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SUMMARY

Both perceiving the world as consisting of stable, unified, three-dimensional objects and recognising them despite changes in vantage point, size, and lighting conditions are fundamental abilities for all mobile animals. Whether an animal is able to retrieve 3-D information also from flat displays (e.g., 2-D projections of 3-D objects presented on a computer screen) has been a matter of interest in the last decades of research. For instance, pigeons (*Columba livia*) may perceive two-dimensional pictures of three-dimensional objects simply as random collections of flat, two-dimensional features instead of experiencing them as generalised 3-D representations. If, however, pigeons are indeed able to form object-like representations of two-dimensional displays, "dynamic presentation", (i.e., presentation of views onto the object in rapid succession) should facilitate recognition across various stimulus modifications, since continuous dynamic change of perspective may help integrating individual views of an object into three-dimensional images. This hypothesis was tested in the current thesis. Pigeons were first trained in a go/no-go procedure to discriminate between 2-D projections of a cube and a pyramid, presented as static images or as rotating around the y-axis. When they had acquired the discrimination the birds were subjected to a series of transfer tests with new, modified, projections. These involved various featural and rotational transformations, such as novel size, altered surface colouration, novel viewpoint, and randomised rotation sequences. The results showed that most types of transformations clearly impaired recognition. In contrast to a study by COOK & KATZ (1999), who used a similar experimental design I could neither find object constancy across various stimulus transformations, nor any indication of a "dynamic superiority effect", i.e., discrimination performance was not improved by dynamic as compared to static presentation, and the order of images within a dynamic sequence was not crucial for object recognition. Furthermore, the ability to recognise an object was found to be strongly viewpoint-dependent and influenced also by modifications in size and colouration to some degree. Together, the results strongly suggest that object discrimination was based on stored 2-D featural information rather than on object-like 3-D representations.

They are in line with the view that pigeons' object recognition is controlled by view-based rather than object-based mechanisms.

ZUSAMMENFASSUNG

Für mobile Tiere ist sowohl die Fähigkeit, dreidimensionale Objekte als solche wahrzunehmen, als auch das Vermögen, diese trotz Änderung des Blickpunktes, Veränderung der Größe und unterschiedlicher Beleuchtung wieder zu erkennen, von großer Bedeutung. Die Frage, ob ein Tier fähig ist, dreidimensionale Information aus rein zweidimensionalen Darstellungen zu erschließen (wie es zum Beispiel bei Bildern dreidimensionaler Objekte der Fall ist, die auf einem Computer-Monitor präsentiert werden), wurde in den letzten Jahrzehnten der Wahrnehmungsforschung zunehmend zu einem zentralen Thema. Es ist durchaus möglich, dass zum Beispiel Tauben (*Columba livia*) zweidimensionale Bilder dreidimensionaler Objekte eher als beliebige Ansammlungen zweidimensionaler Merkmale sehen als diese als generalisierte 3-D-Repräsentationen wahrzunehmen. Sollten Tauben aber tatsächlich fähig sein, objektartige Repräsentationen zweidimensionaler Projektionen zu bilden, sollte die „dynamische Präsentation“ (d.h., das schnelle Abbilden aufeinander folgender Objekt-Ansichten) das Wiedererkennen bei diversen Stimulusmodifikationen erleichtern, da dynamische, kontinuierliche Veränderung der Perspektive die Integration einzelner Objektansichten zu einem dreidimensionalen Bild fördern kann. Diese Hypothese wurde in der vorliegenden Diplomarbeit getestet. Dazu wurden Tauben zuerst mit Hilfe einer Go-/No-Go-Prozedur darauf trainiert, zwischen 2-D-Projektionen eines Würfels und einer Pyramide zu unterscheiden. Diese wurden entweder als statische Einzelbilder oder in Rotation um die y-Achse präsentiert. Nachdem sie die Diskriminierungssaufgabe erlernt hatten, wurden den Vögeln in einer Reihe von Generalisationstests neue, modifizierte, Projektionen gezeigt. Die Änderungen betrafen unterschiedliche Objektmerkmale sowie die Art der Rotation, z.B. die Größe, die Oberflächen-Färbung, den Blickwinkel und die Reihenfolge der Einzelbilder einer dynamischen Sequenz. Die Ergebnisse zeigten,

dass die meisten Arten von Transformationen das Wiedererkennen klar beeinträchtigten. Im Gegensatz zu einer Studie von COOK & KATZ (1999), die ein vergleichbares experimentelles Design verwendeten, fand ich weder Objektkonstanz über verschiedene Reiztransformationen, noch Anzeichen für einen „Dynamischen Superioritätseffekt“, das heißt, dass die Diskriminierungsleistung bei dynamischer gegenüber statischer Präsentation nicht verbessert war. Auch die Reihenfolge der Einzelbilder innerhalb einer dynamischen Sequenz schien für die Fähigkeit zur Objektunterscheidung nicht von Bedeutung zu sein. Die Fähigkeit, ein Objekt zu erkennen, war stark blickpunktabhängig und war bis zu einem gewissen Grad auch durch Größen- und Farbänderungen beeinflusst. Zusammengenommen legen die Ergebnisse den Schluss nahe, dass die Objektdiskriminierung auf gespeicherter zweidimensionaler Merkmalsinformation beruhte und nicht auf der Verwendung von dreidimensionalen Objektrepräsentationen. Sie bestätigen damit die Ansicht, dass das Wiedererkennen von Objekten von Mechanismen kontrolliert wird, die blickbasiert und nicht objektbasiert sind.

1. INTRODUCTION

“All our knowledge has its origins in our perceptions.”

Leonardo da Vinci
(visual artist and scientist,
1452-1519)

For animals living in a world consisting of both animate and inanimate meaningful items it is one of the fundamental visual abilities to identify objects despite changes in various respects, such as viewpoint, size, and lighting conditions. But despite the fact that the visual input that reaches the eye changes dramatically depending on these alterations, the object remains the same. Regarding the basic demand of recognising items of high ecological value even under varying viewing conditions (e.g., navigational landmarks indicating food locations or breeding sites, mates, or objects to avoid, such as predators) it is vitally important to be capable of generalising across depth-rotated views, and across changes in colour or size. Consider further that for an animal also sensitivity to object motion (i.e., an object property in which all or part of it changes continuously in position over time) may be substantially important since, in its natural environment, both the object perceived as well as the perceiver itself is often moving. Thereby, in the real world, movement may be crucial for extracting three-dimensional information about an object since motion can facilitate the perception of depth. Under completely artificial conditions, however, such as it is the case in a discrimination task carried out by means of a computer screen, in which an animal is required to discriminate virtual objects that a human would perceive as dynamically rotating, such assumptions may not be qualified anymore. A pigeon (*Columba livia*), for instance, may be incapable to perceive neither the two-dimensional object shapes as three-dimensional coherent objects nor their apparent motion (i.e., the illusion of motion resulting from rapid presentation of static single images) as true motion. The current thesis tries to increase our knowledge about how a highly mobile bird species, as is the pigeon, might perceive visual stimuli, that for us appear to be three-dimensional dynamically rotating objects.

1.1. From the pigeon's perspective – Visual capabilities in the pigeon

Pigeons like most birds are highly visual animals. This becomes particularly obvious if one considers their relatively large eyes, which are each about 1 ml in volume, and the high proportion of the pigeon's nervous system that is engaged in visual functions (namely, an estimated third; c.f., DELIUS et al. 2000). Since, evolutionary speaking, birds and mammals diverged a long time ago (c.f., KUMAR & HEDGES 1998), pigeon vision differs from human vision in many respects (for reviews see D'EATH 1998; EMMERTON & DELIUS 1980; HUSBAND & SHIMIZU 2001; LEA & DITTRICH 2000; ZEIGLER & BISCHOFF 1993). Differences concern retinal as well as brain structures (e.g., avian double cones, avian oil droplets, number of retinal ganglion cells, post-retinal processing), colour vision (pigeons are suggested to have five different receptor types and are sensitive to ultraviolet light), and the morphology of the eyes (e.g., lateral eyes in the pigeon versus frontal eyes in humans). As regards its visual capacities, the pigeon has been shown to "outplay" humans in many respects. Pigeons are capable to distinguish between bars that differ in length by less than 2 % (SCHWABL & DELIUS 1984), can detect even small differences in the size of a target (HODOS et al. 1985), and their visual acuity is assumed to be excellent (HODOS et al. 1976). Beyond doubt, a pigeon perceives the world in a different way than we do. However, picture technology is primarily adjusted to "fool" human but not bird vision, and pictorial projections of objects, such as those depicted on a computer screen, may thus appear quite different to birds than they appear to us (see also BOVET & VAUCLAIR 2000; DELIUS et al. 2000; D'EATH 1998; FUJITA 2001). Due to different physiological systems, perception and interpretation of the visual input derived from a computer monitor may differ in these two species. Consider, for example, the pigeon's high flicker-fusion frequency, i.e., the frequency at which a flickering stimulus starts to appear continuous, of 140 Hz (DODT & WIRTH 1953). Since this threshold is suggested to be clearly higher in pigeons than in humans, displays of movies on a monitor may be experienced in a "stroboscopic" manner by a pigeon, due to a human-adapted image build-up (see JITSUMORI et al. 1999; JITSUMORI & MAKINO 2004; LOIDOLT et al. 2006, for discussion). Furthermore, certain aspects of the pigeon's visual system that enable it to recover information about depth, have to be considered in the light of the limitations that are possibly set to object perception due to the use of computer displays.

In general, depth perception is based on the use of various depth cues, which are typically classified into monocular and binocular depth cues. The former require input from one eye only, whereas the latter require input from both eyes. Monocular depth cues include for instance *shading*, *perspective*, *relative density*, *relative size*, *occlusion*, and *motion parallax*. Binocular depth cues include, for example, *stereopsis*. In humans, stereopsis (i.e., the perception of depth on the basis of the difference in points of view of the two eyes, described first by WHEATSTONE 1938) is one of the fundamental sources of depth perception. The difference in the two retinal images is caused by the slightly different projections of an object seen by the right and the left eye (i.e., binocular disparity). This disparity results from the horizontal separation of the eyes in the head. Although stereoscopic vision is clearly limited in the pigeon due to a lateral placement of the eyes resulting in only a small overlapping binocular field (c.f., MCFADDEN et al. 1986; MARTINOYA et al. 1981), binocular cues are nevertheless suggested to play a role in the pigeon's depth perception (MCFADDEN 1993). Two-dimensional pictures generally do not provide the viewer with binocular cues, but since pigeons experience their surroundings mainly monocularly, "*... this relative emphasis on monocular vision might be thought to contribute to pigeons perceiving two-dimensional pictures and three-dimensional scenes as equivalent*", as noted by DELIUS et al. 2000 (p. 9). Monocular depth cues can therefore be assumed to be of primary relevance for gaining depth information. There is indeed growing evidence that pigeons, like humans, are capable of using monocular cues, and moreover, are even susceptible to visual illusions that require sensitivity to pictorial depth cues, such as the Ponzo illusion, i.e., a size constancy illusion induced by converging contextual lines (FUJITA et al. 1991). Pigeons are also suggested to be able to use monocular depth cues to perceive spatial three-dimensionality in a scene (CAVOTO & COOK 2006, SPETCH et al. 1998), and even to extract three-dimensionality from pictorial representations of objects by means of monocular depth cues, such as perspective and shading (REID & SPETCH 1998). Alternatively, however, the use of two-dimensional discriminative cues (e.g., differential shading of the objects or spurious discriminative cues resulting from photo editing) might account for at least some of the positive findings, without any recognition of the object's 3-D structure being involved. Additionally, motion parallax is suggested to play an important role in the pigeon's perception of depth as well (e.g., DAVIES & GREEN 1988; FROST 1978; TROJE & FROST 2000). Hence, to what degree a pigeon uses particular depth cues – both monocular and binocular ones – is still uncertain.

It is still a matter of debate whether the information provided in two-dimensional images on a computer screen is sufficient for a pigeon to interpret them as three-dimensional objects. This issue shall be considered in the next chapter.

1.2. How to recognise an object – Theories of object recognition

The aim of examining the cognitive processes underlying the visual recognition of three-dimensional objects has become one of the most challenging topics in research on visual perception. Indeed, the issue of object recognition deals with a twofold question. *First*, in which representational format are objects encoded in visual memory? *Second*, how does an observer match visual percepts of objects to mental representations of objects? Processes of three-dimensional object recognition go thereby far beyond simple mechanisms of detection. The cognitive demands are evident: objects have to be identified across transformations in size, position, illumination, and viewpoint changes.

Theories of object recognition must therefore provide accounts of how an observer can compensate for various changes in the visual appearance of an object. In human visual object recognition research, broadly speaking, two classes of theories have been proposed. Basically, they differ in terms of how objects are represented, and what processes are used to recognise them.

One class of theories assumes that representations of objects are encoded as “structural descriptions” of their 3-D properties. These theories are said to be *viewpoint-invariant* or *object-based* since a structural representation provides sufficient information for recognising the object despite changes in viewpoint (e.g., BIEDERMAN 1987; BIEDERMAN & GERHARDSTEIN 1993, 1995; CORBALLIS 1988; HUMMEL & BIEDERMAN 1992; MARR & NISHIHARA 1978, MARR 1982). A topic of discussion has been the specific representational format. Generally, it has been proposed that an object is represented on the basis of the relations among its distinctive features, defined by a kind of object-centred coordinate system. MARR & NISHIHARA (1978) were the first to describe representations by structural descriptions based on three-dimensional volumes and their spatial relations. However, the most famous example of a volume-based account of recognition is probably the Recognition-by-Components theory (RBC) proposed by BIEDERMAN (1987). It suggests that object representations consist of a restricted set of volumetric parts (*geons*), such as spheres, cubes, and wedges, and their spatial interrelations. RBC theories predict that all views of an object should be recognised with approximately the same speed and accuracy, as long as certain conditions are met (BIEDERMAN & GERHARDSTEIN 1993). The criteria for viewpoint invariance are that, first, the object is decomposable into geons; second, the arrangement of these geons forms a distinct structural description that differs from other arrangements; and third, changes in the view of the object do not change the structural description. In general, viewpoint-invariant theories suggest that the visual system recognises an object by decomposing it and then comparing its parts to stored templates.

The other class of theories assumes that an object is represented in visual memory in the appearance (i.e., the view) in which it is seen by the observer (e.g., BÜLTHOFF 1995, 1998; BÜLTHOFF & EDELMAN 1992; EDELMAN & BÜLTHOFF 1992;

HAYWARD & TARR 1997; JOLICOEUR 1985; JOLICOEUR & HUMPHREY 1998; POGGIO & EDELMAN 1990; TARR & BÜLTHOFF 1995; TARR & KRIEGMAN 2001; TARR 1995; TARR & PINKER 1990; TARR et al. 1997, 1998). The representation thereby preserves *viewpoint-dependent* shape information and surface appearance, and is defined by a coordinate system based on the observer. Since the representation is *view-based* and recognition is *viewpoint-dependent,* these theories are accordingly termed. View-based representations may emerge as a collection of stored views. As regards generalisation to novel unfamiliar views, different processes have been proposed. One of them is a process termed *normalisation*. This is defined as a mechanism that "normalises" (i.e., transforms) a novel view until it matches one of the stored single views (TARR 1995; TARR & PINKER 1990). As originally conceived by SHEPARD and METZLER (1971), the process was suggested to operate in terms of a "mental rotation" that transforms the novel percept until a stored view is matched. More recently, another account has been developed – the *view combination* approach (e.g., BÜLTHOFF & EDELMAN 1992; EDELMAN 1999). This assumes that recognition of an object from novel viewpoints occurs by mathematically interpolating between two or more prototypes of the object (i.e., the representations of an object in a multidimensional "shape space"). In both types of approaches it is predicted that the speed of or the accuracy in recognising an object will decrease as a function of the rotational distance between a given novel view and the closest stored view. However, the two can be distinguished by their predictions regarding the recognition of interpolated novel views (i.e., in between the range of two stored views) versus extrapolated ones (i.e., outside the range of two stored views). Whereas normalisation approaches suggest that object recognition should be equally impaired in both cases, view combination approaches predict that performance should be better with interpolated than with extrapolated views.

To summarise, viewpoint-invariant and viewpoint-dependent theories make different general predictions when an object is presented in an unfamiliar view. Viewpoint-invariant theories assume only insignificant decreases in speed and accuracy of recognition, whereas viewpoint-dependent theories suggest a large continuous decrease in recognition performance. However, in specific cases also view-based theories occasionally predict viewpoint-invariance; namely, when an object contains a single distinctive feature that can serve as diagnostic cue, and is still available in several novel views (c.f., SPETCH et al. 2000, 2001).

Over the last decades research on human object recognition has provided evidence for both types of recognition performances – viewpoint-dependent and viewpoint-independent approaches (see e.g., PEISSIG & TARR 2007, for a review), which suggests that certain elements from both types may play some role in human object recognition. The current view, however, rather favours view-based object recognition. In particular, RBC has been suggested being not robust enough to explain general object recognition. As criticised by TARR & BÜLTHOFF (1998), " … *actual evidence for viewpoint-invariance in human visual recognition (as predicted by RBC) is somewhat thin – the most notable experiments that obtain viewpoint invariance for rotations in depth (Biederman & Gerhardstein, 1993) having only limited generalisabilty to other recognition tasks and stimulus sets …*" (p. 2). Nevertheless, object-based mechanisms may well be applied in specific situations, depending on specific factors. For instance, TARR (1995) noted that "*The mechanisms used in human object recognition are almost certainly a product of many factors, including the task, the learning and retrieval contexts, and the functional and visual relationships between objects both encoded in memory and observed in the environment …*" (p. 73). Indeed, researchers have highlighted the idea that a combination of theories might be more useful to explain processes of object recognition than making dichotomous contrasts (e.g., TARR & BÜLTHOFF 1998).

Consider, however, that both main classes of visual object recognition theories are based on the assumption that the percepts derived from objects are actually interpreted as instances of a three-dimensional shape. In examining visual recognition of three-dimensional objects in the pigeon, it should be kept in mind that both types of theories originate from a purely anthropocentric approach. Therefore, their predictions are valid for human object perception in the first place and suggest that a human subject should, in principle be able to experience the views of a two-dimensionally presented three-dimensional object in its coherent 3-D appearance (both in reality and as a two-dimensional projection like on a computer screen). Provided that a non-human animal, such as a pigeon, parses and perceives visual stimuli, in particular objects presented as 2-D pictures (!), quite differently than the human observer, the animal might be, in the extreme case, completely insensitive to three-dimensional information that can be derived from a two-dimensional projection, and instead perceive and store the object as a random collection of two-dimensional features. Considering the foregoing, it may be essential to bring up a third potential mechanism of discriminating visual stimuli, namely one that is based on generalisation over the different views of each of the objects to be distinguished. In other words, the different "forms of appearance" of an object are sorted into a category according to specific stimulus properties (see also JITSUMORI & MAKINO 2004, for related discussion). Mental representations that are acquired during such classification learning and that define class membership can be captured by different theories (for reviews see HUBER 2001, SMITH & MEDIN 1981). First, categorisation may be based on *exemplar* learning, which means that during training all or many instances of one class are memorised (e.g., ASTLEY & WASSERMAN 1992, CHASE & HEINEMANN 2001, PEARCE 1987). Generalisation to a novel member of the learned class is thereby determined by the degree of similarity to the stored exemplars. Second, categorisation may be based on the abstraction of class defining features, as proposed by *feature* learning theories (e.g., HUBER & LENZ 1993; HUBER & AUST 2006; SCHYNS et al. 1998). Thereby, generalisation to novel class members is controlled by the presence or absence of common features. Third, categorisation may be based on the acquisition of a *prototypical* representation of a category by means of an abstraction process that "summarises" all exemplars that have been experienced during training, resulting into a representation that corresponds to the average or central tendency of the class members (e.g., HUBER & LENZ 1996; POSNER 1969). Generalisation to novel instances of the class is thereby based on their similarity to this "best example".

The stimulus properties that are exploited in order to form a category can be *global* or *local* in nature. Global features are said to be characteristics of the whole stimulus (such as brightness, orientation, configural information, and size), whereas local features are mainly characterised as restricted distinct portions of an object, i.e., elemental units (c.f. AUST & HUBER 2001, 2003).

Studies of object recognition in the pigeon

What do we know so far about a pigeon's ability to recognise objects across different viewpoints? For practical reasons, research concerning this issue has relied almost exclusively on the use of two-dimensional representations of three-dimensional objects, as provided by drawings, photographic stimuli, or digitised stimuli. Over the last decades work on visual object recognition in the pigeon has provided evidence for all types of object recognition theories described in the previous chapter, although most of the findings indicated viewpoint-dependent mechanisms (for a review see e.g., FAGOT 2000; SPETCH & FRIEDMAN 2006). Several authors have reported evidence against pigeons' discrimination performance being controlled by object-based recognition processes. In particular, they consistently found a substantial lack of generalisation to novel views, with systematic decreases in discriminative performance occurring as a function of rotation angle from the training orientation (e.g., CERELLA 1977; JITSUMORI & MAKINO 2004; LOIDOLT et al. 2006; LUMSDEN & PULLEN 1970, LUMSDEN 1977; SPETCH et al. 2001). Research to date suggests that view-combination may thereby be the process underlying generalisation to novel unfamiliar views of a familiar object (FRIEDMAN et al. 2005, 2009, but see SPETCH & FRIEDMAN 2003 for results rather supporting generalisation processes). Evidently, interpolated views are mostly better recognised than extrapolated views.

Conversely, however, some studies (e.g., COOK & KATZ 1999; WASSERMAN et al. 1996) have reported pigeons' significant generalisation of discriminative responding to untrained views over numerous untrained depth orientations (although with some generalisation decrements). The authors thus claimed to have found evidence in support of the hypothesis that recognition of an object might also be based on a three-dimensional object-like representation. They concluded that the birds were able to retrieve three-dimensional structural information from the two-dimensional displays.

But how can we reconcile these obviously contradictive findings? Possibly, the way in which pigeons responded was influenced by several task-specific factors. Whether an outcome is in keeping with one object recognition theory rather than with another, is likely dependent on the specific methods or the use of particular stimuli. For instance, PEISSIG and co-workers (2000a) explored effects of depth rotation on pigeons' discriminative performance by using different computer-rendered versions of single *geons* and clearly found geon-specific responding. With some stimuli the pigeons showed significant generalisation, whereas with others correct responding systematically decreased with the objects' rotation angle in depth. In addition, also methodological factors have been suggested to affect a pigeon's ability to distinguish among stimuli in an object discrimination task. Different studies found strong indication that experiencing an object from multiple views throughout training may enhance the pigeon's recognition of an object (PEISSIG et al. 2000b; WASSERMAN et al. 1996). PEISSIG and co-workers (2002), for example, could demonstrate that transfer to views along a novel axis of rotation was much higher after training with multiple-views than after single-view training. It was therefore concluded that training with multiple views rather than training with single views facilitated the formation of object representations that support generalised recognition, and that exposure to multiple views was thus necessary for a pigeon to show robust object recognition even with novel orientations. Another stimulus aspect that may be crucial in facilitating a pigeon's ability to discriminate between objects was highlighted by SPETCH et al. (2000, 2001), namely the role of distinctive object parts. If such parts remain stable across variations in viewpoint, they may serve as discriminative diagnostic features.

Among the accounts to explain visual object recognition that have been considered in the previous chapter, the one based on a mechanism of classification by means of mere two-dimensional feature discrimination is the most parsimonious one. Thereby, research on visual categorisation in the pigeon has provided evidence for all three main theories of categorisation, namely *exemplar theory* (e.g., HUBER et al. 1999; PEARCE 1988), *feature theory* (e.g., AUST & HUBER 2001, 2002; HUBER & LENZ 1993; LEA 1983, 1984), and *prototype* theory (e.g., AYDIN &

PEARCE 1994; HUBER & LENZ 1996). Hence, it seems plausible to assume that pigeons may be rather flexible in their use of learning strategies when acquiring a categorisation task (see HUBER & AUST 2006; HUBER 2001) and that their choice of strategy may strongly depend on task requirements. Furthermore, there is ample evidence that particularly local features may play a primary role in the pigeon's pattern recognition. First hypothesized by CERELLA (1980), evidence has increased over the last decades that pigeons' responding to complex visual patterns may be controlled by local rather than by global features, (e.g., AUST & HUBER 2003; CAVOTO & COOK 2001; DELIUS & HOLLARD 1992; KELLY & COOK 2003). In the light of this *local dominance hypothesis* (c.f., LEA et al. 2006) it seems possible that pigeons may discriminate objects by means of a simple feature detection mechanism without recovery of the three-dimensional object structure. However, as several researchers have pointed out, there is also evidence that pigeons are able to use configural information in addition to elemental cues (e.g., AUST & HUBER 2001, 2002, 2003; COOK 2001; FREMOUW et al. 1998, 2002; GOTO & LEA 2004; KIRKPATRICK-STEGER & WASSERMAN 1996, KIRKPATRICK-STEGER et al. 1996, 1998, 2000; VAN HAMME et al. 1992, WATANABE & ITO 1991). WATANABE (2001), for example, reported different responding behaviour on scrambled pictures of people depending on whether they were presented as photographs or as cartoons. Altogether, it is most likely that factors like type, composition, or complexity of a stimulus determine by which kind of information – elemental, configural, or both – responding is controlled.

Most of the studies summarised in the current chapter have primarily focused on the investigation of static stimuli. Whether dynamic presentation of an object may facilitate its recognition shall be discussed in the next section.

1.3. The relevance of dynamic cues for object recognition

When animals interact with a dynamic, non-static environment, the role of object motion (i.e., a physically continuous change of an object's position over time, c.f., PALMER 1999) and dynamic object information (in terms of a continuous spatiotemporal sequence of views, c.f., VUONG & TARR 2004) is ambiguous. Primarily, motion cues can be used to identify objects only by their motion characteristics (e.g., the biological motion of a snake versus the movement of a cricket). Additionally, as highlighted by VUONG & TARR (2004), there are several ways that dynamic change of perspective may facilitate the integration of views into an object-like 3-D image, which may contribute to its recognition. First, object motion may enhance the recovery of information about an object's shape. This phenomenon is described as *structure-from-motion*, first hypothesised by ULLMAN (1979). It characterises the capability to recover the three-dimensional structure of a two-dimensionally projected object from motion-based information. For example, human literature on face recognition refers to this facilitating effect as the *representation enhancement hypothesis* (c.f., O'TOOLE et al. 2002), which postulates that facial motion contributes to recognition by enhancing the encoding of the 3-D structure of the face. Second, object motion may provide the observer with more views of the object, and may thereby enhance integration of these views into a more coherent stable representation. Third, object motion may help to segment a scene into discrete objects. Finally, object motion may also enhance the anticipation of novel object views.

In summary, there is convincing evidence that dynamic presentation of objects (of both real objects and pictures or computerised projections of them) facilitates object recognition in humans (see e.g., GREEN 1961; KNIGHT & JOHNSTON 1997; LIU & COOPER 2003; PIKE et al. 1997; VALLORTIGARA et al. 1988, VUONG & TARR 2004, 2006; WALLACH & O'CONNELL 1953). May this be also true for non-human species? To date, a couple of experiments have provided indication that various species including bird species indeed share with humans the ability to recover *structure from motion* (e.g., macaque monkeys in SIEGEL & ANDERSON 1988; marmoset monkeys in CLARA et al. 2007 or chicken in CLARA et al. 2006, and MASCALZONI et al. 2009). It is important to note, that these studies used equipment that create displays involving real object movement (e.g., by using the object's shadow on a translucent screen). However, if motion picture technology (e.g., film, television, computer graphics) has been used the results need to be taken with care. Consider that in movies or video displays presented on monitors or television screens no actual physical movement occurs. The reason why a human observer perceives motion in such displays is a phenomenon called *apparent motion* (EXNER 1988) which refers to the fact that realistic motion perception also arises from rapid presentation of completely static images (see PALMER 1999). Responsible for this visual impression is the alternation rate of the pictures. Within a specific frequency motion is perceived (this is about 10-40 times per second for humans). Motion picture technology uses this illusion by flashing a sequence of motionless images in rapid succession (e.g., frames in a movie are flashed at a rate of 24 frames/sec) in order to produce the perception of continuous motion, which for the human eye is indistinguishable from real motion. For this reason, in humans also stimuli produced as two-dimensional projections on screens are appropriate means for examining motion perception. Since motion picture technology is adapted to human vision one must be cautious to assume that species that differ remarkably in their visual system will perceive motion in motion picture displays as well. In animals with a visual system very similar to ours it may be justified to hypothesise that displays presented in apparent motion would elicit the perception of real motion (see e.g., macaque monkeys in UNNO et al. 2003). But what about the pigeon – a species whose visual system differs remarkably from that of humans?

The role of dynamic presentation for object recognition in the pigeon

There is strong evidence coming from different studies that pigeons are basically sensitive to motion cues (e.g., EMMERTON 1986; HODOS et al. 1975; and DITTRICH & LEA 2001, for review), which is a prerequisite for extracting stimulus structure from motion-based information. For practical reasons, however, a great number of experiments investigated motion perception by using motion picture technology, e.g., movies or computer graphics (e.g., COOK et al. 2001; DITTRICH et al. 1998; GOTO & LEA 2003; HERBRANSON et al. 2002; KOBAN & COOK 2009; RILLING & LACLAIRE 1989, SPETCH & FRIEDMAN 2006; VUONG & TARR 2006;

WILKINSON & KIRKPATRICK 2009). But consider that in all of these studies any object movement (at least perceivable for the human observer) arises from rapid presentation of static frames, or more precisely, it appears as *apparent* but not as *real* movement. Although pigeons are suggested to be able to perceive apparent motion (SIEGEL 1970, BISCHOF et al. 1999), and that "*… it seems likely that both real and apparent movement detection are mediated by processes that are at the least very similar …*" (SIEGEL 1971, p. 192), it is not clear to what extent a pigeon perceives real motion in such displays (but see COOK & ROBERTS 2007 for related discussion). This aspect must always be taken into consideration – at least one should bear in mind that in such displays no actual physical movement occurs[1].

Also research that investigated whether dynamic change of perspective contributes to object recognition in the pigeon predominantly used motion picture technology (e.g., COOK & KATZ 1999; JITSUMORI & MAKINO 2004; LOIDOLT et al. 2006; FRIEDMAN et al. 2009; SPETCH et al. 2006). The findings are rather inconsistent. On the one hand, several studies examining discrimination of human faces dynamically rotating in depth could not find any facilitating effect of dynamic when compared with static presentation on object recognition (JITSUMORI & MAKINO 2004; LOIDOLT et al. 2006; ROVINA 2006). These results suggested that the birds had difficulty using additional structural information provided by dynamic presentation and integrating the multiple views into a three-dimensional object. On the other hand, there is indication that dynamic presentation facilitates visual recognition of depth rotated objects across different stimulus modifications (COOK & KATZ 1999). In this study, the authors trained pigeons in a go/no-go procedure to discriminate between two differently shaped objects, namely computer-generated three-dimensional projections of a pyramid and a cube. On half of the training trials the stimuli were presented as static single views in a randomly selected orientation along the vertical axis. On the other half of the training trials the objects were presented rotating dynamically around the vertical axis. Subsequently, a series of transfer tests was carried out. These included

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[1] In both the current thesis and in all studies using dynamic stimuli that are presented on computer or TV screens the term "motion" refers exclusively to apparent motion (i.e., an illusion of continuous motion arising from a series of purely static frames presented at the proper rate, see PALMER 1999).

changes to new axes of rotation, transformation in size, changes in surface colouration, elimination of contour information, and changes in the direction of rotation. The results revealed that discrimination performance remained invariant for a variety of stimulus transformations. Namely, transfer was significant to novel object sizes, to novel rates and directions of motion, as well as to novel surface colouration, and was at least above chance to stimuli with new axes of rotation. Interestingly, dynamic stimulus presentations resulted in substantially better discrimination performance than equivalent sets of static presentations, an effect that the authors described as *dynamic superiority effect*. Overall, the results – good transfer to a large variety of object transformations and superiority of dynamic presentation – led COOK & KATZ (1999) to conclude that their subjects discriminated the objects by experiencing a generalised 3-D representation of them. They claimed to have found convincing evidence that the pigeons experienced the stimuli as invariant coherent three-dimensional objects, but not as collections of flat two-dimensional features. According to the authors, the finding of dynamic superiority resulted from the fact that more discriminative information was available in dynamic displays than in static images. Dynamic change of perspective might thus have helped to integrate the single views into a unified, object-like 3-D image. These conclusions were both ground-breaking and provocative, because they touched on a longstanding controversy between proponents of conflicting approaches to object recognition, namely feature-based versus object-based explanations. Based on their results COOK & KATZ (1999) argued with regard to pigeons' visual object perception that *"… they see the world as composed of unified objects much like we do …"* (p. 209), and further that *"… the birds discriminated these objects by experiencing a generalized 3-D representation of them"* (p. 207) – notions clearly opponent to the ideas of feature-based theories (e.g., CERELLA 1977, 1980, 1986). However, on closer inspection, also a cognitively simpler account may explain the results by COOK & KATZ (1999), namely, one in terms of two-dimensional cue detection (see also LOIDOLT et al. 2006, for related discussion). Indeed, some conspicuous two-dimensional features (e.g., contour differences) were available in the displays, which might have been sufficient for correct discrimination. In order to properly test whether the birds had indeed perceived the projections as generalised 3-D objects instead of collection of single views or even features, it would have been necessary to rule out the possibility of retrieving three-dimensional structure, but to preserve availability of two-dimensional discriminative features in a display. For example, examination of discriminative response to randomised dynamic sequences might thereby have been the appropriate means of testing. *Randomisation* (i.e., scrambling) of a coherent sequence of images causes disruption of various kinds: It may dramatically alter the temporal sequencing of the single frames and may destroy any cues provided by (apparent) motion. Above all, it may widely rule out the possibility to retrieve from coherent dynamic presentation the three-dimensional structure of an object. Whether pigeons are sensitive to differences in *coherent dynamic presentation* (logically consistent position changes of an object over time) as compared to *non-coherent dynamic presentation* has been focused on in the last years – however, the results seem conflicting. Whereas some studies have found a *coherence superiority effect* (CSE), i.e., coherent sequences facilitated and/or improved discrimination and accelerated learning (COOK et al. 2001; COOK & ROBERTS 2007; FRIEDMAN et al. 2009, Exp. 2; KOBAN & COOK 2009), others failed to provide evidence for an advantage of coherent presentation (COOK et al 2003, Exp. 4; FRIEDMAN et al. 2009, Exp. 1B; LOIDOLT et al. 2006; ROVINA 2006).

1.4. Statement of the problem

Despite extensive research on a pigeon's general capability of recognising objects under many variations in conditions – particularly over rotations in depth – answers to the question on which mechanisms object recognition might be based, are still ambiguous. As discussed previously there is evidence in favour both views, namely that pigeons may rely on generalised object-like three-dimensional representations (COOK & KATZ 1999), and alternatively that they may use simple two-dimensional features to recognise objects instead. Support for the latter theory was strongly provided by some work carried out in the pigeon laboratory of the Department for Neurobiology and Cognition Research of the University of Vienna.

Similar to COOK & KATZ (1999), LOIDOLT et al. (2006) and ROVINA (2006) posed the question whether “motion” does enhance recognition of an object. Interestingly, they could find neither generalisation to novel views nor any enhancing effect of dynamic presentation. The obvious question to arise from these results concerned the nature of the factors that might have led to the different outcomes. For example, differences in stimuli, training and testing procedures, technical equipment as well as reinforcement schedules might have influenced the results. Therefore, it seemed worth examining whether it may be possible to replicate the results of COOK & KATZ (1999) particularly in a laboratory that has, so far, found no evidence of dynamic presentation facilitating recognition – not least because it may have implications for comparing future work from different laboratories.

The aim of this study

The overall objective was hence to re-examine whether pigeons are able to discriminate two-dimensional projections of three-dimensional objects based on generalised three-dimensional representations. To this end, pigeons’ ability to generalise to various stimulus transformations during dynamic versus static presentation was assessed. The experimental design as well as the choice of stimuli was thereby adopted from the experiments described by COOK & KATZ (1999). Furthermore, I extended the original experiment by examining whether randomisation of a dynamic sequence would affect discrimination performance. The rationale behind this additional test was that inhibition of the possibility to recover structure from coherent dynamic presentation should clearly impair performance if the birds had indeed experienced the projections as coherent stable three-dimensional units.

Two contrasting hypotheses were put to the test in the current study.
(A) The pigeons learn the discrimination on the basis of stable generalised three-dimensional object representations (c.f., COOK & KATZ 1999), and **(B)** they learn the discrimination on the basis of two-dimensional features or templates (LOIDOLT et al. 2006; ROVINA 2006). To decide between the two hypotheses, three main

questions were investigated. *First*, would discrimination performance be similar to training performance despite various stimulus transformations? *Second*, would discrimination performance with static presentation be different from performance with dynamic presentation? *Third*, would discrimination performance differ depending on the order of frames in a dynamic sequence?

Based on the foregoing hypotheses, the following predictions could be made:

(A) **The pigeons learn the discrimination by means of stable generalised three-dimensional object representations.**
First, discrimination performance should not be significantly impaired by stimulus transformations concerning size, surface colouration, or rotation in depth. *Second*, dynamic presentation should facilitate object recognition. *Third*, randomising a sequence should clearly deteriorate to discrimination. Generally, the results should be in line with the ones reported by COOK & KATZ (1999).

(B) **The pigeons learn the discrimination by means of two-dimensional features or templates.**
First, discrimination performance should be negatively affected by stimulus transformations, with the extent of decreases depending on the availability of discriminative cues provided by the stimuli. *Second*, performance with dynamic stimuli should not be different from performance with static stimuli, i.e., no facilitating effect of dynamic presentation should occur. *Third*, randomising a sequence should not affect the ability to discriminate. Generally, the results should be inconsistent with those reported by COOK & KATZ (1999), and should rather confirm the ones by LOIDOLT et al. (2006) and ROVINA (2006).

Comparisons of the outcomes of the present experiment and the original study by COOK & KATZ as well as studies that have yielded contrasting results should further elucidate the nature of the procedural parameters that may control discriminative responses in this kind of discrimination task.

2. METHODS

2.1. Subjects

Common pigeons (*Columba livia*) of two different breeds (*C. livia forma urbana*, carrier pigeon, and *C. livia forma domestica*, a huge Austrian livestock breed called "Strasser"), and of mixed sex were employed as experimental subjects. The two breeds are suggested not to noticeably differ regarding cognitive abilities, as has been demonstrated in several previous experiments (e.g., AUST & HUBER 2001; HUBER & LENZ 1993, 1996; HUBER 1994; HUBER et al. 1999; LOIDOLT et al. 2006; ROVINA 2006; TROJE et al. 1999). Only a slight difference concerning their behaviour has been noticed: Strasser pigeons have been shown to be more balanced, as well as more eager to peck in experiments compared to the less tame carrier pigeons that are generally more difficult to handle. I initially employed a total of twelve pigeons as experimental subjects. However, five of them had to be excluded from the study later, either because of their inability to reach the criterion of learning (Felix_T9a, Viktor_T8a) or due to their early decease during the experimental period (Nina_T75a, Hanna_T3, Otto_T10). The following seven subjects eventually completed the entire experiment: Auge (T_47a), Herbert (B_3a), Robin (T_44), Herwig (T_42a), Ricky (T_11a), Moses (T_48a), and Arthur (B_31a).

At the experiment's onset all subjects were already familiar with the procedure and the apparatus because of participation in previous discrimination experiments unrelated to the current study. Furthermore, none of the birds had prior experience with dynamically presented stimuli, except one, Herbert (B_3a). He had previously participated in an experiment using video stimuli (ROVINA 2006). The pigeons' experimental histories, thus, involved extensive exposure to static stimuli of many kinds. The birds were all naïve to the stimuli used in the present study, namely, two-dimensional computer-generated projections of three-dimensional cubic and pyramidal objects.

The subjects were housed with other conspecifics in three 300 x 120 x 170 cm compartments of a 54 m² roofed outdoor aviary located in one of the courtyards of the Biology Centre of the University of Vienna. Each compartment comprised groups of approximately 10 individuals of mixed sex. The birds were allowed free access to grit (a mixture of silex, red stone and oyster shells; Natural Granen Antwerp) and water in the aviary, whereas food was administered only in the experimental chambers (i.e., in the course of testing), as well as immediately after the daily experimental sessions. The provided mixture of grain (complete food for pigeons – Standard, Natural Granen Antwerp) consisted of a variety of corn (35.0 % French maize, 20.0 % milo corn, 20.0 % wheat, 15.0 % yellow peas, 10.0 % green peas, 5.0 % maple peas, 2.5 % dari, 2.5 % safflower seed). On non-testing days the birds were supplied with extra rations of food. In order to increase motivation to work, the birds were maintained at about 90 % of their free-feeding weights.

2.2. Apparatus

The apparatus is depicted in Figure 1. Training and testing was conducted indoors in one of three identical 50 x 30 x 40 cm wooden *operant chambers* (i.e., “Skinner boxes”). Each of them was connected to one compartment of the outdoor aviary by means of a passageway system (see HUBER 1994). The pigeons were let into the chamber via a *Perspex sliding window*, which separated the passageway's inner part from the outdoor compartment. The rear wall of each chamber served as a *sliding door* for letting the pigeons enter. The front wall of the operant chamber served as a so-called *intelligence panel* which comprised two essential components. The first was a clear *Perspex pecking key* (5 cm in diameter, ENV-125M, MED Associates, Georgia, Vermont), that provided free view on the stimuli presented on the *monitor* which adjoined to the Skinner box. The *pecking key* was fixed in a manner that its dislocation, caused by the subject’s pecking, led to interruption of an electric circuit. This was recorded by a PC for later performance assessment. The second component of the intelligence panel was located directly below the key, namely, a 6 x 6 cm aperture for a *28-V DC solenoid-activated* *hopper* of the *grain feeder* (ENV-205M, MED Associates, Georgia, Vermont). A *hopper light* illuminated the aperture whenever grain was accessible. The chamber's interior was weakly lit by a 2-W *house light* (ENV-215, MED Associates, Georgia, Vermont), located in the rear part of the chamber.

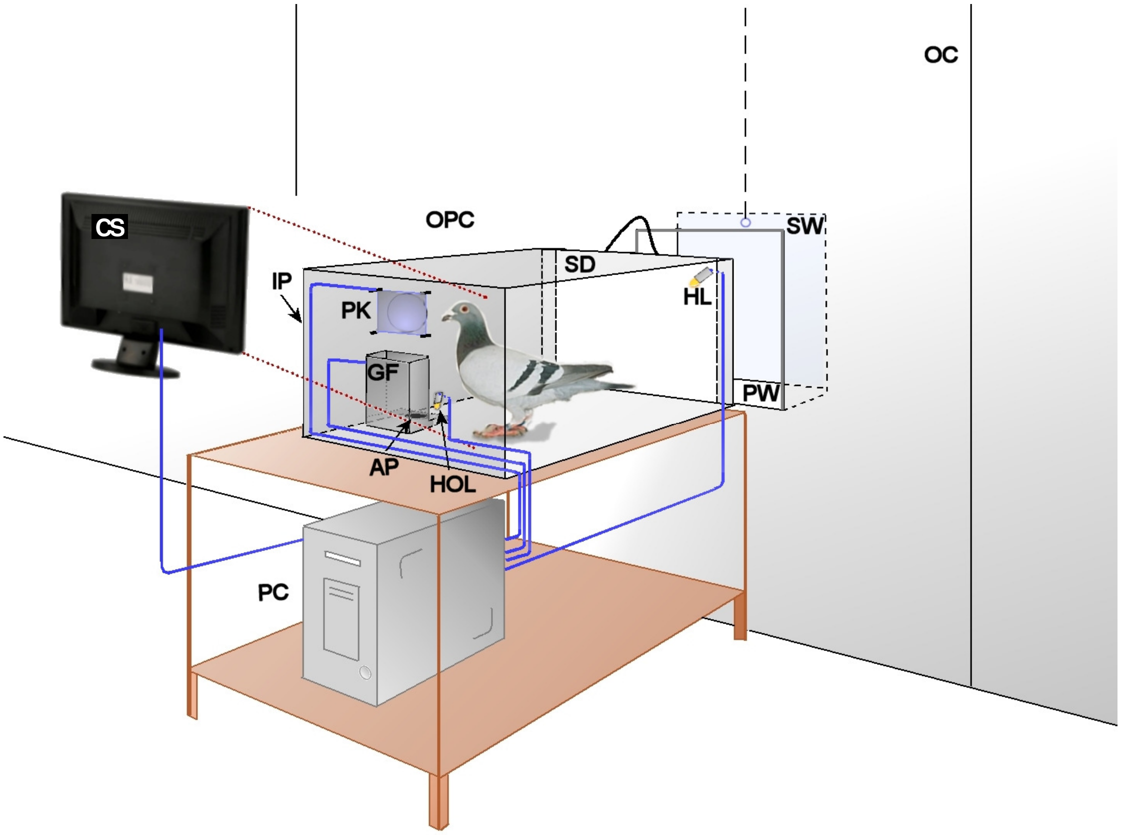


Figure 1. *Schematic drawing of the apparatus.*
By means of a manually lifted Perspex sliding window (SW) the pigeon enters the passageway (PW) that connects the outdoor compartment (OC) with the apparatus. The subject enters the operant chamber (OPC) through a wooden sliding door (SD). The interior of the chamber is illuminated by a house light (HL). The front wall serves as intelligence panel (IP) containing a clear Perspex pecking key (PK) and a grain feeder (GF) that provides food through an aperture (AP). The food receptacle is lit by a hopper light (HOL) while food is administered. At a distance of about 5 cm behind the front panel a computer screen (CS) is located for stimulus presentation (red dotted lines indicate the actual position of the monitor). The two lights, the grain feeder, the monitor, and the pecking key are connected to a PC (PC).

Each Skinner box was connected to a *PC*, equipped with a relay board (8 x input, 8 x output) by Keithley/Metrabyte and with a software package (PigeonLab; STEURER 2002) that controlled all events in the operant chamber during experimental sessions, such as stimulus presentation, registration of responses, and activation of the feeder. The 15-inch *LCD monitor* (Videoseven L15C-TCO99) that displayed the stimuli was located at a distance of 5 cm behind the pecking key.

2.3. Stimuli

Orthographic computer-generated projections of cubic and pyramidal objects served as stimuli for the pigeons. The stimuli were framed by a black area. The (whole) images – consisting of the projection of an object and the surrounding black area – were presented at a size of 150 x 150 pixels and at a resolution of 72 dpi (pixels per inch). Monitor adjustments were set to true colour, and to 1024 x 768 pixel spatial resolution. Thus, the presentations were produced as 4.69 x 4.69-cm images on the screen. Since the stimuli were actually a part of these images they were smaller than the whole presentation image. The actual stimulus size depended on the size class they belonged to (see later). For detailed descriptions of the stimulus sizes see chapters 2.3.2 (Training stimuli) and 2.3.3 (Test stimuli). I created the projections by means of a graphics program (Maya 7.0, Autodesk). Each individual sample of the various projections (i.e., one individual projection of an object featuring a specific combination of the surface colours or modification of its intrinsic properties, see later) was rendered as a sequence of images that depicted the respective object rotating around one ore two axes (see Figure 2 for the coordinate system used in this study). Such a sequence comprised a full rotation of an object around its axis (or axes), and provided the observer with successive views of the object. The single images of a sequence were generated in Windows bitmap format. Each frame differed from the next in viewing angle by 3°. Thus, one full rotation comprised 120 consecutive views onto the respective object (an example of a rendered rotation sequence is pictured in Figure 3). The images were rendered via *orthographic mode*. Orthographic projection is best defined as a form of parallel projection, where the view direction is orthogonal to the projection plane. Due to the absence of a vanishing point, the projections of the present study were generally non-perspective.

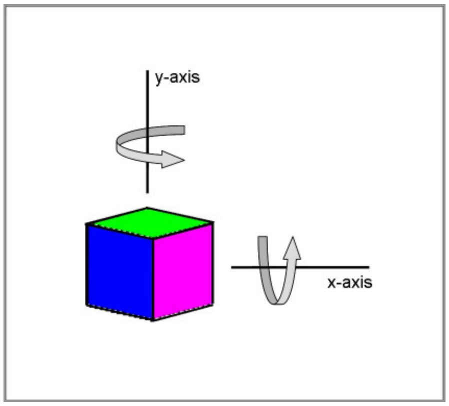


Figure 2. *The coordinate system used in this study. Rotations occurred around the y-axis, the x-axis and simultaneously around both the y- and the y-axis.*

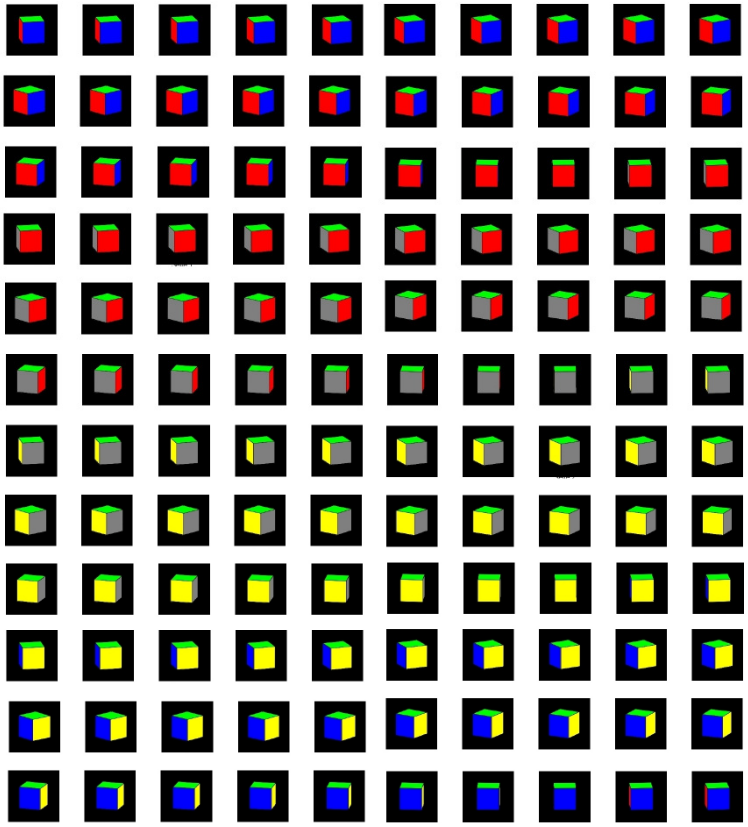


Figure 3. *Example of a rendered rotation sequence depicting 120 single images (views onto a cubic object rotating around the y-axis). Order of succession is top left to down right. Images are smaller-sized than those presented in the experiment.*

A lighting model assuming diffuse reflection and full illumination by ambient light was applied to the rendering process. Diffuse reflection means that rays of light were re-irradiated isotropically from the object in all directions. Hence, the object neither featured shading nor produced shadows. The cubic and pyramidal objects were placed in the centre of a black perspectiveless background. These default settings were equally applied to training and test stimuli.

2.3.1. Presentation mode

Half of the trials within a session (except for the sessions of Test *Randomised,* see below) involved *static* stimulus presentation, the other half of the stimuli involved *dynamic* stimulus presentation. The stimuli were presented in random order during a session.

Static presentation

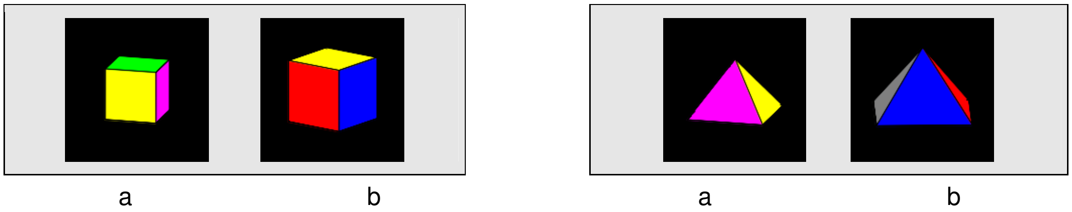
On *static* trials one single image that was arbitrarily selected from each rendered rotation sequence was displayed throughout a pre-specified presentation time interval. Hence, within a *static* trial an object was presented in only one angular orientation (i.e., view).

Dynamic presentation

On *dynamic* trials the individual frames of one complete rendered rotation sequence were displayed in rapid succession throughout the presentation time interval. The single images were shown at a rate of 30 frames per second, controlled by a program that had been generated with Microsoft Visual C++. I chose to apply uncompressed bitmap files, since – in contrast to the commonly used video formats that involve video compression, such as AVI- or MPEG-formats (e.g., COOK et al. 2001; KOBAN & COOK 2009) – they allow for picture-by-picture presentations of video sequences. At least to the human eye, the pyramidal and cubic object appeared to rotate smoothly during dynamic presentation. A complete object rotation (i.e., the successive presentation of all 120 frames of one sequence) took 4 seconds.

2.3.2. Training stimuli

Examples of training stimuli are depicted in Figure 4. I created a total of 96 different rotation sequences (i.e., object samples). Half of them contained two-dimensional projections of a three-dimensional pyramid and the other half contained two-dimensional projections of a three-dimensional cube. For dynamic presentation each rendered sequences was presented in rapid succession; for static presentation one out of the 120 single images of each rendered sequence was arbitrarily chosen and presented as single bitmap image on the screen (it was ensured, however, that all static stimuli showed the object from a different viewpoint). Thus, in total the pool of training stimuli contained 192 stimuli.



Projections of a cube. *Projections of a pyramid.*

Figure 4. *Examples of training stimuli used for static presentation (**a** small, **b** large). Images are smaller-sized than actually presented on the screen.*

Each individual object sample featured a unique combination of six (in case of the cube) or five (in case of the pyramid) colours that were assigned to the object's surfaces. The chosen colours were yellow (RGB 255, 255, 0), red (RGB 255, 0, 0), purple (RGB 255, 0, 255), blue (RGB 0, 0, 255), green (RGB 0, 255, 0) and grey (RGB 127, 127, 127). It was made sure that, overall, each colour appeared equally often across object samples. Thin black contour lines marked the object's edges. During the creation of the objects the virtual camera of the graphics program was set to "recording" the rotation sequence from a viewing angle 15° relative to the object's transecting horizontal plane. Hence, the human viewer had the impression to look from a slanted position above down onto the object's top. Rotation proceeded counter-clockwise around the vertical axis, i.e. the y-axis (see Figure 3). Every individual sample was unique regarding the orientation from which the object started to rotate.

Each object was presented at two different sizes ("large" and "small"). This was conceived in order to prevent the pigeons from using information about size or screen position as a discriminative cue. Since in the original study (COOK & KATZ 1999) a particular size was primarily defined by a particular object volume (large stimuli depicted projections of objects that in reality would have a volume of 4.4 cm³; small stimuli depicted objects with a volume of 2 cm³), also in the current study different size was defined by different object volume. This was done for reasons of comparability. The volumes used in the present experiment, however, were larger than in the original study. Consequently, half of the training stimuli comprised projections of objects that in reality would have a volume of approximately 5 cm³ (small stimuli) and the others comprised projections of objects that in reality would have a volume of approximately 6.8 cm³ (large stimuli). Calculation of the volumes was based on the objects' side lengths which I measured from screen with a ruler (a small volume was equivalent to a side length of 1.7 cm in case of the cube, and 2.9 cm in case of the pyramid; a large volume was equivalent to a side length of 1.9 cm in case of the cube and 3.2 cm in case of the pyramid). Since the stimuli differed according to the viewpoint the actual sizes of the two-dimensional projections of the objects on the computer screen varied relative to the objects' orientation.

Altogether, the 192 training stimuli comprised 48 *small*-sized and 48 *large*-sized projections of an object presented *statically*, as well as 48 *small*-sized and 48 *large*-sized projections of an object presented *dynamically*. Half of these projections were *cubic* objects, the other half were *pyramidal* ones. Therefore, each stimulus was eventually defined by a combination of three parameters, each of which could take one of two forms: shape (*cube*/*pyramid*), mode of presentation (*static*/*dynamic*), and size (*large*/*small*). Thus, there were 2^3 different stimulus types in total. The training stimuli were organised into 5 sets, with one set per session being presented (see Table 1). Each set consisted of five stimuli of each type, resulting in 40 training stimuli per set (and thus per session). The five stimuli of the same stimulus type differed from each other according to the combination of surface colours and the object's orientation (in case of dynamic presentation this means that the orientation from which the object started to rotate differed, in case of static presentation the viewpoint differed). The training sets were shown consecutively in cycles. Due to the fact that one set always comprised 5 stimuli per stimulus type and that 5 sets were used in total, but only 24 stimuli per type were available, one additional stimulus per stimulus type was arbitrarily chosen from the pool of training stimuli and was arbitrarily assigned to any of the 5 sets.

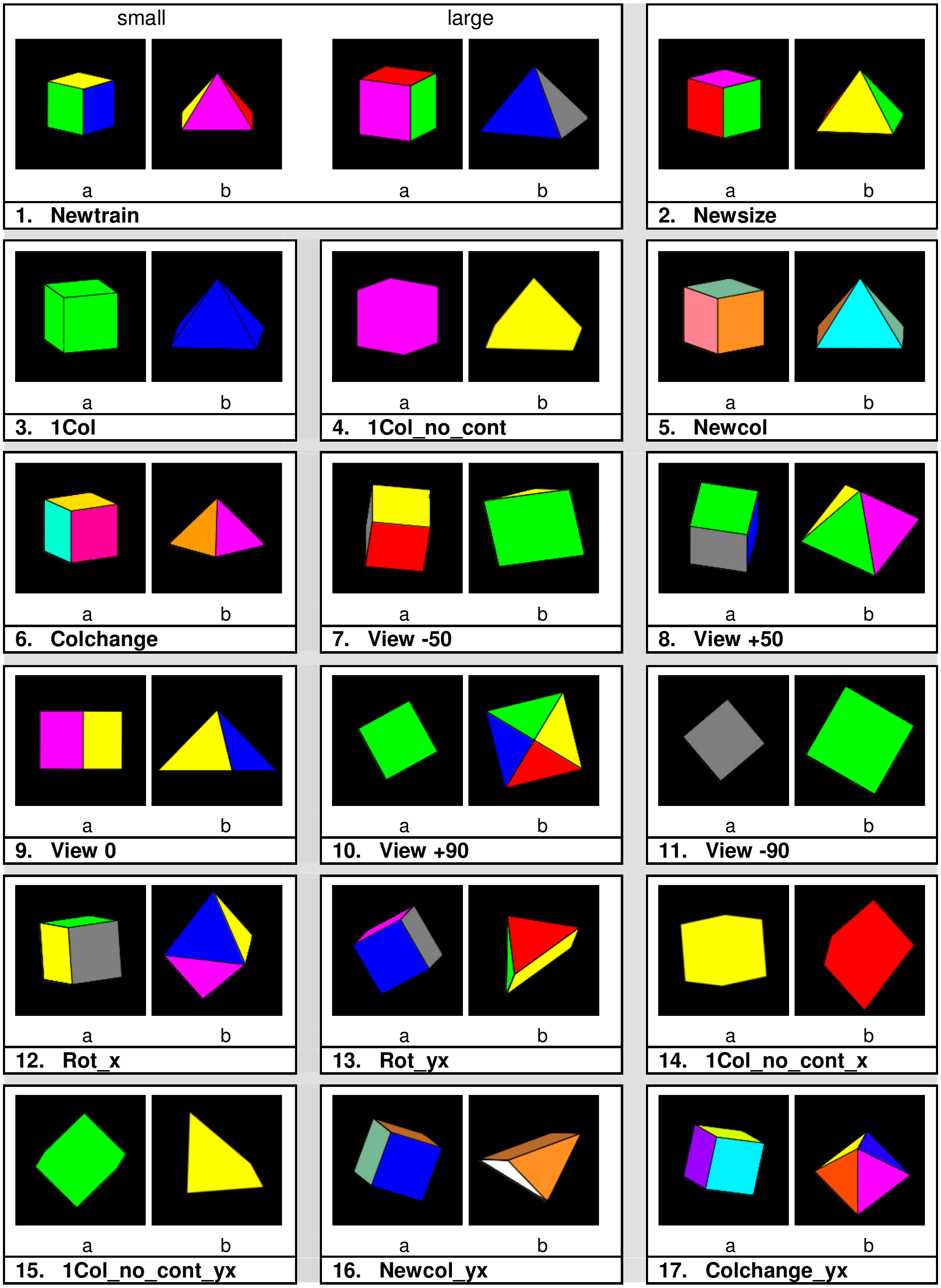
Table 1. *Numbers and types of stimuli shown in every training session.*

Shape	Cube				Pyramid			
Mode of Presentation	static		dynamic		static		dynamic	
Size	small	large	small	large	small	large	small	large
Number of Stimuli	5	5	5	5	5	5	5	5

2.3.3. Test stimuli

A total of 18 novel types of modified stimuli served as test stimuli. Test stimuli used in the study by COOK & KATZ (1999) thereby served as model. However, not all transfer tests conducted in the original experiment were replicated. I created a selection of test stimuli which I considered appropriate for examining the contribution of particular stimulus properties to discrimination. However, I am aware that this selection may reflect an arbitrary selection. Additionally, I introduced three new types of stimuli not included in the study by COOK & KATZ (*Colchange*, *Colchange_yx*, and *Randomised*, see later).

Each transfer test was labelled according to the type of transformation applied to the original training objects from which the test stimuli were derived. Examples of the test stimuli are depicted in Figures 5.1-17.



Figures 5.1-17. *Examples of test stimuli (**a** cube, **b** pyramid). Images are smaller-sized than actually presented on the screen.*

In total, I used 136 test stimuli (for numbers of stimuli per type see later). They were created as rotation sequences in the same manner as the training stimuli, with the exception of the test stimuli that were used for Test *Randomised* (for details see APPENDIX). Both static and dynamic presentation mode were basically the same for test as for training stimuli. Test stimuli were projections of large-sized objects (i.e., those with a volume of 6.8 cm³), except for the ones used in Tests *Newtrain*, *Newsize,* and *Randomised* (for details see APPENDIX). As with the training stimuli, the observer's viewpoint was 15° above the object's transecting horizontal plane, except for transfer tests involving transformations in relation to the observer's perspective (i.e., Tests *View -50*, *View +50*, *View 0*, *View -90* and *View +90*). Test stimuli used in Tests *Rot_x, 1col_no_cont_x, Rot_yx, 1col_no_cont_yx, Newcol_yx*, and *Colchange_yx* differed from the training stimuli in terms of the object's axes of rotation. It is important to note that test stimuli that included a novel angle of elevation of the viewpoint or a novel axis of rotation differed substantially from the training stimuli since, in both cases, the object was presented from a novel perspective relative to the observer. Both transformations also resulted in considerable changes in the two-dimensional shape of the projections. To explicitly highlight this important aspect I divided the tests into two groups, according to the presence or absence of perspective-changing transformations. *Training Perspective* tests (TP tests) included stimuli with a perspective identical to the training perspective (i.e., Tests *Newtrain, Newsize, 1col, 1col_no_cont, Newcol,* and *Colchange)*. By contrast, *Modified Perspective* tests (MP tests) comprised stimuli including modifications in perspective (i.e., Tests *View -50, View +50, View 0, View +90, View -90, Rot_x, 1color_no_cont_x, Rot_yx, 1color_no_cont_yx, Newcol_xy* and *Colchange_yx*). Only Test *Randomised* did not fit into either group for two reasons. First, this test comprised only dynamic stimuli, and second, the individual displays were the same as in the training stimuli, with which the birds had gathered extensive experience. Thus, the test stimuli provided exactly the same visual information as the training stimuli (and differed from the latter only with regard to their mode of presentation; see below). The main aspects by which the stimuli presented in the individual tests differed from the training stimuli are specified in Table 2. The different types of transformations should examine generalisation to particular stimulus modifications. Stimuli with **novel combinations of surface colours** (Test *Newtrain*, Figure 5.1) tested how the pigeons would generalise to novel samples of the training classes. Stimuli with a **new size** (Test *Newsize*, Figure 5.2) examined effects of novel object size on the pigeons' responding. Test stimuli with **novel surface colouration** examined generalisation to novel types of colouration including monochromatic presentation (i.e., Tests *1col,* Figure 5.3*)*, elimination of contour information (i.e., Test *1col_no_cont,* Figure 5.4), novel colours (Test *Newcol,* Figure 5.5), and surface colouration that transformed continuously over time (Test *Colchange,* Figure 5.6). In general, test stimuli that presented the objects from a **novel viewpoint** examined the pigeons' responding to perspective changes. Thereby, stimuli presenting a novel observer's perspective (Tests *View -50*, *View +50*, *View 0*, *View -90* and *View +90,* Figures 5.7-5.11) tested generalisation to changes in the observer's viewpoint, stimuli presenting novel axes of rotation (Tests *Rot_x,* Figure 5.12*, Rot_yx,* Figure 5.13) tested generalisation to depth rotations of the object around different axes of rotation. Tests that included both **novel surface colouration and novel viewpoint** examined the influence of both transformations combined (Tests *1color_no_cont_x, 1color_no_cont_yx, Newcol_xy* and *Colchange_yx*, Figures 5.14-5.17). Finally, presentations of incoherent sequences (Test *Randomised*) examined generalisation to non-coherent sequences of dynamic stimuli. A detailed description of the properties of the individual types of test stimuli and the way in which they were generated is given in the APPENDIX (pp. 87-91). All stimuli of one specific type of transformation (i.e., one test) were pooled together in one *test set*, with the exception of the Tests *Colchange* and *Colchange_yx* that were combined into one single test set[2]. Each test set comprised 8 test stimuli. The composition of the test stimuli within a test session with respect to the different types of presentation can be seen in Table 3.

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[2] Regarding the use of *Colchange*- and *Colchange_yx*-stimuli, the initial focus was basically on examining how the pigeons would react to a continuous change of colouration, but not on the influence of viewpoint. Therefore, the stimuli were combined into one test set.

Table 2. *Main differences (indicated by x) between test and training stimuli.*

Test	Size	Viewpoint	Surface Colouration	Lack of Contour Lines	Mode of Presentation
Newtrain					
Newsize	x				
1Col			x		
1Col_no_cont			x	x	
Newcol			x		
Colchange			x		
View -50		x			
View +50		x			
View 0		x			
View +90		x			
View -90		x			
Rot_x		x			
Rot_yx		x			
1Col_no_cont_x		x	x	x	
1Col_no_cont_yx		x	x	x	
Newcol_yx		x	x		
Colchange_yx		x	x		
Randomised					x

Table 3. *Overview of the composition of the test stimuli within a test session regarding mode of presentation and size of the test stimuli. The figures indicate the numbers of stimuli of the respective type that were shown. Empty fields indicate that the respective test did not include stimuli of that type.*

Test	Cube static			Cube dynamic			Pyramid static			Pyramid dynamic		
	sma	lar	med	sma	lar	med	sma	lar	med	sma	lar	med
Newtrain	1	1		1	1		1	1		1	1	
Newsize			2			2			2			2
1col		2			2			2			2	
1col_no_cont		2			2			2			2	
Newcol		2			2			2			2	
Colchange		1			1			1			1	
View -50		2			2			2			2	
View +50		2			2			2			2	
View 0		2			2			2			2	
View +90		2			2			2			2	
View -90		2			2			2			2	
Rot_x		2			2			2			2	
Rot_yx		2			2			2			2	
1col_no_cont_x		2			2			2			2	
1col_no_cont_yx		2			2			2			2	
Newcol_yx		2			2			2			2	
Colchange_yx		1			1			1			1	
Randomised				2	2					2	2	

Note. *sma = small-sized, lar = large-sized, med = medium-sized*

2.4. Procedure

The subjects already had experience with the procedural requirements at the outset of the experiment. This is, they entered the box voluntarily, accepted food reward from the food hopper, and pecked at the pecking key for food. Therefore, no further habituation phase was required. A counterbalanced design was employed, that is, the subjects were arbitrarily assigned to either of two experimental groups. An overview of the birds' assignment is given in Table 4. For three of the seven eventually remaining birds (i.e., the birds whose data could actually be used for analysis), pyramids were the positive stimuli (S+), and cubes the negative ones (S-), and vice versa for the four other subjects.

Table 4. *Group assignment of the experimental birds. Subjects that had to be excluded in the course of the experiment are put in parentheses.*

Experimental group	pyr+	cub+
Subject	Ricky_T11a	Herbert_B3a
	Moses_T48a	Robin_T44
	Arthur_B31a	Herwig_T42a
	(Hanna_T3)	Auge_T47a
	(Victor_T8a)	(Nina_T75a)
	(Felix_T9a)	(Otto_T10)

Note. *Cub+ indicates that projections of a cube were designated as S+, Pyr+ indicates that projections of a pyramid were designated as S+.*

After a subject had entered the operant chamber, the computer program that was in charge of stimulus presentation and recording of the emitted pecks, and which also controlled the administration of food and time-outs, was started. The pigeons were subjected to a well-established successive discrimination paradigm, the go/no-go procedure as described by VAUGHAN & GREEN (1984; see also e.g., AUST & HUBER 2001, 2002, 2003, 2006a, 2006b; HUBER & LENZ 1993, 1996; HUBER et al. 2000; LOIDOLT et al. 2006). It requires the birds to peck frequently in the presence of a positive stimulus in order to get a reward and to refrain from pecking in the presence of a negative one in order to avoid a delay. Each subject accomplished one *session* a day, i.e., five days a week. Training as well as test sessions consisted of 40 *trials*, i.e., individual presentations. Half of the stimuli of one session were assigned to the *positive* class, the other half to the *negative* one. Only trials on which *positive* stimuli were presented provided an opportunity to receive food. Each trial began with the presentation of a stimulus on the screen. To prevent discouragement already at the very beginning of a session, the stimulus shown in the first trial was always a positive one and never a test stimulus. The remaining trials were presented in quasi-randomised order. That is, stimuli of the same *contingency* (*positive* or *negative,* see below) were never presented in more than three consecutive trials. During the first 10 seconds of a trial, the pecks emitted to the pecking key were counted for later calculations. Except for trials with *neutral contingency* (*test trials*, see below) this period was followed by a *variable interval (VI)*, ranging from one to ten seconds, to avoid conditioning on a specific time schedule. During the VI the stimulus remained visible, but pecks were not registered. During the subsequent decision phase the pigeon was required to respond differently, depending on the contingency of the stimulus, in order to terminate the trial. In positive trials, two pecks emitted within two seconds resulted in eight seconds of food access. The stimulus remained visible until the response requirement was accomplished. In negative trials, the pigeon was required to refrain from pecking for eight seconds in order to terminate the trial, and to proceed to the next one. At failure, i.e., if pecks were emitted during this interval, the subject was exposed to an error-delay of another eight seconds, and so on. No food reward was delivered after the response requirement had been accomplished. In trials with *neutral contingency*, i.e., in *test* trials, no response requirement had to be fulfilled in order to terminate the trial. After the first ten seconds of stimulus presentation, during which pecks emitted to the key were counted, test trials ended immediately without any food reward or time-out. That is, they were conducted in extinction. Thus, learning about the contingency of a stimulus could not occur during the test trials. Every trial (training and test) was followed by an *inter-trial-interval* (ITI) of four seconds. During this period the screen remained dark, and the house light was turned off, to signal the forthcoming presentation of the next stimulus.

This procedure caused the pigeons to learn to discriminate between *positive* and *negative* stimuli by reinforced pecking at the former and non-reinforced pecking at the latter.

2.4.1. Training phase

The training phase consisted of repeated runs of *cycles*, each of which comprised 5 training sets. Within one session, the subjects were presented with one *training set* (consisting of 40 stimuli, i.e., five stimuli of each type of presentation; for details see Chapter 2.3.2). The very first training session started with the presentation of *Training set 1*, the four remaining sets of one cycle (*Training sets 2-5*) were presented consecutively in the following sessions. When all sets of a cycle had been presented, another cycle was started. The subjects were trained until they reached a pre-specified criterion of successful discrimination, namely, 3 rho-values ≥ 0.750 in 5 consecutive sessions (see Chapter 2.5). The criterion thus required discrimination performance above the level of significance for a 40-trial session (rho-value ≥ 0.677). Furthermore, a minimum of 8 accomplished training cycles (i.e., 40 sessions at minimum) was required. However, if a subject did not reach a rho-value of $\rho \geq 0.750$ in at least one of the first 40 sessions training was terminated and the bird was excluded from the experiment.

2.4.2. Test phase

Only subjects that had acquired the discrimination (i.e., reached the learning criterion) were subjected to a series of 18 different transfer tests, each of which involved the presentation of one particular *test set,* with the exception of the Tests *Colchange* and *Colchange_yx* that were combined into one test set (see Chapter 2.3.3). The 40 trials of a test session comprised 8 test stimuli; these were interspersed among 32 training stimuli at pre-specified positions. The 17 *test sets* were presented consecutively. The entire “test battery” was repeated three times. In order to ensure that the birds showed reliable baseline performance during test sessions, some of them had to be repeated several times, since only test sessions that yielded a discrimination performance of $\rho \geq 0.75$ (which was calculated only from the training trials of a test session) entered data analysis.

2.5. Data evaluation and statistics

Calculations concerning discrimination performance (i.e., assessment of the differences in peck rates to positive and negative stimuli) were made on the basis of automatically registered pecks, which were emitted onto the pecking key during the first ten seconds of a trial. In order to assess discrimination performance a well-established non-parametric significance test was used – the *Mann-Whitney U test*. This test was proposed by MANN and WHITNEY (1947) and assesses whether two samples of observation come from the same distribution. Therefore, the stimuli included into estimation are ranked according to the number of registered pecks emitted to them. If the number of pecks in response to every stimulus from the positive class is higher than the number of pecks emitted to any stimulus of the negative class, discrimination is perfect (100 %). To measure to which extent the two distributions (i.e., responses to positive and to negative exemplars) overlapped, the *rho-value* (ρ) i.e., the discrimination ratio was calculated. This statistic was introduced by HERRNSTEIN et al. (1976) and estimates the probability that the average positive exemplar will be ranked above the average negative exemplar. Therefore, the U-value derived from the *Mann-Whitney U test* is divided by the number of positive stimuli multiplied by the number of negative stimuli within a session. ρ can take values between 1 (perfect discrimination) and 0 (perfect converse discrimination). Both extremes thus indicate completely separate distributions, while a ρ of 0.5 reflects a complete overlap (chance performance). The level of significance from which onwards a result is assumed to be significant varies with sample size and α. In a 40-trial training session a *rho-value* ≥ 0.677 or ≤ 0.323 indicates significance ($\alpha = 0.05$). For evaluation of performance on the transfer tests, the data of each test was pooled (${}_1n_2 = 6$, $\rho \geq 0.813$ for all tests except Tests *Colchange* and *Colchange_yx*, ${}_1n_2 = 3$, $\rho \geq 0.922$, and Test *Randomised*, ${}_1n_2 = 12$, $\rho \geq 0.726$). To provide one general baseline value which indicated basic performance on training trials during the test phase, all training trials that entered analysis were used as basis ($_1n_2 = 408$, $\rho \geq 0.540$).

To directly compare the birds' rating of different types of stimuli, *mean standardised response rates* (MSRR) were used. They were obtained for each trial by dividing the pecking rate in response to the respective stimulus by the average peck rate measured over all training trials of the session. Thus, peck rates of different birds as well as peck rates in response to different types of stimuli became relative values and thereby comparable because inter- as well as intra-individual variations in pecking behaviour were compensated for.

On the basis of mean discrimination ratios and mean standardised response rates non-parametric statistical tests were conducted. *Wilcoxon signed-ranks tests* examined potential subject group differences, effects of stimulus size and mode of presentation during training, general differences between training and test performance, and between TP and MP test performance, potential differences in test performance between static and dynamic presentation, particular test performances compared with training level, the influence of non-coherent presentation on discrimination performance, and finally assessed discrimination performance with regard to particular stimulus properties. Comparisons between training and test components were based on the MSRRs emitted to the test stimuli in each test (averaged across the three test sessions that entered analysis), and the averaged corresponding MSRRs emitted to the training stimuli presented in the same test sessions. Data analysis was done in Data Desk, SPSS 14.0 and Microsoft Office Excel 2003.

2.6. Comparison to COOK & KATZ (1999)

Basically, the present study was devised and developed following COOK & KATZ's experiment (1999). Therefore, the experimental design of my study was derived from and similar to that used by COOK & KATZ. Nonetheless, the present study deviated from the original one in some respects, due to procedural constraints and theoretical considerations. The most fundamental differences can be seen Table 5. For further details see also COOK & KATZ (1999), and Chapter 2.

Table 5. *Overview of major procedural differences between* COOK & KATZ *(1999) and the present study.*

	COOK & KATZ 1999	**KRAMER 2010**
Apparatus	NEC Multisync 2A (CRT display)	15-inch LCD monitor
Procedure	**Registration of pecks**	
	by infrared touch screen pecks registered during first 15 sec (S- trials … only first 15 pecks used)	by dislocation of pecking key (interruption of electric circuit), pecks registered during first 10 sec of trial
	pecking on white circular signal initiated trial S+ … 15 pecks → reward S- … stimulus visible for 15 sec → no reward 5 sec inter-trial-interval	no specific initiation of the trial required; variable interval S+ ... 2 pecks within 2 sec → reward S- ... no peck within 8 sec (otherwise error-delay of further 8 sec) 4 sec inter-trial-interval
	Requirement for Reward	
	<u>Training</u>: completion of S+ peck requirement … reward, from 30th training trial on partial reinforcement schedule (12.5 % of S+ end with no reward after 15th peck) <u>Tests</u>: variable (partial reinforcement or completion in extinction)	<u>Training</u>: completion of S+ requirement … reward <u>Tests</u>: neutral contingency (no reward)
Stimuli	**Generation**	
	on the fly via QuickBasic Version 3 and Computer Graphics	in advance via Maya©
	Presentation	
	directly rendered during presentation; no detailed specifications available	(successive) presentation of uncompressed images (bitmap) via Visual C++
	Assignment of colours to surfaces	
	on each trial at random	equal distribution of colours over trials
Size of object	Training: 2 cm^3/4.4 cm^3	Training: 5 cm^3/6,8 cm^3
Rate of rotation	Training: 1 rev/5 sec, 1 rev/1 sec	Training: 1 rev/4 sec
Frames/sec	unknown; no detailed specification available	30 frames/sec
Frames/ Rotation	unknown; no detailed specification available	120 frames/rotation, each differs from the next by 3°
Subjects	4	7
Number of trials/Session	<u>Training</u>: 96 <u>Tests</u>: variable number	<u>Training</u>: 40 <u>Tests</u>: 40 comprising 8 test trials
Discrimination Measure	Discrimination Ratio (0-100 %)	*rho-value* (0-1) standardised response rate
Tests	novel rates, novel sizes, novel direction of rotation	novel size, continuous change of colouration, randomised sequence
Criterion of success	None	3 *rho-values* ≥ 0.750 on 5 successive sessions, minimum of 40 sessions

3. RESULTS AND DISCUSSION

3.1. Training Phase

The subjects were trained to discriminate between two-dimensional projections of two three-dimensional objects, a cube and a pyramid. The stimuli comprised projections of two object sizes, i.e. *small* and *large*, and were presented either *statically* or *dynamically.* In the latter case the objects rotated around the y-axis.

Results and Discussion

The birds' training performance is illustrated in Figure 6 and summarised in Table 6. Since the criterion of mastery was determined as 3 rho-values of 0.750 or higher in 5 successive sessions combined with completion of at least 40 sessions the training required at least 8 weeks (5 sessions a week provided). Of the twelve subjects three (Nina_T75a, Hanna_T3, Otto_T10) died in the course of training and two (Felix_T9a, Viktor_T8a) had to be discontinued since their discriminative performance did not reach a rho-value of $\rho \geq 0.750$ in any of the first 40 training sessions. Therefore, all results reported in the remainder of this thesis were calculated from pecking responses of the seven successful birds only. Five of them acquired the task within 40 training sessions (this corresponds to the completion of 8 cycles). One bird (Arthur_B31a) needed 60 sessions (this corresponds to the completion of 12 cycles) and one (Herwig_T42a) needed 80 sessions (this corresponds to the completion of 16 cycles). Hence, 38.29 (± 23.16) sessions on average were required by the seven subjects to reach learning criterion (see Table 6, left panel). Figure 6 shows acquisition performance (assessed as rho-values, performance on all stimulus types combined) of the individual birds. For reasons of clarity rho-values were calculated separately for each cycle of training sessions; that is, five sessions were pooled together for calculation. The learning curves clearly show that the subjects differed from each other in terms of learning speed.

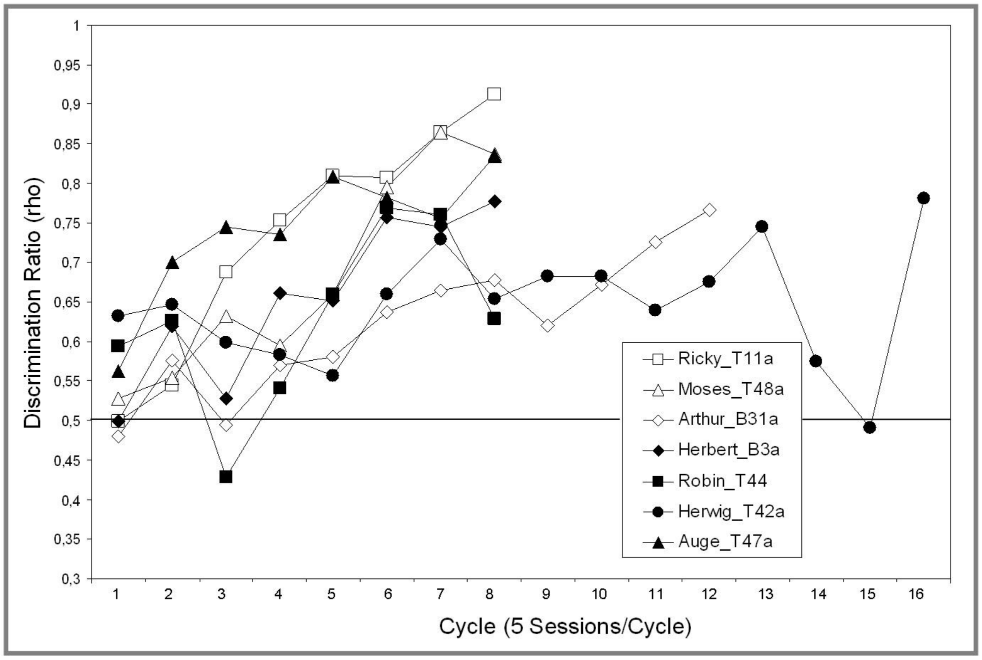

Figure 6. *Discrimination performance assessed as rho-values throughout the training phase, shown separately for each of the seven successful subjects, performance on all stimulus types (i.e., small, large, dynamic, static) combined. Filled symbols indicate performance of subjects assigned to group cub+, open symbols indicate assignment to group pyr+. The solid horizontal line indicates the level of chance performance. The criterion of successful discrimination was pre-specified as combining 3 rho-values ≥ 0.750 in 5 successive sessions with a minimum of 8 accomplished training cycles. If a subject's discriminative performance did not reach the learning criterion during the first 8 cycles training was continued until the criterion was met.*

Table 6. *Training performance of the individual subjects.*

Subject	Experimental Group	Number of Sessions	Final rho-value
Ricky_T11a	pyr+	20	0.928 (40)
Moses_T48a	pyr+	26	0.788 (40)
Arthur_B31a	pyr+	60	0.812 (60)
Herbert_B3a	cub+	36	0.723 (40)
Robin_T44	cub+	28	0.781 (40)
Herwig_T42a	cub+	80	0.904 (80)
Auge_T47a	cub+	18	0.757 (40)
Mean		**38.29** *± 23.16*	**0.813** *± 0.076*

Note. *Listed are the numbers of sessions required to achieve 3 rho-values ≥ 0.750 in 5 successive sessions, and the rho-value of the last training session. The total numbers of training sessions needed to fulfil the learning criterion (at least 40) are given in parentheses. Cub+ indicates that projections of a cube were designated as S+, Pyr+ indicates that projections of a pyramid were designated as S+.*

Most birds started to discriminate above chance level ($\rho \geq 0.677$), already at the end of the first cycle, and then performance continuously increased further in the course of training. One bird (Herwig_T42a), however, failed to show steady improvement for several cycles. Considerable fluctuations of his discriminative behaviour can be noticed, especially between the 13th and 15th cycle. At this time, he was afflicted with a serious disease, but recovered during the 16th cycle. Furthermore, Figure 6 suggests that there was no difference in acquisition performance between the two experimental groups. This was confirmed by a Wilcoxon's signed-ranks test, which compared rho-values (averaged across the birds of each group separately) obtained in the first eight cycles. No inter-group difference was revealed ($z = -0.700$, $p = 0.547$). That is, group assignment influenced neither the speed nor the accuracy of learning. The right panel of Table 6 presents the rho-values reached by the individual subjects in the last training session. The mean of $\rho = 0.813$ (± 0.076) indicates a high level of performance, far above the level of significance (≥ 0.677) as well as the level set for the learning criterion (≥ 0.750).

Altogether, this shows that the pigeons were basically able to learn to discriminate reliably between projections of a cube and projections of a pyramid. This finding is consistent with the study by COOK & KATZ (1999) which yielded comparable results. Apparently, acquisition of the discrimination was not affected by procedural differences between the two experiments (e.g., the use of different stimulus material). Nevertheless, the birds of the present study seemed to acquire the task slightly less accurately and a little bit more slowly than the subjects in the original experiment, and they needed more trials to reach high levels of performance. Overall, however, the learning progress of the subjects of both studies was similar throughout the first sessions, with an increase in discrimination performance being evident from about the 200th trial onwards (this corresponds to the end of the first cycle in the present study and to the beginning of the third session in COOK & KATZ 1999).

Moreover, it seems that the birds did not noticeably benefit from either mode of presentation (i.e., neither *dynamic* nor *static*), regarding learning speed or accuracy. Figure 7 compares discrimination performances assessed as rho-values for the two different modes of presentation. Discrimination ratios were calculated for each subject in each cycle, with the five sessions of a cycle being pooled. Then, rho-values were averaged across all subjects for each cycle (±SD).

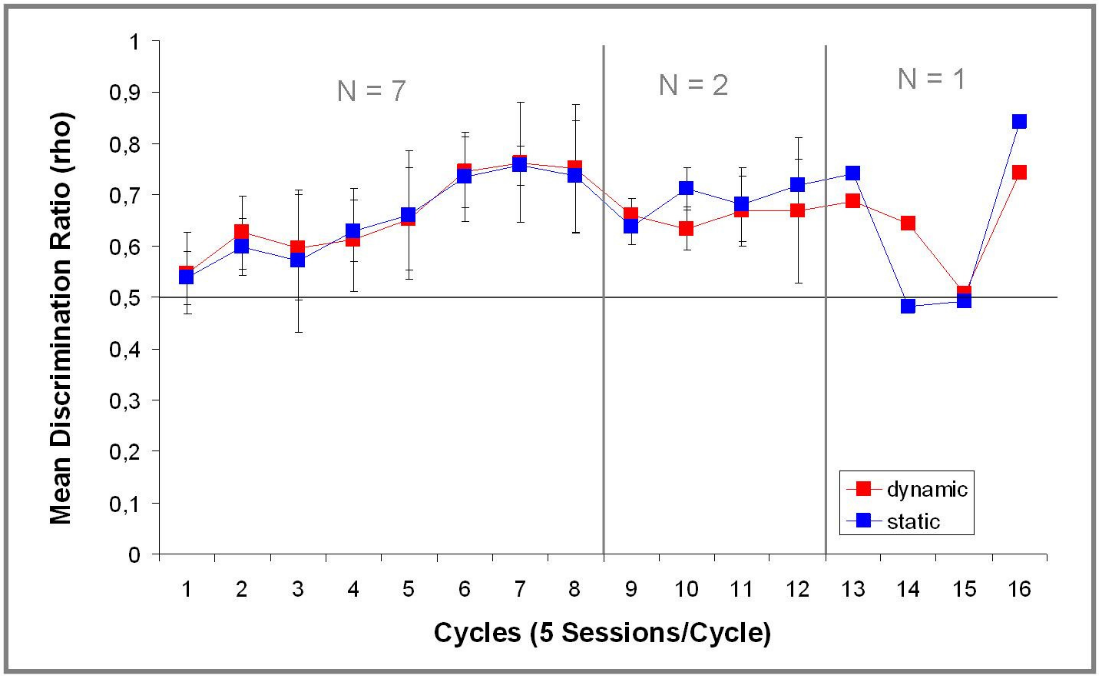

Figure 7. *Learning curves assessed separately for each type of presentation (static and dynamic) as rho-values (± SD). Performance is shown separately for each training cycle, but averaged across subjects. The solid horizontal line indicates the level of chance performance. For the first eight cycles (= first 40 training sessions) assessment of discrimination performance was based on the data of all seven subjects, from the ninth to the twelfth cycle (= 41st to 60th training session) on the data of two subjects, and for the last four cycles (= 61st to 80th training session) on the data of one subject.*

The progression of the curves confirms that the subjects' performance was not influenced by the mode of presentation. Additionally, for each cycle a Wilcoxon's signed-ranks test was carried out which compared rho-values obtained for *dynamic* presentations with the rho-values obtained for *static* presentations. Thereby, rho-values were pooled across birds. Only the first eight cycles entered analysis, since the remaining cycles included only two birds. In neither cycle the test revealed a significant difference between static and dynamic presentation (all *p*-values > 0.05). On the one hand, the use of a new stimulus type (i.e., *dynamic* presentation) did not aversely affect the subjects' willingness to peck, and the birds did not show any signs of neophobia towards the dynamic stimuli (which one may have expected, considering that this was the first time the birds encountered non-static images at all). Thus, the extended experimental history with static stimuli had obviously not biased the results towards a preference for these. But on the other hand, the use of dynamic stimuli failed to enhance discrimination learning, as would have been expected if dynamic change of perspective was indeed an effective cue to facilitate object recognition. The result is therefore consistent with the original study (COOK & KATZ 1999) which also did not find different effects of *dynamic* and *static* presentation on training performance.

Acquisition performance with the two different sizes (*large/small*) was assessed separately, and is summarised on a cycle-by-cycle basis as *rho*-values in Figure 8. Calculations of discrimination ratios were first conducted for each subject individually and then averaged across birds (±SD).

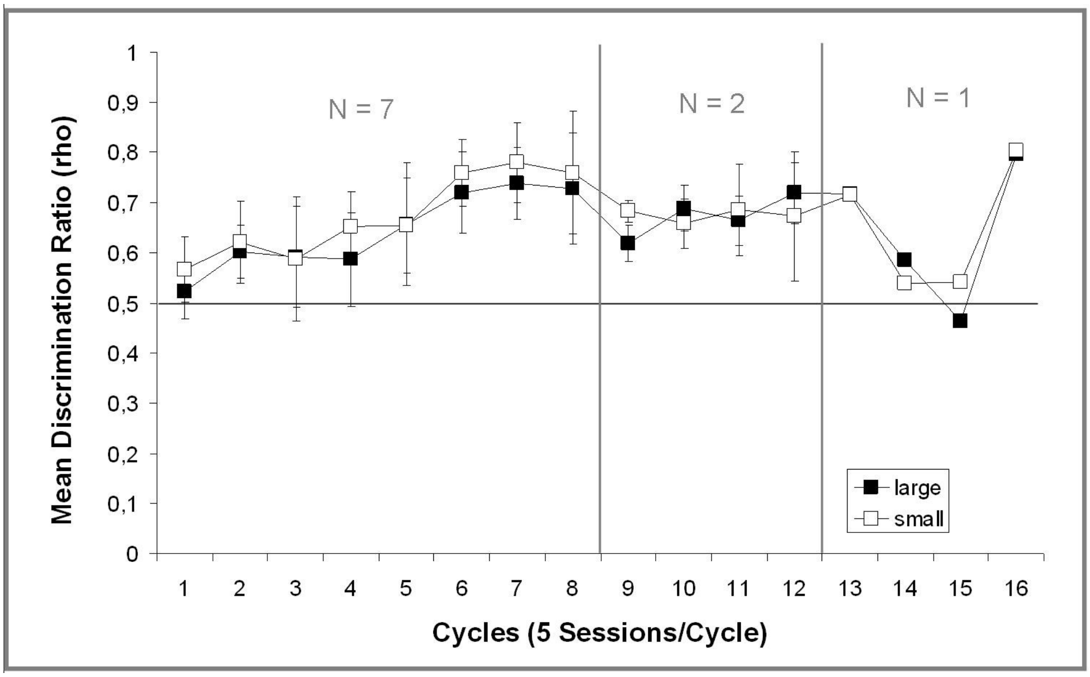

Figure 8. *Learning curves assessed separately for each size (small and large) as rho-values (± SD). Performance is shown separately for each training cycle, but averaged across subjects. The solid horizontal line indicates the level of chance performance. For the first eight cycles (= first 40 training sessions) assessment of discrimination performances was based on the data of all seven subjects, from the ninth to the twelfth cycle (= 41st to 60th training session) on the data of two subjects, and for the last four cycles (= 61st to 80th training session) on the data of one subject.*

At first sight, the progression of the learning curves seems to suggest a slightly better performance with *small*-sized than *large*-sized stimuli. However, Wilcoxon's signed-ranks test comparing for each cycle separately the rho-values obtained for *small* stimuli with the rho-values obtained for *large* stimuli (rho-values were pooled across birds, only the first eight cycles entered analysis) revealed no significant difference (all *p*-values > 0.05). Consequently, the present results indicate *size invariance* across training stimuli. In contrast to this, COOK & KATZ (1999) reported a significant effect of stimulus size throughout the entire training, with discrimination of the larger objects being slightly better than discrimination of the smaller ones. Given the fact that the latter had a volume of only 2 cm^3 in the COOK & KATZ study (compared to 5 cm^3 in the present study), the difference in discrimination performance they found for large and small stimuli might have been the consequence of pigeons' reduced visual acuity for very small stimuli. COOK & KATZ (1999) used stimuli that were considerably smaller than the ones of the current study. Thus, problems with visual acuity, enhanced by poor monitor resolution (640 x 350 pixels), might explain why the pigeons in the original study discriminated less accurately between the small than between the large stimuli. In contrast, the results of the current study suggest that the birds did not have difficulties discriminating the small stimuli. The larger absolute size of the smaller stimuli (as compared to COOK & KATZ) in combination with higher monitor resolution (1024 x 768 pixels) may have been advantageous for accurate recognition of small stimuli.

The pigeons showed reliable discrimination in the end of training, irrespective of the type of stimulus (*dynamic*/*static*, *large*/*small*) they responded to. But what may have been the basic mechanism by which the pigeons learned the task? Attributing the acquisition of the discrimination to the use of a strategy beyond two-dimensional feature detection may be jumping to a conclusion too hastily. It is, of course, possible that the birds indeed used an answering strategy based on the recall of structural object-like descriptions (i.e., 3-D representations) of a pyramid and a cube. But there are other strategies that could just as well have controlled discriminative behaviour, such as memorising the individual training exemplars, i.e., *rote learning,* as assumed by the *exemplar view of categorisation* (see e.g., HUBER et al. 1999). If one considers the relatively small number of training stimuli as well as pigeons' outstanding capacities of picture memorisation, it seems indeed plausible to suggest rote learning as an alternative to the formation of generalised 3-D-representations. Recent examinations of the pigeon's visual memory revealed a tremendous exemplar-specific memory capacity of over 800 single pictures stored in the brain (FAGOT & COOK 2006; COOK et al. 2005). In comparison, the birds of the current study were subjected to a total of only 96 static and 96 dynamic stimuli. It should be considered, however, that the stimulus set used in the studies by COOK and colleagues (2005, 2006) varied substantially in terms of the visual appearance of the stimuli (wide variety of landscapes, objects, and abstract photography), whereas the stimuli used in the current study bore strong overall similarities. Memorising all pyramid and cube pictures individually may therefore have been quite difficult. The pigeons may thus have not learned every single stimulus as a whole, but may have memorised just some specific stimulus parts or simple conspicuous 2-D features of specific individual pictures as encoded in viewer-centred 2-D templates (c.f., SPETCH et al. 2000, 2001). Alternatively, learning may not have been based on individual exemplars (or parts of them) at all, but on the extraction and combination of some category-defining features that were common to all or most instances of one class and distinguished them from instances of the other class. Possible candidates may be the right angles characterising cubes or the acute angle at the top of the pyramids. Such a mechanism would be in keeping with the *feature theory of categorisation* (see e.g., AUST & HUBER 2001, 2002; HUBER & AUST 2006). Finally, the pigeons may have abstracted a summary representation that corresponded to the average, or central, tendency of each class in order to distinguish between pyramids and cubes. Such a strategy would be predicted by the *prototype view of categorisation* (HUBER & LENZ 1996).

Concluding, for reasons of parsimony, it seems to be the most likely explanation that the subjects based their discrimination on the memorisation of particular stimuli (or conspicuous parts of them). Nevertheless, also learning mechanisms beyond mere rote learning might account for the training results. Thus, investigation of generalisation to novel instances of the familiar object classes was essential in order to shed light on the mechanisms that may have controlled pigeons' responding in the training task. For this purpose, a variety of transfer test was carried out.

3.2. Test Phase

To disentangle possible contributions of different mechanisms of object recognition the subjects were confronted with various transformations of the objects. Since object-based approaches account for recognition invariance with regard to changes in size, position, and viewpoint (c.f., KIRKPATRICK 2001), the birds' responses to novel – transformed – exemplars of the object classes might allow for a better understanding of what was represented in the pigeons' brains.

Familiar objects in a new guise – Basic findings from the transfer tests

Performances on the 18 different types of tests were assessed separately, as both mean discrimination ratios (ρ) and mean standardised response rates (MSRR), averaged across subjects. The results are summarised in Table 7, and illustrated in Figures 9, 10, and 12. Each figure combines the results of several tests, grouped according to the types of transformation the stimuli underwent (marked by coloured frames). Performances on the test stimuli were averaged across subjects, and the same was done for the training stimuli.

Overall, discrimination performance was quite inconsistent over tests and subjects. The large inter-individual variations are reflected by substantially high standard deviations that occurred in all tests. Generally, mean test discrimination ratios dropped below training level (see right section of Table 7), with only one test yielding significant discrimination, namely, Test *Randomised*. Regarding mean standardised response rates (MSRRs; see left section of Table 7) it can be noticed that on average the subjects performed worse with the test stimuli than with the training stimuli. More specific, a general decrease in responses to positive test stimuli and an increase in responses to negative test stimuli can be observed.

Table 7. *Overview of the test results shown as mean standardised response rates (left panel) and mean discrimination ratios ρ (right panel), averaged across subjects (± SD).*

	Mean Standardised Response Rate (MSRR)								**Discrimination Ratio *(ρ)***			
Test	**dyn +**		**dyn -**		**stat +**		**stat -**		**dyn**		**stat**	
Newtrain	1.600	±0.52	0.829	±0.61	1.326	±0.65	0.921	±0.74	*0.805*	±0.21	0.686	±0.22
Newsize	1.420	±0.58	0.592	±0.33	1.472	±0.38	0.390	±0.21	0.722	±0.17	*0.796*	±0.16
1Col	1.156	±0.54	0.504	±0.62	0.862	±0.46	0.894	±0.67	0.712	±0.15	0.553	±0.24
1Col_no_cont	1.031	±0.31	0.586	±0.58	1.591	±0.48	0.419	±0.37	0.599	±0.09	*0.806*	±0.10
Newcol	1.570	±0.38	0.673	±0.44	1.293	±0.36	0.336	±0.31	*0.780*	±0.12	*0.807*	±0.13
Colchange	2.018	±1.15	0.309	±0.21	1.122	±0.61	0.590	±0.61	*0.913*	±0.15	0.738	±0.30
View -50	0.938	±0.22	1.099	±0.41	1.704	±0.66	0.985	±0.43	0.476	±0.16	0.645	±0.20
View +50	1.267	±0.41	1.071	±0.52	1.282	±0.52	0.914	±0.64	0.565	±0.19	0.549	±0.15
View 0	1.216	±1.23	0.272	±0.32	0.838	±0.53	0.218	±0.36	0.738	±0.24	0.725	±0.11
View +90	0.498	±0.32	1.300	±0.84	0.652	±0.33	1.210	±0.40	0.280	±0.14	0.361	±0.18
View -90	0.529	±0.33	1.329	±0.59	0.891	±0.46	1.221	±1.11	0.286	±0.18	0.464	±0.17
Rot_x	1.446	±0.36	0.895	±0.40	0.980	±0.50	0.963	±0.50	0.655	±0.13	0.486	±0.11
Rot_yx	1.527	±0.63	0.790	±0.50	1.355	±0.49	1.117	±0.35	0.631	±0.12	0.567	±0.19
1Col_no_cont_x	1.057	±0.58	0.626	±0.54	0.608	±0.32	0.668	±0.35	0.641	±0.17	0.502	±0.11
1Col_no_cont_yx	0.945	±0.60	0.940	±0.91	0.806	±0.54	0.832	±0.69	0.571	±0.33	0.512	±0.19
Newcol_yx	0.935	±0.46	0.623	±0.26	0.927	±0.43	0.395	±0.37	0.667	±0.16	0.671	±0.13
Colchange_yx	1.382	±0.69	0.594	±0.38	0.947	±0.99	0.609	±0.63	0.730	±0.14	0.548	±0.17
Randomised	1.255	±0.28	0.524	±0.36					**0.794**	±0.14		
Training stimuli	1.730	±0.16	0.369	±0.14	1.642	±0.19	0.339	±0.12	**0.836**	±0.06	**0.817**	±0.06

Note. *Response tendencies are indicated by type of font: italic type indicates values approaching levels of significance; bold type highlights values exceeding levels of significance ($\rho \geq 0.813$, except for Tests Colchange and Colchange_yx, $\rho \geq 0.922$, and for Test Randomised, $\rho \geq 0.726$; Training stimuli, $\rho \geq 0.540$)*
dyn+ = MSRR on positive dynamic stimuli, dyn- = MSRR on negative dynamic stimuli, stat+ = MSRR on positive static stimuli, stat- = MSRR on negative static stimuli,
dyn = rho-values of dynamic stimuli, stat = rho-values of static stimuli.

In order to determine whether the use of test stimuli in general had any effect on performance, Wilcoxon's signed ranks tests were carried out. Therefore, all MSRRs emitted to the different test components (except Test *Randomised* since this test only included static presentations) were pooled across subjects and tests and then compared with the MSRRs emitted to the corresponding training components, for positive and negative trials separately. Peck rates for each training component were based on the averaged MSRRs emitted to the training presentations in the respective test. Analyses revealed a highly significant decrease of MSRRs in both dynamic and static positive test trials compared to positive training trials (dynamic: ${}_1n_2 = 119$, $z = -6.457$, $p > 0.0001$; static: ${}_1n_2 = 119$, $z = -6.945$, $p > 0.0001$), and a highly significant increase of MSRR in both dynamic and static negative test trials as compared to negative training trials (dynamic: ${}_1n_2 = 119$, $z = -6.327$, $p > 0.0001$; static: ${}_1n_2 = 119$, $z = -6.229$, $p > 0.0001$), which indicates a significant effect of the introduction of novel stimuli. Obviously, the ability to discriminate was impaired by the introduction of novel stimuli of any kind whatsoever. This may not be entirely due to a general effect of confusion caused by stimulus novelty *per se*, but may also indicate that at least parts of the training stimuli were learned by rote. However, there were a couple of tests that yielded discrimination ratios approaching significance, namely, Tests *Newtrain, Newsize, 1col_no_cont, Newcol,* and *Colchange*. The birds therefore showed at least a tendency to generalise to some of the presented modifications. Consequently, mere memorisation of specific training stimuli on a pixel-by-pixel basis as exclusive learning mechanism can hardly account for these findings. Rather, it seems that learning mechanisms besides mere rote learning of individual stimuli were used in addition.

Another general tendency that is apparent across tests is that the subjects transferred noticeably better to test stimuli comprising objects that were presented in the same orientation relative to the observer as the training stimuli, i.e., *Training Perspective* (TP) tests (see Figure 9), than to stimuli that contained views of objects which deviated from the training stimuli in terms of perspective, i.e., *Modified Perspective* (MP) tests (see Figure 10). In five out of six TP tests, i.e., *Colchange, Newtrain, Newsize, 1col_no_cont*, and *Newcol*, mean discrimination ratios for one or both presentation modes at least approached significance. Only in Test *1col* no such tendency was found. Moreover, with the exception of only one test (*1col*, $\text{MSRR}_{static+} = 0.862$) the averaged MSRRs on positive test stimuli were always > 1 (i.e., above the level of average performance), and MSRRs on negative test stimuli were always < 1 (see left section of Table 7, and lower panel of Figure 9). In contrast to the TP tests, the birds' performance was quite poor in the MP tests, with none of the mean discrimination ratios being even close to significance (see right section of Table 7 and upper panel of Figure 10). Accordingly, the two types of tests differed considerably also with respect to the MSRR obtained for both positive and negative trials (see left section of Table 7 and lower panel of Figure 10). Two additional Wilcoxon's signed-ranks tests confirmed that the birds discriminated differently in *Training Perspective* and *Modified Perspective* tests. One compared the subjects' mean standardised response rates on the averaged positive trials of the TP tests with the averaged positive trials of the MP tests. The other test compared the respective peck rates on negative trials. Thereby, performances with dynamic and static presentation were averaged for analysis. Results of Test *Randomised* were excluded from analyses. The tests revealed significantly higher MSRRs on positive trials of *Training Perspective* tests compared to *Modified Perspective* tests ($_{1}n_{2} = 7$, $z = -2.028$, $p = 0.047$), and significantly lower MSRRs on negative trials of *Training Perspective* tests compared to *Modified Perspective* tests ($_{1}n_{2} = 7$, $z = -2.028$, $p = 0.047$). Figure 11 compares discrimination performances in the *Training Perspective* and *Modified Perspective* tests, with both modes of presentation averaged and means taken across the individual tests and birds (±SD). The results indicate that in particular the shape of the stimuli might have served as a crucial discriminative cue. However, the impaired performance to any kind of stimulus transformation suggests that also manipulation of stimulus properties other than alterations in perspective (and thus shape) appeared to affect conjointly the pigeons' ability to discriminate – although to different extents.

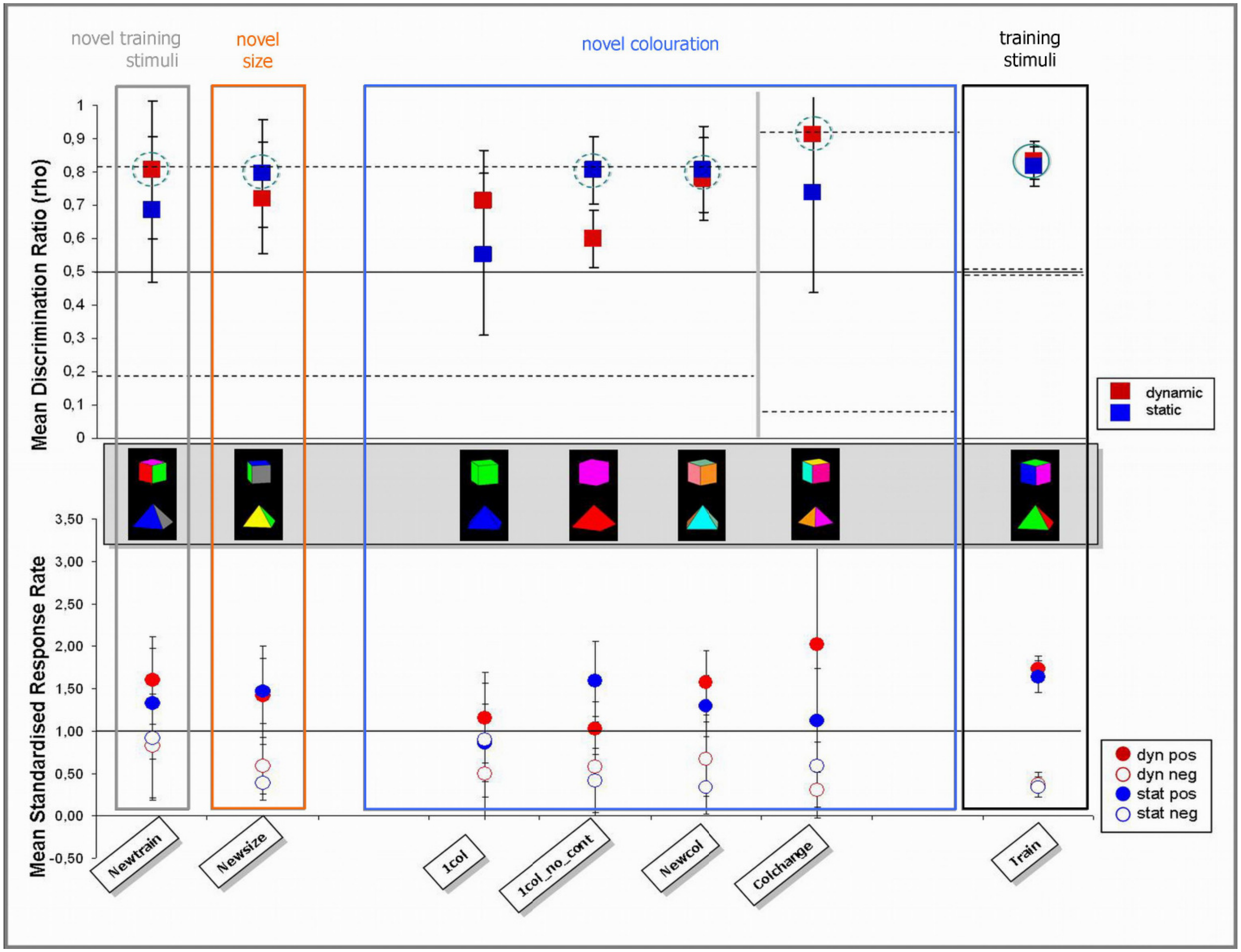

Figure 9.
Results of the Training Perspective (TP) tests. Transfer is shown as mean discrimination ratios ± SD (upper panels), and mean standardised response rates ± SD (lower panels), separately for static and dynamic stimuli, and averaged across birds. Dashed horizontal lines indicate the respective limit of significance, solid horizontal lines indicate average performance, solid turquoise circles around symbols mark significant performances, and dashed turquoise circles around symbols mark performances approaching significance. Particular stimulus transformations are highlighted by coloured frames (light grey = novel training stimuli, orange = novel size, light blue = novel colouration), overall baseline performance on the training stimuli during testing is marked by a black frame.

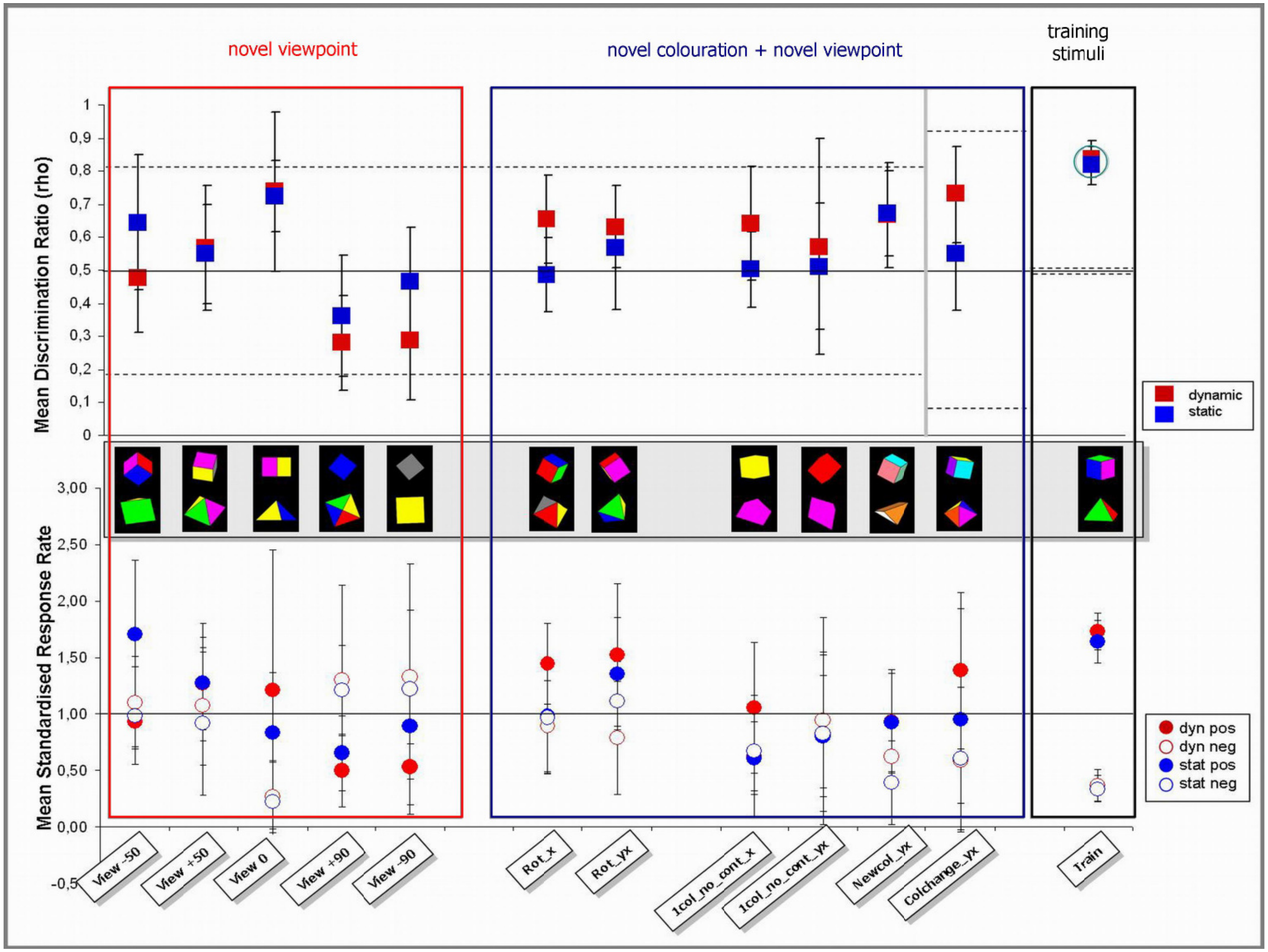

Figure 10.
Results of the Modified Perspective (MP) tests. Transfer is shown as mean discrimination ratios ± SD (upper panels), and mean standardised response rates ± SD (lower panels), separately for static and dynamic stimuli, and averaged across birds. Dashed horizontal lines indicate the respective limit of significance, solid horizontal lines indicate average performance, and solid turquoise circles around symbols mark significant performances. Particular stimulus transformations are highlighted by coloured frames (red = novel viewpoint, dark blue = novel colouration in combination with novel viewpoint), overall baseline performance on the training stimuli during testing is marked by a black frame.

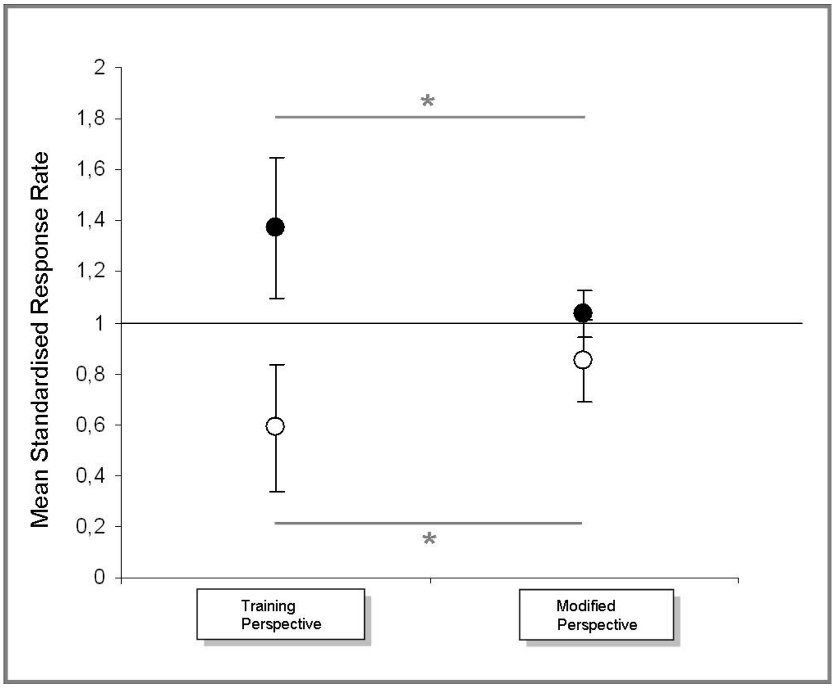

Figure 11. *Comparison between TP and MP tests shown as mean standardised response rates in positive test trials (filled circles) and negative ones (plain circles). Response rates were calculated for each subject individually and then averaged across tests and birds (± SD). The solid horizontal line indicates average performance; an asterisk marks a significant difference.*

The role of particular stimulus properties

To evaluate in detail to what degree the specific types of stimulus transformations (represented by coloured frames in Figures 9 and 10) had controlled responding, a series of additional Wilcoxon's signed-ranks tests was carried out. The results are shown in Table 8. Therefore, MSRRs emitted to each test component showing stimuli that had in common a particular stimulus property that distinguished them from the training stimuli (i.e., new combination of surface colours, novel size, novel viewpoint, novel colouration, and novel colouration in combination with novel viewpoint) were pooled across the respective tests and subjects. Then they were compared with the corresponding training MSRRs in the respective tests. Thereby, performances with dynamic and static presentation were averaged for analysis. Response rates on positive and negative trials were evaluated separately.

Table 8. *Wilcoxon's signed-ranks tests assessing performance with regard to particular stimulus properties.*

	novel training stimuli			novel size			novel viewpoint			novel colouration, y-axis			novel colouration, novel viewpoint		
	Newtrain			Newsize			View -50, View +50, View 0, View +90, View -90, Rot_x, Rot_yx			1col, 1col_no_cont, Newcol, Colchange			1col_no_cont_x, 1col_no_cont_yx, Newcol_yx, Colchange_yx		
	$_1n_2$	z	p	$_1n_2$	z	p	$_1n_2$	z	p	$_1n_2$	z	p	$_1n_2$	z	p
pos	7	-0.676		7	-1.014		49	-5.595	****	28	-2.163	*	28	-4.304	****
neg	7	-2.028	*	7	-2.366	*	49	-5.655	****	28	-0.296		28	-3.211	***

Note. *MSRRs on the test components summarised according to particular stimulus properties were compared with MSRRs on the corresponding training component (performances were pooled across subjects and tests); results are given for positive and negative stimuli separately, pos = positive stimuli, neg = negative stimuli. Significance levels:* * $p \le 0.05$, ** $p \le 0.01$, *** $p \le .0001$, **** $p \le 0.0001$.

For purposes of clarity the results are reported and discussed in detail in the following results sections together with individual results of the transfer tests. Hence, they are summarised according to the type(s) of transformation the test stimuli had been subjected to.

Similar but not familiar – Newly combined surface colours (Novel training stimuli)

Figure 9 (upper panel; marked by a light grey frame) and Table 7 (right panel) indicate a drop in performance in Test *Newtrain* compared with training performance. This is evident from non-significant discrimination performances, and lower MSRRs on positive test stimuli as well as higher MSRRs on negative test stimuli compared to training level (Figure 9, lower panel; and Table 7, left panel). A Wilcoxon's signed ranks test which compared responses on test stimuli with responses on training stimuli (both modes of presentation combined) for positive and negative MSRR separately, showed that this difference was significant for negative trials (Table 8). Summarising, the results revealed that even performance on novel stimuli that matched the training stimuli in all respects except colour combinations was decreased. This strongly suggests that responding was – at least to some degree – controlled by memorisation of the individual training exemplars or specific parts of them. But the fact that some tendency to discriminate correctly was nevertheless present indicated that rote learning as the exclusive mechanism could not account for the results.

Variation of metric properties – Novel stimulus size

Discrimination performance did not reach significant levels in Test *Newsize* (see Table 7, right panel; and Figure 9, upper panel, marked by orange frame). On average, MSRRs on positive test stimuli were below, and MSRRs on negative test stimuli were above training MSRR (Figure 9, lower panel; and Table 7, left panel). Combining both modes of presentation, a significant difference was found between negative MSRRs of the test and training component but no significant difference was found between positive MSRRs (Table 8). Together, these findings indicate that metric object properties were obviously not used as the primary discriminative cue but nevertheless acquired *some* control over the pigeons' responding. In general, size dependence indicates that metric information is stored as part of the representation of the object (e.g., BUNDESEN & LARSEN 1975, LARSEN & BUNDESEN 1978). As a result, recognition is impaired by changes in size. Invariance to size changes, by contrast, indicates that metric information is stored separately from the representation used for recognition (or is not stored at all). Consequently, generalisation of discriminative performance to familiar stimuli presented in a novel size ought to be expected (e.g., COOPER et al. 1992). While size independence favours recognition mechanisms based on structural descriptions as proposed by object-based theories, size dependence rather points to mechanisms based on 2-D templates as proposed by viewer-based theories of object recognition. Studies on the influence of stimulus size on pigeon object recognition have concordantly reported significant generalisation of discriminative performance to familiar stimuli presented in novel sizes, indicating size invariance in this species (e.g., JENKINS et al. 1958; LOMBARDI & DELIUS 1990; TOWE 1954; PISACRETA et al. 1984). Nevertheless, small decrements in accuracy were found as well in these studies, with small sizes obviously causing some drop in performance, which could not be explained by general problems with visual acuity. It is important to note, however, that the stimuli used in these studies either consisted of simple two-dimensional objects (geometrical shapes, or silhouette stimuli) or spots of light. Therefore, it is hard to tell, whether the discrimination of projections of more complex, three-dimensional objects would be supposed to vary in a similar manner with different sizes. Since a change in size does not disrupt the structural description, 3-D objects should be recognisable despite such variations. PEISSIG and her colleagues (2006) addressed this issue by presenting pigeons with shaded static visual stimuli that implied three-dimensionality at least to the human eye. They found systematic performance decrements as a function of increasing deviations of the testing size from the original training size and thus inferred that metric information was stored as part of the object representations. It is, however, not clear, whether the pigeons indeed perceived these stimuli as three-dimensional. Therefore, it might not be justified to draw from this study any conclusions on whether or not the recognition of three-dimensional objects may be invariant over changes in size. COOK and KATZ (1999) reported no significant effect of object size when testing for the pigeons' response to novel sizes and took this as further evidence that the subjects had based their discrimination on a 3-D representation of the objects (c.f., COOK 2001). Similarly, in category or concept discrimination tasks (e.g., AUST et al. 2001; BHATT et al. 1988; HERRNSTEIN & LOVELAND 1964) the size of the transfer stimuli was found to be almost irrelevant for correct classification, except for extremely small targets (see, e.g., AUST & HUBER 2002).

Considering the foregoing, what might then have been the reason for size effects revealed in the present study? As mentioned previously, a perceptual problem of acuity cannot account for them since the pigeons had been subjected to even smaller-sized stimuli in training. (The novel size introduced in Test *Newsize* actually lay between the two sizes of the training objects.) It seems thus that the pigeons had indeed stored metric information as part of the object representations, which then impaired transfer to sizes other than the ones encountered during training. The effect of size transformation found in the current study is thereby in accordance with other studies reporting systematic accuracy decrements when object size was manipulated. However, one should nevertheless keep in mind that the test stimuli featured – besides novel size – new combinations of the surface colours, and might thus have generally been harder to discriminate than training stimuli.

A matter of viewpoint – Novel perspective (novel angles of elevation, novel axes of rotation)

The results of tests examining the influence of novel viewpoints (i.e., modification of the viewer's perspective, and novel axes of rotation) are shown in Figure 10 (marked by red frame). The results of tests examining the effect of the viewer's perspective (i.e., *View_-50, View_+50, View_0, View_+90*, and *View_-90*) clearly suggest that performance varied systematically as a function of the degree of deviation from the training orientations (angle of elevation 15° relative to the transecting horizontal plane). That is, discrimination was most accurate for views closest to the training views (0°), and least accurate for viewpoints farthest away (90°). However, in neither test discrimination was significant. In Tests *View +90°* and *View -90°* (see Figure 10, upper panel, and Table 7, right panel) all rho-values were even < 0.5 (i.e., average performance), thereby indicating "inverse discrimination", which was also reflected by the corresponding MSRRs. Accordingly, Wilcoxon's signed-ranks tests revealed no significant difference between MSRRs derived from negative test trials of Test *View +90* and *View -90* and positive training trials, and the same was found for a comparison between positive test trials and negative training trials, for both modes of presentation. Evidently, in Tests *View_+90* and *-90* the birds "mistook" pyramids for cubes and vice versa (Test *View_+90*: Comparisons of MSRRs on dynamic positive test stimuli with dynamic negative training stimuli, $z = -1.521$ $p = 0.156$, on dynamic negative test stimuli with dynamic positive training stimuli, $z = -1.352$ $p = 0.219$, on static positive test stimuli with static negative training stimuli, $z = -1.521$, $p = 0.156$, and on static negative test stimuli with static positive training stimuli, $z = -1.521$, $p = 0.156$; Test *View -90*: Comparisons of MSRRs on dynamic positive test stimuli with dynamic negative training stimuli, $z = -0.338$, $p = 0.813$, on dynamic negative test stimuli with dynamic positive training stimuli, $z = -0.845$, $p = 0.469$, on static positive test stimuli with static negative training stimuli, $z = -1.690$, $p = 0.091$ and on static negative test stimuli with static positive training stimuli, $z = -0.676$, $p = 0.578$). Figure 10 (upper panels, red frame) and Table 7 also show poor discrimination performance with stimuli comprising novel views of the objects due to the use of untrained axes of rotation. Transfer was evidently weak for both rotation around the x-axis, and the combined rotation around the y- and the x-axis. Dynamic presentation failed to facilitate discrimination with mean discrimination ratios ranging clearly below the limit of significance. Finally, a comparison of the viewpoint-modified test stimuli with the corresponding training components (Table 8) revealed a highly significant decrease on positive test MSRRs, as well as a highly significant increase on negative test MSSRs compared to training MSRRs. Altogether, the results suggest that the birds' ability to discriminate pyramids and cubes was negatively affected by any change in the observer's perspective relative to the object. The present experiment is therefore in line with pigeon studies reporting viewpoint-dependence (e.g., CERELLA 1977, 1990; FRIEDMAN et al. 2005; LOIDOLT et al. 2006; LUMSDEN 1970; SPETCH et al. 2000, 2001, 2003; SPETCH & FRIEDMAN 2003; WASSERMAN et al. 1996). Such viewpoint-dependence can be explained by two theories of object recognition, namely by view-based accounts to visual recognition of three-dimensional objects (c.f., BÜLTHOFF & EDELMAN 1992; POGGIO & EDELMAN 1990; TARR 1995, TARR & PINKER 1990, TARR & BÜLTHOFF 1995, 1998; TARR & KRIEGMAN 2001)[3] and also by 2-D feature- or exemplar-based accounts (c.f., CERELLA 1980, 1986; HUBER et al. 1999; PEARCE 1988). In the former case, the pigeons would have perceived the two-dimensional projections in a more unitary way and encoded them as collections of the 2-D views they encountered during training. If the pigeons had actually used object-like structural descriptions to serve as representational formats, as proposed by object-based theories (e.g., BIEDERMAN 1987; BIEDERMAN & GERHARDSTEIN 1993, 1995; MARR & NISHIHARA 1978), accurate transfer to novel views should have occurred, since

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[3] Assuming such accounts it is, however, not possible to tell from the findings whether recognition might have been based on view normalisation (e.g., TARR 1995, TARR & PINKER 1989), or on a view combination mechanism (e.g., BÜLTHOFF & EDELMAN 1992, EDELMAN 1999) since I did not systematically control for extrapolated versus interpolated views (c.f., SPETCH 2006).

in my judgement, the objects used in the present study met the criteria for allowing viewpoint invariance (i.e., decomposability into geons, arrangement of these geons as a distinct structural description that differs from other arrangements, and no alteration of these structural descriptions by changes in view) stipulated by BIEDERMAN & GERHARDSTEIN (1993). Admittedly, the second and the third criterion might have been violated in views in which the pyramid was hard to distinguish from the cube and/or in which some presumably conspicuous object parts (e.g., the top of the pyramid) were not visible (View +90 and View -90). Viewpoint-dependence occurred, however, with all views, and was not exclusively restricted to those that did not fully meet the criteria. Interestingly, not even training with multiple views of the objects seemed to improve performance on stimuli involving x-axis or yx-axis rotations. This is not in line with the results of other studies which found that experiencing an object from multiple views throughout training enhanced its recognition (PEISSIG et al. 2000b; WASSERMAN et al. 1996), even with views along a novel axis of rotation (PEISSIG et al. 2002). All the more it is surprising that the birds in the present study, which had already experienced a large number of different training views along the y-axis, failed to form stable representations that allowed for generalised recognition along other axes. This together with the finding that the birds also showed impaired transfer to the *Training Perspective* test stimuli (which were actually presented in the same perspective as the training stimuli, and should thus be recognised without any decrease in performance) rather points to the alternative explanation of a feature- or exemplar-based account for object recognition. That is, the pigeons might not have recognised the individual views as depicting a three-dimensional object, but encoded the stimuli either as a collection of discriminative features (CERELLA 1980, 1986; HUBER & LENZ 1993) or memorised all or many instances of them (HUBER et al. 1999; PEARCE 1988). Hence, discrimination could have been based on simple, two-dimensional, diagnostic object properties – the more perceptually "similar" an image appeared to a familiar training stimulus, the stronger would be transfer. In fact, the subjects might have been insensitive to the three-dimensional information that was derivable from the two-dimensional projections. Consider that the stimuli of the present study were relatively easy to distinguish, for instance on the basis of conspicuous contour differences (e.g., a vertex top versus a flat top, roughly triangular shape versus square shape). Therefore, both local and/or global features might indeed have controlled pigeons' responding (see e.g., AUST & HUBER 2001, 2002, 2003; KELLY & COOK 2003; MATSUKAVA et al. 2004; KIRKPATRICK-STEGER & WASSERMAN 1996; WATANABE 2001). It is possible, for example, that properties like the number of coloured pixels in a specific stimulus area provided salient cues for discrimination. It has been shown that pigeons are indeed highly sensitive to the specific appearance of individual pixels or pixel blocks (AUST & HUBER 2001). Regarding the current study, it should be noted that the two classes of training stimuli (cubes and pyramids) differed in the ratio of coloured (object) to black (background) pixels within a single frame. More precisely, the number of coloured pixels varied among different stimulus areas. In training, the upper part of pyramid frames always featured a relatively small amount of coloured pixels compared to the upper part of cube frames. The ratio of chromatic versus achromatic pixels in the upper part of a training image was thus generally lower in pyramids than in cubes. In some types of test stimuli, however, this was no longer the case. This could account for the drops in performance on stimuli involving changes in perspective and may even explain the puzzling results of *Tests +90*, and *-90*, where the birds seemed to "mistake" pyramids for cubes and vice versa. In these tests – as opposed to training – the number of coloured pixels was lower in the upper part of cubes than in the upper part of pyramids. As a consequence, a cube as presented in *Tests +90*, and *-90* might have been perceptually more similar to the training pyramids than to the training cubes, and vice versa for the pyramids presented on test. Additional investigation would thus be needed to test this hypothesis, e.g., by examining whether inverting the training stimuli would impair discrimination performance.

Does colour matter? – Novel surface colouration

Mean discrimination performances and MSRRs in tests involving modifications in terms of surface colouration, but no modification in terms of viewpoint, i.e., Tests *1col, 1col_no_cont, Newcol,* and *Colchange,* are illustrated in

Figure 9 (marked by light blue frame). Performances in tests involving modifications in terms of surface colouration combined with modifications in terms of perspective, i.e., *1color_no_cont_x, 1color_no_cont_yx, Newcol_yx, Colchange_yx,* are illustrated in Figure 10 (marked by dark blue frame). As can be seen, three tests – *1col_no_cont, Newcol,* and *Colchange* – yielded quite good although non-significant discrimination of transfer stimuli, with performance at least approaching significance for one of the two modes of presentation (see also Table 7, right panel). In general, performance on colour-modified stimuli was worse when they were additionally presented from novel viewpoints than when they differed from training stimuli only with respect to surface colouration. Accordingly, Wilcoxon's signed ranks tests revealed a highly significant difference of response rates compared with the training stimuli in case of colour plus viewpoint transformations, but in case of colour transformations without viewpoint manipulations a significant difference was only found in positive trials (Table 8). The results suggest that the introduction of modified or novel surface colours *per se* may have had a minor impact on discrimination performance compared to the effects of altered perspective. Overall, it seems that successful discrimination was mainly based on cues other than colour (otherwise the tendency to respond correctly to this kind of colour-modified stimuli should not have been found). More precisely, recognition was not exclusively controlled by specific internal surface features like colour or internal contours. Instead, poor transfer in some of the tests comprising colour transformations was presumably based on viewpoint rather than on colour dependence.

In summary, the results indicated that the pigeons were able to use two-dimensional shape information as a basis of responding (while colour information was also important, but not crucial). Work on pigeon object recognition has consistently shown that pigeons can recognise objects from silhouettes alone, but negative results were mainly obtained for transfer from shaded images to line drawings of the objects (e.g., CABE 1976; DELIUS 1992; LUMSDEN 1977, PEISSIG et al. 2005; YOUNG et al. 2001). This suggests that pigeons may not be able to extract internal edges or contours of a shaded object in order to assess its general shape. Although I did not explicitly test for transfer to line drawings, comparatively good transfer in Test *1col_no_cont* indicates that successful discrimination was not crucially dependent on the presence of internal contour lines. (The fact that performance in this test nonetheless missed significance demands caution, however.) Overall, the results suggest that the subjects encoded and used for discrimination the two-dimensional shape or distinctive parts of the shape of the two-dimensional projections. This is largely consistent with a recent result reported by GIBSON and his colleagues (2007) who found that pigeons based their recognition of an object on so-called *coterminations* (i.e., corners) instead of relying on other features such as colour and shading. At first sight, the preference for shape information relative to surface cues found in this study appears to be in contradiction to studies reporting that pigeons were sensitive to surface features, such as colour or brightness, but seemed to widely neglect shape information (e.g., KIRSCH et al. 2008; LAZAREVA et al. 2005; WILKIE & MASSON 1976). These studies showed conclusively that, when both types of cues – shape and colour – are provided in a task, pigeons tend to use colour as the primary cue to guide their decisions. In the present task, however, the wide variety of different surface colour combinations occurring in the training stimuli may have made it difficult for the pigeons to remember them all. This may have devalued colour features as “good” cues (i.e., cues that substantially facilitate stimulus recognition), whereas shape features provided a quite reliable basis for classification. Furthermore, the two classes (cubes and pyramids) were not perfectly separable by means of colour information. That is, colour alone would not have been sufficient for reliably predicting class membership and the subjects were thus forced to use (also) other features, such as shape information, in order to correctly classify the objects.

Neither test including monochromatic stimuli revealed an advantage of dynamic over static presentation. In particular, it is worth mentioning that the mean discrimination ratio on static trials in Test *1col_no_cont* clearly exceeded the mean level of performance on dynamic trials ($\rho_{stat} = 0.81 \pm 0.1$; $\rho_{dyn} = 0.59 \pm 0.09$); a Wilcoxon’s signed-ranks test revealed that this difference was even significant ($z = -2.371$, $p = 0.016$). Hence, it seems that dynamic monochromatic stimuli did not contain any additional information relevant for discrimination that was not present in the static images. To the human observer, however, the addition of apparent motion inevitably led to a strong impression of three-dimensionality. Provided that also pigeons are able to extract stimulus structure from motion-based information, dynamic presentation should enhance perception of a three-dimensional object. The results of the present experiment, though, did not support the notion of a facilitating effect of dynamic presentation on the recognition of monochromatic displays. This contrasts sharply with the findings of COOK & KATZ (1999), who reported significantly better transfer with dynamic monochromatic stimuli than with static monochromatic stimuli.

Screwing up the order – Incoherence of the rotation sequence (modification of the sequence of images)

Figure 12 illustrates mean performance in Test *Randomised* compared to performance with dynamic training stimuli (see also Table 7, right panel). Evidently, the pigeons were able to significantly discriminate randomised sequences of training stimuli. Wilcoxon's signed-ranks tests revealed no significant differences between the test and the corresponding training component (positive MSRR, $z = -1.183$, $p = 0.297$, negative MSRR, $z = -0.676$, $p = 0.578$).

Provided that the subjects perceived all successive views of an object within a coherent sequence as if representing one stable three-dimensional object, and provided that the discrimination was facilitated by the extraction of 3-D information from dynamic presentation, scrambling should have severely disrupted the structural description. As a consequence, incoherent presentation should have negatively affected performance. However, this was not the case. Discrimination of scrambled sequences was not significantly worse than discrimination of the training stimuli shown in coherent apparent motion. The result of Test *Randomised* thereby completes evidence that the pigeons did not represent the projections of the objects as three-dimensional structural descriptions. Rather, the results are compatible with the assumption that the pigeons relied on two-dimensional information. Since such cues were still present in scrambled sequences, recognition should not have been impaired by frame randomisation. This finding is in line with studies that failed to provide evidence for an advantage of coherent presentation (COOK et al 2003, Exp. 4; FRIEDMAN et al. 2009, Exp. 1B; LOIDOLT et al. 2006; ROVINA 2006), and in contrast with studies reporting a *coherence superiority effect* (COOK et al. 2001; COOK & ROBERTS 2007; FRIEDMAN et al. 2009, Exp. 2; KOBAN & COOK 2009). In considering what might account for the contrasting results, it is important to note that researchers used a wide range of different stimuli in their studies. For examining the role of frame randomisation in dynamic displays, stimulus quality may indeed play a critical role, with object recognition possibly being controlled by specific stimulus-based properties. It might make a difference whether (1) the object's "motion" is unique (i.e., if the characteristic trajectory of an object can be used in order to distinguish it from other objects, randomising a sequence is suggested to have a negative effect on the ability to discriminate), (2) whether the subjects have already had experience with scrambled versions of the stimuli (e.g., the sudden experience of in-coherent presentation might elicit a neophobic reaction), (3) whether object-unique invariant features are available in all displays irrespective of the order of the frames (i.e., scrambling would not cause a loss of information required for recognition), and finally (4) which video-format is used for presentation (compressed algorithms such as AVI- or MPEG-formats are producing visual displays quite different from uncompressed ones, see METHODS). Considering that, the similar findings in my study and in LOIDOLT et al. (2006) and ROVINA (2006) might be based on procedural similarities. These studies have at least two aspects in common which set them apart from studies that reported a facilitating effect of coherent "motion" (COOK et al. 2001; COOK & ROBERTS 2007; FRIEDMAN et al. 2009, Exp. 2; KOBAN & COOK 2009). *First*, invariant discriminative features were at all times available in the displays, irrespective of the order in which the images were presented. *Second*, the trajectories of the objects were insufficient and thus not crucial for properly distinguishing among them, since both objects were rotated around the same axis in the same way. *Third*, the use of different video formats may account for the different outcomes. It has been suggested that pigeons may be more sensitive than humans to unintended deformations of the displays caused by video compression, such as AVI compression. LOIDOLT and her colleagues (2006), and also ROVINA (2006) could demonstrate that recognition in pigeons was severely impaired by AVI presentation in comparison to uncompressed video formats. As AVI formats are not presented on a picture-by-picture basis, the process of combining single frames into a movie sequence might add additional spurious discriminative cues caused by the compression algorithm. This means that randomised sequences shown in compressed formats may carry additional visual cues that are not available in properly ordered sequences, although both sequences are composed of the same single images. As a consequence, a pigeon might judge the two types of presentation differently.

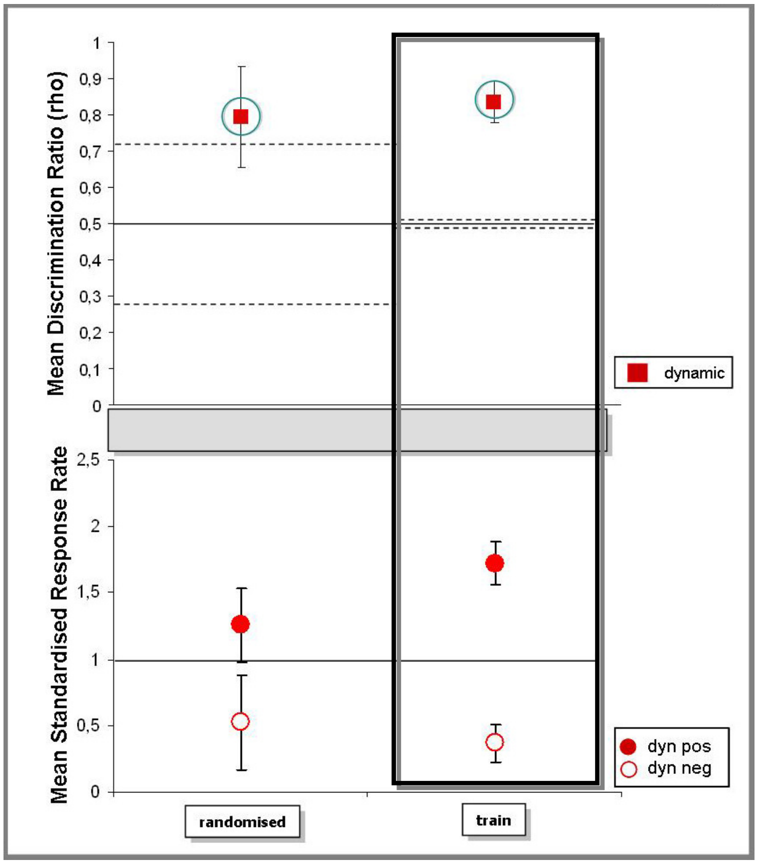

Figure 12. *Test Randomised.*
Transfer is shown as mean discrimination ratios ± SD (upper panels), and mean standardised response rates ± SD (lower panels), averaged across birds. Dashed horizontal lines indicate the limit of significance; solid horizontal lines indicate average performance, solid turquoise circles around symbols mark significant performance. Overall baseline performance on the training stimuli during testing is marked by a black frame.

Does dynamic presentation help? – Dynamic versus static stimuli

To examine potential effects of the mode of presentation (*dynamic/static*) on test performance two Wilcoxon's signed-ranks tests were carried out. They compared MSSRs across tests and subjects obtained for the averaged dynamic test stimuli with those obtained for the averaged static test stimuli. Results of Test *Randomised* were excluded from analyses. Analysis revealed no significant differences between static and dynamic presentation, neither for the positive test stimuli ($_1n_2 = 7$, $z = -1.014$, $p = 0.375$) nor for the negative test stimuli ($_1n_2 = 7$, $z = -0.338$, $p = 0.813$). This is illustrated in Figure 13, which shows mean standardised response rates averaged across tests and birds (± SD).

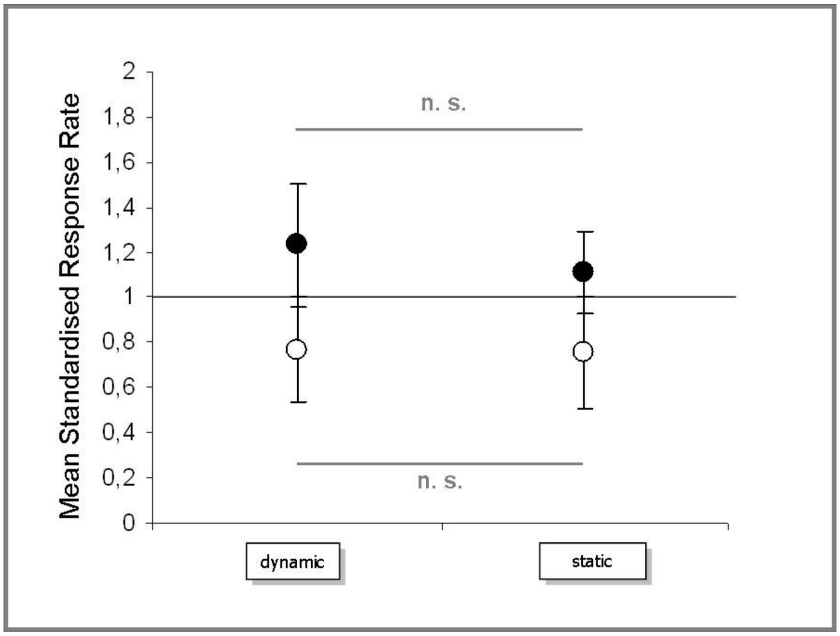

Figure 13. *Mean performance during static versus dynamic presentation of test stimuli, shown as mean standardised response rates, separately for positive (filled circles) and negative test trials (plain circles), and averaged across tests and birds (± SD). The solid line indicates average performance, n. s. = "not significant"*

The present results therefore failed to support the hypothesis that dynamic change of perspective enhances object recognition in the pigeon (*dynamic superiority effect;* c.f., COOK & KATZ 1999). Actually, the pigeons could not benefit from dynamic presentation, when they had to transfer to novel versions of the training objects. This suggests that dynamic information whatsoever provided by the apparent movement was basically redundant, and not essential for object recognition. Hence, the current study is rather in line with JITSUMORI & MAKINO (2004), LOIDOLT et al (2006) and ROVINA (2006), who consistently found that dynamic presentation of rotating human faces did not facilitate discrimination compared to the presentation of static views of a face. JITSUMORI & MAKINO (2004) suggested that the birds did not benefit from the additional structural information provided by dynamic presentation. The authors concluded that the pigeons did not form a three-dimensional structural representation of each face, but instead relied on multiple 2-D features as cues by which to discriminate the stimuli. As discussed previously, it might be possible that the birds did not perceive the apparent motion provided in the dynamic displays as real motion, but rather perceived the displays as collections of single images instead, without any impression of movement. Thus, the pigeons might have based their discrimination on classification of the individual views within a sequence instead of integrating the single views into one coherently rotating object. Indeed, it has been shown that pigeons are able to classify geometric stimuli when flashed very briefly (KRAMER, unpublished). Perfect discrimination could be reported for presentation times of 100 ms, which suggests that stimulus classification might even be possible with times below that. In the current study the single frames of a sequence were shown at a rate of 30 frames per second. It is therefore possible that the pigeons had problems with view integration and rather experienced the displays as collection of individual pictures, or in a “stroboscopic” manner (see JITSUMORI et al. 1999, for discussion). Nevertheless, one can’t directly infer from this that the pigeons did not notice the dynamic cues available in the displays. It might be possible that the birds in the current study could *perceive* the dynamic cues, but failed to *use* them as facilitators of object recognition. Obviously, they neither made use of the 3-D structure provided by dynamic presentation (or they were not able to recover it), nor did they profit from additional views. Presumably, it was simply not necessary in this specific discrimination task to use such information, since discrimination was also possible by means of static, two-dimensional, object-distinguishing cues alone.

4. GENERAL DISCUSSION

Imagine a pigeon observing a rotating pyramid displayed on a computer screen. Would the bird perceive it in the same manner as a human observer? That is, would the pigeon experience its shape as three-dimensional or rather parse the display into a collection of simple two-dimensional features? And, besides that, would the object be recognised by the pigeon despite changes in size, colour, or perspective? And most importantly, what may the coherent presentation of views in rapid succession contribute to recognition?

In the current thesis I tried to address these challenging issues against the background of different theories of object recognition. My experiment was based on a study by COOK & KATZ (1999) regarding the experimental design – however, used more advanced technical equipment. Interestingly, the results deviated from those of the original study. *First* the subjects of the present study did not show object constancy across different types of object transformations (e.g., novel size, altered surface colouration, new axis of rotation). *Second*, my results failed to show any advantage of dynamic over static presentation (i.e., *dynamic superiority effect*). *Third*, randomisation of dynamic sequences (Test *Randomised*) revealed that properly ordered presentation of successive views of dynamic stimuli was not critical for discrimination. In summary, the results do not support the hypothesis that the pigeons recognised and discriminated the object projections by means of generalised three-dimensional representations. They are more in line with the assumption that the birds discriminated them by means of viewpoint-dependent recognition mechanisms (c.f., CERELLA 1977; FRIEDMAN et al. 2005; JITSUMORI & MAKINO 2004; LOIDOLT et al. 2006; ROVINA 2006; SPETCH & FRIEDMAN 2006), and rather used two-dimensional cues instead. The findings of the current study may thus be best accounted for by feature theory or by tolerant versions of the exemplar view (see HUBER & AUST 2006).

Thereby, the pigeons might not have recognised the individual views as depicting a three-dimensional object, but rather encoded the stimuli either as a collection of discriminative features (as suggested by feature-based accounts, c.f., CERELLA 1980, 1986; HUBER & LENZ 1993) or memorised all or many instances of them (as suggested by exemplar-based accounts; c.f., HUBER et al. 1999; PEARCE 1988). Hence, discrimination could have been based on detection of simple, two-dimensional, diagnostic features or broad similarity judgements. The more perceptually "similar" an image appeared to a familiar training stimulus, the stronger would be transfer. Support in favour of such an exemplar-based account was mainly provided by the general lack of good transfer to all test stimuli irrespective of the type of transformation and, in particular, poor transfer to stimuli that were the same as the training stimuli with respect to shape, but displayed different combinations of surface colouration. However, the finding that the pigeons showed at least some tendency to generalise to stimuli with novel colouration and size provides support for feature-based accounts and rather speaks against mere memorisation of specific training stimuli on a pixel-by-pixel basis. If indeed particular features were used as discriminative cues – what stimulus aspects in particular might have acquired control over the pigeons' responding? Impaired performance to any kind of stimulus transformation suggests that the pigeons relied on a collection of discriminative features, such as represented by a "polymorphous feature rule" c.f., AUST & HUBER 2002; HUBER & LENZ 1993; HUBER et al. 2000; HUBER 2001; LEA & HARRISON 1978; VON FERSEN & LEA 1990). Thereby, some features seemed to be more relevant for object recognition than others. Evidently, information about two-dimensional object *shape* was used as discriminative cue in the first place. *Size* and *colouration* also contributed to discrimination, though to a much lesser extent. One should keep in mind, however, that the training stimuli comprised various combinations of surface colours and that the training stimuli were presented in two different sizes. Consequently, neither size nor colour as such would have been sufficient for reliably discriminating the stimuli. Whether discrimination was based on the recognition of particular elemental features (such as a vertex top versus a flat top), or rather on the use of global shape or contour properties (such as a roughly triangular form versus square form), the present study cannot tell (nor was it designed to answer such specific questions). A possibility to investigate what type of shape information controlled the birds' responding would be to test them with fragmented stimuli, generated by scrambling the individual views (see, AUST & HUBER 2001, 2003; CERELLA 1980; KIRKPATRICK-STEGER & WASSERMAN 1996; KIRKPATRICK-STEGER et al. 1996, 1998). Thereby the overall spatial arrangement of shape properties would get distorted. Another way that could also help to pinpoint the functional features that pigeons use to make the discrimination would be isolation of particular local features by means of covering the objects with a mask that reveals only a portion of the underlying stimuli through openings (e.g., "*Bubbles* procedure", GOSSELIN & SCHYNS 2001; see also GIBSON et al. 2005, 2007, NIELSON & RAINER 2007).

Further support for the assumption that discrimination was based on 2-D properties of the objects was provided by the fact that dynamic presentation failed to facilitate the pigeons' ability to recognise the projections. This was obvious from the training as well as from the test phase. If the subjects had based their discrimination on object-like representations, they should have benefited from dynamic change of perspective. But even with monochromatic displays, the current study failed to reveal any advantage of dynamic as compared to static presentation. Other than humans, in whom the addition of apparent motion to the monochromatic displays inevitably led to a strong impression of three-dimensionality and thereby enhanced the ability to identify the objects, the pigeons were apparently not able to extract such information.

Presumably the strongest evidence that the birds did not perceive the projections as depicting stable three-dimensional objects was provided by the findings of Test *Randomised.* The results failed to reveal any *coherence superiority effect* (CSE), i.e., a facilitating effect of coherent as compared to non-coherent presentation of a sequence. Since frame randomisation had widely destroyed the objects' three-dimensional structure available in coherent sequences, significant transfer to non-coherent sequences suggests that the birds did not integrate the single views of a sequence into a unified, three-dimensional structural object representation.

In summary, the current findings – discrimination dependence across all stimulus transformations and no advantage of coherent dynamic stimulus presentation for discrimination – are in sharp contrast to results of the original study by COOK & KATZ (1999). But what might have caused these substantial differences?

First, regarding the question of invariance across various stimulus transformations including novel viewpoints, it has to be considered that all transfer tests in the current experiment were non-reinforced, and therefore did not provide any feedback about the presented stimulus. However, this was not true for the transfer tests in the original study by COOK & KATZ (1999). Since they used a partial reinforcement schedule for particular test sessions, effects of reinforcement might have influenced the formation of object representations. Moreover, novel views were subsequently integrated into the training sets (e.g., novel x-axis rotation). The additional information provided by reinforcement may well have extended the variety of stored perspectives, and may thereby have facilitated subsequent transfer to novel views. Furthermore, different experimental histories of the birds participating in the two studies may have led to differences in the type(s) of information the subjects relied on. Two aspects could thereby have played a role. On the one hand the pigeons' pre-experience with two-dimensional pictorial stimuli acquired in previous experiments might have influenced responding. On the other hand experience with three-dimensional objects in real life might have facilitated recognition of the objects when presented in novel views. There is indeed some indication that familiarisation with real three-dimensional objects may enhance viewpoint invariance of their 2-D images (WATANABE 1997, 1999, 2000). Similar discrimination-enhancing effects have also been reported for the discrimination of stimuli of pictures of familiar versus unfamiliar conspecifics in hens (BRADSHAW & DAWKINS 1993), and recently in pigeons (WILKINSON et al., under review), and also in the context of landscape discriminations (WILKIE et al. 1989).

Second, the differences concerning the contribution of apparent motion to discrimination might be explained by several factors: Above all, the quality of the visual input the pigeons received differed in the two studies. Video formats and technical equipment, in particular the computer screens, were not the same. Also, it is very likely that the two studies differed as regards the appearance of the dynamic stimuli. While I presented uncompressed bitmap images in rapid succession, dynamic sequences in the COOK & KATZ study were rendered directly during their presentation. This might have severely affected the visual appearance of the dynamic displays (at least for the pigeon eye), and could thus have contributed to the observed differences in responding. Additionally, the use of CRT monitors used in the COOK & KATZ study (i.e., NEC Multisync 2A monitors) versus TFT monitors used in the current experiment (i.e., Videoseven L15C-TCO99 monitors) could have caused differences in the quality of the dynamic stimuli. Although, interestingly, no difference was found in a study comparing pigeons' discrimination performances with CRT and TFT monitors (ROVINA 2006), the human literature consistently shows that in sequences with rapid movements the subjective quality of a sequence displayed on a TFT is generally lower than the subjective quality of the same sequence displayed on a CRT (see e.g., TOURANCHEAU et al. 2007). As a consequence, the effect of motion blur caused by the TFT monitor might have decreased, e.g., the pigeons' ability to recover structure from the dynamic displays in the current study.

Finally, the subjects in the two studies may indeed have perceived and encoded the objects differently. While transfer may have been based on generalised object-like 3-D representations (indicated by discrimination invariance, enhanced by dynamic presentation) in COOK & KATZ (1999), discrimination in the present experiment may have been controlled by two-dimensional properties (indicated by discrimination dependence, with no additional value of dynamic presentation). But if so, one should ask why the birds in the two experiments based their responding on different learning mechanisms. The question may be answered as follows. It is possible, although not very likely, that the greater variety of stimuli used in COOK & KATZ's study supported the generation of structure-based rather than feature-based object representations. (They used two rates of rotation instead of just one, and, due to the simultaneous rendering process, a higher number of object samples than the present experiment.) Namely, the large number of different stimuli may have impeded the use of exemplar-based learning mechanisms such as learning individual stimuli by rote or extracting item-specific invariant local or global features. The pigeons in the study by COOK and KATZ might thus have been virtually "forced" to rely on structural properties rather than on two-dimensional cues since the latter were insufficient for discrimination. Hypothetically, it is also possible that the birds in the original study indeed had different prior experiences with real life objects similar to the projections of a cube and a pyramid than the subjects in the present study. (However, in this regard the authors do not provide further information). As discussed above, exposure to real objects has been suggested to affect a pigeon's behaviour towards their pictorial equivalents. Possible differences in the degree of pre-experience in the two studies might therefore have biased the formation of object representation. Further examination of the role of pre-exposure to real objects in a controlled set-up would thus be required to rule out this possibility.

In view of the conflicting results obtained in the present study and the original experiment by COOK & KATZ (1999) on the one hand, and consistent outcomes obtained in studies carried out in our lab on the other hand (i.e., viewpoint dependence and no advantage of dynamic presentation for object recognition, LOIDOLT et al. 2006, ROVINA 2006), further inspection seems warranted. Could the experimental conditions provided by different laboratory environments have influenced the pigeons' responding to a larger extent than could be compensated for by the use of similar methodology? And could, in turn, the same laboratory environment have biased the results of different studies in the same direction? This possibility must indeed be considered. While not all the technical equipment used in the present study was the same as the one used in previous studies that were conducted in our laboratory (e.g., different computer monitors), many other parameters were nearly or entirely identical. They concerned stimulus presentation (e.g., dynamic presentation mode, spatial resolution of the monitors), laboratory conditions (e.g., pigeons' housing, skinner boxes), and details of the experimental procedures (e.g., reinforcement schedules).

Finally, let me return to the scenario brought up at the beginning of this section. What does a bird actually see in an object presented on a screen? As nicely put forward by LEA (2006), "*Humans, including human experimenters, 'see' (…) logical relations within stimuli that are not necessarily 'there' for other species*" (p. 254). In other words, the answer to this question demands caution, and without doubt, appropriateness of 2-D stimuli for examining three-dimensional object recognition in the pigeon needs reconsideration. Although the stimuli used in the present study “appeared” three-dimensional (at least to the human observer) they were actually strongly impoverished 2-D versions of the real 3-D-objects they depicted. Forming object-like structural descriptions thus required the subjects to interpret the 2-D projections as if representing (or being) 3-D objects. Humans with their extensive experience in interpreting pictorial stimuli would most probably be able to do so spontaneously and effortlessly. But this may not be true for pigeons, which might be completely insensitive to the 3-D information provided in the 2-D displays. Given that the presence of monocular depth cues (e.g., shading, perspective, relative density, relative size, and occlusion) in a 2-D picture may support three-dimensional perception of an object (CAVOTO & COOK 2006; DELIUS 1992; REID & SPETCH 1998; SPETCH et al. 1998), the outcome of my study should be interpreted with caution. As the stimuli used in the present experiment provided neither perspective nor shading cues the subjects may not have been able to encode the 3-D structure of the objects. Comparing discrimination performance on projections devoid of pictorial depth cues with that on projections comprising such cues may be a challenge for future research.

The question, however, remains unanswered whether the outcome of a study using 2-D projections may indeed allow for conclusions regarding the general ability of a pigeon to perceive objects as 3-D units. There are various kinds of cues that are present in real objects but absent from their two-dimensional projections, and it is unknown to which extent they are used by a pigeon. Pigeons may, for example, be well able to perceive three-dimensional shapes in their natural environment, but may fail to derive them from two-dimensional displays. There is in fact evidence that pigeons perform faster and better with novel views of a real object than with photographs of the very same views (FRIEDMAN et al. 2003, 2005). The non-realistic nature of computer-generated pictures may thereby contribute to the pigeons’ failure to perceive a two-dimensionally presented object as three-dimensional. As computer monitors are adapted to the demands of human but not pigeon vision, factors such as colour mode, picture resolution, and the lack of UV emission or temporal frequencies of a computer screen might account for impaired performance in an object discrimination task. Generally, it should be borne in mind that the outcome of an experiment must always be examined with regard to the stimuli used in the task. Furthermore, the difficulty of the discrimination task as experienced by the pigeons might also influence the results (see LOIDOLT et al. 2006, for related discussion). To put it in the context of the current study, there might have been no particular need for a pigeon to acquire a complex structural description of a pyramid in order to distinguish it from a cube. Instead, it may have been sufficient to base discrimination on two-dimensional object features. In order to pinpoint more precisely whether a pigeon has the general capability of forming a three-dimensional representation of an object, it would be necessary, first, to create stimuli that better represent real three-dimensional objects (e.g., by including monocular depth cues), and, second, to reduce availability of discriminative features other than three-dimensional cues. For example, one may use stimuli that consist of the same local units, but differ with regard to their configural arrangement, as were, e.g., employed in a mental rotation experiment by SHEPARD & METZLER (1971). As advice for future research aimed at further elucidating the nature of object representations used by the pigeon, I would thus recommend the choice of more "appropriate" stimuli than those used in the COOK & KATZ study and in the present experiment.

In the end, it should be emphasised that, of course, the validity of the results and conclusions of the COOK and KATZ (1999) study should by no means be depreciated on the basis of the present study. Although their interpretations in terms of three-dimensional object representations may have been premature in the light of the methodological problems discussed earlier, and despite the fact that a cognitively simpler (and thus more preferable) account may actually be one in terms of two-dimensional cue detection, the possibility that their pigeons indeed used structure-based object descriptions cannot be ruled out.

Concluding, the "take-home-message" to receive from my thesis is that it should always be borne in mind that even two studies examining the same issue in almost identical set-ups may nevertheless yield diverging results and thus may lead to deviating conclusions, due to slight differences in experimental design and methodology.

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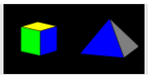
APPENDIX

The following part gives a detailed description of the properties of the individual types of test stimuli and the way in which they were generated. For reasons of clarity the single descriptions are grouped according to the main aspect(s) in which they differed from the training stimuli, and are generally divided into *Training Perspective* tests and *Modified Perspective* tests.

TRAINING PERSPECTIVE TESTS

Novel combination of surface colours – novel training stimuli

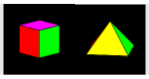
Newtrain (see Figure 5.1)



Angle of elevation (15°) and axis of rotation (y-axis) were the same as for the training stimuli. However, each projection featured a novel combination of the six colours used for the training stimuli (yellow, red, purple, blue, green and grey). As with the training stimuli, black contour lines were applied to the object's edges.

Novel size

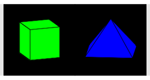
Newsize (see Figure 5.2)



The stimuli comprised projections of novel size and thus volume. Their size lay between the two training sizes, with their volume being approximately 5.8 cm³. This corresponds to a side length of 1.8 cm for the cube, and 3.1 cm for the pyramid, derived from dimensions on screen. With respect to rotation axis (y-axis), contour lines, and observer viewpoint they were the same as the training stimuli. The object's surfaces featured novel combinations of the six colours assigned to the training stimuli.

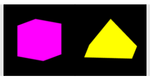
Novel colouration

1col (see Figure 5.3)



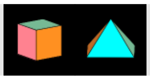
Regarding rotation axis (y), contour lines, and observer viewpoint the stimuli were the same as the ones used in training. However, only one of the six training colours was assigned to each object's surfaces. By making all surfaces the same colour, all surface cues were eliminated.

1col_no_cont (see Figure 5.4)



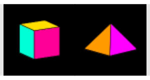
Regarding rotation axis (y) and observer viewpoint the stimuli were the same as the ones used in training. The test stimuli were, like in Test *1col*, monochromatic and thus devoid of surface cues. But other than in the previous test, also the contour lines were removed from the object’s edges.

Newcol (see Figure 5.5)



The test stimuli were the same as the training stimuli, however, novel colours were assigned to the object’s surfaces. Six novel colours were introduced, namely orange (RGB 255, 144, 33), white (RGB 255, 255, 255), turquoise (RGB 0, 255, 255), brown (RGB 187, 105, 39), pink (RGB 255, 130, 144), and olive (RGB 118, 185, 148). The colours were arbitrarily assigned to the object’s surfaces and appeared equally often throughout the test. Observer viewpoint and axis of rotation were the same as for the training stimuli.

Colchange (see Figure 5.6)

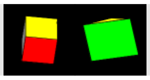


The test stimuli were the same as the training stimuli, except for the fact that the colour presentation mode was altered. Surface colours were the same as used in training (yellow, red, purple, blue, green and grey). However, the originally assigned colours continuously changed within a rotation sequence by smoothly transforming into another colour. Thereby, the object’s surfaces featured a successive change from one surface colour (i.e., the “initial colour”) to the next colour (i.e., the “target colour”) by presenting decreasing proportions of the initial colour and continuously increasing proportions of the target colour over time (e.g., purple changed continuously into yellow, from yellow into blue, from blue into green, from green into grey, and from grey into red). At the beginning of a trial, each object sample featured another combination of initial colours. The process of transforming one colour into the next target colour required 20 single frames, since every rotation sequence showed a complete transformation cycle that included all six surface colours. Observer viewpoint and axis of rotation were the same as for the training stimuli.

MODIFIED PERSPECTIVE TESTS

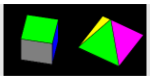
Novel viewpoint – observer’s perspective

View -50 (see Figure 5.7)



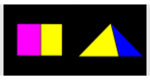
The axis of rotation was the same as for the training stimuli. Contour lines as well as new combinations of the six different colours used for the training stimuli were applied to the projections. The observer’s viewpoint was changed from 15° (training stimuli) to -50° relative to the object’s transecting horizontal plane. Hence, the viewer had the impression to look from a slanted position below the object up to its bottom.

View +50 (see Figure 5.8)



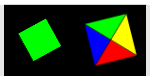
All specifications were the same as for the *View -50*-stimuli. Only the observer’s angle of elevation was changed to +50° relative to the object’s transecting horizontal plane. Therefore, the viewer's impression was to look from a steep position above the object down onto its top.

View 0 (see Figure 5.9)



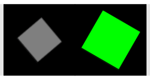
The axis of rotation and the application of contour lines were the same as for the training stimuli, but the viewing angle was 0° relative to the object’s transecting horizontal plane. Hence, the viewer's impression was to look from a frontal position directly onto the object. To the human eye, the impression of three-dimensionality was thereby remarkably diminished or got even lost, especially during static presentation. New combinations of the six different colours used for the training stimuli were applied to the projections.

View +90 (see Figure 5.10)



As with the training stimuli, the axis of rotation was the y-axis, and contour lines were applied to the edges. The surfaces featured new combinations of the six training colours. These stimuli, however, comprised projections that were “recorded” by the virtual camera of the graphics program from a perpendicular position, i.e. +90° relative to the object’s transecting horizontal plane. The viewer's impression was to look directly from above down on the object's top. To the human eye, the impression of three-dimensionality got lost, for both static and dynamic presentation. The stimuli appeared as square-shaped objects (a monochromatically coloured smaller square in case of the cube and a larger square divided into four differently coloured triangles in case of the pyramid). Furthermore, the dynamic projections appeared to rotate counter-clockwise in the plane of the screen.

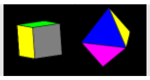
View -90 (see Figure 5.11)



The axis of rotation, surface colours, and contour lines were the same as for the training stimuli. The viewpoint's angle of elevation was -90° relative to the object’s transecting horizontal plane. Hence, the viewer's impression was to look directly from below up to the object's bottom. As was the case with the V*iew +90*-stimuli, to the human eye, the impression of three-dimensionality got lost and the stimuli appeared as square-shaped objects (both projections were monochromatically coloured, and the projection of the cube was somewhat smaller than that of the pyramid). The dynamic stimuli appeared to rotate clockwise in the plane of the screen.

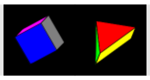
Novel viewpoint – novel axes of rotation

Rot_x (see Figure 5.12)



In terms of their features the test stimuli were the same as the training stimuli, i.e., the surfaces showed the same colours (though in new combinations), and contour lines were applied to the object’s edges. Also the observer viewpoint was the same as for the training stimuli. However, the axis of rotation was changed. Namely, the test stimuli comprised projections of an object rotating around its horizontal axis, i.e., the x-axis. To the human eye, the object appeared to rotate in a bottom-up motion, first toward, and than away from the observer (see Figure 2). The orientation from which the object started to rotate was arbitrarily chosen along the horizontal axis.

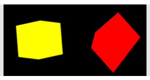
Rot_yx (see Figure 5.13)



The stimuli rotated simultaneously around both the y- and the x-axis (see Figure 2). To the viewer's eye, the object appeared to rotate in a tumbling manner. The object’s surfaces featured different combinations of the six colours used for the training stimuli. Contour lines were applied to the edges. The observer viewpoint was the same as for the training stimuli.

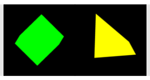
Novel colouration

1color_no_cont_x (see Figure 5.14)



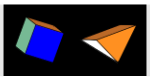
As in the Test *Rot_x*, the object rotated around the x-axis. However, surface cues as well as contour cues were eliminated, that is, all surfaces and edges of an object featured only one of the colours used for the training stimuli. To the human eye, the impression of three-dimensionality was remarkably diminished for static presentation. In fact, static stimuli rather appeared to be planar two-dimensional objects, whereas the addition of apparent motion in dynamic presentation led to a strong impression of three-dimensionality. The observer viewpoint was the same as for the training stimuli.

1color_no_cont_yx (see Figure 5.15)



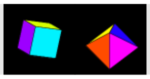
As with the stimuli of Test *Rot_yx* the axes of rotation were the y- as well as the x-axis. The object’s surfaces and their edges featured only one of the six colours used for training stimuli. Thus, surface cues as well as contour cues were eliminated. As was the case also with the *1color_no_cont_x*-stimuli, to the human eye, the impression of three-dimensionality was remarkably diminished for static presentation. However, dynamic stimuli evoked a strong impression of three-dimensionality. The observer viewpoint was the same as for the training stimuli.

Newcol_yx (see Figure 5.16)



Stimulus modifications were the same as in Test *Newcol*, but the object rotated simultaneously around both the y- and x-axis. Each projection featured a novel combination of the six novel colours (i.e., orange, white, turquoise, brown, pink, and olive), and the observer viewpoint was the same as for the training stimuli.

Colchange_yx (see Figure 5.17)



The mode of colouration was the same as in Test *Colchange*, but the stimuli were rotated around the y- and x-axis simultaneously. The observer viewpoint was the same as for the training stimuli.

INCOHERENT ROTATION SEQUENCE

Randomised

The test stimuli were arbitrarily selected from the training set and presented only dynamically. Thereby, the single images of a rendered coherent rotation sequence were randomly put into a new order so that they eventually formed a novel – incoherent – sequence of views. To the human eye, the continuity of the rotation was thereby disrupted. This is, the impression of a smoothly moving object was lost. Instead, the object seemed to strongly jiggle and to move in an erratic way. (It should be kept in mind, however, that the birds had already experienced during training the images that constituted these sequences, although in consistent order.)

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Publications

Poster Presentation	Kramer J., Aust U., Steurer M., Huber L. (2007) "Perception of rotating objects by pigeons" European Conference on Visual Perception (ECVP), Arezzo, Italy
Published Abstract	Kramer J., Aust U., Steurer M., Huber L. (2007) "Perception of rotating objects by pigeons" *Perception* **36** ECVP Abstract Supplement