with previous studies (Hubel & Wiesel, 1966; Derrington et al., 1984; Livingstone & Hubel, 1987; Hendry & Yoshioka, 1994) which postulate significant temporal conducting latencies between the P and M pathways. Furthermore, the results support the dorsal/ventral delays in processing information (Nowak & Bullier, 1997; Tanaka & Shimojo, 1996; Tanne et al., 1995).

However, due to the fact that within the pilot study only one target object was utilized, future investigation was required and two experiments were therefore designed. The central foundation of this second experimental approach was to explore the real time capacity of the visuo-motor system to use chromatic information to program (Experiment 1) and control (Experiment 2) the grasping movement having two coloured object displayed on the background. Luminance was manipulated in half of the trials, the other half remaining iso-luminant varying in chromaticity instead (similarly as in Pilot Study). This treatment allowed the

examination of the involvement of M and P systems in movement production and furthermore the implication of the subsequent dorsal and ventral areas in performing action.

Our findings are consistent with the results of the pilot study and subsequently with previous lines of investigation (Pisella et al., 1998; Brenner & Smeets, 2004) and reinforce the idea of a proficient usage of chromaticity for adjusting the movement parameters when colour had to be processed for action. Although participants were able to complete the grasping task, significant differences were observed when comparing the iso-luminant condition with the hetero-luminant condition. Both programming and on-line control showed an increased adaptability in using luminance to guide the movement production. Still, when the luminance attribute was adjusted to a neutral value for targets and background, chromatic attributes offered substantial information for completing the task.

Summing up, our findings are generally consistent with the PA model proposed by Milner and Goodale (1995). While the dorsal stream is mainly involved in the modulation of the motor act, the ventral stream represents a reliable source of information when the task is performed under no vision condition. The real-time hypothesis (Westwood & Goodale, 2003) is also supported by our results. Scaling the grip during visually guided tasks occurs under the command of the dorsal stream; conversely, when vision is occluded, the ventral stream modulates the kinematics of the grasp based on previous recorded

experience, in our case colour being successfully used for controlling on-line the movement.

Limitations and future directions

In order to design visual interfaces which afford better comprehension and elicit faster and more accurate reactions, one must first understand how different attributes of a target interact to influence perception and responding. The key question which was raised along this thesis was whether humans can use colour for preparing/performing a movement.

Although our results are consistent with previous lines of investigation (Pisella et al., 1998; Brenner & Smeets, 2004; Nowak & Bullier, 1997; Tanaka & Shimojo, 1996; Tanne et al., 1995) our obtained temporal latencies between the M and P processing (i.e. location/colour) were less than the values reported previously for pointing/reaching paradigms. One pertinent explanation could reside in the fact that it is nearly unattainable to control for a perfect iso-luminance a real 3-dimensional environment given that within a real life situation a large variety of perturbation factors might interfere with our sensorial system (i.e. shadows, noise, depth of the field). For example, future examination of monocular guiding performance could provide supplementary data with respect to the degree of segregation between M and P pathways when examining the grasping movement (i.e. 3-dimesional design).

Another feature that might require supplementary examination is the yellow/blue chromatic dimension. In this line of investigation we focused only on

red/green modulation and knowingly avoided the yellow/blue dimension and konio (K) pathway inputs to movement production. Although existing evidence supports the possibility that K signals might interfere with grasping circuits (Wandell, Poirson, Newsome, Baseler, Boynton, Huk, Gandhi, & Sharpe, 1999; Calkins, 2000), other neurophysiological studies argued against this hypothesis (Lee, Martin, & Valberg, 1998; Dacey & Lee, 1994). Whether K contribution to colour/motion modulation is significant or not remains to be examined.

References

Arbib, M., A. (1981). Perceptual Structures and Distributed Motor Control, in Handbook of Physiology, Section 2*: The Nervous System*, Vol. II, Motor Control, Part 1 (V.B. Brooks, Ed.), American Physiological Society , 1449-1480.

Binsted, G., & Elliott, D. (2001). Eye-hand coordination in goal directed aiming. *Human Movement Science, 20,* 563-585.

Boussaoud, D., Ungerleider, L., G., & Desimone, R. (1990). Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *Journal of Comparative Neurology, 296,* 462-495.

Brenner, E., & Smeets, J., B., J. (2004) Colour vision can contribute to fast corrections of arm movements. *Experimental brain research, 158,* 302-307.

Calkins, D., J. (2001). Seeing with S cones. *Neuron, 24,* 313-321.

Calkins, D., J. (2000). The representation of cone signals in the primate retina. *Journal of the Optical Society of America, 17,* 597-606.

Carruthers, P. (1989). Brute Experience. *Journal of Philosophy, 86,* 258 - 269.

Casagrande, V., A. (1994). A third parallel visual pathway to primate area V1.*Trends in Neuroscience 17,* 305–310.

Chelazzi, L., Miller , E., K., Duncan, J., & Desimone, R. (2001). Responses of neurons in macaque area V4 during memory guided visual search. *Cerebral Cortex, (11),* 761-762

Crossman, E., R., F., W., & Goodeve, P., J. (1983). Feedback control of hand-movement and Fitts' law: Communication to the Experimental Society. *Journal of Experimental Psychology, 35A,* 251-278.

Culham, J., C., Danckert, S., L., & Goodale, M., A. (2002). fMRI reveals a dissociation of visual and somatomotor responses in human AIP during delayed grasping. *Journal of Vision, 2(7),* 701-708.

Dacey, D., M., & Lee, B., B. (1994). The 'blue-on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. *Nature 367,* 731-735.

Deiber, M. P., Ibanez, V., Sadato, N., & Hallett, M. (1996). Cerebral structures participating in motor preparation in humans: A positron emission tomography study. *Journal of Neurophysiology 75,* 233–47

De Valois, R., Abramov, I., & Jacobs, G. (1966). Analysis of response patterns of LGN cells. *Journal of the Optical Society of America, 56(7),* 966-977.

De Valois, R., L., Cottaris, N., P., Elfar, S., D., Mahon, L., E., & Wilson, J., A. (2000). Some transformations of color information from geniculate nucleus to striate cortex. *Proceedings of the National Academy of Sciences of the United States of America, 97,* 4997-5002.

Derrington, A., M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology (London), 357,* 241-265.

Desmurget, M., Grea, H., Grethe, J., S., Prablanc, C., Alexander, G., E., & Grafton, S., T. (2001) Functional anatomy of nonvisual feedback loops during reaching: A positron emission tomography study. *Journal of Neuroscience, 21(8),* 2919–28.

Dobkins, K., R. (2000). Moving colors in the lime light. *Neuron, 25,* 15-18.

Dobkins K., R., & Albright, T., D. (1994). What happens if it changes color when it moves? The nature of chromatic input to macaque visual area MT. *Journal of Neuroscience, 14 ,* 4854-4870.

Egusa, H. (1983). Effects of brightness, hue, and saturation on perceived depth between adjacent regions in the visual field. *Perception 12,* 167–175

Elliott, D., Heath, M., Binsted, G., Ricker, K., Roy, E., E., & Chua, R. (1999). Goal directed aiming: Correcting force specification error with the right and left hands. *Journal of Motor Behavior, 31 (4),* 309-324.

Faubert, J., & Von Grunau, M. (1995). The influence of two spatially distinct primers and attribute

priming on motion induction. *Vision Res. 35,* 3119–3130

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119,* 593-609.

Gegenfurtner, K. (2003). Cortical mechanisms of colour vision. *Nature, 4,* 563-572.

Gegenfurtner, K., R., & Hawken, M., J. (1996) Interactions between color and motion in the visual pathways. *Trends in Neurosciences*, 19, 394-401.

Gegenfurtner, K., R., Kiper, D., C., Beusmans, J., M., H., Caradini, M., Zaidi, Q., & Movshon, J., A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience, 11,* 455-466.

Glover, S. (2004). Separate visual representation in the planning and control of action.. *Behavioural and Brain Science, 27,* 3-78.

Grafton, S., T., Fagg, A., & Arbib, M., A. (1998). Dorsal premotor cortex and conditional movement selection: A PET functional mapping study. *Journal of Neurophysiology 79,* 1092–97.

Grafton, S., T., Mazziotta, J., Woods, R., & Phelps, M. (1992). Human functional anatomy of visually guided finger movements. *Brain 115*, 565–87.

Haffenden A., M., & Goodale, M., A. (2000). Independent effects of pictorial displays on perception and action. *Vision Research, 40,* 1597-1607.

Hendry, S., H., & Yoshioka, T. (1994). A neurochemically distinct third channel in the macaque dorsal lateral geniculate nucleus. *Science, 264,* 575-577.

Hendry S., H., & Reid, R., C. (2000). The koniocellular pathway in primate vision. *Annual Review of Neuroscience, 23,* 127-153.

Hoff, B., & Arbib, M., A. (1993). Models of trajectory formation and temporal interaction of reach and grasp, *Journal of Motor Behavior, 25,* 175-192.

Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior,* 16, 235–254.

Jeannerod, M., Arbib, M., A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuo-motor transformation. *Trends in Neuroscience, 18,* 314–320.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A (Eds.) *Attention and performance IX* (153–169). Lawrence Erlbaum, Hillsdale.

Jeannerod, M., & Biguer, B. (1982). Visuo-motor mechanisms in reaching within extrapersonal space. In: Ingle D, Goodale MA, and Mansfield R. (Eds.). *Advances in the Analysis of Visual Behavior*, (387-409). Boston, MA: MIT Press.

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements.* Oxford University Press.

Johnson, E., N., Hawken, M., J., & Shapley, R. (2001). The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience, 4,* 409-416.

Kaiser, P., K., & Boynton, R., M. (1996). *Human Color Vision.* Washington, DC: Optical Society of America.

Kanizsa, G. (1974). Contours without gradients or cognitive contours *Italian J. Psychoogy*. *1,* 93–113

Kiper, D., C., Fenstemaker, S., B., & Gegenfurtner, K., R. (1997). Chromatic properties of neurons in macaque area V2. *Visual Neuroscience, 14(6),* 1061-1072.

Krams, M., Rushworth, M., Deiber, M., P., Frackowiak, R., & Passingham, R. (1998). The preparation, execution, and suppression of copied movements inthe human brain. *Experimental Brain Research 120,* 386–98.

Lee, B., B., Martin, P., R., & Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina. *Journal of Physiology 404,* 323-347.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience, 10,* 649-669.

Leventhal, A., G., Thompson, K., G., Liu, D., Zhou, Y., & Ault, S., J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex. *Journal of Neuroscience, 15,* 1808-1818.

Livingstone, M., S., & Hubel, D., H. (1987). Psychophysical evidence for separate channels for the perception of form, color, Movement and Depth. *Journal of Neuroscience, 7 (11),* 3416-3468.

Livingstone M., S., & Hubel, D., H. (1987). Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey. *Journal of Neuroscience, 7,* 3371-3377.

Livingstone M., S., & Hubel, D., H. (1982). Thalamic inputs to cytochrome oxidase-rich regions in monkey visual cortex. *Proceedings of the National Academy of Sciences U S A, 79,* 6098-6101.

Marcel, A., J. (1983). Conscious and Unconscious Perception. *Cognitive Psychology, 15,* 197 - 300.

Martin, P., R., White, A., J., R., Goodchild, A., K., Wilder, H., D., & Sefton, A., E. (1997). Evidence that blue-on cells are part of the third geniculocortical pathway in primates. *European Journal of Neuroscience, 9,* 1536-1541.

Maunsell, J., H., Ghose, G., M., Assad, J., A., McAdams, C., J., Boudreau, C., E., & Noerager, B., D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience, 16,* 1–14

Milner, A., D., & Goodale, M., A. (1995). *The visual brain in action.* Oxford, England: Oxford University Press.

Merigan, W., & Maunsell, J. (1993). How parallel are the primate isual pathways? *Annual Review of Neuroscience, 16,* 369–402.

Morand, S., Thut, G., de Peralta, R., G., Clarke, S., Khateb, A., Landis, T., & Michel, C., M. (2000). Electrophysiological Evidence for Fast Visual Processing through the Human Koniocellular Pathway when Stimuli Move. *Cerebral Cortex, 10 (8),* 817-825.

Nowak, L., G., & Bullier, J. (1997). The timing of information transfer in the visual system. *Cerebral cortex, 12,* 205-241.

Parkin, A., J. (1996). *Explorations in Cognitive Neuropsychology.* Blackwell Publishers Ltd.: Oxford.

Paulignan, Y, MacKenzie, C., L., Marteniuk, R., G., & Jeannerod, M. (1991a). Selective perturbation of visual input during prehension movements. II. Effects of changing object size. *Experimental Brain Research, 87,* 407-420.

Pessoa, L., Beck, J., & Mingolla, E. (1996) Perceived texture segregation in chromatic element-arrangement patterns: High Intensity interference *Vision Res. 36,* 1745–1760

Posner, M., I., & Keele, S., W. (1968). On the genesis of abstract ideas. *Journal of Experimental Psychology, 77,* 353-63.

Rizzolatti, G., & Gentilucci, M. (1988). Motor and visual-motor functions of the premotor cortex. In Rakic, P., & Singer, W. (Eds.), *Neurobiology of neocortex* (269-284). Chichester: Wiley.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey: II. Area F5 and the control of distal movements. *Experimental Brain Research, 71,* 491-507.

Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3,* 131-141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (1997). Parietal cortex: from sight to action. *Currrent Opinion in Neurobiology, 7,* 562-567.

Sakata, H., Taira, M ., Kusunoki, M., Murata, A., Tanaka, Y., & Tsutsui, K. (1998). Neural coding of 3D features of objects for and action in the parietal cortex of monkeys. *Phil Trans Roy Soc London B, Biological Science, 353,* 1363-1373.

Salvia, J., & Ysseldyk, J. (1972). Criterion validity of 4 tests for green-red color blindness. *American Journal of Mental Deficiency, 76*, 418-430.

Schiller, P., H., & Logothetis, N., K. (1990). The color opponent and broadband channels of the primate visual system. *Trends in Neurosciences,* 13, 392-398.

Schmidt, T. (2002). The finger in flight: real-time motor control by visually masked color stimuli. *Psychoogical Science, 13,* 112-118.

Schoenfeld, M., A., Heinze, H., J., & Woldorff, M., G. (2001). Unmasking motion-processing activity in human brain area V5/MT+ mediated by pathways that bypass primary visual cortex. *NeuroImage, 17,* 769-779.

Seideman, E., & Newsome, W., T. (1999). Effect of spatial attention on responses of area MT neurons. *Journal of Neurophysiology, 81,* 1783-1794.

Tanaka, Y., & Shimojo, S. (1996). Location vs. feature: reaction time reveals dissociation between two visual functions. *Vision Research, 36,* 2125-2140.

Tanne, J., Boussaoud, D., Boyer-Zeller, N., & Rouiller, E. (1995). Direct visual pathways for reaching movements in the macaque monkey. *Neuroreport, 7,* 267-272.

Thorell, L., G., De Valois, R., L., & Albrecht, D., G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research, 24*, 751-769.

Ungerleider, L., G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, R. J. W. Mansfield, & M. S. Goodale (Eds.), *The Analysis of Visual Behavior* (549-586). Cambridge, Mass: MIT Press.

Wandell, B., A., Poirson, A., B., Newsome, W., T., Baseler, H., A., Boynton, G., M., Huk, A., Gandhi, S., & Sharpe, L., T. (1999). Color signals in human motion-selective cortex. *Neuron 24*, 901-909.

Weiskrantz, L. (1986). Blindsight: A Case Study and Implications. Clarendon Press: Oxford.

Weiskrantz, L. (1997). Consciousness Lost and Found: *A Neuropsychological Exploration.* Oxford University Press: Oxford.

Weiskrantz, L. (1998). Consciousness and Commentaries. In Stuart R. Hameroff, Alfred W. Kaszniak, and Alwyn C. Scott (Eds.), *Toward a Science of Consciousness II: The Second Tucson Discussions and Debates* (371-377). The MIT Press: Cambridge, Massachusetts.

Wolpert, D., M., Ghahramani, Z., & Jordan, M., I. (1995). An internal model for sensorimotor integration. *Science*, *269,* 1880-1882.

Westwood, D., & Goodale, M., A. (2003). Perceptual illusion and the real-time control of action, *Spatial Vision, 16,* 243-254.

Woodworth, R., S. (1899). The accuracy of voluntary movements. *Psychological Review Monograph, 3 (13)* , 1-119.

Xiao, Y., & Felleman, D., J. (2004). Projections from primary visual cortex to cytochrome oxidase thin stripes and interstripes of macaque visual area 2. *Proceedings of the National Academy of Sciences U S A 101 (18),* 7

Zeki, S., M. (1993) *A vision of the brain.* Blackwell: Oxford.

Zeki, S., M., & Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain, 121*, 1669-1685.