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UNIVERSITY OF ALBERTA

# AVIAN PATTERN AND OBJECT PERCEPTION

BY

DEBBIE M. KELLY ©

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

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# ABSTRACT

Humans and birds recognize objects and scenes readily, so one tends to believe that their perceptual mechanisms must be similar. This thesis shows that there are substantial species differences in the architecture of the perceptual systems, differences that were studied using three main approaches. At the initial level, elemental processing of simple patterns was examined. These experiments revealed that pigeons encode simple patterns in terms of local properties. Humans, on the other hand, did not show local level processing but rather showed global level processing. This type of elemental encoding, used by the pigeons, would not seem to provide the flexibility needed to recognize dynamic objects in a naturalistic environment. Thus, the second approach used to understand avian perception examined how pigeons use complex information from entire scenes. Using this approach, we found that pigeons were not simply encoding the elemental properties of the images, but were rather using contextual information. The complex scenic images presented may have provided the pigeons with several cues (e.g., depth cues or multiple views) which were not available in earlier investigations using more simple stimuli. Therefore, the in the third approach, we examined the influence of motion in pattern and object recognition. Motion, either on the part of the observer or the object, may provide important discriminative cues that are not available when an object is viewed statically. In these investigations we found that pigeons encode both the featural and geometric properties of their environment, and that the geometric properties are encoded as relational metrics. To examine the influence of object-motion, owl predatory behavior was examined. It was shown that owls rely not only on the presence or absence of motion but also on the quality of the motion. Each approach to examining pattern and

object perception is necessary to understanding how birds recognize objects within their environment. The experimental evidence provided by each of these approaches provides a new and better understanding of avian visual perception.

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# CHAPTER 1

# INTRODUCTION

# Introduction

Recognition of objects within the environment is one of the most fundamental behavioral requirements for most bird species. For example, birds must be able to recognize animate objects (such as their chicks, mates or potential predators) as well as inanimate objects (such as their nest sites, inanimate food items or environmental landmarks). Birds manipulate objects within their environment quite skillfully, suggesting that they perceive and recognize objects. However, empirical studies examining the processes and mechanisms involved in object perception and recognition have not clearly demonstrated that birds do indeed see environmental objects as structured wholes. Several approaches have been administered to examine how birds perceive objects. These approaches begin with an understanding how birds encode simple patterns. At this initial level, one can easily manipulate the stimulus properties to examine how stimulus changes influence bird behavior. The understanding of avian pattern perception provides a foundation for understanding simple and complex object perception. Objects can be examined in isolation or within a visually rich context. Investigations of object perception have examined how birds perceive and recognize natural and artificial objects using several different methods of presentation. Furthermore, research has shown that birds may use different visual information depending upon the task requirements.

## Local and Global Processing

Although birds behave as if they perceive an object-filled world, many investigators have argued that birds, in particular pigeons, represent objects at a local level only. In an attempt to further understand how important individual elements are to recognition of objects, many researchers have systematically examined how pigeons encode two dimensional (2-D) properties of an object. For example, Cerella (1980) trained pigeons to respond to pictures of the Peanuts cartoon character Charlie Brown, and to withhold responding to any other character of the comic series. Charlie Brown was easily distinguished from other characters in the cartoon series. When the character's bodies were altered such that the body parts were no longer in biological order (eg., biological order = head-torso-legs, non-biological order = torso-head-legs), the pigeons were still able to distinguish the scrambled Charlie Brown from the other scrambled characters. These results indicate that pigeons process and encode individual elements; the image is not encoded as a drawing of a 3-D person (i.e., Charlie Brown is not seen as a line drawing depicting a young boy).

Further support for local level processing was shown by Kirkpatrick-Steger, Wasserman and Biederman (1996) in their examination of the importance of spatial arrangement of an objects' elements (or geons). Pigeons were trained to discriminate between line drawings of 4 objects (sailboat, watering can, lamp and an iron). Following training, the individual elements of each object were systematically scrambled horizontally and/or vertically. For example, the mast of the sailboat might have been moved so that it was below the keel. The researchers found that, even though the spatial arrangement of the elements had been radically modified, the pigeons were still able to successfully categorize the four scrambled objects. The results of this study and Cerella

(1980) show that pigeons were not encoding the general structure of the objects but rather the individual elements that comprised the objects.

The results reported in these investigations are quite surprising. Humans perceive objects as unified wholes; and it is difficult to imagine an elemental world the pigeons seem to perceive. Several unresolved issues remain from studies such as the above. For example, it is unclear if the pigeons were actually viewing the images as representations of 3-dimensional (3-D) objects or whether they were seeing a pattern of unstructured lines. If the latter was true, then the results are less surprising, but as indicated by Kirkpatrick (2001) it is difficult to imagine how a flighted organism would function so adequately with only elemental level processing.

A closer examination of Kirkpatrick-Steger et al. (1996) reveals support for not only local level processing, but also global processing. Although the pigeons correctly categorized the scrambled objects, the pigeons did not show complete insensitivity to the spatial arrangement of the individual elements: accuracy in categorizing the scrambled objects was significantly lower than for the configured objects. If pigeons were insensitive to the structural properties of an object then scrambling the object's components should not affect discrimination performance. This indicates that while the pigeons were encoding the elemental properties of the objects, and used this information to correctly categorize the scrambled objects, they were still sensitive to the spatial arrangement or the global properties of the objects.

The study of avian texture perception, by Cook and colleagues, has further shown that pigeons, similar to humans, are able to encode visual information on a global level.

The texture displays used consisted of hundreds of individual elements arranged in a matrix of rows and columns. The displays contained a target region and a distractor region. The target region consisted of a smaller array of elements which differ from the surrounding distractor elements along some dimension (see Cook, 2000 for examples). Pigeons were shown to discriminate between the target region and the distractor region with high accuracy. Learning this task required that the pigeons group together the similar elements that form the target area, and perceive the target area as different from the surrounding distractor area. This perceptual grouping of the target elements and distractor elements must be done on a global level. Cook and colleagues have demonstrated that pigeons are able to use color, shape and orientation to group elements into a global structure (Cook, 1992b; 2000; Cook, Cavoto & Cavoto, 1996; Cook, Katz & Cavoto, 1997; Cook, Katz & Kelly, 1999).

Several investigations of texture discrimination conducted by Cook and colleagues have shown similar processing by pigeons and humans. Specifically, both humans and pigeons can readily locate a target area that differs from the distractor along a common dimension (i.e., shape, color or orientation). However, when a dimensionally mixed or conjunctive search was required, both pigeons and humans showed a dramatic performance decrement. An example of a conjunctive display would be a target area consisting of blue circles and red triangles surrounded by a distractor region comprised of blue triangles and red circles. The difference in performance between the unidimensional texture displays and the conjunctive displays show that the pigeons were grouping the common elements together in order to locate the target area.

In summary pigeons are sensitive to both the local and global properties of an object. However, what is not completely understood is why in some instances pigeons encode objects on a local level, whereas in other situations they process the global structure. In an attempt to understand this divergent behavior, researchers have used stimuli with a hierarchical structure. Hierarchical stimuli are constructed from a set of small elements, the spatial organization of the elements form a larger shape. For example, several small letter "O's" can be organized such that their spatial arrangement resembles a capital letter "L". Humans have been shown to process the global information (the larger L) at a much faster rate than the local level components (the smaller O's). However, pigeons show the opposite effect. The pioneering study by Fremouw, Herbranson and Shimp (1998) showed, through the use of priming procedures, that pigeons can shift their attention between local and global level processing.

Several researchers have suggested that many visual discrimination tasks, as in the studies mentioned above, produce a bias for elemental encoding of stimulus properties. Pigeons are known to have two foveal areas, a more frontally located fovea, thought to be important for close range manipulation, such as pecking, and a laterally located fovea thought to be important for long range perception, such as would be needed for predator detection. It has been suggested that the frontal foveal system may be more important for perception of detail, and thus local level processing would dominate. The lateral foveal system, on the other hand, may be used for tasks that require large-scale discriminations, and thus global level processing would be needed. Covoto and Cook (2001) suggest that presenting the stimuli on lateral displays may predispose a global level processing.

However, several other factors including the visual angle of the stimuli may also produce a bias for local-level processing.

## Object and Scene Perception

Birds have been shown to use both local and global level encoding during pattern discrimination. It has been suggested (e.g., Cook,1992b; 2000; Cook, et al., 1996a; 1996b;1997; 1999) that since pigeons can use contours and surfaces to segregate target and distractor regions (e.g., during texture displays) they should be capable of using this information for object perception. Object perception and recognition require that the viewer segregate between different objects , as well as to separate objects form background information. Therefore, results showing that birds are capable of using contours and textures for pattern segregation suggest that birds may be able to use these global level cues in object perception and discrimination.

Investigations into avian object recognition have shown that birds are able to discriminate between different objects (e.g., Cabe, 1976; Shimizu, 1998; Spetch, Friedman & Reid, 2001; Watanabe, 1993; 1997; 1999; Watanabe & Ito, 1991; Watanabe, Yamashita & Wakita, 1993). Many of these studies have trained pigeons to respond to an object that is associated with food and to withhold responding to a different object. The mere learning of this task demonstrates that birds are able to discriminate between the presented objects. However, it is not clear from these studies how the birds were representing the information. Given that the stimuli were presented as 2-D images, the birds could simply have encoded the stimuli as 2-D visual patterns and not as representations of 3-D objects.

Many theoretical frameworks have been proposed to explain how objects are represented by humans. Such theories may be categorized into object-centered theories [e.g., recognition-by-components theory (RBC); Biederman, 1987] and viewer-centered theories (e.g., the multiple-views theory of Tarr & Pinker, 1989; Tarr, Williams, Hayward & Gauthier, 1988). Both the object-centered and the viewer-centered theories state that in order for an object to be recognized the viewer must possess a mental representation that is compared to the actual viewed object. However, the two frameworks deviate in their predictions of what object qualities are preserved in the stored mental representation. One of the main differences in the predictions of the two theories is that the RBC theory hypothesizes that objects are represented viewpoint invariant, whereas the multiple-views theory suggest that views are represented from the original viewpoint in which the object was seen. Although several theories, other than the two mentioned above, have been proposed to explain how objects might be represented by humans, the aforementioned theories have been directly adopted to investigate avian object recognition.

Investigations have been undertaken to determine if pigeons recognize objects according to the predictions of the object-centered or the viewer-centered theories. Although these theories make seemingly contradictory predictions, support for both theories have been reported within a single investigation. Peissig, Young, Wasserman and Biederman (2000) trained pigeons to respond to a single particular view of a geon. Although pigeons responded at levels above chance when tested with novel rotations of the training geons, a significant and systematic rotational decrement was found for rotations moving away from the trained viewpoint. The finding that pigeons are able to generalize to novel views of the training geon support an object-centered theory. However, the systematic decrement in responding as the object was rotated away from the training image supports the viewer-centered hypothesis. Thus, in order to achieve complete generalization the pigeons would need training with multiple views of each geon in order to store different representations. Peissig et al. (2000) suggest that perhaps the pigeon visual system makes use of both the object-centered (discrimination between objects) and the viewer-centered (recognition of same object from differing viewpoints) principles for object recognition.

Very rarely do birds need to recognize an object defined by a single geon. Rather, birds must recognize and respond to objects that are comprised of several distinct geons. Using an object discrimination task Spetch, Friedman and Reid (2001) further investigated the role of viewpoint in object recognition. They found that pigeons showed a systematic decrement in performance as the object was rotated away from the training view, independent of the number of distinctive parts and regardless of whether it was within or outside of the training orientations. Therefore, this study as well as the study by Peissig et al. (2000) strongly indicate that, when viewing 2-D objects, pigeons use a type of generalized similarity rule and do not have viewpoint- invariant object recognition.

It seems improbable that under natural situations a bird is incapable of generalizing from one view of an object to another. Such an inflexible recognition system would seem ill prepared to recognize important objects such as predators, a nest site or perhaps a mate under less than optimal situations. So why have so many studies failed to find viewpoint invariant object recognition in birds? Perhaps the difficulty in finding transfer or generalization is not a limitation of the species under investigation but rather is due to the nature of the stimuli presented.

In an attempt to make visual stimuli more biologically relevant, investigators have examined cognitive and perceptual processes through the use of complex images. Complex images have allowed them to examine object perception not only through studies of geometric object recognition but have involved studies of object categorization, conspecific recognition and landmark use (Delius, 1992; Delius, Emmerton, Hörster, Jäger & Ostheim, 1999; Edwards & Honig, 1987; Herrnstein & Loveland, 1964; Honig & Stewart, 1988; Huber, 1999; Spetch, Kelly & Lechelt, 1998; Spetch, Kelly & Reid, 1999; Watanabe, 1993; Watanabe, 1997; Watanabe, 1999; Watanabe & Ito, 1991).

Investigations of object perception using complex pictorial stimuli may be grouped according to three main experimental approaches and are described in detail below. One approach examines if a learned response is transferred to novel exemplars. The classic study by Herrnstein and Loveland (1964) is an example of such an approach. The researchers trained pigeons to peck at pictures that contained a human and to withhold responding to pictures that did not contain the presence of a human. After completion of discrimination training the pigeons were shown novel pictures, both with humans present and absent. The pigeons showed differential responding to the new images with accuracy levels similar to training images. Given the pigeons' ability to generalize to novel images, Herrnstein and Loveland concluded that pigeons are able to categorize images based on the presence or absence of a human.

A second approach used to examine if birds encode a 2-D object in a similar manner as the actual 3-D object is to train with one medium and test with another. Several investigations have used this approach. For example, Delius (1992) presented pigeons with several 3-D objects differing in shape. The pigeons were reinforced for pecking only the spherical objects and not reinforced for pecking at non-spherical objects. When the pigeons were presented with photographs of spherical and non-spherical objects the pigeons directed the majority of their pecks at the photographs depicting spherical objects. Thus, it would seem that pigeons were able to encode the pictures as representative of the actual object and transferred the training with the real objects to accurately discriminate among pictures of the objects.

Finally, studies of scene recognition have also examined if birds can transfer between 2-D and 3-D media. Using this approach some researchers have reported limited transfer (Cole & Honig, 1994; Kendrick, 1992; Wilkie, Willson & Kardel, 1989). Several studies examining transfer of responding from one medium to another have not adequately controlled for the possibility that the subjects were using a common 2-D element (e.g., color) during both media presentations. Spetch, Kelly and Lechelt (1998) developed a unique method for examining if pigeons use 3-D cues in pictorial stimuli. This third approach for examining avian object perception was based on Spetch's earlier examinations of landmark learning in pigeons (Spetch, Cheng & MacDonald,1986; Spetch, Cheng, MacDonald, Linkenhoker, Kelly & Doerkson,1997; Spetch & Mondloch,1993). Spetch et al. (1998) presented pigeons with several digital images of a complex scene. The pigeons were required to locate and peck at a small target area within the images. Once the pigeons had learned the position of the target area for the training images, they were presented with images depicting novel orientations of the same scene. If the pigeons had encoded the target's position using 3-D coordinates they would be able to use this coordinate system to easily locate the target's position in the novel images. On the other hand, if the pigeons had simply memorized the 2-D location of the target in the training images they would not show accurate transfer to the novel images. This type of task is a more direct method for measuring transfer than previous approaches, because it requires the subject to make a response based not simply on general recognition but the specific relationship between the target position and one or several landmarks.

Although the presentation of complex images has furthered our understanding of the underlying cognitive processes, many questions remain as to exactly what aspects of the pictorial information are being used and how the objects within the images are perceived by birds. For example, what type of information is crucial to allow for transfer between media? Is the type of task an important factor? Will some bird species show transfer and others not? One suggestion that has received a great deal of attention is the potential importance of motion for encoding for avian object perception. For example, when a bird normally locomotes through its natural environment, its movement allows it to see objects from many different viewpoints.

## Dynamic Object Perception

Motion plays an important role in perception. Theories of object perception suggest that motion provides information that is not available when either the observer or the scene is static (Gibson, 1979). In human research, the role of motion and its relation to object perception has been examined for many years. It has been argued that motion cues and static cues are very different and are processed in different ways (e.g., Gibson, 1979). Motion-based visual cues may be obtained from either object-motion, viewer-motion or a combination of both.

Object-motion. Movement is an important component of the avian world. Birds need to be able to detect and quickly respond to dynamic properties of their environment (e.g., perching on a wind blown branch, avoiding a stalking predator, or engaging in mating displays). It is quite difficult to examine how birds perceive and react to dynamic visual stimuli in their natural environment and researchers have thus relied on the use of video technology to present birds with moving images [but see Burford, McGregor & Oliveira (2000) for field studies using video playback for examining communication in fiddler crabs, *Uca tangeri*]. Video technology allows for systematic and detailed manipulation of motion properties and behavioral cues that might co-occur with motion in a natural environment. Behavioral responses to video images have been assessed to examine object discrimination, recognition of video image conspecifics and whether biologically appropriate responses are directed to video images.

To investigate how pigeons use video-based motion cues to aid in the discrimination of two different objects Cook and Katz (1999) presented two different geometric shapes (triangle and cube) either in static form or a dynamic form (rotating around either the x, y and/or z-axis). The pigeons showed strong discrimination invariance even when the stimuli were altered according to rate of movement, direction of movement (although initially poor discrimination on the x-axis) and changes in surface color. The results of this investigation suggest that the pigeons were encoding the geometric shapes as 3-D objects since a 2-D form of encoding would not allow for the recognition of the objects throughout the numerous 2-D transformations. The series of experiments by Cook and Katz provide evidence that pigeons are capable of using dynamic video presentations in the discrimination of geometric stimuli. This study allows one to compare static and dynamic object recognition. The results support the importance of dynamic presentations in object discrimination by birds. However, similar to studies using static geons or elements it is not clear from this study if birds recognize simple geometric shapes, either static or dynamic, in the same way they recognize more complex naturalistic objects (e.g., other birds). Thus, a second general approach used for examining avian object recognition is to present video images to the birds and see if they react to the video images in a similar manner as the real object.

Studies of avian communication [Evans, Macedonia & Marler, 1993 and Evans & Marler, 1991; (chickens, *Gallus gallus domesticus*)] and social learning [McQuoid & Galef Jr., 1993 (Burmese junglefowl, *Gallus gallus spadiceus*); Watanabe, Yamashita & Wakita, 1993 (Bengalese Finch, *Lonchura striata domestica*)] have used dynamic video displays to better understand the stimulus properties that underlie avian object recognition. In a series of investigations into the effects of alarm calling by roosters (*Gallus domesticus*), Evans and colleagues found that when video images of aerial predators were presented to male roosters, the roosters emitted an alarm call similar to what has been reported under natural circumstances (Karakashian, Gyger & Marler, 1988). Thus, the results of the study suggest that video images supplied the roosters with enough visual information to emit an alarm call similar to that seen in natural situations. Interestingly, the predominate cues controlling the emitting of an alarm call was the size and speed of the raptor stimulus. Further, the researchers found that when the audience, for which the alarm call was emitted, was replaced with video image chickens the roosters continued to emit alarm calls.

Galliformes are not the only bird order to show biologically appropriate behavior to video images. Male pigeons have been shown to engage courtship behavior (i.e., tail dragging, bowing and vocalizations) for a similar duration when presented with either a video of a female pigeon or a live female pigeon (Shimizu, 1998). Further analysis of the stimulus properties involved in the onset of courtship behavior showed the head region of the female to be more important than the body region. Further, when presented with video images of cockatoo (*Cacatua galerita*) the duration of time male pigeons spent in courtship behavior decreased.

One might be tempted to conclude, based on the evidence provided above, that video images are adequate substitutions for real objects when studying avian object recognition. Unfortunately, not all investigations using video images have had such positive results. Studies of social recognition have shown that female domestic fowl will not only begin feeding near familiar hens more quickly than non-familiar hens, they are also able to discriminate hens based on rank. However, when hens were presented with video images of conspecifics no such discrimination was evident (D'eath & Dawkins, 1996). Likewise, pigeons engage in elaborate courtship displays (e.g., bowing, cooing and dragging tail feathers by males in response to females) when in the presence of pigeons of the opposite sex. However, when pigeons were presented with life-size moving video images of other pigeons none of the observer pigeons engaged in courtship behavior (Ryan & Lea, 1994).

Why is the evidence so unclear? Based on a categorization of the studies to date a trend can be seen. Tasks that may be solved according to gross motion discrimination or general shape information (e.g., an aerial predator or another chicken; "basic categorization", Logothetis, Pauls & Poggio, 1994) have shown that video images are adequate stimuli to elicit naturalistic behavior. However, if the task requires that the bird encode more specific information about the stimuli (e.g., individual pigeons or chickens; "subordinate categorization", Logothetis, et al., 1994), transfer between the two media is more unlikely. Thus, it would appear that investigations of object recognition using dynamic video images have been unable to address the many questions left unanswered from static video images. In particular, how are birds representing pictorial images? Using static pictorial stimuli it appears that birds may not be encoding the global properties of the images but rather attending to elements within the images. The selective use of elemental properties of pictorial representations has not been ruled out by using dynamic images. With moving stimuli birds may selectively attend to motion cues (e.g., speed or type of motion). While motion may be an important part of the natural discrimination process it is still not known whether natural motion and artificial motion are encoded as similar.

Observer-motion. Dynamic video images, although providing stimulus motion, do not incorporate motion on the part of the observer or allow for observer-stimulus interaction. Dawkins and Woodington (2000) have shown that chickens' ability to recognize objects is reduced when their normal or preferred path of object inspection is altered. Video images do not allow animals to choose how they approach objects. Such rigidity or lack of interaction may make the video images appear artificial and thus alter the viewer's behavior toward the image. Investigators are beginning to address the importance of observer-stimulus interaction by attempting to incorporate interactive playback into studies using video images (McGregor, 2000).

Another approach used to examine the role of observer motion has been to keep the environment stationary while allowing the observer to locomote. This approach has been used quite successfully to examine how birds use objects within their environment as landmarks to locate hidden food items (e.g., Spetch et al.,1996; 1997). Recent studies using this approach have found that birds, specifically chickens, can use both the featural properties (e.g., color and shape of surfaces) and geometric properties (e.g., distance and angles between surfaces) to locate a target area (Vallortigara, Zanforlin & Pasti, 1990). This approach to understanding how birds encode environmental information has raised interesting questions regarding potential differences among. For example, Spetch et al. trained pigeons to locate a hidden target centered between four identical landmarks. Although the pigeons became quite accurate at locating the target, when Spetch et al. expanded the landmark array the pigeons did not continue to search in the center of the landmark array but rather searched at an absolute vector from individual landmarks. This result showed that the pigeons had learned a vector from the landmark to the target during training and when the landmark array was expanded the pigeons continued to use the vector learned during training. Tommasi, Vallortigara and Zanforlin (1997) trained chicks of domestic fowl on a similar task. However, instead of an array of individual landmarks, the chicks were trained in a fully enclosed search space. Interestingly, when the walls of the search space were expanded the chicks continued to search in the middle. The difference in results reported by Spetch et al. and Tommasi et al. may show that pigeons and chickens use environmental information differently. On the other hand, the procedural differences (individual landmark array versus a fully enclosed search space) may elicit different encoding processes. Future studies are needed to examine if the differences reported here are truly species related or if birds encode information differently depending on the spatial task.

## Summary

Avian pattern and object perception is a field very much in its youth. Attempts at understanding how birds recognize and respond to environmental objects have taken many seemingly diverse approaches. Such approaches have ranged from the investigation of how elemental properties of an object are constructed to form a coherent object, to studies of landmark use in a bird's natural environment. Each of these approaches has furthered our understanding of object perception and recognition. Examining the various stages of object recognition is critical to understanding how birds recognize objects. Investigations of local and global pattern processing is important for understanding when birds perceive common elements as belonging to a single object, rather than as a series of unrelated pieces. This initial step allows us to determine what object properties are important for segregating an object from its background. This question can be addressed further by asking what properties are critical for perceiving and recognizing important objects when presented among other relatively unimportant objects, as would occur in a bird's natural environment. To examine this issue, many investigators have introduced static pictorial stimuli and dynamic video images in an attempt to more closely parallel the natural world of the species of study. These studies have shown that not only is object-based motion important for perception and recognition but viewer-based motion may be equally or more important. To examine the influence of motion in object perception and recognition many systematic examinations of avian behavior under naturalistic conditions have been conducted to better understand how birds perceive objects important for daily survival. Through investigations examining the stages of pattern and object detection the studies presented here further our current knowledge of avian object recognition.

Within the framework outlined above, this thesis investigates a number of issues regarding the encoding of visual information in birds. Chapter 2 examines the role of contextual information during the discrimination of line orientation and position by pigeons. In chapter 3 Glass patterns are used to investigate if pigeons are able to pool across elemental information to extract a global pattern. Chapter 4 uses complex images of an outdoor scene to examine if pigeons encode a 2-D image as a representation of 3-D space. Whether pigeons use the absolute or relative metric properties of an environment to relocate a hidden target is investigated in chapter 5. Chapter 6 examines how initial experience within an environment influences what environmental properties are encoded and how these properties are subsequently used. Finally, chapter 7 incorporates both object-motion and viewer-motion in examining what object-based properties are important for object recognition, more specifically prey recognition, by hunting owls.

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# CHAPTER 2

# CONTEXT LINES FACILITATES HUMAN AND IMPEDES PIGEON PATTERN PERCEPTION

Discrimination of line orientation stimuli may be altered by the presence of redundant or seemingly uninformative contextual information. An improvement in discriminating or grouping stimuli based on line orientation has been shown in several experimental paradigms (Enns & Prinzmetal, 1984; Pomerantz, 1991; Pomerantz & Pristach, 1989; Pomerantz, Sager & Stoever, 1977; Weissten & Harris, 1974). Generally, humans have been shown to discriminate oblique lines faster or more accurately when these lines are presented in a context of horizontal and vertical lines (e.g., Figure 2-1b) than when presented alone (e.g., Figure 2-1a). This effect has been referred to as the Configural Superiority Effect (Pomerantz, 1991; Pomerantz & Pristach, 1989; Pomerantz, Sager & Stoever, 1977) or the Object-line Effect (Enns & Prinzmetal, 1984). The superior performance with the lines in context has been attributed to the production of emergent features (e.g., closedness, intersections or symmetry; Julesz, 1975;1981).

Donis and Heinemann (1993) have reported that pigeons do not show facilitated performance when line stimuli are presented within a context, but rather seem to be disadvantaged by the addition of the uninformative contextual information. Poorer performance with contextual stimuli has been referred to as the Configural Inferiority Effect or the Object-Line Inferiority Effect. The opposite influence of contextual information is an interesting species difference between humans and pigeons, particularly in light of the many studies reporting a remarkable species similarity in pattern recognition and categorization (Blough, 1984; 1985; Cook, 2000; Cook, Cavoto & Cavoto, 1996).

Two main explanations have been offered to account for this difference. One such explanation, suggested by Donis and Heinemann (1993), is that humans are able to use a non-visual encoding processes, such as verbal labeling, in addition to visual encoding in discrimination tasks. For example, humans may attach verbal labels to the stimulus configurations, such as arrow and triangle, in addition to visual encoding of the stimuli. It is this dual encoding which facilitates the retrieval of the relevant information needed for discrimination by humans. Donis and Heinemann suggest that since verbal coding is not available to pigeons, they are distracted by the addition of the contextual information (also see Heinemann & Chase, 1990).

A second explanation for the contextually-based species difference is based on possible perceptual coding differences. Many investigations of pigeon pattern and object perception have reported that pigeons show strong elemental encoding (e.g., Cerella, 1980; Kirkpatrick-Steger, Wasserman and Biederman, 1996). One example of elemental or local encoding by pigeons (referred to as the Particulate Feature theory) was shown by Cerella (1980). He showed that pigeons were able to discriminate line drawings of the cartoon character Charlie Brown from other characters in the Peanuts comic series. However, when the individual images of the characters were scrambled such that large body divisions were no longer in biologically correct order, the pigeons were still able to discriminate Charlie from the other characters. Accurate performance in the scrambled condition supports the idea that pigeons were encoding Charlie at an elemental level.

If pigeons show a strong bias to encode images or patterns at a local or elemental level, then one would expect that in line orientation discrimination experiments (such as Donis and Heinemann, 1993), the type of contextual information should selectively influence discrimination performance. Specifically, pigeons' performance in discriminating line orientation could either be degraded or enhanced, depending on presence and orientation of the contextual lines.

Donis (1999) reports that pigeons are better at discriminating between lines oriented along the main axis (horizontal and vertical) than between obliquely oriented lines. Whether this oblique effect is truly a perceptual effect or a consequence of learning (e.g., the carpentered hypothesis proposed by Annis & Frost, 1973) is unclear. However, if pigeons are better or more sensitive to lines oriented along the main axis, this bias must be considered in configuration studies. Specifically, in the configuration study reported by Donis and Heinemann (1993), the pigeons were required to discriminate between obliquely oriented lines. These lines were presented either alone or embedded in a context comprised of a horizontal and vertical line. The pigeons showed better discrimination when the oblique lines were presented alone than within the context. If the orientation of the context lines is important then perhaps the pigeons' performance with the oblique lines in context was due to a masking effect by the horizontal and vertical contextual information. Given that pigeons can discriminate horizontal/vertical lines better, these lines may have disrupted encoding of the oblique line orientations relevant to the discrimination task.

The contextual information provided in studies of the configural effect may also serve to enhance performance. Donis, Heinemann and Chase (1994) show that pigeon's discrimination of line position may be enhanced by providing a visual "frame of reference". They showed that pigeons' ability to discriminate the absolute position of elemental stimuli was enhanced by placing uninformative elements around the to-be-discriminated elements. Thus, if pigeons were required to discriminate positional stimuli it might be expected that the contextual information may facilitate the discrimination. Thus, if pigeons are presented with a difficult discrimination, such as the absolute position of a line element, the contextual line elements could act as a frame of reference, and enhance performance rather than mask the elemental discrimination.

The configural effect can be examined using similar stimulus sets that require a discrimination of either orientation or position. The orientation discrimination requires pigeons to discriminate between obliquely oriented lines presented either alone or within an uninformative context comprised of horizontal and vertical lines. This discrimination is exactly that reported by Donis and Heinemann (1993; and an example is provided in Figure 2-1a and b). The position discrimination requires pigeons to discriminate between an L and a mirror-image L presented alone or within an uninformative context comprised of a single positively sloped line (for example see Figure 2-1c and d). This discrimination requires that the pigeon encode the absolute position of the vertical line along the horizontal line. If the orientation of the uninformative contextual lines are important then one would predict that the pigeons would show a configural inferiority effect in the orientation discrimination because the horizontal and vertical contextual lines will overpower the oblique lines. The opposite would be predicted in the position discrimination, where the oblique lines enhance an otherwise difficult discrimination based on absolute line position.

# EXPERIMENT 1

This study is an analysis of a large amount of data compiled from several different experiments with slight procedural differences, all examining texture perception in pigeons. The elements used in this study were part of a larger training stimulus set presented regularly over a five year period. Thus, the trials we examined were interspersed with other trials presenting textures comprised of non-line elements (e.g., solid triangles, stars etc) not included in the analysis. We systematically examined this data set to evaluate if our pigeons showed the same configural inferiority in discriminating orientation stimuli as reported by Donis and Heinemann (1993). In addition, we examined the pigeons' discriminative performance with Position stimuli.

## Methods

### Subjects

Five highly experienced male White Carneaux pigeons (*Columba livia*: Palmetto Pigeon Plant) were tested (Cook, 1992a; 1992b; Cook, Cavoto, & Cavoto, 1996; Cook, Cavoto, Katz, & Cavoto, 1997). They were maintained at between 80% to 85% of their free-feeding weights. Supplemental feedings were provided following experimental sessions. The pigeons were maintained on a 12-hour light dark cycle and given free access to water and grit in the colony room.

### Apparatus

Training and testing were conducted in a flat-black Plexiglas chamber (38cm wide x 36 cm deep x 38 cm high). All stimuli were presented on a color computer monitor

(NEC MultiSync 2A; Wooddale, IL) viewed through a 26 x 18 cm window in the middle of the front panel of the chamber. A thin piece of glass was mounted in the viewing window to protect the surface of the monitor. Pecks directed to the monitor screen were detected by an infrared touch screen (resolution of 80 x 48; EMS Systems, Champaign, IL) mounted behind a 40-mm wide Plexiglas ledge surrounding the inside edge of the viewing window. A 28-V houselight located in the ceiling was illuminated at all times, except when an incorrect choice was made. A food hopper was located in the middle of the front panel, its access hole flush to the floor. Infrared beams located in the food hoppers measured head entries. All experimental events were controlled and recorded by a computer. Computer-controlled relays (Metabyte, Taunton, MA ) operated the hopper and house-light.

### Stimuli

All Line elements were presented using a Texture display (see Figure 2-1). The overall display size was 20 x 13 cm. The displays consisted of 468 individual elements (approximately 7 mm x 1 mm; length x width) evenly spaced across 18 rows and 26 columns. The elements were white presented against a uniform black background. The Texture displays could be presented such that all the elements in the display were the same (Same display type) or such that a smaller portion (8 x 7 elements) of the display located at a random position, differed (Different display type) from the larger element array. Only displays consisting of the following stimulus pairs were used in this analysis:

The Orientation stimuli consisted of either oblique Line elements or O-Configural elements (see Figure 2-1a and b, respectively). The Line elements were positively and negatively sloped lines. The O-Configural elements were the positively and negatively sloped lines embedded within a redundant L context.

The Position stimuli consisted of either L elements or P-Configural elements (see Figure 2-1c and d, respectively). The L elements were a capital L and a mirror image L. The P-Configural elements were the capital L and the mirror-image L embedded on a positively sloped line.

In the Different display type, all elements were used for both the target region and the distractor region. For example, on one trial the target region might be comprised of positively sloped lines and the distractor region negatively sloped lines. However, on another trial the target region would consist of negatively sloped lines and the distractor region would consist of positively sloped lines (note that Figure 2-1 shows only one stimulus type).

### Discrimination Training

An orienting stimulus, consisting of a white circle on a black background, began each trial. A single peck terminated the orienting stimulus and a texture display was randomly presented. If the pigeon responded correctly (i.e., five pecks accumulated to the target region before five pecks accumulated to the distractor region) the display was terminated and the pigeon was permitted 2 s access to the food hopper. If the pigeon responded incorrectly (i.e., five pecks accumulated to the distractor region) the display was terminated and the overhead houselight was shut off for a brief period of time. Correct or incorrect, all trials were separated by a 5s intertrial interval in which the houselight was illuminated.

## Results

Each bird had a total of 500 sessions. For the purposes of analysis, these were organized into 100 session blocks. A repeated measures ANOVA with Orientation stimuli (Line elements vs O-Configural elements) revealed a significant main effect $F(1,4) = 12.7$; $p<0.05$. A configural inferiority effect was found in the Orientation conditions: the pigeons were more accurate at locating the target region with Line elements (55.7%) than with O-Configural elements (40.5%; see upper graph in Figure 2-2). Chance level in this type of task is 30% (Cook et al.,1996). In addition, a repeated measures ANOVA with Position stimuli (L-elements vs P-Configural elements) also showed a significant main effect $F(1,4) = 7.96$; $p<0.05$. A configural superiority effect was found in the Position conditions: the pigeons showed lower accuracy locating the target region with L-elements (32.3%) than with P-Configural elements (51.9%; see lower graph in Figure 2-2).

## Discussion

This experiment yielded two important results. First, contextual information can serve to degrade or enhance the discrimination of line elements. The pigeons consistently showed better accuracy at discriminating the Line elements when they were presented alone rather than within an uninformative context (O-Configural condition). Thus, the contextual information degraded the pigeons' ability to discriminate between the oblique lines. However, when the pigeons were required to make a position discrimination, they were better at discriminating between the L stimuli when presented in context (P-

Configural condition) than when presented alone. Unlike the Orientation stimuli, the Position stimuli require the pigeons to make a more subtle discrimination based on the absolute position of the vertical line along the horizontal line. Donis, Heinemann and Chase (1994) argued that if a target stimulus is presented with an accompanying context, the context provides a frame of reference for determining differences in absolute position. This positional frame of reference is not available when the targets are presented in isolation. Thus, in the current experiment, the positively sloped line present during the P-Configural condition may have acted as a frame of reference allowing the pigeons to accurately discriminate the absolute position of the two vertical lines in reference to the horizontal line.

The second important result is the robustness of the configural inferiority effect. The results of this experiment show that Donis and Heinemann's (1993) result generalizes from single elements to texture displays, and that the presence of an Orientation configural inferiority effect in pigeons is quite robust and can be seen even when the pigeons are presented with a very different stimulus display. Furthermore, the configural inferiority effect remained even when the pigeons were very familiar with the stimuli, and when other stimulus sets were added during training and testing.

## EXPERIMENT 2

The results of Experiment 1 show that pigeons' discrimination of two oblique line stimuli, with different orientations, is less accurate in the O-Configural condition. This result supports the results reported by Donis and Heinemann (1993). In Experiment 2, the configural effect was further examined by testing new birds in a same/different task, and with a wider variety of stimuli and display arrangements. In addition to Texture displays, Geometric displays were used that were comprised of larger elements arranged in a matrix of 2 rows by 3 columns. Three different element sizes were used during the Geometric displays. To examine the role of stimulus size the three sizes used were smaller, larger and of similar size (see the bottom right illustrations in Figure 2-3) to the elements used by Donis and Heinemann (1993). Finally, to further understand the role of the context in the discrimination of oblique lines, the stimuli were also presented in a Separated condition where the to-be discriminated element (the Line in the Orientation condition or the L in the Position condition) was separated from its context by a gap. The Separated condition provides the same amount of visual information, but the gap separates the target information from the context reducing the "goodness" or the emergent features (i.e., closedness). If pigeons are unable to use emergent features then performance in the Separate condition should be similar to performance in the Configural condition.

## Methods

### Subjects

Four highly experienced male White Carneaux pigeons (Cook, Katz & Cavoto, 1997; Cook & Wixted, 1997; Cook, Katz & Kelly, 1999), maintained at 80% of their free-feeding weights, were used in this experiment. Supplemental feedings were provided following experimental sessions. The pigeons were maintained on a 12-hour light dark cycle and given free access to water and grit in the colony room. No preliminary training was needed, as each pigeon had several years experience with target localization tasks (Cook, 1992a, 1992b, 1993a; Cook et al., 1996; Cook, Cavoto, Katz & Cavoto, 1997)

Apparatus

Training and testing were conducted in a flat-black Plexiglas chamber (38cm wide x 36 cm deep x 38 cm high). All stimuli were presented on a color computer monitor (COMPAQ 151FS; Houston, TX) visible through a 27.5 x 21.0 cm viewing window centered in the front panel. The viewing windows bottom edge was 18.0 cm from the chamber floor. Mounted within this window was a touch-screen (Elographics AccuTouch Model E274-SFC; Oak Ridge, TN), used to detect pecks directed at the monitor's screen. A thin sheet of acetate was placed in front of the touch-screen to protect it from direct contact. A 28-V houselight was located in the ceiling and was illuminated at all times, except when an incorrect choice was made. Three identical food hoppers (Coulbourne #E14-10, Allentown, PA) were located one in the center of the front panel, one on the left wall and one on the right wall. Only the two side hoppers were used during this experiment, the center food hopper was inactive. Infrared LED's mounted 1.5 cm within each hopper were used to detect head entries.

All experimental events were controlled and recorded with a 486-class computer. A video card (VGA Wonder ATI Technologies, Scarborough, Ontario) controlled the monitor in the SVGA graphics mode (800 x 600 pixels). Computer-controlled relays operated the hoppers and house-light (Metabyte, Taunton, MA).

Display organization

The overall display size was 18.0 x 12.0 cm and arranged as either a Texture display or a Geometric display. All elements were white presented on a uniformly black background. The elements were the same types as in Experiment 1 (i.e., Lines, O-Configural, L's and P-Configural). The texture displays consisted of 384 small elements (7 mm in size) and arranged in a matrix of 16 rows and 24 columns (spaced by 0.75 cm intervals). The Different displays of the texture organization contained a randomly located 8 element by 7 element target region. The Same displays with the texture stimuli did not contain a target region but were constructed of identical elements.

The Geometric displays contained 6 large elements arranged in a matrix of 2 rows and 3 columns. The length of the individual elements of Geometric displays were presented in three different sizes. The elements were 7, 13, and 20 mm, for the small, medium and large elements, respectively. In any particular trial with the Geometric displays all elements were the same size. The Different geometric displays contained one randomly located target element that differed in identity from the other five elements. For example, a Different display might consist of five positively sloped oblique lines and one negatively sloped oblique line. The Same displays consisted of six identical elements.

The elements of the Texture and Geometric displays were also displayed in a Separated fashion. The individual elements making up the Configural stimuli were separated from each other by a small gap (see top right illustrations in Figure 2-3). For the Geometric display types only the small and medium element sizes were used during the Separated condition since the large elements were too large to be displayed in such format.

Interspersed among the Texture and Geometric displays were object and photo displays containing digitized pictorial images (see Cook, Katz & Cavoto, 1997). These displays were used as part of another experiment and were not included in the analysis.

### Discrimination Training

A target-directed fixed response procedure was used. Because the Same displays did not have a target area, the peck requirement was yoked to the number of pecks emitted to the last Different display (for a more complete description of the response requirement refer to Cook, 1995). Once the bird completed the peck requirement both side hoppers were illuminated. For two of the subjects, choosing the right hopper was considered correct for a Same display and the left hopper correct for a Different display. This hopper assignment was opposite for the remaining two birds. The stimulus display remained on the monitor until a head entry was recorded to one of the hoppers. If the pigeon made a correct hopper choice the hopperlight remained illuminated and the hopper was raised for 2 s. On the other hand, if the pigeon made an incorrect hopper choice the hopperlight was turned off, the hopper was not presented and the overhead houselight was extinguished for 15 s. Each trial was followed by an 8 s ITI.

### Testing

The pigeons were presented with four successive testing phases.

Phase 1. Both Texture and Geometric display types were presented. However, for the Geometric displays only the large size Orientation stimuli were used. Each session contained 24 distinct pairings of the stimuli, subdivided into Texture and

Geometric displays each containing 6 Same and 6 Different display types. The Different displays contained 2 Line, 2 O-Configural and 2 O-Separated presentations, counterbalanced for which stimulus type was located in the target region and the distractor region. Each pigeon was given 22 sessions of testing with Phase 1.

Phase 2. As in Phase 1 only the Orientation stimuli were presented. The two stimulus types used in Phase 2 were both smaller than the stimuli presented in Phase 1. The largest of the two was approximately 13 cm and the smaller was approximately 7 cm. Similar to Phase 1, each session contained 24 distinct parings of the stimuli, subdivided into Texture and Geometric displays each containing 6 Same and 6 Different display types. Again, the different displays contained 2 Line, 2 O-Configural and 2 O-Separated presentations, counterbalanced for which stimulus type was presented in the target and distractor regions. Each pigeon was given 14 sessions of testing with Phase 2.

Phase 3. Both Texture and Geometric display types were presented. In this Phase only the Position stimuli were presented. For the Geometric displays, two sizes of stimuli were presented, the same sizes as used in Phase 2. Each session contained 48 distinct pairings of the stimuli, subdivided into Texture and Geometric displays, each containing 12 Same and 12 Different display types. The Different displays contained 2 "L", 2 P-Configural and 2 P-Separated presentations, counterbalanced for which stimulus type was different.

Phase 4. The final phase contained all of the stimuli used in the previous three phases. Each session contained 96 distinct parings of the stimuli, subdivided into 48 Same and 48 Different displays.

## Results

Performance with the Texture and Geometric display types remained relatively good throughout testing (mean choice accuracy for texture and geometric displays were 70.1% and 66.6% respectively). On test trials with the Orientation stimuli, mean performance was 70.8% (Texture = 72.7% and Geometric = 68.9%). On trials testing Position stimuli, mean performance was 66.1% (Texture = 67.7% and Geometric = 64.4%). The individual birds' discrimination was good overall(Astro = 66.7%, Barkley = 66.8% and Rosie = 73.3%), except for Judy's chance level discrimination (54.8%).

Although the Texture displays used in this experiment differed slightly from the Texture displays in Experiment 1, a configural inferiority effect was once again found for the Orientation stimuli $F(2,6) = 12.935$; $p < 0.01$. A Tukey's HSD showed a significant difference between the Line elements (78.9%) and O-Configural (71.8%) stimuli ($p<0.05$) and between the Line and O-Separated (67.1%) stimuli ($p< 0.01$; see upper graph in Figure 2-4). No significant difference was found for the Position stimuli during the Texture display presentations $F(2,6) = 0.244$; $p>0.05$ (see upper graph in Figure 2-4).

One pigeon (Judy) was excluded from all analyses with Geometric conditions due to poor baseline performance with these stimuli. A repeated measures ANOVA (with Line elements vs O-Configural elements) revealed a significant main effect $F(2,4) = 16.23$; $p<0.05$. A configural inferiority effect was found in the Orientation condition: the pigeons showed higher accuracy locating the target region with Line elements (72.2%) than with the O-Configural elements (66.4%; see lower graph in Figure 2-4). No main effect of stimulus size was found $F(2,4) = 0.778$; $p>0.05$. No main effect was found for the Position condition F(2,4) = 1.257; $p>0.05$ and again no significant difference was found among the different sizes of the stimuli F(2,4) = 3.604; $p>0.05$ (see lower graph in Figure 2-4).

## Discussion

Similar to Experiment 1, the pigeons in Experiment 2 show a configural inferiority effect with Orientation stimuli in texture displays. Thus, a configural inferiority effect was shown with two slightly different Texture displays and two different groups of pigeons. In addition to the configural inferiority effect with the Texture displays, the pigeons in this experiment also showed a configural inferiority effect with the Geometric displays. The results from the Geometric displays support the conclusion that the configural inferiority effect is quite robust in pigeons, being evident not only when using Texture displays but also with Geometric displays comprised of three different element sizes. The combination of results from the Texture and Geometric displays support the hypothesis that the addition of the context degrades pigeons' performance in line orientation discrimination. The context, rather than facilitating the line orientation discrimination (as it does in humans), acts to distract the subject. The similar poor performance in the O-Separated and O-Configural condition further supports the conclusion that the context does not facilitate discrimination.

A configural superiority effect was not found for the Position stimuli with either the Texture or Geometric displays. The difference between Experiment 1 and 2 may be due to the fact tha the pigeons in Experiment 1 had extended experience with the Positional stimuli. Since it has previously been reported that pigeons have difficulty accurately discriminating between stimuli differing with regard to the position of the stimulus elements, the differences we found in Experiment 1 and 2 are most likely a result of experiential factors.

## EXPERIMENT 3

The previous experiments show that pigeons' accuracy in discriminating between two oblique lines decreases when these lines are presented embedded in a redundant context of horizontal and vertical lines. Since pigeons are unable to make use of a dual encoding process (visual and verbal) we suggest that the addition of the horizontal and vertical lines from the context interferes with the line discrimination. Humans could also be distracted by the addition of the context (since humans, like pigeons, are also reported to be better at discriminating horizontal and vertical lines) and show poorer discrimination with the configural elements when compared to the Line condition. Alternatively, they could use dual encoding or coding of emergent features and show enhanced discrimination with the configural elements. If humans can use emergent features to enhance discrimination then performance should be better with the configural elements than with the separated elements. Degraded performance is expected with the Separated elements because the gap reduces the "goodness" of the emergent features. To examine these hypotheses we presented human subjects with the same stimuli that were presented to the pigeons in Experiment 2.

# Methods

## Subjects

Ten subjects served in this study. All had normal or corrected-to-normal vision.

## Apparatus

All stimuli were presented on a color computer monitor. Subjects were seated approximately 50 cm from the monitor with a keyboard within easy reach. All experimental events were controlled and recorded with a 486-class computer, A video card (VGA Wonder ATI Technologies, Scarborough, Ontario) controlled the monitor in the SVGA graphics mode (800 x 600) pixels. All programming was done in QuickBasic (1989) with an attached graphics library (GX Graphics, 1993).

## Stimuli

The stimuli used in this experiment were identical to the stimuli used in Experiment 2 with the pigeons.

## Discrimination Testing

A trial began with an orienting stimulus presented for 0.75 seconds. Following the orienting stimulus the subjects were presented with either Same displays or Different displays. Subjects were instructed to press the “f” key if all the stimuli on a display were the same, or otherwise to press the “j” key. If the subject’s response was correct, a new trial began, otherwise a blue screen was displayed for 2 s, followed by a new trial. The subjects were given 10 warm-up trials prior to testing.

## Testing

Subjects received one session of 106 trials comprised of 96 test trials and 10 warm-up trials.

## Results

Human subjects showed all of the standard effects previously reported, with the geometric displays supporting a configural superiority effect (Enns & Prinzmetal, 1984; Pomerantz, 1991; Pomerantz & Pristach, 1989; Pomerantz, Sager & Stoever, 1977; Weissten & Harris, 1974) and texture displays not supporting such an effect (Julesz, 1975; Pomerantz, 1981; Pomerantz & Pristach, 1989). In the following analyses, only correct responses are analyzed and the few errors (<1%) discarded.

For the geometric displays, analyses of the Orientation stimuli for the different displays found that search times for O-Configural elements were faster (862 ms) than for the Line elements (1070 ms), i.e., the Orientation stimuli showed a configural superiority effect, $\underline{F}(1,9)=9.54$. There was no effect or interaction with size, $\underline{F}(2,18)< 3$. Analysis of the same displays showed no significance difference for the Line (858 ms) and O-Configural (882 ms) conditions, $\underline{F}(1,9)<1$. Search times in both the Line and the O-Configural conditions were significantly faster than in the O-Separated condition, on both different (1445 ms) and same (1388 ms) trials, all $\underline{F}s(1,9)>6.0$ (see lower graph in Figure 2-5).

Comparable analyses of the Position stimuli found that search times in the P-Configural condition for the different display types were faster (872 ms) than in the L-condition (1166 ms), i.e., the Position stimuli showed a configural superiority effect, $F(1,9)=19.7$. There was no effect or interaction with size, all $\underline{F}s(2,18)< 2.4$. Analysis of the position stimuli for the same displays showed no significant difference between the L-condition (899 ms) and the P-Configural condition (882 ms), F(1,9)<1. Search times in the L-condition and the P-Configural condition were significantly faster than in the P-Separated condition, on both, different (1564 ms) and same (1388 ms) trials, all Fs(1,9)>12.0 (see lower graph in Figure 2-5). There were no effects for stimulus size F(2,18)<2.5, except for a significant main effect for the comparison between the L-condition and the P-Separated condition F(2,18)=3.75.

For the texture displays, the pattern of results was similar, but because human observers were considerably more variable in their response to the texture displays than to the geometric displays, the statistical results give a different picture. Analysis of the Orientation stimuli for the different displays showed that the O-Configural condition (928 ms) was not significantly faster than for the Line condition (1097 ms), F(1,9)<2. Further, there was no significant difference on the Same display trials (O-Configural = 1394ms; Line = 1194 ms) for these conditions, F(1,9)<2 (see upper graph in Figure 2-5). Both of the Line and the O-Configural conditions were faster than for the O-Separated condition for the Different display trials (1519 ms), all Fs(1,9)> 9), but not for the same display trials (1638 ms), F(1,9)<2.

Analyses of the Position stimuli for the different displays showed that the P-Configural (1076 ms) condition was not significantly different from the L-condition (1198 ms), F(1,9)< 1 (see upper graph in Figure 2-5). The Same display trials also showed no significant differences (P-Configural = 1465 ms; L = 1314 ms), F (1,9)<1. Further, the P-Separated condition did not differ from either the L nor the P-Configural conditions with either the Different display trials (1248 ms) or the Same display trials

(1638 ms), Fs(1,9)<1) and Fs(1,9)<2, respectively.

## Discussion

Overall the human subjects showed configural superiority effects with both the Orientation and Position stimuli in the Geometric display conditions. They showed overall lower accuracy when the discriminated stimuli were presented alone than when these stimuli were presented embedded in a redundant context. This result is important because not only does it support other investigations using similar stimuli, but it also suggests an important species difference. The similar results with the Orientation and Position stimuli suggest that the humans were using the emergent features present in the configural stimuli to discriminate the target location. This hypothesis is further supported by the results with the Separated stimuli. The Separated condition reduced the saliency of the emergent features by separating the context from the discriminating elements. Thus, the context could no longer aid the subject in the discrimination, but rather it distracted the subjects.

The texture displays did not show as strong a configural superiority effect as seen with the geometric displays. This result is not all that surprising: Pomerantz and colleagues have found that the role of emergent features (such as closure) and stimulus features such as line-slope differences are quite different for form perception (similar to our geometric displays) and texture displays (Pomerantz, 1981; Pomerantz & Pristach, 1989; also see Julesz, 1975).

## GENERAL DISCUSSION

Providing identical contextual information during a simple discrimination task may alter discrimination based on non-visual properties (dual encoding hypothesis) as well as on visual properties (emergent features). Many comparative investigations into feature processing by pigeons and humans have reported processing differences for the two species. Some examples of these differences can be seen during experiments of pattern recognition, visual search and object orientation (Kelly et al., In Press; Allan & Blough, 1989; Delius & Hollard, 1995). The results from the present experiments also support featural processing differences between pigeons and humans.

The configural effect has been examined using human subjects over several decades. However, only recently has the configural effect been studied using pigeon subjects. Our results, consistent with other investigators, show that the role of redundant contextual information differs for human and pigeons. However, the current investigations substantially further our knowledge of the extent to which these differences exist. First, we have shown that pigeons consistently showed a Configural inferiority effect with the Orientation stimuli. This was demonstrated in Experiment 1 where the pigeons had a great deal of experience with the stimuli as well as in Experiment 2 where the pigeons had far less experience with the stimuli. We also showed that the configural inferiority effect is robust to changes in the display type (Texture and Geometric) and over several stimulus sizes (small, medium and large Geometric elements). If pigeons were using emergent features of the Configural stimuli, performance with the Separated condition should have been disrupted in comparison to the Configural condition. This was not the case.

Humans showed a configural superiority effect with the Geometric displays for both the Orientation and Position conditions. However, reaction time in the Separated condition increased significantly in comparison to the Configural condition. This result supports the conclusion that humans were using the emergent features in the Configural conditions to identify the target location. In the Separated conditions, the "goodness" of the emergent features was reduced and reaction time increased. Finally, humans showed a strong configural superiority effect over changes in size of individual elements. Thus, providing contextual information to a simple line discrimination task allows human subjects (during the geometric displays) to configure the elements based on emergent features. The results of these experiments strongly support a species difference in the use of contextual information in a line discrimination task. The context clearly proved to be disruptive to the discrimination for the pigeons but enhanced discrimination for humans. The influence of the context in the line position discrimination task was less clear. Humans showed enhanced discrimination in the Geometric conditions and although pigeons initially showed enhanced performance (Experiment 1) this was not seen across experiments and thus may have been simply due to experiential factors.

Figure 2-1. Examples of the texture displays used in Experiment 1. The top row shows Orientation displays with (a) the Line condition and (b) the O-Configural condition. The bottom row shows Position displays with (c) the L-condition and (d) the P-Configural condition.

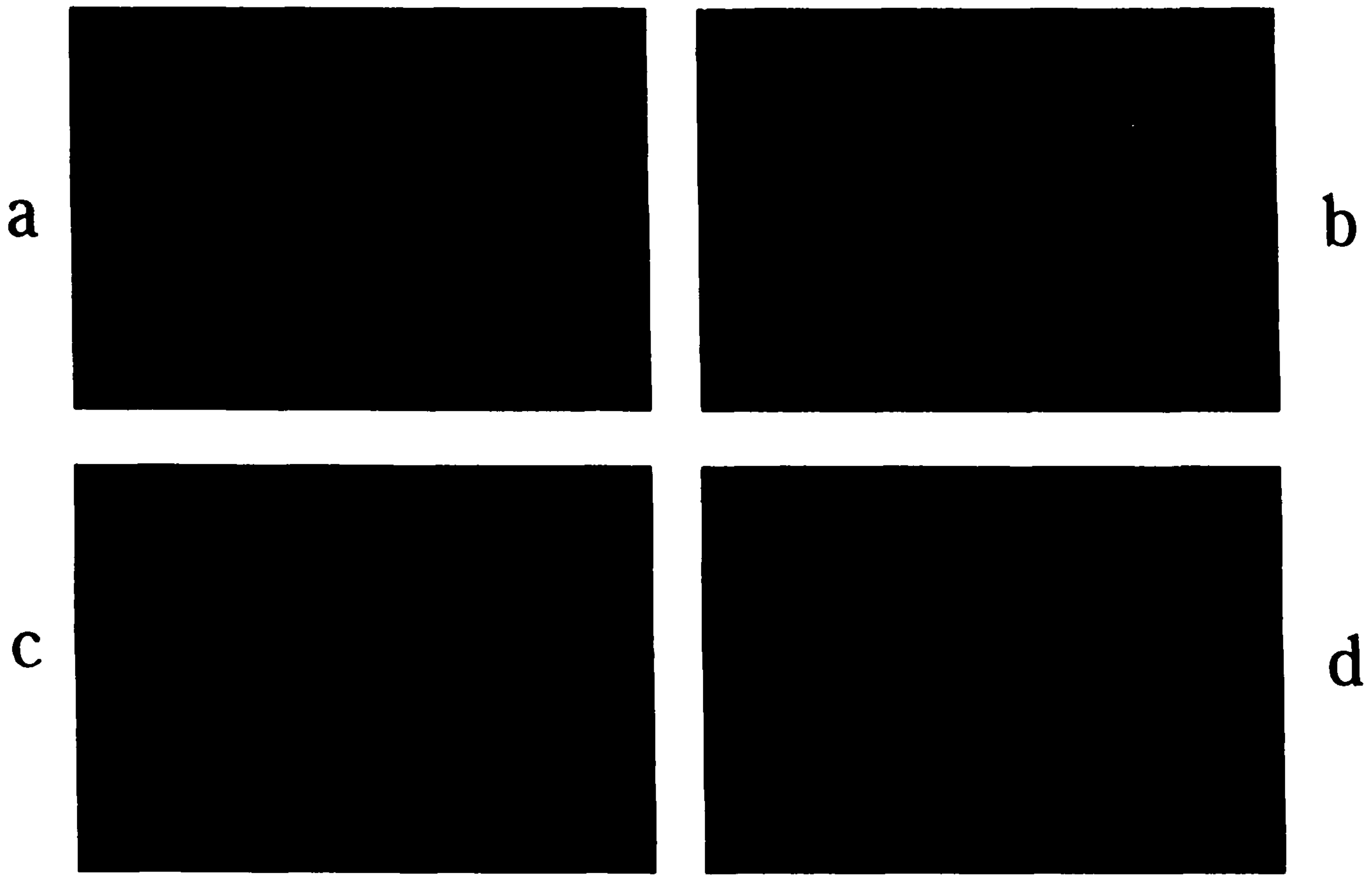

a
b
c
d

Figure 2-2. Pigeons' average accuracy to the Texture displays presented in Experiment 1. The upper panel shows accuracy for the Line and the O-Configural conditions, and the lower panel shows accuracy for the L and the P-Configural conditions.

# TEXTURE DISPLAYS

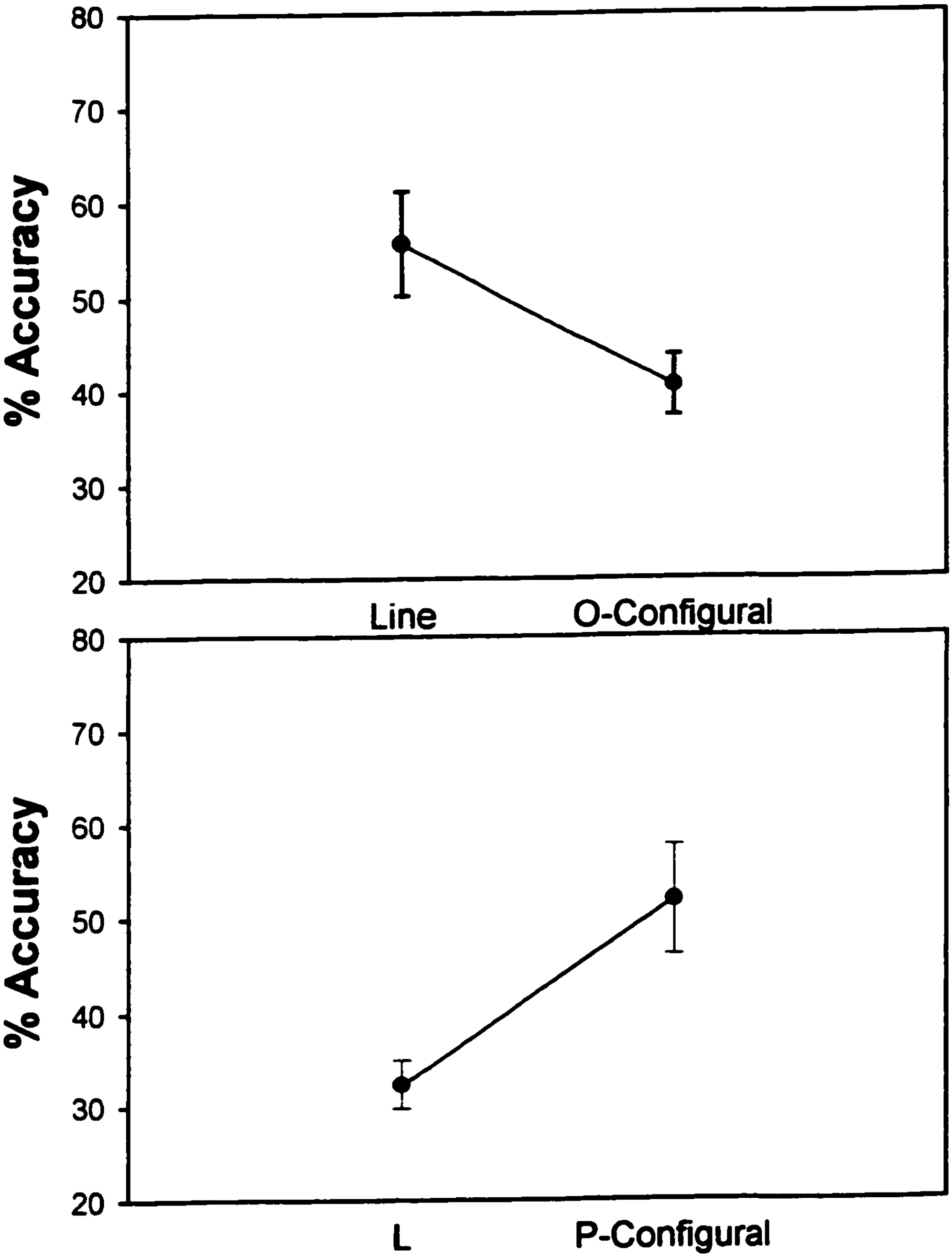


Figure 2-3. Examples of the display used in Experiments 2 and 3. Texture displays are shown in the two leftmost illustrations: the top illustration is an example of a Same display and the bottom is an example of a Different display. Also shown are examples of the Geometric displays, again with the top illustration being an example of a Same display, and the bottom one being an example of a Different display. Examples of all elements used are shown in the upper-right panel. The Orientation subpanel shows the two versions of the Line, O-Configural, and O-Separated elements, respectively. The Position subpanel shows the two versions of the L's, P-Configural, and P-Separated elements, respectively. The three different sizes of Geometric are shown in the lower-right.

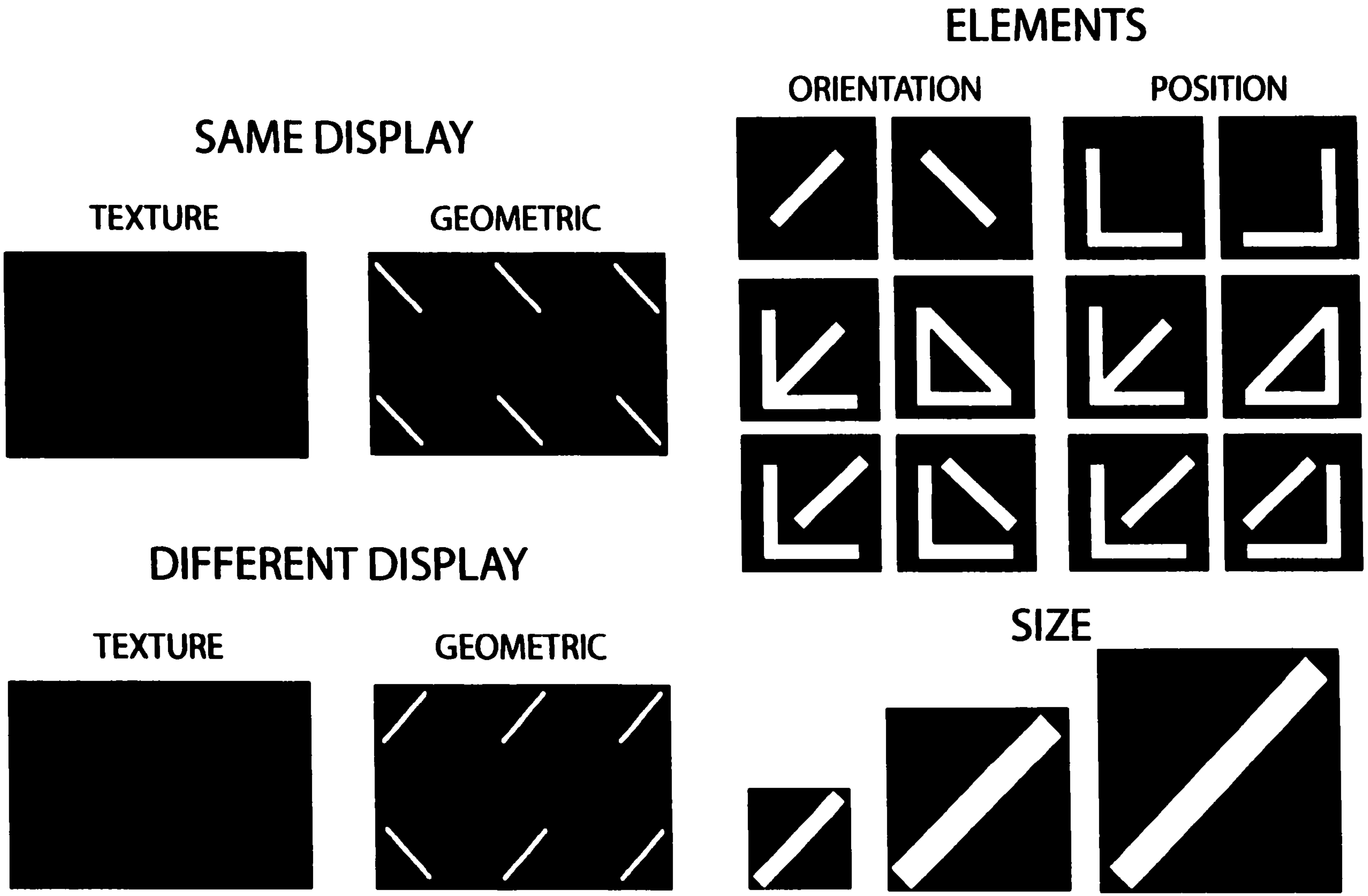
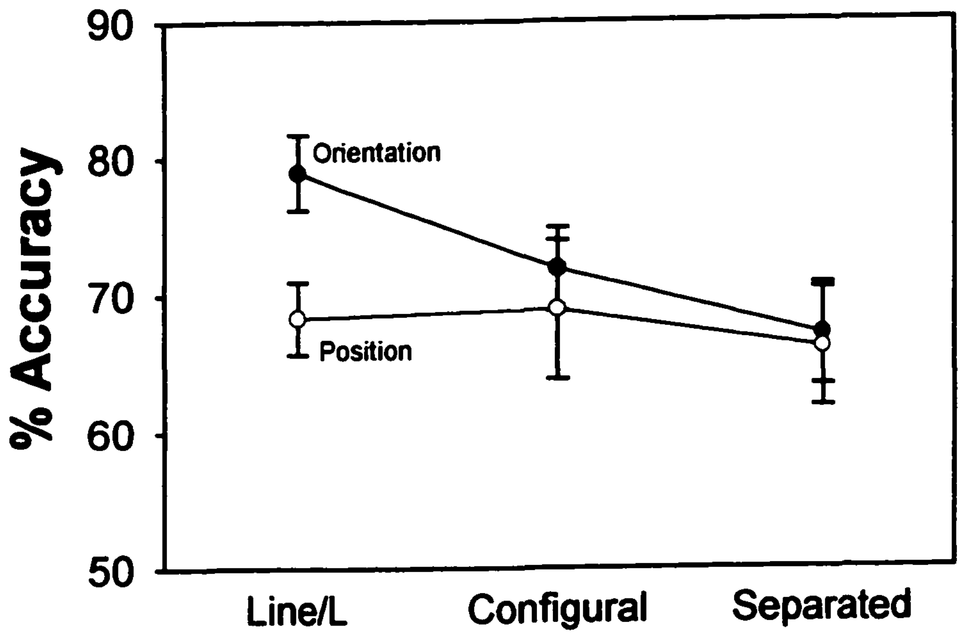

SAME DISPLAY
TEXTURE
GEOMETRIC
DIFFERENT DISPLAY
TEXTURE
GEOMETRIC
ELEMENTS
ORIENTATION
POSITION
SIZE

Figure 2-4. Pigeons' average accuracy for the Texture and Geometric displays used in Experiment 2. The upper panel shows accuracy for the Texture displays: the filled circles show accuracy in the Orientation conditions and the open circles show accuracy in the Position conditions. The lower panel shows accuracy for the Geometric displays: the filled circles show accuracy in the Orientation conditions and the open circles show accuracy in the Position conditions.


TEXTURE DISPLAYS

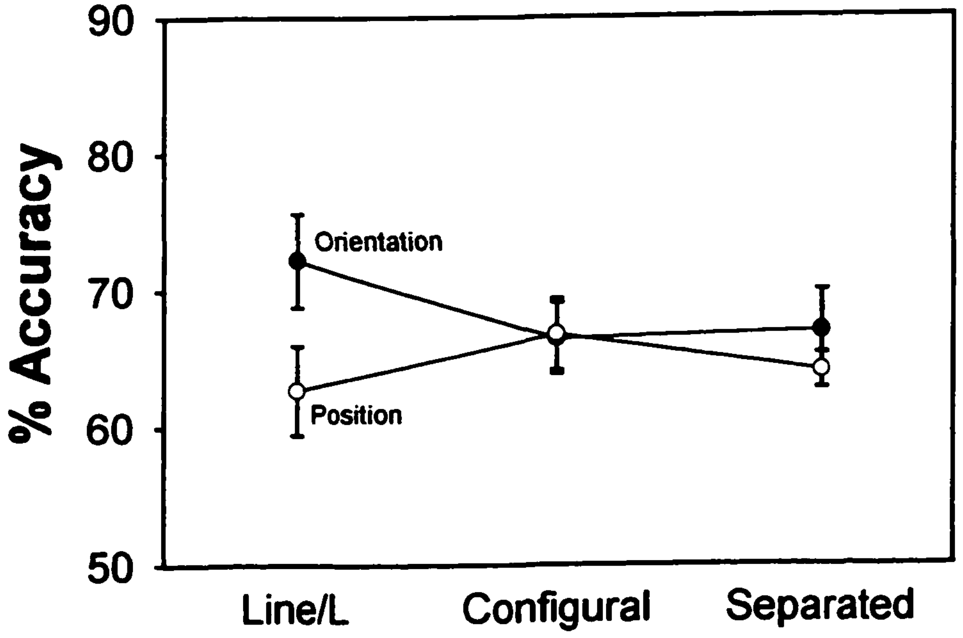
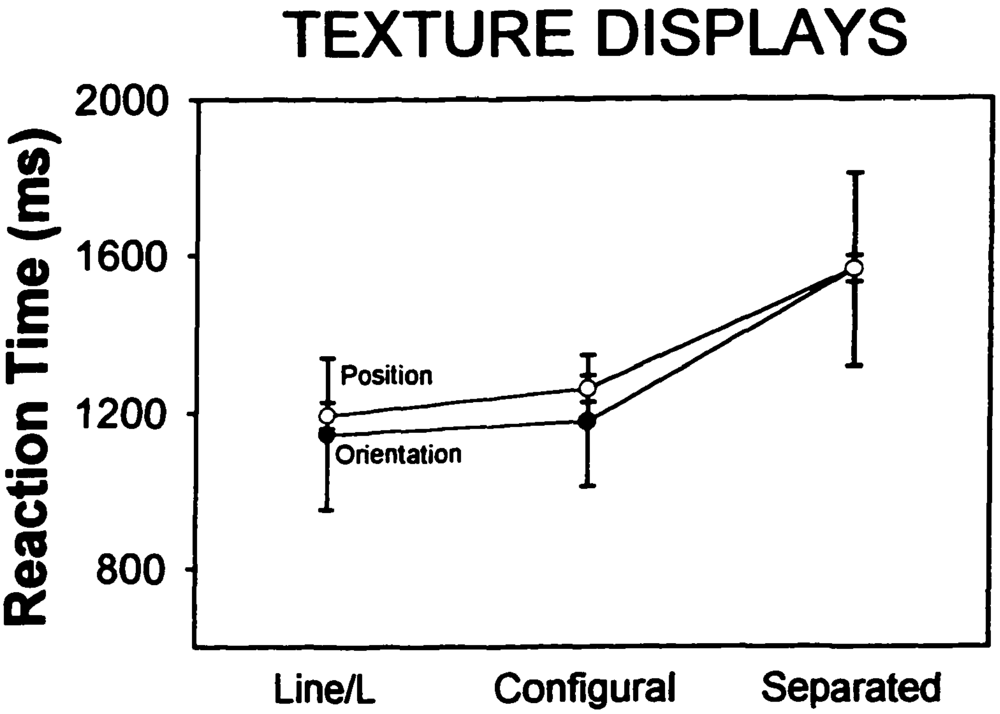
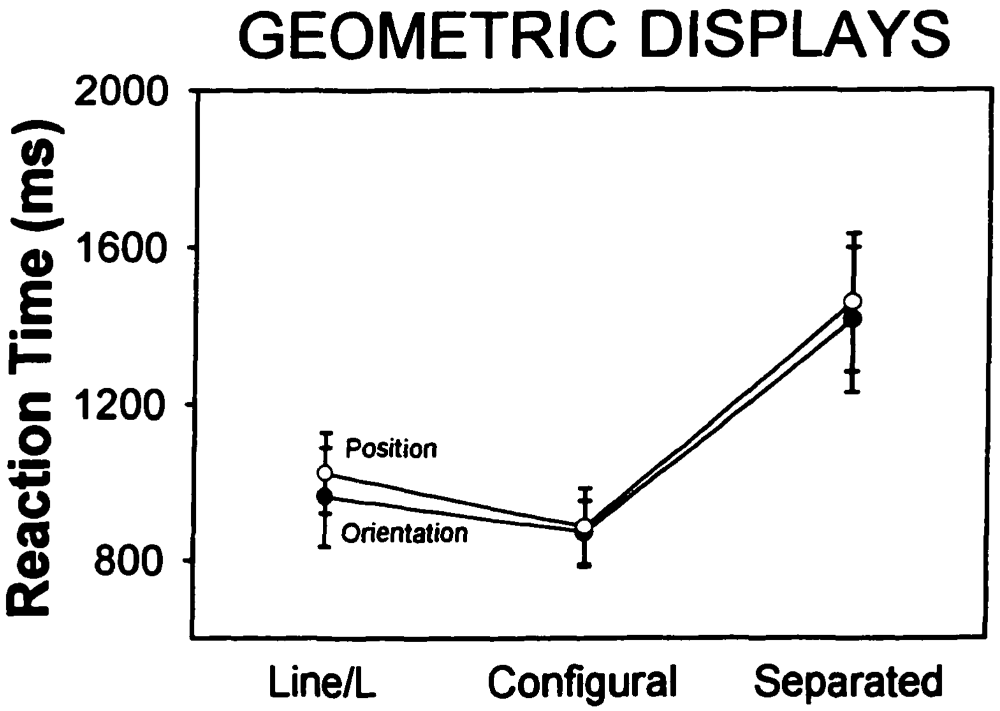

GEOMETRIC DISPLAYS

Figure 2-5. Humans' average reaction time (in ms) for the Texture and Geometric displays used in Experiment 2. The upper panel shows reaction time for the Texture displays: the filled circles show reaction time in the Orientation conditions and the open circles show reaction time in the Position conditions. The lower panel shows reaction time for the Geometric displays: the filled circles show reaction time in the Orientation conditions and the open circles show reaction time in the Position conditions.



TEXTURE DISPLAYS



GEOMETRIC DISPLAYS

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# CHAPTER 3

# DETECTION OF GLASS PATTERNS BY PIGEONS AND HUMANS: IMPLICATIONS FOR DIFFERENCES IN HIGHER LEVEL PROCESSING

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Although investigations of neurons in the visual cortex have demonstrated neuronal sensitivity to specific line and edge orientations (Hubel & Wiesel, 1962, 1968) it is less understood how this information is formulated into the ability to recognize global patterns. Wilson and colleagues (Wilson, Wilkinson, & Asaad, 1997; Wilson & Wilkinson, 1998) addressed this issue using Glass patterns (Glass, 1969; Glass & Pérez, 1973). Glass patterns are composed of random dot pairs positioned, within a specified field, such that a larger global pattern is perceived (see Figure 3-1). Wilson and colleagues (1997, 1998) measured detection thresholds for different Glass patterns embedded in noise, and found that human observers showed lower thresholds for concentric and radial patterns compared to parallel patterns. Wilson et al. concluded that there is global pooling of orientation information for the processing of concentric and radial patterns, but only local processing for the detection of parallel patterns. Further, they suggested that this type of global pooling occurs in V4 and that V4 is an important level for form recognition in the pathway between V1 and the inferior temporal cortex (IT). Similar studies using grating stimuli have shown V4 to be an important step in form perception within the non-human primate visual system (Gallant, Braun & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis & Van Essen, 1996).

Electrophysiological studies have shown that there are orientation-sensitive units in the pigeon visual system (e.g., Wilson, 1980) and behavioral studies have shown that pigeons are capable of discriminating complex stimuli and global patterns (e.g., Cook, Katz & Cavoto, 1997; Kirkpatrick-Steger, Wasserman & Biederman, 1998; Watanabe & Ito, 1991). For this reason, we were interested in examining form perception by pigeons.

If pigeons show differential sensitivity to patterns, as has been shown with Glass patterns in humans (Wilson and colleagues, 1997; 1998) and with similar grating stimuli in non-human primates (Gallant and colleagues, 1993; 1996), then we may be able to conclude that similar processing is involved in form perception by these species. Conversely, if pigeons do not show differential sensitivity we may conclude that form perception is organized differently in avian and primate species. Interestingly, honeybees have been shown to prefer radial over other patterns (Lehrer, Horridge, Zhang & Gadagkar, 1995), which is presumably important for flower recognition. Thus existence of differential sensitivity to patterns such as Glass patterns may reveal fundamental species-specific differences in the architecture of the form processing system. In the current study we compared humans' and pigeons' sensitivity to Glass patterns to see if pigeons also show differential sensitivity to Glass patterns.

## Methods

### Subjects

Pigeons. Eleven Silver King pigeons, with previous unrelated touch-screen experience served as subjects. Four pigeons failed to learn the task and were removed from the study leaving seven birds. The birds were housed in individual cages under a 12-hour light:dark cycle (light onset at 6:00 am). All birds were maintained at approximately 85% of their free-feeding weights by mixed grain during experimental sessions and supplemental feedings of Kay Tee pigeon pellets after sessions. Water and grit were available ad lib in the home cages.

Humans. Nine subjects participated in the study. Seven subjects were experimentally naive and two subjects were informed regarding likely experimental outcomes. All subjects had normal or corrected-to normal vision. The subjects ranged in age from 23 to 35 years.

**Apparatus**

Pigeons. The experiment was conducted in touch-screen operant chambers. The chamber dimensions (h x d x w) were either 36 x 34 x 50 cm or 42 x 32 x 73 cm. A Zenith 1492 color monitor with attached infrared touch frame (Carroll Touch, 1492 Smart Frame) was placed against an opening centered in the back wall of each chamber. The touch-screen was recessed from the opening by 3 cm and was spaced 1.6 cm from the monitor. Each chamber contained two Gerbrands pigeon feeders, one on each side of the monitor on the back wall of the larger chamber or on the side walls of the smaller chamber. A lamp in each feeder illuminated feeder presentations, and photo cells in each feeder recorded head entries so as to limit food access. Microcomputers, located in an adjacent room, controlled experimental contingencies and recorded responses. The touch frame was programmed to detect individual responses (i.e., detection of a beam break, and subsequent return to an unbroken state before another response could be detected). Although the pigeons were free to view the monitor display from any position within the chamber, previous reports (Bischof, Reid, Wylie & Spetch, 1999) and our observations indicated that the birds typically maintained a viewing distance of 9 cm or less.

Humans. Stimuli were presented on a Hitachi Superscan Elite 21 monitor under the control of a VGA display card. Viewing distance was 14cm, and stimulus size was such that the visual angle was as similar as possible for pigeons and humans. A keyboard to make responses was within easy reach of the subjects.

**Stimuli**

The stimuli consisted of four Glass patterns (concentric, radial, parallel-vertical and parallel-horizontal; refer to Figure 3-1) as the positive stimuli and a random dot pattern as the negative stimulus. On each trial, two 47.9 x 47.9 arc deg stimulus displays, one consisting of the positive pattern and one consisting of the negative pattern, were presented side by side, separated by a gap of 29.9 arc deg [Note: the size of the patterns are substantially larger than that used by Wilson and colleagues, (1997, 1998)]. The right/left position of the positive display was counterbalanced across trials in each session. Each stimulus display consisted of 200 black dots (luminance approximately 5 cd/m$^2$) on a white background (luminance 98 cd/m$^2$). Dot size was 0.5 x 0.5 arc deg. For the positive display, a proportion of the dots was shown in pairs (dot separation 1.4 arc deg) aligned tangential to the Glass pattern and any remaining dots were positioned randomly within the display window. For pigeons, 20 to 100 dot pairs were aligned according to the Glass pattern (coherence level of 20 to 100), and for humans 5 to 55 dot pairs were aligned according to the Glass pattern (coherence level 5 to 55). For the negative stimulus, all dots were positioned randomly. The dot patterns were presented in a simultaneous forced choice procedure with responses to the Glass pattern considered correct and responses to the random pattern considered incorrect. For pigeons, the display was presented until two responses were made to one of the display areas of the screen (typically between 1 and 3 s). For humans, the display was presented for a total duration of 1 s.

### Procedure for Pigeons

All sessions began with 10 warmup trials not included in analysis. Each trial began with the presentation of a 6 cm yellow square which served as a warning stimulus indicating the beginning of a new trial. The pigeon was required to peck the warning stimulus once to begin the stimulus presentation. During training trials if 2 pecks accumulated first to the positive stimulus the stimulus display was terminated followed by a 2 s access to a randomly selected food hopper. However, if two pecks accumulated first to the negative stimulus the stimulus display was terminated without access to a food hopper. Trials were separated by a 2 s inter-trial interval (ITI). Following the ITI on an incorrect trial, a correction procedure was instituted. During a correction procedure the same patterns, as previously shown, were redisplayed until the correct response was made. Correction trials were not used in the data analysis.

#### Initial Training Procedures

During initial training sessions, pigeons were presented with a Glass pattern, at 100% coherence, on one half of the screen; the other half of the screen remained blank. Pecks to the stimulus side of the screen resulted in access to the food hopper for 10 s. Pecks to the non-stimulus side of the screen were inconsequential. Once the pigeon completed 60 trials for three consecutive days it began training procedures.

#### Blocked Pattern Training Procedures

During training sessions, each trial consisted of the simultaneous presentation of a Glass pattern, at 100% coherence, and a random dot pattern (0% coherence). Each daily session included 100 trials. Four of the pigeons were initially trained with two of the four Glass patterns (counterbalanced across birds), presented in an alternating fashion across sessions. Because only two birds acquired the task within 35 sessions on this two-pattern training procedure, the other two pigeons, and all remaining pigeons were trained to criterion with only a single pattern at a time, with order of exposure to patterns varied across birds. Once performance reached an accuracy level of 80% or greater for three consecutive sessions, the bird received coherence level testing with the trained pattern or pair of patterns.

### Blocked Pattern Testing Procedures

During blocked pattern testing, the trained Glass pattern(s) were presented at coherence levels of 20, 30, 40, 50,60, 80, and 100. All coherence levels were presented in a quasi-random fashion, with each coherence level presented a maximum of 18 times per session. Daily sessions were increased to 120 trials. Following a minimum of 12 test sessions, the bird was then trained and tested with the remaining patterns.

### Mixed Pattern Testing Procedures

Once the birds finished the blocked testing procedures they were tested with all four patterns presented in a quasi-random fashion within a session. Again, each pattern was presented at the seven coherence levels. The birds were tested for a total of 25 sessions.

## Procedure for Humans

Four of the nine subjects received six sessions of mixed stimulus presentation and eight sessions (two sessions for each pattern) of blocked stimulus presentations. The remaining five subjects received only the six sessions of mixed stimulus presentation. The mixed sessions began with 24 warmup trials consisting of all four patterns at six coherence levels, followed by four blocks of 96 trials, with each block consisting of two presentations of four patterns at six coherence levels. The blocked sessions also began with 24 warmup trials with each pattern being presented four times at six coherence levels, followed by 3 blocks of 96 trials, with each block consisting of one pattern presented sixteen times at 6 coherence levels. For the subjects that received both the mixed and blocked sessions two subjects received all of the random sessions followed by the blocked sessions and two subjects received all blocked sessions initially, followed by the random sessions.

A trial began with the simultaneous stimulus presentation for 1 s. Subjects were instructed to determine which stimulus was the Glass pattern and press the arrow key on the keyboard that corresponded to the side of the screen (left or right) on which the Glass pattern was located. The subjects were not provided with feedback regarding accuracy of their choices. An ITI of 1 s separated each trial. After each block of trials subjects were prompted to take a brief self-timed break.

## Results

For all statistical tests, the alpha level was set at 0.05 unless otherwise noted. Figure 3-1 shows percent accuracy for pigeons and humans at each pattern and coherence level.

Pigeons. Only the mixed pattern testing sessions were used in analysis. A repeated measures ANOVA on accuracy scores showed a significant effect of coherence (F=54.22) but no significant effect of pattern (F=2.06). Performance with each pattern increased linearly with coherence (linear regression with $r^2$=0.939, 0.910, 0.926, 0.970 radial, concentric, vertical and horizontal, respectively).

Humans. Only the mixed pattern sessions were used in analysis. A repeated measures ANOVA on accuracy scores showed significant main effects for both pattern and coherence (F= 16.26 and 156.55, respectively). A significant interaction of pattern x coherence was also present (F=9.33). Performance with each pattern increased linearly with coherence, but due to a ceiling effect the 55% coherence data was not included in the regression analysis ($r^2$=0.990, 0.998, 0.973, 0.943 radial, concentric, vertical and horizontal, respectively). Newman Keuls multiple comparisons revealed the following significant comparisons for the patterns: Radial > Vertical and Horizontal; Concentric > Vertical and Horizontal; Vertical > Horizontal.

## Discussion

Similar to Wilson and colleagues (1997, 1998), the human observers in our study showed highest detection accuracy with the radial and concentric Glass patterns. We also found lower accuracy for the horizontal pattern than for the vertical pattern, suggesting that horizontal patterns may engage only local processing.

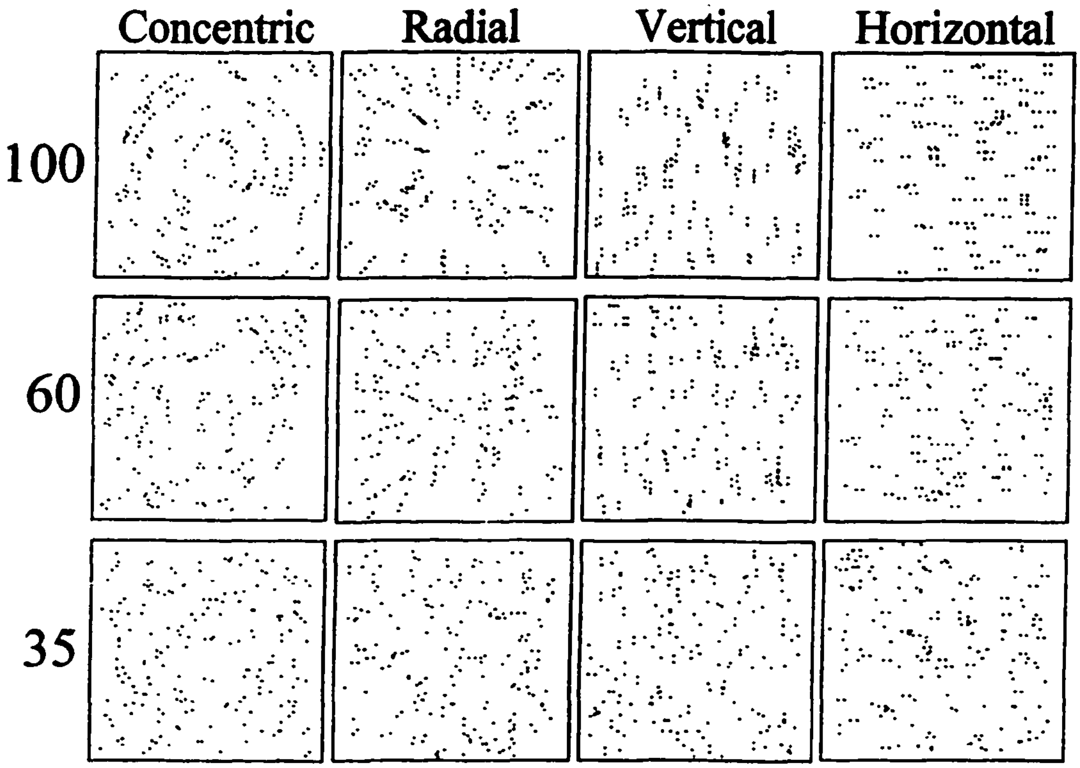
Pigeons did not show differential sensitivity to the four Glass patterns. Thus, according to Wilson and colleagues, whereas humans show global pooling of orientation units for construction of concentric and radial patterns, this is not the case in pigeons.

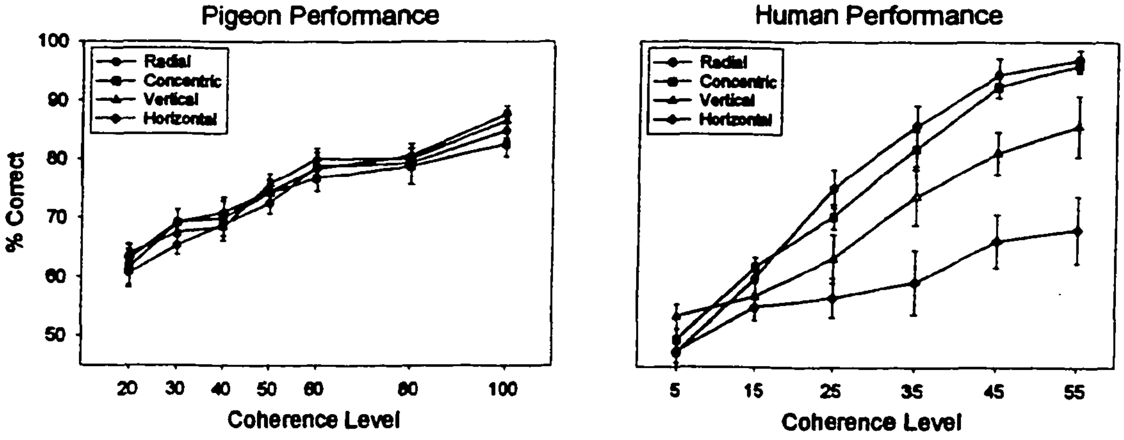
Pigeon's accuracy with all patterns at 100% coherence was lower than the human performance with the vertical pattern (argued by Wilson and colleagues to be processed at a local level), thus suggesting that the pigeons processed all patterns at a local level. Overall, the lack of differential pattern sensitivity by the pigeons shows that form perception processes are organized differently in pigeons than in humans or non-human primates.

Recent anatomical and physiological studies have highlighted numerous similarities in the organization of avian and mammalian visual pathways presumed to be important for form analysis. The mammalian primary visual cortex (V1) is thought to be equivalent to the visual "Wulst" in birds (e.g. Karten and Shimizu, 1989; Shimizu and Karten, 1993), although the authors caution against a simplistic comparison of the two structures (Shimizu, Cox & Karten, 1995). An electrophysiological study of the wulst in chicks noted that most cells showed orientation-sensitivity (Wilson, 1980), as is the case in V1 (e.g. Hubel and Wiesel, 1968). Neurons in the primate extrastriate areas such as the inferotemporal cortex (IT) encode more complex stimuli (e.g. Tanaka, 1996) including faces (e.g. Perret, Rolls & Caan, 1982). As previously stated, Wilson and colleagues suggested that the global pooling of orientation units for the detection of concentric patterns represents an intermediate step for face processing, and that it occurs in V4. If they are correct, then superior detection of concentric patterns by humans but not pigeons may reflect differences in the evolution of specialized mechanisms for processing faces. The pigeon equivalent to mammalian extrastriate cortices is the Ectostriatum (Ec; Karten and Shimizu, 1989). Watanabe (1992) reported that Ec lesions disrupted pigeons' discrimination of conspecifics but not their discrimination of different species. However, in contrast to humans and at least some non-human primates (Pascalis, Petit, Kim & Campbell, 1999), pigeons' recognition of individuals may not involve specialized face processing. Instead, pigeons' recognition of individuals may depend on a combination of several visual features (Ryan and Lea, 1994), as well as on motion (Shimizu, 1998) and behavioral cues during social interaction (Watanabe, 1992). Primates and pigeons also appear to process faces differently. In a working memory task, Phelps and Roberts (1994) found that humans and monkeys were affected by facial inversion, whereas pigeons were not.

Our findings suggest that the processes underlying complex form perception are organized differently in pigeons than in humans. Perhaps pigeons do not show superior detection of concentric Glass patterns, as do humans, because discrimination of individual pigeons involves numerous cues other than facial structure.

Figure 3-1. Examples of the four Glass patterns at coherence levels 100, 60 and 35 are shown at the top. The graphs at the bottom show pigeons' and humans' performance with the Glass patterns (left and right graphs respectively).


Concentric
Radial
Vertical
Horizontal
100
60
35


Pigeon Performance
Radial
Concentric
Vertical
Horizontal
100
90
80
70
60
50
% Correct
20
30
40
50
60
80
100
Coherence Level
Human Performance
Radial
Concentric
Vertical
Horizontal
5
15
25
35
45
55
Coherence Level

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# CHAPTER 4

# ENCODING OF SPATIAL INFORMATION IN IMAGES OF AN OUTDOOR SCENE BY PIGEONS AND HUMANS.

An expanded version of this chapter has been published in Animal Learning & Behavior, 1998

Many organisms have been shown to use visual landmarks to remember and locate a goal area (see Gallistel, 1990 and Collett, 1992 for reviews). Use of visual landmarks is demonstrated experimentally by manipulating the visual cues between the opportunity to encode the spatial information and subsequent search tests in which the subject attempts to locate the goal. Two types of evidence indicate that a subject uses a particular landmark: 1) The subject shifts its search location in response to landmark shifts, and 2) Accurate search is disrupted by the absence of the landmark. In a series of experiments using a laboratory task in which food is hidden on the floor of a spatial arena, Cheng and his colleagues have clearly demonstrated that pigeons use visual landmarks to locate a hidden goal, and they have identified several principles of pigeons' landmark-based search. (Cheng, 1988, 1989, 1994; Cheng & Sherry, 1992).

Pigeons' landmark-based search has also been investigated in a touch-screen task in which pigeons search for an unmarked goal on the surface of a monitor (Spetch, Cheng, & Mondloch, 1992; Spetch & Mondloch, 1993; Spetch & Wilkie, 1994). Visual stimuli displayed on the monitor served as landmarks. This two-dimensional search task has yielded results that are remarkably similar in certain ways to those found in real space tasks. In particular, near landmarks are weighted more heavily than far landmarks (Cheng, 1989; Spetch & Wilkie, 1994), and landmarks near an edge of the search space exert more control in the dimension parallel to the edge than in the dimension perpendicular to the edge (Cheng & Sherry, 1992; Spetch et al., 1992). Recent work (Spetch, Cheng, & MacDonald, 1996; Spetch, Cheng, MacDonald, Linkenhoker, Kelly, & Doerkson, 1997) has revealed that, on both the touch-screen and the laboratory floor, pigeons can use the configuration of an array of landmarks to locate a goal. In both environments, however, they respond to expansions of the array by maintaining the absolute training distance from individual landmarks in the array, rather than adjusting distance so as to maintain the appropriate relative position with respect to the entire array of landmarks.

Although the results obtained to date suggest that the touch-screen task calls forth many of the spatial processes used in more naturalistic search tasks, the visual information provided in studies using the touch-screen task has clearly differed from that in most real-world spatial search situations. In particular, whereas landmarks found in natural settings are typically located within a rich visual context consisting of many distal as well as local stimuli, the landmarks presented in the touch-screen studies have been presented against visually uniform backgrounds. In most studies, the landmarks have been colored two-dimensional geometric stimuli presented against a uniform grey background (Cheng & Spetch, 1995; Spetch et al., 1992; Spetch & Mondloch, 1993; Spetch 1995). One study presented visually richer stimuli in the form of digitized images of an outdoor scene consisting of three objects on a grassy field (Spetch & Wilkie, 1994). However, the grassy field was reasonably uniform except for a gradient in the texture of the grass from the top (background) to the bottom (foreground) of the image. Most importantly, there were no objects in the background of the scene which would provide a spatial context for the landmarks.

Distal background cues in a scene could play an important role in spatial search. For example, distal cues may be used to define the general region in which to search, with local landmarks serving to pinpoint the goal within that region. Distal cues may also provide a context which determines the meaning of local landmarks (e.g., the clump of trees beside the river may signify something different than a similar looking clump of trees in an open field). Finally, distal cues may be used as additional redundant sources of information to locate a goal. Indeed, laboratory studies of spatial memory have suggested that both global and local cues may be encoded to remember a goal location (Brodbeck, 1994; Spetch & Edwards, 1988).

Another way in which the visual information during real world search is very different from that available in the touch-screen studies is that a goal area can often be approached from different directions in the real world. This means that the visual information used in searching for the goal changes because it is viewed from different perspectives. Spetch, Kelly and Lechelt (1998, Experiment 1), addressed this issue by presenting pigeons with images of an outdoor scene. Six images, each showing a different view of the scene, were used. The pigeons were required to locate a target area that varied from image to image according to two-dimensional (2-D) properties but remained stable in terms of three-dimensional (3-D) coordinates. The researchers found that when the pigeons were presented with novel testing images the pigeons were not able to accurately locate the target position. Thus, it was suggested that the pigeons were not encoding the images as representative of 3-D space. The researchers suggest that perhaps the pigeons were simply memorizing the 2-D relationship between the target and some aspect or landmark in the images. Another suggestion was that since the pigeons were all laboratory raised, not having experience with real-world scenes might have effected the pigeons ability to encode the pictures as representations of real-world scenes.

The present research used the touch-screen task to further address the questions remaining from Spetch, Kelly and Lechelt (1998, Experiment 1). Racing pigeons with prior outdoor experience were trained with 28 different views of a complex scene that provided some variation in direction and distance from which the scene was viewed. This meant that the 3-D spatial relationships in the scene depicted by the images were invariant, but the 2-D spatial relationships among the visual features varied somewhat from image to image. A variety of tests were conducted following training to determine which information in the scene was used when searching for the goal, and whether accurate searching would transfer to novel views of the same scene. For comparison, adult humans were trained with the same set of training images and then were given some of the same tests presented to pigeons.

## Method

### Subjects

Pigeons. Five female racing pigeons served as subjects. The pigeons had previous outdoor experience through their participation in races, but they were naive with respect to experimental procedures. The birds were housed in large individual cages under a 12 hour light/dark cycle (lights on at 6:00 a.m.). All birds were maintained at approximately 85% of their free-feeding weights by Kay Tee pigeon pellets obtained after experimental sessions and mixed grain during experimental sessions. Water and grit were available ad libitum in the home cages.

Humans. The human participants were 11 undergraduate students, 9 female and 2 male, ranging from 18 to 28 years of age. They participated in the study for credit in their introductory Psychology class.

Apparatus, Search Space, and Images.

Pigeons. The experiment was conducted in a large custom built chamber, 44 cm high, 32 cm deep, and 74 cm wide (inside dimensions). A Zenith 1492 color monitor with attached infrared touch frame (Carroll Touch, 1492 Smart Frame) was placed against an opening centered in the back wall of the chamber. This opening was 10 cm from the raised grid floor of the chamber and provided access to the entire surface of the monitor. Spacers were used to recess the touch frame by approximately 3 cm from the opening, and to separate the frame from the monitor by approximately 1.6 cm. Two Gerbrands pigeon grain feeders were mounted on the back wall, one on each side of the monitor. The feeder openings began 8.5 cm from the sides of the monitor opening, and 17 cm from the floor. Lamps located within each feeder illuminated feeder presentations and photocells in each hopper measured head entries so as to limit eating times. Microcomputers, located in an adjacent room, controlled experimental contingencies and recorded peck coordinates. The touch frame was programmed to detect individual responses (i.e., detection of a beam break, then a return to unbroken beams before another response would be recorded).

The search space was a rectangular area, approximately 26 x 20 cm, on the surface of the color monitor. The images consisted of an outdoor scene taken from the University of Alberta campus during the winter. Training images provided 28 differing views which differed in distance to the goal as well as horizontal and vertical visual angle. These 28 training images are shown in Figures 4-1 and 4-2. In the vertical dimension, the scene was viewed from ground level or from the third and fourth stories of a building. The horizontal angle covered approximately 180°. For some views the camera angle was rotated to 45° or 315° in either direction. The 28 training views provided variation not only in viewing perspective but also in the absolute position of the goal on the touch-screen.

The goal was located near a large black metal sculpture, approximately 12.5 meters tall that had two vertical components. The scene provided a complex assortment of additional cues, including the city's downtown skyline, a winding roadway, lamp posts, trees, and buildings. A black box placed near the sculpture served as the goal marker and was present in the images only during preliminary training. The snow cover provided a reasonably uniform surface for the unmarked goal location.

The images were digitized using procedures similar to those described in Wilkie, Mak, and Saksida (1994) and Spetch and Wilkie (1994). The videotape was then played into a computer using a frame grabber system (Creative Labs Video Blaster) and still frames were saved in a GIF format (Compuserve, Inc). Removal of the goal marker from the images, and manipulation of the visual information in the scenes for the various test phases was accomplished by editing the images with Photofinish software (Zsoft). A large set of images was created, of which 28 were used for training and 18 for transfer testing. For each view, the location of the goal needed to be matched to the touch-screen coordinates. This matching was done by displaying the scene with the goal marker present, touching in the center of the goal marker, and reading off the coordinates recorded by the touch-frame. This was repeated several times for each image to ensure reliability.

### Procedure for Pigeons

Preliminary Training. All pigeons were trained to eat from a raised illuminated hopper and then were trained to peck at the monitor using a modified autoshaping procedure to establish reliable pecking at the monitor. Initially, the images used to establish pecking consisted of a 2-cm black square on a uniform light grey background (produced by cloning a patch of snow over an entire image). Once the pigeons reliably pecked at the black square, training scenes with a 2-cm black square centered over the goal marker were gradually introduced.

Search Training. During the first stage of search training, the black square marking the goal was decreased from 2.0 cm to 1.0 cm to 0.5 cm and then finally was eliminated, thereby requiring the bird to rely upon landmark cues in the scene to locate the goal. Reductions and removal of the marker were accomplished by cloning surrounding snow over the marker. Training with the marker absent continued until two criteria were met on each of three consecutive sessions: 1) the bird completed at least 80 trials in each session, and 2) the proportion of pecks in the goal area was greater than .10 (estimated chance level accuracy is only .03 as described below).

During the second stage of search training, the peck requirement was increased to 2 and then 3 pecks in the goal. Next a requirement was added that the last two pecks recorded had to be consecutive pecks in the goal area.

In the final stage of training and for all subsequent baseline sessions, the percentage of reinforcement for successfully completed trials was decreased to 50%. Each bird remained on 50% reinforcement for a minimum of 4 sessions and advanced to testing only after completing at least 80 trials on each of three consecutive sessions, and only if the proportion of pecks in the goal was at least .15 on each of these sessions.

Tests. Each bird was given three test series. Baseline sessions were interspersed between test session within and between series. The number of interspersed baseline sessions varied according to the bird's accuracy levels. Each test session consisted of a mixture of reinforced and unreinforced baseline trials, control trials that were visually identical to baseline trials but were procedurally the same as test trials, and test trials in which visual information in the image was altered in some way. On control and test trials, the image remained on for 8 s following the second peck recorded anywhere on the screen. In all test sessions, at least 50% of the trials were reinforced baseline trials. Each type of scheduled test trial occurred once in each block of 15 or 16 trials, with the order varying randomly between blocks.

Series 1 and 3 tested for transfer to novel views. In Series 1, test sessions consisted of 50% reinforced trials with training views, 25% unreinforced control trials with 12 of the training views (the first 12 shown in Figure 4-1), and 25% unreinforced trials with test images that provided 12 new views of the scene (the first 12 images shown in Figure 4-3). In Series 3, test sessions consisted of 50% reinforced baseline trials with the training views, and 25% unreinforced transfer tests with 6 novel views of the scene (the last 6 images shown in Figure 4-3), and 25% unreinforced tests with the same 6 transfer images, but with all visual cues removed from the scene. These latter test images were created by cloning snow over the entire image (a sample of these is shown at the bottom of Figure 4-4). Series 2 tested for landmark control by the tall sculpture near the goal. Test sessions consisted of 50% reinforced trials with training views, 25% unreinforced control trials with 12 training views (the bottom two rows of images in Figure 4-1 and the top two rows of images in Figure 4-2), and 25% unreinforced trials composed from these same 12 training views but with the sculpture shifted by 2 cm up, down, left, or right. Each type of shift was represented by three different views as shown in Figure 4-4. The extent of the shift in the represented three-dimensional space varied across views. In all series, each test image was presented for a total of 20 trials.

### Procedure for Humans

The experiment took place in a small private room that contained a touch-screen equipped computer. The computer monitor (Zenith 1490) and touch-screen (Carroll Touch 1490 Smart Frame) provided the same search space and stimuli as used for the pigeons. Subjects sat in a chair in front of the monitor and searched by touching the screen with the eraser end of a pencil. At the beginning of each session, subjects were provided with the following information: Their task would be to remember and locate a goal area, which initially would be marked but later would be unmarked. A point would be available on randomly selected trials. They could obtain this point only by touching in the goal area. The required number of touches in the goal would vary across trials and sometimes consecutive touches in the goal would be required. Whenever they earned a point, their cumulative points would be displayed. When points were not available, the trial would end after a certain number of touches, whether or not they were correct. The session would end after they obtained a certain number of points or after 45 min, whichever came first.

The experimenter then ran a demonstration program that presented two training trials. The experimenter demonstrated the importance of holding the pencil straight and removing it between touches. The first demonstration trial presented an image with the marker present and the second demonstration trial presented an image with the marker absent. Two touches in the goal were required during each demonstration trial. Each trial ended as a "reinforced" trial in which a point was earned (i.e., the screen was blanked and cumulative points were displayed). Any procedural questions were answered with "I'm sorry but I cannot provide any further information until after you have completed the experiment." After confirming that the subject wished to participate, the experimenter started the program and left the room.

The subjects program began with 12 different training images with the goal marker present. The next 12 trials presented the same 12 images but with goal marker absent. The next 12 trials randomly selected from the remaining set of 28 training images with the goal marker present. For all remaining baseline trials, the goal marker was absent. Trials 37 to 40 presented the four training images that had not yet been presented, and thereafter the 28 training images were selected to occur equally often. Beginning on trial 52, control and test trials were interspersed among baseline trials. Test trials presented the same set of 12 novel views used in Test Series 1 for the pigeons. Each test image was presented 3 times.

### Data Recording and Analysis

All data presented are from unreinforced control and test trials. Each response was recorded in terms of touch-screen coordinates that ranged from 0 to 640 in the horizontal dimension and 0 to 480 in the vertical dimension. Analysis of individual trial performance indicated that pigeons often made a burst of pecking immediately upon presentation of an image, and the location of first few pecks was random with respect to the goal. These pecks appeared to reflect orienting behavior rather than search behavior. In addition, casual observation indicated that the pigeons occasionally pecked directly at the frame of the touch-screen, or occasionally placed a foot on the bottom frame. These behaviors triggered the touch-frame but did not appear to constitute search pecks. Therefore, the first three pecks made on every trial, and all pecks that fell within 20 pixels from the far edges of the search space, were excluded from the analysis of the data for pigeons.

Responses were considered correct if they were within 25 pixels of the center of the goal in both dimensions. For all tests conducted with images in which the visual information was manipulated (e.g., landmarks or background removed or shifted), accuracy was determined according to the location of the goal in the image prior to these manipulations. Accuracy was calculated as correct responses divided by the total responses. All accuracy scores presented are averaged across all test trials and, except for the detailed results presented in the table, are also averaged across views.

It should be noted that chance level accuracy is very low. For example, if subjects responded randomly on the screen, the probability of a response falling within the goal area is less than .01. For our determination of chance level, however, we took into account the possibility that subjects might learn to respond only within the range of screen locations in which the goal is sometimes found. If subjects responded randomly in this range, the probability of a response falling in the 50 by 50 pixel goal area is .03.

## Results

Acquisition of accurate searching by the pigeons was slow. Two of the pigeons failed to meet criterion within 200 sessions following the start of search training, and were dropped from the study. The remaining three birds required 89, 112 and 114 sessions from the start of search training until they were ready for testing.

Transfer to Novel Views. The results of the transfer tests are shown for pigeons (top panel) and humans (bottom panel) in Figure 4-5. The left two bars for pigeons show the results of Series 1, which included tests with 6 training images (Control) and 12 novel images (Trans 1). The right two bars for pigeons show the results of Series 3, in which pigeons were tested with 6 additional novel images (Trans 2) and with those same images with all visual information removed (No Visual). Humans did not receive the Series 3 tests. Accuracy scores for each individual control and test image are shown in Table 4-1.

For pigeons in Series 1, overall mean accuracy on transfer tests with novel views (.303) was only slightly lower than the overall mean accuracy on control tests (.353), and the difference failed to reach significance, $t(2) = 3.84$. Moreover, accuracy on transfer tests was significantly higher than expected by chance (.03), $t(2) = 8.58$. In Series 3, the overall mean accuracy on novel view tests (.336) was again significantly higher than expected by chance, t(2) = 13.73, and was also higher than the overall mean accuracy on tests with the visual information removed from the images (.012), t(2) = 1.59. Accuracy with no visual cues was significantly lower than the estimated chance level, t(2) = 4.99.

Humans also showed good transfer to novel views of the scene. Their overall mean accuracy on control trials (0.380) did not differ significantly from their overall mean accuracy on transfer test trials (0.401), t(10) = 0.89.

Landmark Shifts (Pigeons only). Shifts of the large landmark near the goal (i.e., the sculpture) produced small but significant shifts in searching in the direction of the landmark shift. Horizontal shifts of the landmark by 2 cm resulted in significant shifts of searching in the appropriate direction (mean = 0.67 cm), t(2)= 8.64, whereas 2 cm vertical shifts of the landmark did not produce significant shifts in the appropriate direction (mean = 0.13 cm), t(2) = 0.76. Closer inspection of the vertical shift results indicated that when the landmark was shifted down, the birds showed a significant downward shift in searching (mean = 0.97), t(2) = 5.30. However, when the landmark was shifted up, the birds showed a nonsignificant shift in the wrong direction (mean = 0.70 cm down), t(2) = 1.37. Averaged across all directions of landmark shifts, 2 cm shifts of the landmark resulted in 0.40 cm shifts in searching in the appropriate direction, which was significantly greater than 0, t(2) =8.20.

## Discussion

These results indicate that at least under some conditions, pigeons can transfer accurate search behavior to novel views of a scene. On unreinforced tests with novel views, pigeons searched with accuracy levels that comparable to their accuracy levels with the trained views. Their accuracy levels with the novel views were also well above the estimated chance levels, and the level of accuracy they achieved when all visual cues were removed from the images. Human participants showed complete transfer to the novel views, searching as accurately with the novel views as with the training views. Interestingly, both pigeons and humans showed considerable variability in accuracy across views, both in the training and transfer sets, suggesting that some perspectives were more difficult than others.

The shift tests revealed that pigeons used the tall sculpture near the goal as a landmark, but they used other cues as well. The birds shifted only part way with the sculpture when it was shifted left, right or down. The birds did not follow the sculpture when it was shifted upwards. Although inspection of Figure 4-4 suggests that two of the upward shift images might be problematic because the landmark appears to "float" above the snow, the birds also failed to follow the upward landmark shift even in the image in which the landmark remained in the snow. At present, we have no explanation for the anomalous results of the upward landmark shifts. In this experiment, pigeons learned to locate a goal in images of an outdoor scene viewed from varying perspectives. The scenes provided a rich set of visual cues that maintained a constant relationship to the goal in the represented 3-D space. The 2-D relationship of these cues to the goal, however, varied across images. The cue manipulation test suggested that search behavior was controlled by more than one source of spatial information, because search shifted only part way toward the shifted landmark. This evidence that search behavior is controlled by multiple sources of spatial information is consistent with results from search tasks conducted on the laboratory floor (Cheng, 1992).

Although pigeons in both Spetch, et al. (1998, Experiment 1) and the current experiment learned to search accurately in images depicting varying views of a scene, only in the current experiment did the pigeons show strong transfer of accurate search to novel views of the same scene. The weak transfer in Spetch et al. (1998; Experiment 1) suggested that the pigeons may have memorized the two-dimensional spatial relationships between landmark cues and the goal specific to each of the six training views, rather than learning the three-dimensional spatial relationships in the represented scene. On the other hand, the occurrence of strong positive transfer in the current experiment suggests that under some circumstances pigeons may be able to learn the three-dimensional spatial relationship depicted in different training views of a scene.

Although the positive transfer to novel images seen in the current experiment suggests the use of 3-D information, we cannot conclusively rule out the use of a 2-D strategy. Each transfer view was novel and differed to some extent from any of the training views. However, the training set used in the current experiment was large, and some transfer views looked quite similar to one or more of the training views, differing only by a lateral, or vertical displacement. In such cases, transfer could be obtained if the pigeons a) memorized the 2-D relationships in each training image or in subsets of training images, b) generalized from the most similar training image to the transfer image, and c) shifted their searching in accordance with the horizontal and/or vertical displacement of the visual information from the training to the transfer scene (or, in other words, searched at the same 2-D vector from landmark(s) as in the training scene). Such a strategy could account for accurate performance with several of the transfer images, but does not appear to account well for all of the transfer results. For example, Transfer Image 2, appears most similar to Training Image 2, but the orientation is rotated, so that vectors from landmarks to the goal differ (unless one uses information in the picture to adjust the directional frame of reference). Yet accuracy with Transfer Image 2 is not substantially lower than accuracy with Training Image 2. Transfer Image 18 appears most similar to Training Image 12, but it is viewed from a different vantage point (as can be seen by the position of the tree in the bottom of the image, and by the appearance versus occlusion of the second vertical component of the sculpture). Generalization between these images and application of the same vector from any of the salient visual cues (e.g., the building, the tree at the bottom or the sculpture) should produce a systematic errors in search location. Yet accuracy was slightly higher with the transfer image than with the trained image. Thus, at least some of the transfer results seem more consistent with the possibility that the birds did in fact attend to the 3-D relationships in the scene. Nevertheless, unequivocal evidence of 3-D processing is difficult to provide, and likely will require the convergence of results from many different experiments.

Several differences between Spetch, et al. (Experiment 1) and the current experiment could underlie the difference in transfer results. First, birds in the current experiment were trained with many more different views of the scene than were birds in Spetch et al. (28 versus 6), which may have discouraged memorization of the spatial relationships specific to each view and facilitated attention to the three-dimensional relationships that were constant across views. Training with more exemplars also enhances stimulus generalization (e.g., Wasserman et al., 1996). Second, to the human eye at least, the scene depicted in the current experiment seems to provide more depth cues. Third, the pigeons in the current experiment, unlike those in Spetch el al., had prior outdoor experience, and therefore had some basis for recognizing at least some types of objects depicted in the scene. However, recent results from Spetch, Kelly and Reid (1999) suggest that real-world experience may not be an important factor in these experiments. Determining which of these factors is responsible for the difference in results is a challenge for future research.

Table 4-1

Screen coordinates of the target location for all training and transfer images and mean proportion of responses in the goal (with standard error of the mean in parentheses) by pigeons and humans for images used for control and transfer testing.

| | Target Coordinates | Pigeons | Humans |
|---|---|---|---|
| Training Images | | | |
| 1 | 305, 198 | .389 (.044) | .422 (.074) |
| 2 | 422, 306 | .352 (.067) | .580 (.058) |
| 3 | 108, 328 | .301 (.024) | .414 (.058) |
| 4 | 195, 270 | .616 (.061) | .289 (.084) |
| 5 | 117, 218 | .347 (.024) | .416 (.069) |
| 6 | 392, 342 | .332 (.060) | .303 (.072) |
| 7 | 265, 252 | .424 (.039) | .571 (.067) |
| 8 | 196, 270 | .261 (.063) | .271 (.055) |
| 9 | 473, 372 | .426 (.085) | .296 (.079) |
| 10 | 210, 372 | .275 (.035) | .350 (.093) |
| 11 | 295, 312 | .221 (.046) | .311 (.081) |
| 12 | 208, 328 | .296 (.029) | .335 (.076) |
| 13 | 412, 239 | .269 (.058) | - |

Table 4-1 continued

| | | | |
|---|---|---|---|
| 14 | 335, 295 | .285 (.020) | - |
| 15 | 294, 265 | .252 (.051) | - |
| 16 | 282, 225 | .287 (.047) | - |
| 17 | 420, 223 | .283 (.013) | - |
| 18 | 285, 208 | .353 (.024) | - |
| 19 | 310, 179 | .484 (.064) | - |
| 20 | 280, 303 | - | - |
| 21 | 479, 278 | - | - |
| 22 | 112, 334 | - | - |
| 23 | 125, 325 | - | - |
| 24 | 390, 370 | - | - |
| 25 | 336, 330 | - | - |
| 26 | 358, 340 | - | - |
| 27 | 509, 320 | - | - |
| 28 | 255, 290 | - | - |
| Transfer Images | | | |
| 1 | 269, 339 | .290 (.088) | .342 (.073) |
| 2 | 450, 252 | .339 (.027) | .448 (.097) |
| 3 | 345, 240 | .232 (.008) | .337 (.054) |

Table 4-1 continued

| | | | |
|---|---|---|---|
| 4 | 420, 214 | .402 (.062) | .311 (.068) |
| 5 | 122, 320 | .446 (.026) | .378 (.088) |
| 6 | 415, 241 | .477 (048) | .468 (.057) |
| 7 | 088, 248 | .213 (.041) | .225 (.048) |
| 8 | 252, 342 | .168 (.051) | .303 (.087) |
| 9 | 260, 351 | .175 (.052) | .182 (.056) |
| 10 | 468, 340 | .150 (.042) | .494 (.082) |
| 11 | 325, 359 | .202 (.055) | .764 (.057) |
| 12 | 330, 198 | .547 (.128) | .499 (.058) |
| 13 | 413, 291 | .332 (.027) | - |
| 14 | 380, 306 | .352 (.028) | - |
| 15 | 122, 322 | .447 (.063) | - |
| 16 | 292, 265 | .113 (.041) | - |
| 17 | 374, 306 | .399 (.026) | - |
| 18 | 254, 304 | .37 (.071) | - |

Note. Images are numbered in the order shown in Figures 4-1, 4-2 and 4-3. Target coordinates are reported in pixels and are ordered x, y respectively.

Figure 4-1. Images showing 18 of the 28 training views presented. Images are numbered consecutively from left to right and then from top to bottom. The goal was located near the tall black sculpture. The small box used to mark the goal was edited out of the images after preliminary training and was not present during any baseline or test trials.

# Training Images









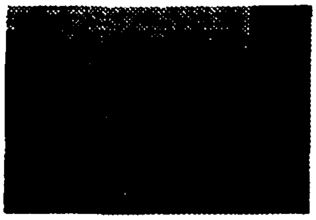



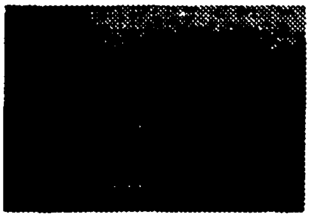


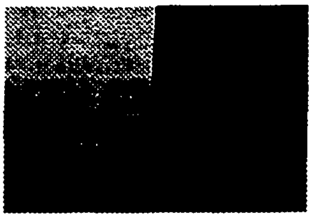




Figure 4-2. The 10 remaining training views. The last image is shown in larger size so that details can be seen, and the goal is indicated with an arrow. The small box at the goal was edited out of the images following preliminary training.

# Training Images continued





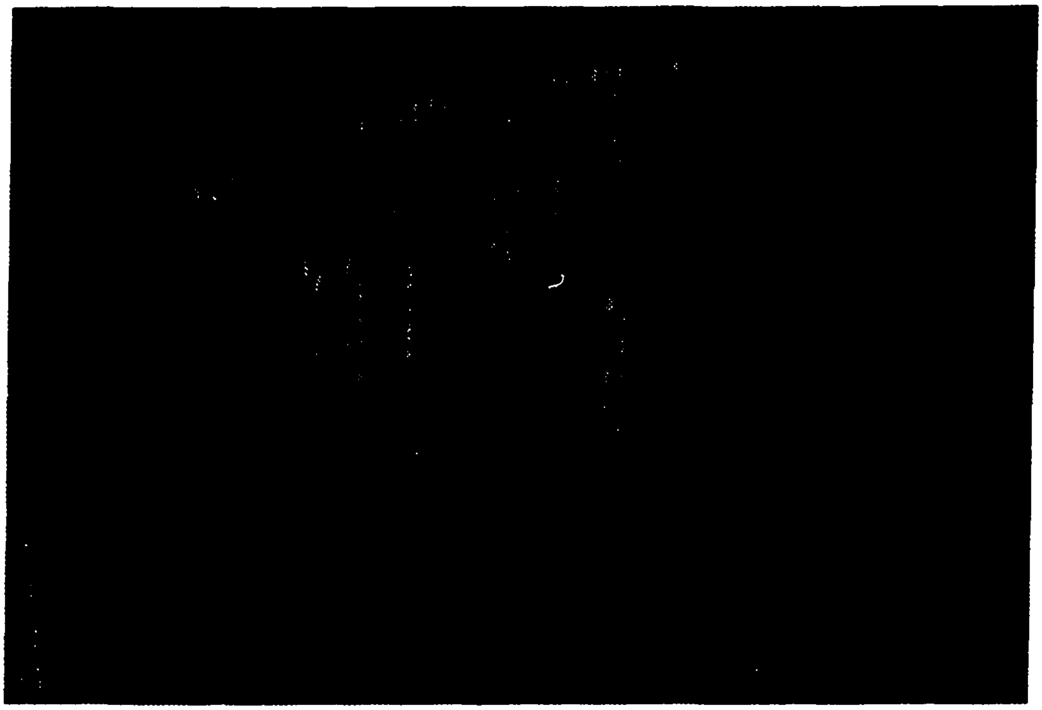
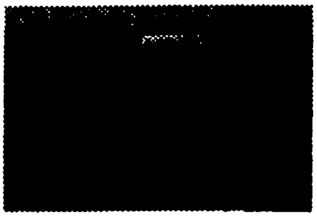


Figure 4-3. Novel views used for transfer testing. The first 12 images were used for humans and in Series 1 for pigeons. The last 6 images were used in Series 3 for pigeons.

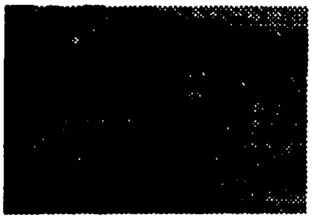
# Transfer Images













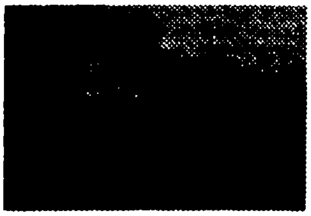


Figure 4-4. Images used for landmark shift tests and a sample of the images used for no visual cue tests for pigeons.

# Shift Tests

## Left Shift



## Right Shift

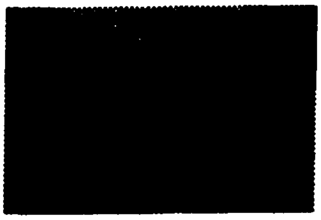


## Upward Shift



## Downward Shift





## No Visual Cues

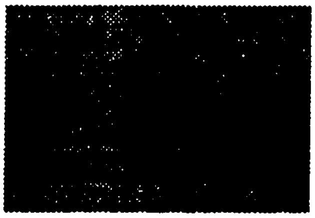
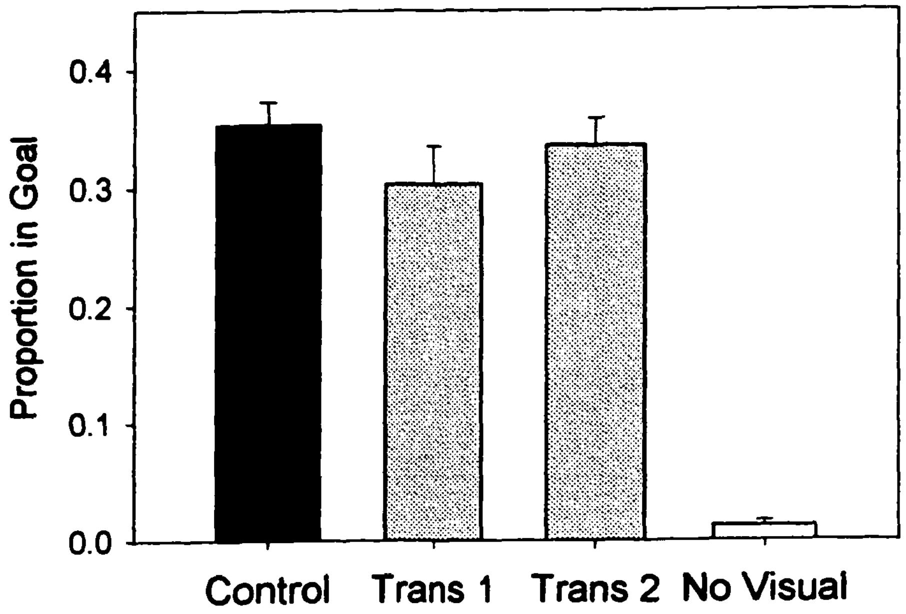


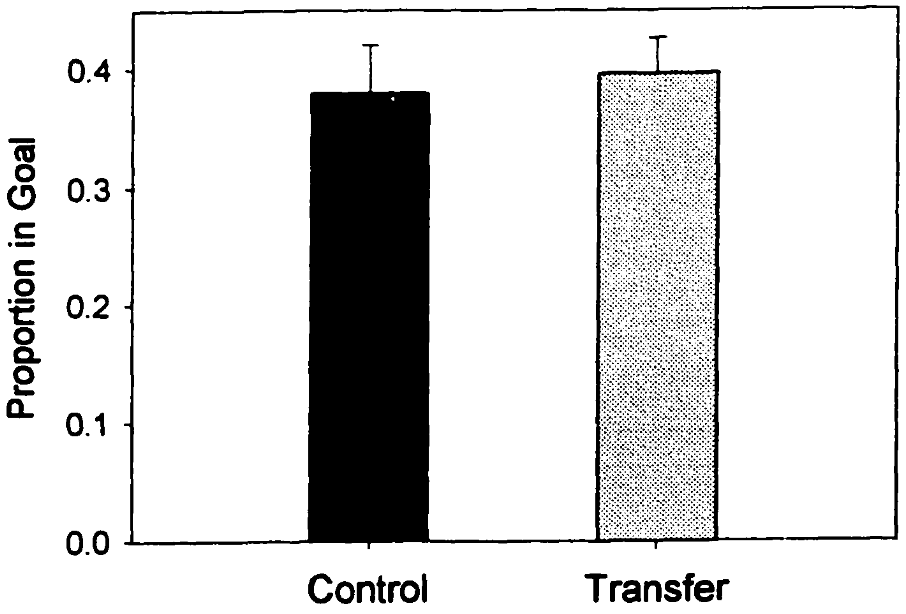
Figure 4-5. Transfer test results for pigeons and humans. For pigeons, the two left bars show mean accuracy on control tests (training views) and transfer tests with the novel views presented during Series 1 (Trans 1). The right two bars show pigeons mean accuracy on the transfer tests with novel views (Trans 2) and the tests with images containing no visual cues (No Visual) during Series 3. Humans received Series 1 tests only.

## Experiment 2

### Pigeons



### Humans



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# CHAPTER 5

# PIGEONS ENCODE RELATIVE GEOMETRY

A version of this chapter is in press in Journal of Experimental Psychology: Animal Behavior Processes, 2001.

Establishing a directional frame of reference is an essential first step in many navigation and spatial search problems. Consider, for example, an animal that needs to remember the location of a goal, such as a nest or source of food. The animal may encode the location in terms of distance and direction from the nearest landmark, for example a tall tree, and then later use that landmark to navigate to and search for the goal. Many studies have demonstrated such landmark-based search in both vertebrate and invertebrate species (see Cheng & Spetch, 1998; Collett & Zeil, 1998). Clearly, however, an accurate match between a landmark-to-goal vector perceived during searching and that stored in memory depends on the establishment of a stable directional frame of reference. As discussed by Gallistel (1990), "sense of direction is profoundly important to an animal" (p. 201). This process is sometimes referred to as "determining heading", "getting bearings" or "getting oriented".

Given the fundamental importance of directional determination for spatial search, it is hardly surprising that many animals seem well equipped to accomplish this step using various sources of information. Global celestial cues, such as the sun and stars appear to provide a common source of directional information for navigation by birds and insects but other cues serve as back-up sources of information (e.g., for reviews see Able, 1991; Dyer, 1996). In smaller or enclosed spaces heading may be determined by the configuration of landmarks or surface features (e.g., Suzuki, Augerinos & Black, 1980; Kelly, Spetch & Heth, 1998) or by the geometric shape of the environment (e.g., Cheng, 1986).

Determining heading from the geometric shape of the environment is a particularly interesting process that was first demonstrated by Cheng (1986) in rats. Cheng trained rats to search for food that was hidden in one corner of a rectangular enclosure. Distinctive features differentiated the walls and corners. Rotation of the rats prior to the trial disrupted inertial cues, and cues external to the apparatus were blocked or masked. In a working memory task, the rat was shown and allowed to eat a portion of food in one randomly selected corner and was then removed. The food was then buried in the same corner and the rat's task was to relocate it. Strong control by geometry was indicated by systematic rotational errors, in which rats frequently confused the correct corner with the geometrically equivalent corner (which contained incorrect features). In a reference memory version of the task in which food was hidden in the same corner on every trial, the rats eventually learned to use the features to distinguish the two geometrically correct corners. However, transformation tests revealed that geometric shape dominated over features in controlling the rats' search behavior because the rats did not follow the correct feature when it was moved to a geometrically incorrect corner. Additional evidence for the primacy of geometric cues in rats was provided by Margules and Gallistel (1988). Young children also have been found to attend to geometric shape to the exclusion of features in a disorientation task that is analogous to Cheng's working memory task (Hermer & Spelke, 1994; 1996).

Birds, specifically pigeons (Kelly et al., 1998) and chicks (Vallortigara, Zanforlin, & Pasti, 1990) also have been found to encode geometric shape of an enclosure, although control by geometry does not appear to dominate over control by featural information. Instead, geometric shape and features appear to share control of searching, with the weighting given to each dependent on initial experiences. Specifically, Kelly et al. examined choice performance on conflict tests in which features and geometry were placed in opposition, for two groups of pigeons. One group was trained with distinctive features present in each corner of the enclosure from the start of training (i.e., with both features and geometry). The other group was trained first without the features (geometry only) and then was retrained with the features added. The pigeons trained with features from the outset showed primary control by the features, whereas the pigeons trained with geometry first showed shared control by both features and geometry.

Although species and experiential factors may alter the weighting of geometric and featural cues, the aforementioned studies show that rodents, birds and humans encode the geometric shape of an enclosed environment and are able to use this information to locate a goal. Thus, sensitivity to the geometric properties of an environment has considerable species generality. However, little is known about the mechanisms underlying the encoding of geometric shape, or the form in which this geometric information is encoded.

Consider for example, a case in which the animal searches in a rectangular environment and finds the goal in a corner that has a 200 cm wall on the left and a 100 cm wall on the right. The geometric information could be encoded in terms of one or both of these absolute metrics. That is, when facing the corner at which the goal is found, the animal could encode the length of the wall on its right or the length of the wall on its left, or both. Even if only one of these absolute lengths is encoded, this information would specify the correct corner and its geometrically equivalent corner, and the information would not match that perceived at either of the other two corners. Thus, encoding of absolute metrics, whether specified by visually perceived length of a wall or steps taken to travel along a wall, is one simple way in which geometric shape could be encoded. Another way in which geometric shape could be encoded is by attending to relative metrics (e.g., the correct corner has a longer wall on the left side than on the right side). In other words, the animal might extract a shape that is independent of absolute metrics.

This question of whether geometric information is encoded in terms of absolute or relative metrics can be addressed through size transformation tests which preserve shape but alter the absolute metrics. Of all the previous studies which have demonstrated use of geometric shape of an enclosure for determining heading, only the Kelly et al. (1998) study with pigeons included a size transformation test. Unfortunately, this test (referred to as the "New Wall Test") was conducted in the presence of distinctive featural information and all pigeons showed strong reliance on the features during these tests. Thus, it did not provide a sufficiently sensitive test of whether geometric information is encoded according to absolute or relative metric properties.

On intuitive grounds, one might expect that encoding would be based on relative metrics because such encoding requires less precision and is more flexible. Moreover, theoretical discussions of rats' encoding of geometric information have assumed that metric relations, rather than absolute metrics, are encoded. For example, Gallistel (1990) assumes that relational learning must underlie the rotational error displayed by rats and he argues that: "only the combination of a sense relation (left-right) and a uniquely metric relation (longer-shorter) renders one pair of diagonally opposite corners in a rectangle geometrically distinct from the other pair" (p.199). Nevertheless, these assumptions have not been tested, and as we argued previously, a strategy based on absolute metrics is possible given that only one size of rectangle is used in training. Moreover, one must be cautious about assuming that an animal will solve a task in the intuitively most likely fashion. For example, in several situations pigeons seem prone to using a seemingly more difficult strategy based on absolute information than one based on relational information. For example, in matching-to-sample tasks, transfer tests suggest that pigeons often do not to learn a relational "same-as" rule (e.g. Wilson, Mackintosh & Boakes, 1985a), although they can do so under certain training conditions, such as long sample exposure (Wright, 1997) or trial-unique stimuli (e.g., Wright, Cook, Rivera, Sands & Delius, 1988). Pearce (1991) found little evidence that pigeons could categorize stimuli on the basis of whether two bars are similar or different heights and he concluded that his results "suggest that when for humans there exists an obvious relational solution to a problem, pigeons are extremely reluctant to adopt it."(p. 157). Wills and Mackintosh (1999), in discussing the previous literature on absolute versus relational learning suggested that "one interpretation of the pattern of results is that, by comparison with some other animals, pigeons are remarkably insensitive to the relationships between stimuli" (p.32). They compared discrimination learning and transposition effects in pigeons under simultaneous versus successive presentations of stimuli differing in luminance or number of vertices and they found that simultaneous viewing facilitated discrimination and transposition only for the luminance stimuli. Wills and Mackintosh suggested that even this evidence for relational learning in pigeons with luminance stimuli does not necessarily imply learning of a conceptual relation (e.g., "brighter than"). Instead, the effect could be based on a lower-level sensory process in which the perceived difference between stimuli is enhanced by the contrast between neighboring stimuli.

Recent studies of rule learning in landmark-based spatial search have revealed another situation in which pigeons, and at least some other species, seem surprisingly likely to learn on the basis of absolute information rather than learning what seems to humans an obvious and simpler relational rule. For example, when trained to find a goal that is hidden in the middle of an array of identical landmarks, adult humans learn an abstract middle rule, as revealed by expansion tests in which the landmarks are spread farther apart (Spetch et al., 1996; 1997). Adult humans also learn a relational rule when the goal is located between and below an array of two identical landmarks (Spetch et al., 1996). By contrast, pigeons (Spetch et al., 1996; 1997) and gerbils (Collett, Cartwright & Smith, 1986) trained with similar landmark arrangements did not learn abstract relational rules, but instead appeared to learn the absolute spatial relationship between individual landmarks and the goal. Squirrel monkeys (Sutton, Olthoff, & Roberts, 2000) and marmoset monkeys (MacDonald, Spetch & Cheng, 1998) also do not appear to learn a relative middle rule when trained to find a goal in the center of an array of four landmarks.

A few studies with other species, however, have found results that suggest some control by relative spatial information. Kamil and Jones (2000) trained Clark's nutcrackers to find a goal that was hidden at a fixed relative location from two landmarks that varied across trials in their inter-landmark distance. The goal was located at the midpoint between the landmarks or at a fixed distance or direction away from the landmarks. The Nutcrackers learned a geometric rule as evidenced by the ability to search at the appropriate relative location on transfer tests with new interlandmark distances. The contrast between these results and those found for pigeons could reflect training and/or species differences. Both are reasonable candidates because varying interlandmark distance provides training with multiple exemplars of the relational rule which is known to enhance relational learning (Wright et al.,1988), and because differences in relational learning between Corvids and pigeons have been found in other tasks (Wilson et al., 1985b). In another recent study, chicks were trained to find food hidden in the center of an square enclosed arena (Tommasi & Vallortigara, 2000). Tests in which the size of the arena was transformed revealed that the chicks learned both the relative and the absolute distance from the arena walls. That is, search was concentrated both in the center of the new arenas, and at locations that maintained the same absolute distance from the walls as in training. To our knowledge no other species have yet been tested on this task. Finally, recent studies on place cell firing in rats suggested strong sensitivity to absolute distances from walls and some control by relative distances (O'Keefe and Burgess. 1996). Whether these results are general across species and how they translate into search behavior remains to be determined.

It should be noted that none of the aforementioned rule-learning studies focused on the use of absolute versus relative geometry for determining heading in the environment. In the landmark-based search studies, numerous external cues were available for orientating within the environment and these were not controlled or investigated. In the Tommasi and Vallortigara (2000) study with chicks, orientation within the environment was not required, and indeed was not possible because there were no directional cues provided by either the shape or features of the enclosure and all external cues were blocked. In the O'Keefe and Burgess (1996) study on place cell firing, cues external to the arena appeared to exert some directional control. We are not aware of any investigations to date, in any species, which have addressed the question of whether animals attend to relative or absolute metrics when determining heading exclusively from the geometric shape of their environment.

Accordingly, we trained pigeons to locate a single reinforced container in a large rectangular enclosure with identical features at all corners. Steps were taken to eliminate inertial and external cues so that geometric shape of the enclosure was the only available cue. Once the pigeons learned the geometry, as evidenced by preferentially searching in the geometrically correct corners, the geometric properties of the environment were altered by changing the shape and/or size of the enclosure on unreinforced test trials. If the pigeons had encoded only the absolute geometry of the environment, then resizing the apparatus should disrupt accurate search behavior. However, if the pigeons extracted the relative geometric properties of the enclosure, then they should continue to search in geometrically correct corners despite resizing of the apparatus, but they should be disrupted if the shape is changed.

## Methods

### Subjects

Pigeons. Three Silver King pigeons, all experimentally naive in open field searching tasks, served as subjects. The birds were housed in large individual cages under a 12-hour light:dark cycle (with light onset at 6:00 am). All birds were maintained at approximately 85% of their free-feeding weights by maple peas during experimental sessions and supplemental feedings of Kay Tee pigeon pellets after sessions. Water and grit were available ad lib in the home cages.

### Apparatus

The experimental apparatus was a completely enclosed, uniformly white large rectangular enclosure constructed to control for cue availability (similar to Kelly, et al. 1998). The walls of the apparatus were constructed from 5cm thick Styrofoam covered with opaque white plastic. Thick white cloth sheets were used for the upper walls and for the suspended ceiling. Specific measurements of the entire apparatus are provided in Figure 5-1. Approximately 5 cm of aspen chip bedding covered the floor of the apparatus. A video camera, for recording responses, was positioned in the center of the apparatus. The majority of the camera was hidden behind the suspended ceiling so that only the lens of the camera was visible. Four identical tin containers (8.5 cm diameter and 3.5 cm height) were secured to the floor of the apparatus by a piece of velcro located 20 cm from each corner of the apparatus. Situated behind each container was a single glass bottle (height 25 cm and width 14 cm) filled with grit and covered with yellow construction paper. Around the middle of the bottle was a single brown stripe. The bottles were placed behind the containers to ensure each corner was equally salient. White noise was played through 2 speakers (centered along the exterior of the long walls) to mask any exterior noise that could be used as cues.

### General Procedures

Experimental sessions consisted of 10 trials, and were conducted once per day, five days per week at approximately the same time each day for a given bird. Each pigeon was carried to the experimental room in an opaque plastic container and placed within one of two completely enclosed metal holding cages that were located in different ends of the testing room. The selected holding cage randomly alternated across trials. Prior to the beginning of each trial the pigeon was rotated while inside the holding cage for 1 min at approximately 12-14 rpms. This rotation was necessary to eliminate use of inertial cues. The subject was removed from the metal cage and placed directly into the plastic container. From the container the pigeon was placed into the apparatus according to a predetermined random entry position (one per wall).

The corner that provided food was constant across trials for a given pigeon but differed across the three pigeons. On each trial, the pigeon was given a maximum of 5 min to locate the reinforced container and/or peck through the paper towel covering of two containers. The first peck directed to any container that broke the paper towel covering was consider the choice on each trial. Once the pigeon pecked at two of the containers or 5 min elapsed the lights in the room were extinguished and the pigeon was removed from the apparatus and placed in a holding cage. The lights were then illuminated, the apparatus was prepared for a new trial and the bird was rotated.

Between trials all debris was removed from the bedding and the four identical containers and bottles behind each container were randomly re-arranged. Periodically between sessions, the four speakers, the walls of the enclosure, the curtains and the bedding were rearranged or replaced. These procedures were designed to eliminate or disrupt use of any subtle cues that might have provided non-geometric information.

### Shaping Procedures

While in their home cages, pigeons were provided with tin containers filled with grit and a small amount of maple peas. Once the pigeons were quickly eating from the containers, a piece of paper towel covering was placed over the top and secured with an elastic band. The pigeons were required to peck through the paper towel to gain access to the food. Once the pigeons were readily pecking through the paper towel, shaping in the experimental apparatus begun.

Experimental training was divided into five stages to progressively acclimatize the bird to the novel surroundings and train for accurate searching behavior. In the first stage a single uncovered container with 4 maple peas was placed in the positive corner. The pigeon was required to simply approach and eat from the container within 5 min. If the pigeon did not eat from the container within the allotted time it was removed from the apparatus. Once the pigeon successfully ate from the container on all 10 trials, with no trial taking longer than 5 min, the pigeon was moved onto Shaping 2. Shaping 2 was identical to Phase 1 except that three identical unreinforced tins were added, one in each of the remaining three corners. Again, if the pigeon ate from the reinforced tin within 5 min on each of the trials it was moved onto Shaping 3. In Shaping 3 all of the tins were covered with paper towel and the pigeon was required to peck through the paper towel covering in order to obtain the hidden food. Successful completion of Shaping 3 required that the pigeon maintain the requirements of Shaping 2 while maintaining 80% accurate choice responding. Since no cues were present to discriminate the positive corner from its geometrically equivalent corner, choices to the two geometrically equivalent corners were scored as correct choices in this accuracy calculation.

The fourth and fifth shaping phases were administered to prepare the birds for a reduction in the overall amount of reinforcement available during a session. In Shaping 4, three out of the 10 trials were non-reinforced and in Shaping 5, five out of the ten trials were non-reinforced. The criteria for successful completion of these phases were identical to those in Shaping 3 with the added requirement that to complete Shaping 5 the pigeons must maintain 80% accuracy over two consecutive days. Once the birds completed the requirements for Shaping 5 they were moved onto testing.

### Testing

Three tests, which altered the structure of the experimental apparatus, were administered to determine whether pigeons were using the absolute or the relative geometry of the rectangular enclosure to locate the correct corner. All test and control trials were conducted as non-reinforced trials to eliminate any food related cues. The control trials were visually identical to the baseline trials but were non-reinforced. On test trials, the enclosure was altered to change the size or shape.

The three types of test trials and the control trials occurred in mixed order and were interspersed randomly among reinforced baseline trials within each test session.

The control and test trials were presented on randomly selected trials within each session with two constraints: 1) they never occurred on the first trial, and 2) they never occurred on two consecutive trials. Each experimental session contained a maximum of two control trials and three test trials. To maintain accurate responding, some experimental sessions contained only one control trial and two, randomly selected, test trials.

Testing continued until each bird had completed a minimum of 68 control trials (one bird received 72) and 18 trials of each test type. Occasionally a bird would fail to make a choice within the 5 min period on a test or control trial. When this happened the test or control trial was repeated on a later day. If accuracy during a session fell below 80% (calculated for baseline trials only), or if a bird failed to complete one of the trials withing the 5 min period, the bird was retrained for a minimum of two days following the criteria outlined for Shaping 5. One bird was given a total of 12 retraining sessions and another was given a total of 14 retraining sessions to maintain accuracy. Approximately half way through testing, the experiment was interrupted for several days and a new researcher began testing the birds when the experiment resumed. Therefore each bird was retrained to criterion with the Shaping 5 procedures before testing was resumed. This required a range of 3 to 16 retraining sessions for the three birds.

The Medium Rectangle test was a size transformation in which a replication of the experimental apparatus was constructed from the same material as the training apparatus but with length and width 2/3 the size of the original (133 cm, 67.7 cm; see Figure 5-1). This new apparatus was centered in the middle of the training apparatus. It should be noted that the medium rectangle perfectly preserves the relative geometry of the training enclosure, but the length of both the long and the short walls are changed. Moreover, length of the long wall of the medium rectangle (133 cm) is more similar in absolute length to the short wall (100 cm) than to the long wall (200 cm) of the original enclosure. Thus, search behavior that is based on absolute metrics should be completely disrupted by this manipulation.

The Small rectangle test was a more drastic size transformation in which the short walls of the enclosure now became the longer walls. For this test, two identical walls were inserted 50 cm apart and parallel to the two short walls of the training apparatus. The addition of the two walls created a new, much smaller enclosure (length 100 cm and width 50 cm; see Figure 5-1).

The Square test was a control test to ensure that accurate choice of the geometrically correct corners did in fact depend on the geometric shape of the enclosure. The square test altered the overall structure of the experimental apparatus such that now the distance between each of the walls was equidistant (see Figure 5-1). Two identical walls were inserted 100 cm apart and parallel to the two short walls. Thus, in the square test all of the walls were identical to the short walls of the training apparatus and none of the corners could be distinguished on the basis of geometry. Thus, choice of the corners should be random whether the birds had encoded relative or absolute geometry.

During both of the size transformation tests, accuracy was scored according to relative geometry. For example, for a bird with “a” as the positive corner, “a” and “c” would be scored as correct choices on control and medium rectangle tests, whereas “b” and “d” would be scored as correct on Small rectangle tests (see Figure 5-1). On Square tests, accuracy was scored according to the orientation of the corners in the test room. That is, "a" and "c" would be scored correct for a bird that had "a" as the positive corner. Choices were recorded manually during the sessions and all control and test trials were videotaped. The video tapes were independently re-scored, for corner of first choice peck, by the researcher and by a student naive to the experimental predictions. No discrepancies were found.

## Results

All birds progressed at a reasonable rate through the shaping procedures. Two birds required a total of 12 shaping sessions and one bird required a total of 22 shaping session to complete all five shaping phases.

The overall pattern of test results indicated that the birds had encoded relative geometry. Figure 5-2 shows the overall accuracy in choosing the corners that were correct according to relative geometry on control trials and on each of the transformation tests. As expected, accuracy was very high on control trials, with almost all choices being made to the two geometrically correct corners. Accuracy remained high on the Medium Rectangle test in which relative geometry was preserved but absolute geometry was distorted. Accuracy decreased on the Small Rectangle test and fell to chance on the Square test. A repeated measures ANOVA with test type as the factor revealed a significant effect of test type on accuracy $\underline{F}(3,6)=20.7$; $\underline{p}<0.001$). Newman-Keuls post-hoc comparisons showed only the following differences to be significant: Control versus Small Rectangle, Control versus Square, and Medium Rectangle versus Square (all $\underline{p}$s <

0.01).

Three types of evidence confirmed that the accurate choices on Control and Medium Rectangle tests were controlled by geometry rather than extraneous external or internal cues associated with the positive corner. First, on Square tests, which removed geometry, the birds chose randomly and did not preferentially choose the corner that was oriented the same way in the room as the positive corner during training. Specifically, the mean proportion of choices of the positively-oriented corner was 0.22, which is not significantly different from chance level of 0.25, $\underline{t}(2) = -0.43$, $\underline{p} > 0.1$. Second, on the Control and Medium Rectangle tests, the birds were not significantly more likely to choose the positive corner than the geometrically equivalent corner. The proportion of geometrically correct choices that were to the positive corner was not significantly above 0.5 for either the Control tests [mean = 0.621, $\underline{t}(2) = 1.86$, $\underline{p} > 0.1$] or the Medium Rectangle test [mean = 0.493, $\underline{t}(2) = -0.17$, $\underline{p} > 0.1$]. The third and perhaps most convincing piece of evidence is provided by an analysis of choices to the three non-correct corners. If extraneous cues rather than geometry controlled choice of the positive corner, one would expect that incorrect choices would be randomly distributed among the three remaining corners, or might even favor the corner than is closest to the correct one. Therefore, we excluded choices of the positive corner and analyzed choices made to the remaining three corners. The proportion of choices made to the corner opposite to the correct one (i.e., the geometrically equivalent one) was significantly above chance (0.33) during both the Control tests [mean = 0.968, $\underline{t}(2) = 35.34$, $\underline{p} <.001$] and during the Medium Rectangle tests [mean= 0.773, $\underline{t}(2) = 4.94$, $\underline{p} < 0.05$]. By contrast, a similar analysis revealed that on Square tests, choice of the corner opposite to the positive one was not significantly above chance [mean = 0.400, $t(2) = 1.13$, $p > 0.1$].

For the Small Rectangle test, the corners that were correct according to relative geometry were incorrect according to both absolute geometry and any extraneous cues associated with the positive corner. Although two of the three birds made more choices to corners that were correct according to relative geometry, the third bird chose randomly on this test. Consequently, although the mean proportion of choices of the corners that were correct according to relative geometry (0.61) was higher than 0.50, the difference failed to reach significance [$t(2) = 1.73$, $p > 0.1$].

## Discussion

The pigeons in this experiment learned to locate hidden food based only on the geometric properties of the experimental environment. When the size of the environment was reduced such that the absolute length of the long wall was made closer to that of short wall in training (i.e., the Medium Rectangle test) the birds continued to search in corners that were correct according to relative geometry. When the walls of the environment were made equilateral (i.e., Square test) the birds responded randomly, indicating that they had not encoded cues external to the testing apparatus but rather were relying on the geometry of the environment. Indeed, the lack of any significant difference between the proportion of responses to the two geometrically correct corners, and the significant preference for the geometrically-equivalent non-correct corner over the other non-correct corners, supports this conclusion.

The lower accuracy in choosing the geometrically correct corners during the Small Rectangle test may suggest a qualification of the conclusion that encoding was based on relative rather than absolute geometry. However, we suspect that the lower accuracy is instead a reflection of performance problems in the very small search space. During test trials with the small rectangle the birds frequently chose the feeder most near their point of entry.

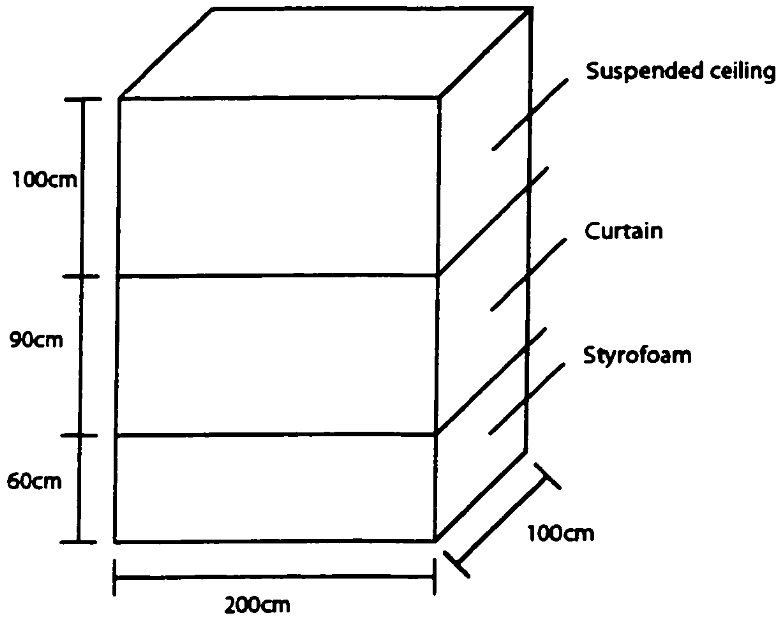
The encoding of relative geometry in this task is particularly interesting for several reasons. Encoding of geometry in terms of relative metrics meant that the birds were sensitive to the relative lengths of the walls (e.g., at the correct corner, the wall on the left was longer than the wall on the right). Our study therefore demonstrates an instance of relational learning that occurred despite training with only a single exemplar (i.e., only a single size of enclosure was used during training). This is interesting given the previous literature suggesting that pigeons are often insensitive to relational cues and tend to favor strategies based on absolute learning. Our results are also surprising given the previous evidence that pigeons show a strong tendency to encode landmark arrays in an absolute rather than a relative fashion (Spetch et al., 1986; 1987). Finally our results provide empirical support for the assumption that geometric encoding is based on encoding of metric relations (Gallistel, 1990).

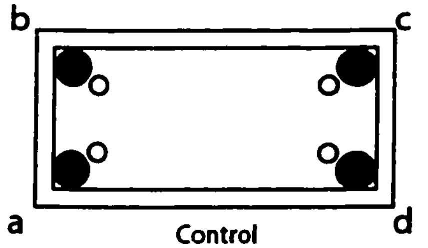
The contrast between our present finding that pigeons encode geometry in terms of relative metrics, and our previous findings that pigeons encode landmark arrays in terms of absolute metrics suggests that the form of the encoding may depend on the nature of the spatial information encoded. In the present study, pigeons encoded geometric information in order to orient themselves in the environment. All extraneous cues were removed, so that the directional heading could only come from the geometric shape. In our previous landmark configuration studies (Spetch et al., 1996;1997), many extraneous cues were present that could be used to establish a stable direction frame of reference. The landmark array was translated within the search space so that these external cues could be used for heading but could not be used for goal localization. However, the stable frame of reference allowed the learning of vectors from landmarks. One possibility therefore, is that encoding of a local configuration of landmark for pinpointing a goal in a well-oriented search space is typically based on absolute metrics, whereas the encoding of geometric shape for determine heading is typically based on relative geometry. Encoding of relative geometry for directional determination might be favored because it provides a flexible means of orienting within a search space regardless of the distance one is from the surfaces that make up the geometry. A strategy based on absolute metrics may be less efficient because it might require traveling to each corner in order to determine whether the absolute metrics do or do not match that stored in memory. On the other hand, absolute distance from local landmarks that are used to pinpoint a goal is likely to be important in many natural search situations.

Our results are also interesting in relation to the recent studies in which young chickens were trained to locate food hidden in the center of an enclosed environment (Tommasi, Vallortigara, & Zanforlin, 1997; Tommasi & Vallortigara, 2000). In this case, as in the present study, there were no external cues and no local landmarks that could be used to pinpoint the goal. On tests in which the size or shape of the enclosure was altered, the chicks spent a considerable portion of time searching at the center of the altered environment, suggesting that they had encoded the relative distance from the walls. Unlike the present study, however, this encoding of the center did not require any directional determination. There was no need to, and in fact no means of, orienting within the search space. Furthermore, searching in the center could be based on a simple rule of searching as far as possible from a wall. The center of the arena satisfies this rule for all walls, regardless of size. Thus, it is not clear whether the relative center rule learned by the chicks entailed a relational, comparison process.

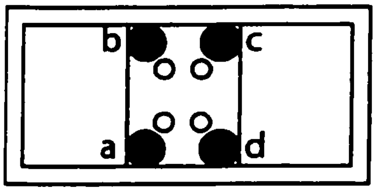
In summary, our results show that when deprived of distinctive featural information, pigeons can encode geometric properties of the environment. During unreinforced test trials in which the overall size of the environment was reduced, while maintaining the relative geometric relations between the walls of the environment, the pigeons continued to distribute their choices among the two geometrically correct corners. This result indicates that the pigeons had extracted the relative geometric shape of the environment rather than encoding only the absolute metrics. Being able to encode the environmental shape using relative geometry may provide pigeons with a more flexible search mechanism than simply relying on the absolute metrics alone.

Figure 5-1. The top illustration shows the dimensions of the experimental apparatus. The bottom illustrations show a overhead view of the experimental setup for the Control and Test sessions. The darkened circles represent the landmark bottles and the open circles represent the food containers. Letters a-d are labels for the four corners.

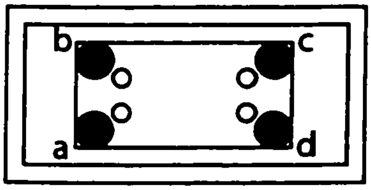




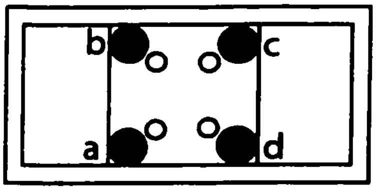
Control



Small Rectangle

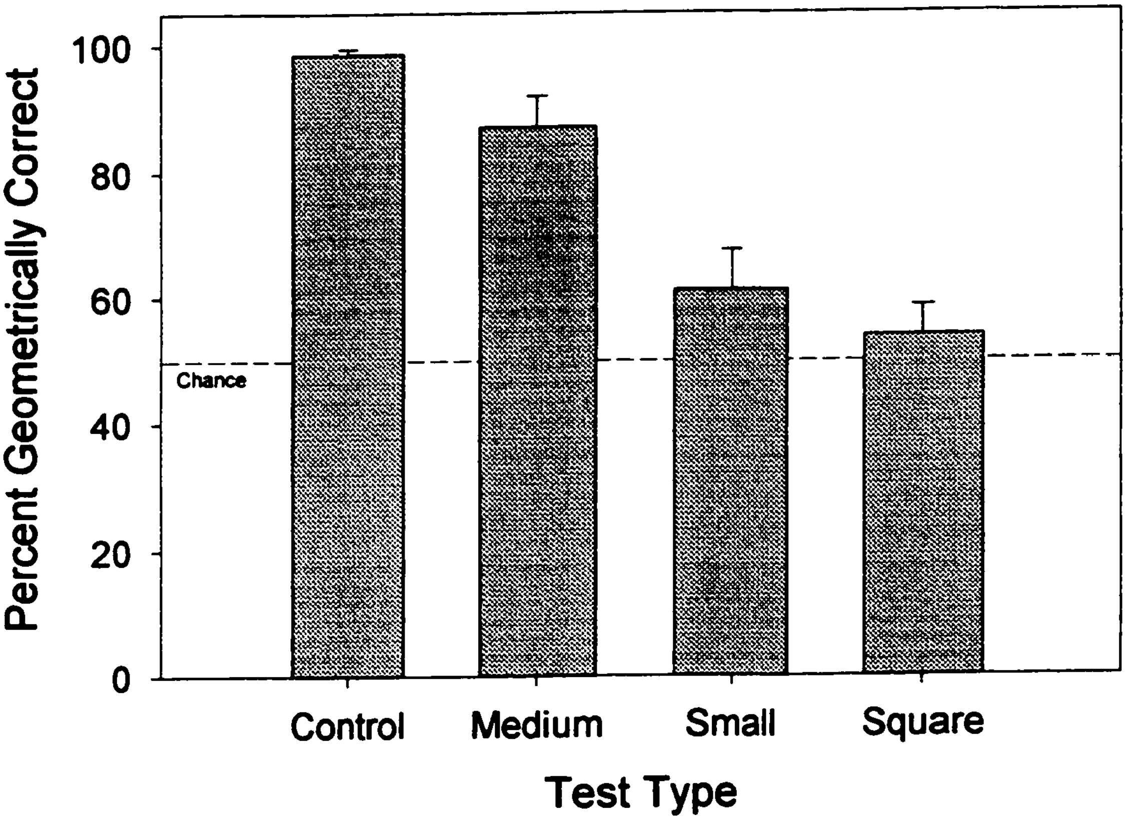


Medium Rectangle



Square

Figure 5-2. The mean percentage of responses to the geometrically correct corners are plotted for the Control and three test conditions. Chance level is 50%.


Percent Geometrically Correct
100
80
60
40
20
0
Chance
Control
Medium
Small
Square
Test Type

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# CHAPTER 6

# PIGEONS' ENCODING OF GEOMETRIC AND FEATURAL PROPERTIES OF A SPATIAL ENVIRONMENT.

**A version of this chapter has been published in Journal of Comparative Psychology, 1998**

Survival within an environment frequently requires efficient processing of spatial information. Spatial abilities underlie activities that are critical for the individual (e.g., establishment of lodging, avoidance of predation and attainment of nourishment) and for a species (e.g., migratory behavior or reproduction), and may involve a variety of mechanisms. Navigation, for example may be achieved through inertial guidance, orientation to a beacon, piloting by use of landmarks, or by the development of a spatial representation of the environment (Gallistel, 1990).

Questions concerning which aspects of an environment are encoded and used in navigation have been addressed in recent research (see Poucet, 1993; Gallistel, 1990 and Cheng & Spetch, in press for reviews). Many studies have shown that animals can encode and use multiple sources of information to locate a goal (e.g., Spetch & Edwards, 1988) and that the primacy of control by different sources of information may differ according to context (e.g., Strasser & Bingman, 1996) or species (e.g. Brodbeck, 1994). One particularly interesting set of results has emerged from studies that have controlled and manipulated the information available for encoding by restricting access to navigational cues in an enclosed environment and by disrupting other positional cues through disorientation techniques (Cheng, 1986; Vallortigara, Zanforlin & Pasti, 1990; and Hermer & Spelke, 1994; 1996). These studies have compared control by navigational cues that depend upon the geometry of the environment with control by cues provided by specific perceptual features in the enviroment. Cheng (1986) and Cheng and Gallistel (1984) demonstrated that rats rely primarily on the geometry of the environment to determine a target position. For example, Cheng (1986) trained rats in a reference memory task to find food that was located in one corner of a rectangular environment containing distinctly different features in each corner. Control by geometry was indicated by the occurrence of systematic rotational errors, in which rats were more likely to choose the corner that was geometrically equivalent to the correct corner (but contained the wrong feature) than the corners that were geometrically incorrect. These errors to the geometrically correct corner indicate that the rats had encoded the metric properties of the environment. Although the rats did eventually learn to use the features to distinguish between the two geometrically correct corners, tests with various transformations of the environment revealed that geometry rather than the featural cues exerted primary control over the rats' search behavior. Specifically, the rats did not follow the correct feature when it was moved to a geometrically incorrect corner. Additional evidence for the primacy of geometric cues in rats was provided by Margules and Gallistel (1988).

Vallortigara et al. (1990) showed that chicks, trained in a similar environment, also demonstrated systematic rotational errors when the training features were removed or when novel uninformative features were provided. However, unlike the rats, responses by the chicks on transformation tests showed a strong reliance on the feature associated with the positive corner even when it was placed in a geometrically incorrect position. Therefore, the chicks encoded both the featural and geometric information, but they showed a preference for the featural information. Geometric information was used only when features were unavailable or uninformative.

In addition to these phylogenetic differences, experiential or developmental factors might also affect the use of spatial information. Hermer and Spelke (1994) presented human subjects with a task similar to that used by Cheng (1986) and Vallortigara et al. (1990). The researchers hid an object in one corner of either an uniformly painted rectangular room or a room with one wall painted blue. University students and young children (18 to 24 months) were disoriented after witnessing the experimenter hide the objects. The subjects were then instructed to locate the object in the room. Although the University students were able to identify which corner contained the hidden object when provided with one blue wall, the young children confused the two geometrically equivalent corners. Even after distinct objects were placed in the corners and the children's attention was drawn to the placement of the object, the children still did not use these features to reorient.

The present experiment examined questions similar to those addressed by Cheng (1986) and Vallortigara et al. (1990). The results of the studies by Cheng (1986) and Vallortigara et al. (1990) suggest that different species may employ different types of information to locate objects in space. Another avian species might, like the chicks of the Vallortigara et al. (1990) study, rely on featural information more than geometric. Hermer and Spelke's (1994) results suggest that age-related factors, such as the greater navigational experience of adults, also affect the use of featural information. In this experiment, pigeons are tested to determine their reliance on featural information under different types of initial experience with geometric or featural information.

Accordingly, the present experiment differed from previous studies in a number of respects. First, the pigeons in this experiment were divided into two groups dependent upon the type of initial training they were to receive. Manipulating the type of training allowed us to investigate potential training effects. Perhaps, pretraining one group of subjects with a featurally absent environment may strengthen geometric encoding, whereas initially experiencing the environment with distinct featural information may reduce the importance of encoding the environment's geometry. Second, the featurally trained subjects were further subdivided according to the type of featural information they were to receive. For half of these subjects, the features consisted of three-dimensional landmarks; for the other half of the subjects, the features were flat panels affixed to the corners of the apparatus. We expected that the landmark objects would be more salient because Chappell and Guilford (1997) found that pigeons were unable to locate a target on the basis of two-dimensional panels on the walls of an octagonal enclosure, but they were able to locate the goal on the basis of a three-dimensional landmark. Third, our experiment included a larger number of transformation tests than in previous studies thereby providing a more comprehensive investigation of responses to tests which pitted geometry against featural information. Fourth, we included transfer tests to identify which property or properties of the features (shape, color, or three dimensionality) were encoded. Finally, we included a test in which the apparatus was altered physically to examine the nature of the geometric information encoded.

## Method

### Subjects

Eight adult Silver King pigeons (Columba livia) participated as subjects in this experiment. The pigeons had previous experience in an unrelated time discrimination task conducted in a standard operant chamber. The pigeons were maintained at 85% of their free feeding body weight throughout the duration of this experiment. Maple peas were provided as reinforcement during the experiment. Supplemental feedings of KayTee pigeons pellets were provided as required to maintain the pigeons at their individual experimental weights. The pigeons were individually housed and exposed to a 12 hour light/dark schedule with light onset at 06:00 hours.

### Apparatus

The experimental apparatus was a uniformly white rectangular enclosure assembled to control for cue availability (similar to that used by Cheng, 1986). The walls were constructed from opaque plastic and 5-cm thick Styrofoam®. The construction of the apparatus was such that no discernable differences could be detected between the two short walls or between the two long walls. Specific measurements of the outside dimensions of the entire apparatus are provided in Figure 6-1. The inside dimensions of the enclosure were 90 x 190 cm. The floor of the enclosure was covered with approximately 5 cm of aspen chip bedding. A video camera, mounted above the apparatus, monitored the inside of the experimental apparatus and was used to record responses. The video camera was hidden behind a 30.0 cm suspended ceiling such that only the lens of the camera remained visible. Four small Velcro® squares were fixed to the flooring, 24 cm from each corner. Four identical round tin containers (diameter 8.5 cm and 3.5 cm height) containing 2 cm of pigeon grit were later positioned on the Velcro® squares. White noise was played through four speakers, one speaker outside of each corner of the apparatus, to mask any exterior noise cues. The position of individual speakers were intermittently exchanged at random.

Features

The stimuli used as features in this experiment can be divided into two categories: landmarks and panels. For each subject, the features were either all landmarks or all panels. Landmarks and panels were placed flush into each corner, so that they physically touched both walls. The landmarks were 3-dimensional (3-D) objects of unique color and shape. The panels approximated the landmarks in color and shape, but were constructed from 3 mm cardboard, thus providing a 2-dimensional (2-D) feature array. Figure 6-1 provides the dimensions of the various landmarks and panels used during training and testing.

Shaping Procedures

The pigeons were initially trained to eat out of a tin container while in their home cages. Once a pigeon ate out of the container without hesitation a piece of paper towel was placed over the container and secured with a rubber band so that the pigeon was required to peck through the paper towel cover to obtain the food. Shaping in the experimental apparatus began once a pigeon readily pecked through the paper towel covering.

The eight pigeons were divided into two groups (of four subjects each) according to the type of training they were initially to receive. One group of subjects received training in the apparatus without the presence of any distinct featural information (Group Geometric). The other group of subjects (Group Feature) was trained with relevant and distinctly different featural information provided at each of the four corners. Each of the birds in Group Geometric was assigned to a different “positive” corner. On reinforced trials, food was available only at this “positive” corner and containers at the other three corners never contained food. The birds in Group Feature were also each assigned to a different positive corner. However, the birds in Group Feature were further subdivided into two groups (two subjects in each) depending on the type of featural information provided at the four corners, landmarks or panels.

The pigeons were given one experimental session, consisting of ten trials, per day. The pigeons were transported to and from the experimental room in an opaque plastic jug. Prior to each trial, the pigeon was placed in an opaque holding cage on a swivelling chair (the placement of the chair relative to the experimental apparatus was randomized on each trial) and rotated for 1 min at approximately 12 revolutions per minute to eliminate any use of inertial cues. The subject was then placed into the apparatus according to a schedule of randomly chosen entry positions (one on each wall). The subject was given 10 min to make a choice. The first peck that broke the paper towel covering a container was considered a choice. A subject was permitted to make two choices per trial after which the lights in the room were dimmed and the subject was removed from the apparatus. The point of exit from the apparatus was determined by a prearranged schedule of randomly chosen exit positions. Entry and exit positions were located at the midpoint of each of the four walls. Upon completion of a trial the subject was placed into the holding cage while the bedding in the apparatus was sifted, and any extraneous debris was removed, and the apparatus was prepared for a new trial. The subject was then rotated and a new trial was begun.

The pigeons' training was divided into five shaping phases designed to train persistent searching behavior under conditions of degraded information. The first shaping phase allowed the pigeon to adjust to the novel surroundings. One tin container was placed at the bird's positive corner. The container was not covered and four maple peas were placed on the grit. A subject was allotted 10 min to eat from the container. If a subject ate from the container it was given one additional minute after which the lights were dimmed and the subject was removed from the apparatus. Failure to eat from the container after 10 min resulted in termination of the trial and the start of a new trial immediately thereafter. Successful completion of Shaping Phase One required that a pigeon eat the maple peas from the container within 5 min on each trial and complete all ten trials. Two pigeons failed to make a choice when placed in the experimental chamber and thus after seven days they were dropped from the study and two new birds with identical experimental histories were added.

The second shaping phase was identical to the first with the exception that an uncovered container was placed at each of the four corners; only the container in the positive corner contained food. The criteria for shaping two were the same as for shaping one.

The third shaping phase was similar to Shaping Phase Two, except that all of the containers were covered with paper towel. Successful completion of Shaping Phase Three included the criteria used in previous shaping sessions plus an accuracy criterion. For feature training , 80% or more of the first choices were required to be directed to the container at the positive corner. For Group Geometric, there were no cues that would allow the pigeon to distinguish the positive corner from the geometrically equivalent corner. Therefore, the criterion used was that 80% of first choices were required to be directed to either of the two geometrically equivalent positive corners.

The fourth and fifth shaping phases were instituted to prepare the birds for the density of reinforcement that they would experience during testing sessions. The schedule of reinforcement was set at 70% in Shaping Phase Four and 50% in Shaping Phase Five. The subjects were allowed 10 min to make a first choice. After an initial choice was made, the subject was provided with one additional minute to make a second choice. All trials ended after the second choice or 1 min after the first choice, whichever occurred first. The criteria to complete Shaping Phases Four and Five were the same as those of the third shaping phase. The birds were required to meet the criteria for two consecutive days before they completed Shaping Phase Five and started testing.

### Testing

Numerous tests were administered to determine which cues controlled the pigeons' choices. Test and control trials were conducted without reinforcement. Control trials were visually identical to training trials but were unreinforced in order to measure behavior in the absence of potential food related cues. Choices were recorded manually, and in addition test and control trials were video taped. A subject was allotted 5 min to make a choice, after which the trial was terminated.

Geometric Only, No Features and Identical Features Tests. The first test series given to both groups of birds was designed to assess control by the geometry of the enclosure in the absence of featural information. For the birds in Group Geometric, two

Geometric Only test sessions, consisting of five baseline trials and five test trials, were given. The environment on test trials was identical to that of baseline trials but test trials were non-reinforced. The birds in Group Feature were administered an Identical Features test and a No Features test. Both tests were administered over three sessions with five baseline trials, two control trials and three test trials per session. The baseline and control trials provided the training environment (i.e., distinctive features in each corner) and were reinforced or non-reinforced respectively. Four identical landmarks or panels (depending on a subject's group designation) replaced the original featural information for the Identical Features test (see the test landmarks and panels labeled I in Figure 6-1 for stimulus dimensions), whereas for the No Features test all featural information was removed (see Figure 6-2).

Once this testing stage was completed, Group Feature moved directly on to the next test series (Distant Features Only tests), whereas Group Geometric subjects were provided with featural information and retrained to chose only one corner. Each subject maintained its positive corner and the configuration of featural information was identical to that of Group Feature. Two birds were assigned to the landmark subgroup and the other two were assigned to the panel subgroup. Retraining was conducted in the same manner in which Group Feature was initially trained (from shaping phase one to shaping phase five). Upon completion of retraining Group Geometric moved on to the Distant Features Only test.

Distant Features Only Test. This test assessed whether the pigeons had encoded only the features proximal to the goal (the features in the positive corner and its geometric equivalent), or instead had also encoded the featural information present in corners distant to the goal (i.e., in the geometrically incorrect corners). Accordingly, the feature in the positive corner and in the geometrically equivalent corner were removed. Thus only the featural information in the far corners was available to distinguish between the positive corner and its geometrical equivalent (see Figure 6-3). If the subjects relied exclusively upon information provided by features near the goal, accuracy would decrease. If, however, the birds had encoded the distant features and could use those features to orient, then accurate responding would be maintained despite the removal of the more proximal cues. These tests were conducted over a block of three sessions, with each session consisting of five baseline trials, two control trials and three test trials.

Transformation Tests. Group Geometric and Group Feature received the same series of transformation tests. These tests were conducted over blocks of three sessions per test. Each testing session consisted of five baseline trials, two control trials and three test trials. The order in which the transformation tests were administered varied randomly across subjects, with the constraint that each type of transformation test occur in a particular ordinal position for no more than one subject in each group.

For two of the transformation tests (Rotational and Diagonal), the relationship between the positive feature and the geometry of the enclosure remained unchanged. The Rotational Transformation Test rotated each feature by two corners (or 180°). This test was conducted as a control for unintentional cues that might allow subjects to distinguish between the two geometrically correct corners (e.g., a spot on the wall). If the birds continue to respond to the originally positive corner (now containing a negative feature) such an unintentional difference between corners may be suspected. The Diagonal Transformation switched the feature at the positive corner with the feature at the geometrically equivalent corner. For the two geometrically correct corners, one corner is correct according to the proximal features whereas the other corner is correct according to distant features. A schematic of the Rotational and Diagonal Transformations can be seen on the bottom of Figure 6-3.

Three tests (The Affine, Reflection and One Wall Switch transformation tests) placed the positive feature and correct geometric corners in conflict (see Figure 6-4). Therefore, if the subjects relied more upon geometry than upon featural information we would expect the majority of responses to be directed to the geometrically correct corners. If the subjects relied primarily upon featural information the majority of their responses should be directed to the positive feature.

The Affine Transformation altered the environment by rotating the feature in each corner one position. This test series was presented twice, once with the features rotated by one position clockwise and once with the features rotated by one position counterclockwise.

The Reflection Transformation involved exchanging one pair of features with the features along an opposite wall. This test series was presented twice, once with the features along the long walls switched and once with the features along the short walls switched.

The One Wall Switch Transformation involved an exchange of the positive feature with one of the adjacent features. This transformation is different from the

Reflection Transformation in that the Reflection Transformation switches both pairs of features whereas the One Wall Switch Transformation only involves the exchange of features along one wall. The One Wall Switch Transformation was presented twice with one test series switching the two features on the long wall and the other switching the two features along the short wall.

Transfer Tests. Upon completion of the Transformation Tests the pigeons were given transfer tests designed to identify which properties of the features had been encoded. The first transfer test administered to all subjects was a Feature Transfer test in which birds initially trained with landmarks were tested with panels (in the same arrangement) and birds initially trained with the panels were tested with the landmarks. The Feature transfer test was completed over four sessions, with each session being comprised of five baseline trials, two control trials and three test trials. The birds were then given Shape Transfer tests and Color Transfer tests, with the order of administration counter-balanced across subjects in each group. A schematic of these tests can be seen in Figure 6-5. The Color Transfer test presented the original coloration of the featural information but on novel and identically shaped features (see Figure 6-1 for an illustration). The type of feature (landmark or panel) was determined by each bird's initial training group. The Shape Transfer test maintained the original shape of the features but all the features were of an identical novel color (purple).

New Wall Test. The New Wall test altered the structure of the experimental apparatus. A new wall was inserted parallel and 50 cm from one of the existing short walls (randomly determined on each trial), thereby forming a new, smaller, enclosure with inside dimension of approximately 50 x 90 cm. This new wall was visually identical to the existing short wall. Two features were moved to the new wall such that the four features maintained the same sense relationship to each other as in training, but the metrics changed because they were now closer together (see Figure 6-6). Moreover, this changed the relationship between the goal and the geometric shape of the environment. In essence, this manipulation was an affine transformation produced by a contraction along one axis. If the birds' encoding of geometry was based on the encoding of specific distances between objects and walls of the enclosure (i.e., "absolute" geometry), this manipulation would severely distort the geometric information, thereby eliminating geometry as a useful cue. We might expect in such a case that the birds would show exclusive control by the positive feature. If, however, the birds encoded a geometric configuration that was invariant to contractions (i.e., relative geometry), the positive feature would now be in a geometrically incorrect corner. It would therefore be expected that the birds would show the same pattern of results on this test as they show on the Affine transformation tests.

Geometric Only Test 2. Upon completion of the New wall test the Geometric group was given a second Geometric Only test. This second Geometric Only test was identical to the one given to this group immediately after shaping.

## Data Analysis

For all statistical tests, the alpha level was set at 0.05. The data were analyzed in four steps. First, an analysis was conducted to determine whether the results could be collapsed across tests that were presented twice (first and second Geometric Only Tests) or across tests for which two variations of the same type of test were presented (No Feature and Identical Features Tests, clockwise and counterclockwise versions of the Affine Test, long wall and short wall versions of the Reflection Test and long wall and short wall versions of the One Wall Switch tests). For this analysis, we used a within-subjects t-test on the proportion of correct choices (choices to a geometrically correct corner for the Geometric Only, No Feature and Identical Features Tests, and choices to the featurally correct corner for the Affine, Reflection and One Wall Switch tests). In each case, the proportion scores were first subjected to an arcsin transformation (Winer, 1971) to normalize the variance. Because none of these t-tests revealed a significant difference, the data were collapsed in each of these cases.

Second, each set of test results was analyzed for differences between the Featural and Geometric groups. For this analysis we used between-subject contrasts with dichotomous categories (Marascuilo & Serlin, 1988). In each case, choices were divided into two categories. For the tests assessing control by geometry only (i.e., the Geometric Only tests and the Identical/No Features tests), the data were divided into choices of a geometrically correct corner, and other choices. For all other tests, the data were divided into choices of a featurally positive corner, and other choices. Dichotomous categories contrasts were preferable to a t-test because these contrasts are sensitive to the frequency of observations made for each subject. In cases for which the contrast did not reveal a significant difference between groups, the data were collapsed across groups for the third analysis.

In the third analysis, we used single-sample t-tests to determine whether the proportion of choices made to a particular corner or pair of corners was significantly above chance. For each analysis, the proportion scores were again subjected to an arcsin transformation. The specific proportions analyzed depended on the type of test, as described in the results section.

In a final analysis, we collapsed across the two groups and then conducted contrasts (again using the dichotomous categories method) to determine whether birds trained with landmarks responded differently than birds trained with panels during any of the tests. For the Geometric Only tests, the data were divided into choices of a geometrically correct corner, and other choices. For all other tests, the data were divided into choices of a featurally positive corner, and other choices.

## Results

The birds in Group Feature completed shaping in a mean of 8.75 sessions. Birds in Group Geometric completed shaping without features in a mean of 10.25 sessions. This difference was not significant, $t(6) = 1.68$. When the birds in Group Geometric were subsequently trained with features, they completed shaping in a mean of 12 sessions (with three birds taking 8 sessions and one bird taking 24 sessions), which was again not significantly different than the sessions required by Group Feature, $t(6) = 0.81$. Collapsing across the two groups, the number of sessions required to complete shaping with features was not significantly different for bird trained with landmarks (mean = 12) than for birds trained with panels (mean of 8.75), $t(6) = 0.81$.

## Identical/No Feature and Geometric Only Tests

As can be seen in Figure 6-2, regardless of initial training, the pigeons did not respond randomly when placed within the environment void of relevant featural information; instead they chose a geometrically correct corner most of the time. The Identical/ No Features test results for Group Feature, and the Geometric Only test results for Group Geometric were collapsed and analyzed together since the contrast revealed no statistically significant difference between the groups, $z = 0.80$. To assess the reliability of preferences for a geometrically correct corner, the proportion of total choices that were made to a geometrically correct corner was analyzed with a one-sample t-test. This revealed that the subjects chose geometrically correct corners more often than expected by chance (0.50), $t(7) = 19.49$. Choices of a geometrically correct corner were further analyzed according to whether they were made to the positive corner (i.e., the one that contained food during training) or its geometrical equivalent. The mean proportion of responses to the positive corner was 0.544, which was not significantly above 0.50, $t(7) = 1.09$. Thus, responses were divided approximately equally between these two geometrically correct corners.

## Distant Features Only Tests

Results of the Distant Features Only tests are shown in the top panel of Figure 6-3. The two groups of subjects did not show a statistically significant difference in their proportion of choices to the correct corner ($z = 0$) and therefore their results were collapsed. The Distant Features Only test assessed whether the pigeons were able to locate their positive corner when the features at the positive corner and the geometrically equivalent corner were removed. If subjects showed no control by the distant cues, they would be expected to respond in the same way as they did on geometric only tests, and hence would be expected to choose randomly between the two geometrically correct corners. In a first analysis, we confirmed that the pigeons chose one of the two geometrically correct corners more often than expected by chance (0.50), t(7) = 42.5. To determine whether the pigeons distinguished between the two geometrically correct corners, we next analyzed choices of the positive corner as a proportion of total choices made to either of the two geometrically correct corners. A one-sample t-test revealed that the proportion choices to the positive corner was significantly above chance (0.50), t(7) = 6.01. Therefore, the birds did not respond randomly between the two geometrically correct corners, indicating that they were able to use the distant features to orient.

Transformation tests with correct geometry and positive feature

Results of the two transformation tests that maintained the relationship between the positive feature and the geometric shape of the environment (Rotation and Diagonal) are shown in the bottom panel of Figure 6-3. No statistically significant difference between groups was found on either the Rotational Test (z = 1.06) or the Diagonal Test (z = 1.60), and hence the results were collapsed across groups for each of these tests. For both of these transformations, the positive feature remained at a geometrically correct corner. In a first analysis, we confirmed that the pigeons chose one of the two geometrically correct corners more often than expected by chance (0.50), t(7) = 42.5. To determine whether the pigeons distinguished between the two geometrically correct corners, we next analyzed choices of the positive corner as a proportion of total choices made to either of the two geometrically correct corners. One sample t-tests revealed a statistically significant preference (i.e., greater than 0.50) for the corner containing the positive feature for both the Rotational test, t(7) = 42.46 and for the Diagonal test, t(7) = 10.41.

Transformation tests with geometry and features in conflict

For each of the transformation tests that pitted geometry against features (the Affine, Reflection and the One Wall Switch Transformation), the contrasts showed a significant difference between the two groups (Affine, z = 3.38; Reflection, z = 5.36, One Wall Switch, z = 4.00), with Group Feature choosing the corner containing the positive feature more often than Group Geometric. Results for each group are shown in Figure 6-4.

For each of these tests, there was one featurally correct corner, two geometrically correct corners, and one corner that was incorrect on the basis of both geometry and features. For both groups and in each of the three tests, choice of the corner that was incorrect on the basis of both features and geometry either never occurred, or occurred significantly less often than expected by chance (0.25), t(3) = 79.02 (Group Feature during the Affine tests). Clearly then, the birds did not choose randomly but instead chose on the basis of either the featural or the geometric information, or both. To determine whether the birds in each group showed a significant preference for featural information over geometric information, we next analyzed choices to the featurally correct corner as a proportion of total choices made to either the featurally correct or the geometrically correct corners. Random choice among the three corners that were correct according to either geometry or features would yield a chance level proportion of 0.33. Group Feature chose the featurally positive corner significantly more often than expected by chance during the Affine Transformation, $\underline{t}(3) = 7.64$ and the Reflection Transformation, $\underline{t}(3) = 8.80$, but not during the One Wall Switch Transformation, $\underline{t}(3) = 2.51$. Group Geometric did not chose the featurally correct corner significantly more than chance on any of the three transformations, $\underline{t}(3) = 2.89$, $\underline{t}(3) = 0.64$, and $\underline{t}(3) = 0.71$, respectively.

### Transfer Tests

The two groups did not differ significantly on any of the transfer tests (Feature Transfer, $\underline{z} = 0.78$; Color Transfer, $\underline{z} = 0.10$; Shape transfer, $\underline{z} = 1.62$), and therefore the results for the two groups were combined. Results of these tests are shown in Figure 6-5. For the Feature Transfer, Color Transfer and Shape Transfer tests, respectively, the birds chose one of the two geometrically correct corners significantly more often than expected by chance (0.50), $t(7) = 25.64$, 25.64, and 37.98. To determine whether the birds were able to use the manipulated featural information in order to distinguish between the two geometrically correct corners, we next analyzed choices to the positive corner as a proportion of total choices made to either of the two geometrically correct corners for each test, and compared these proportions to chance level of 0.50. During the Feature Transfer tests, choice of the featurally correct corner was greater than chance, $\underline{t}\,(7) = 5.26$, demonstrating that the pigeons transferred accurately between the landmarks and panels or vice versa. During the Color Transfer tests, providing the subjects with the correct color while altering the shape of the features did not eliminate accurate choice;

subjects chose the corner containing the feature with the positive color significantly more often than expected by chance, t (7) = 6.67. However, accurate choice was not maintained during the Shape transfer tests in which the color of the features was altered while maintaining the original shape; the subjects did not choose the feature of positive shape significantly more often than chance, t (7) = 2.07.

### New Wall Test

Results of the New Wall test are shown in Figure 6-6. No statistically significant difference was found between the two groups, z = 1.55, and therefore the data were collapsed. On this test, there was one featurally correct corner, two corners that were correct according to relative geometry (none of the corners were correct according to absolute geometry), and one corner that was incorrect according to both geometry and features. Choice of the corner that was incorrect on the basis of both sources of information never occurred, indicating that at least one of these two sources of information controlled the birds' choices. To determine whether the birds showed a significant preference for the corner with the correct feature, choices of the featurally correct corner were assessed as a proportion of choices of the featurally correct corner plus choices to the two corners that were correct according to relative geometry. The one-sample t-test showed that choice of the featurally correct corner was significantly above chance (0.33), t (7) = 5.60.

### Comparisons between landmark-trained and panel-trained subjects

Comparisons between birds trained with landmarks and birds trained with panels did not reveal systematic differences. Although contrasts between the birds trained with landmarks versus the birds trained with panels revealed significant differences in four of the eleven tests, the direction of the difference varied. Choice of the featurally correct corner was significantly higher for the birds trained with landmarks than for the birds trained with panels in the One Wall Switch Test, $\underline{z} = 4.91$, the Shape Transfer Test, $\underline{z} = 3.26$, and the New Wall Test, $\underline{z} = 3.30$. However, during the Affine Test, choice of the featurally correct corner was significantly higher for the birds trained with panels than for the birds trained with landmarks ($\underline{z} = 2.25$).

## Discussion

The pigeons in this experiment learned to locate hidden food on the basis of information contained within a rectangular apparatus. This experiment differed from previous studies investigating encoding of features and geometry in that two groups of birds were initially trained with either the featural information present or absent. The initial training received by the pigeons was found to be an important determinant of how the environmental information controlled choice behavior.

The Identical/No Features and Geometric Only tests examined whether both groups encoded the geometric information supplied by the environment regardless of whether it was required to solve the task. Pavlovian conditioning mechanisms exhibit overshadowing of a cue by other, more salient, cues with equal predictive validity (e.g., Kamin, 1969). Although overshadowing has been shown in the spatial domain (March, Chamizo, & Mackintosh, 1992; Spetch, 1995), there was no evidence that it occurred here. In this experiment, training pigeons to locate the goal in the presence of featural information did not interfere with their subsequent ability to find the goal on the basis of geometric information only.

The Distant Features Only test investigated the content of featural information being encoded: Did pigeons encode just the feature in the positive corner or some larger portion of the array (e.g., the features in the distant corners)? Both groups demonstrated the ability to use the distant features to correctly locate the positive corner. This result contrasts with previous studies which found that neither rats (Cheng, 1986) nor chicks (Vallortigara et al. 1990) showed evidence of encoding the distant features within a geometric enclosure. A difference in encoding between rats and pigeons is perhaps not surprising given that these two species belong to different classes of animals and inhabit contrasting ecological niches. The present study, however, suggests a difference between two avian species in the encoding of cues distant to the goal: Distant cues were used by the pigeons in our study but not by the chicks in the study by Vallortigara et al. These contrasting results between pigeons and chicks could reflect any of a number of differences between the studies, including differences in the procedures, the nature of the search response (pecking versus scratching), or the specific apparatus and featural cues used. Another interesting possibility is that developmental factors (either maturation or experience) may affect encoding. In support of this possibility, developmental factors have been implicated in the encoding of featural information by humans (Hermer & Spelke, 1994). An interesting area for future research would be to directly investigate whether use of featural information for navigation emerges or broadens during development in an avian species.

During Transformation tests, the two groups of pigeons responded to alterations in the featural configuration in a systematically different way. Transformation tests that maintained the relationship between the correct feature and the geometry of the environment (Diagonal and Rotation Transformation) did not reveal a difference in responding between the two groups. However if the positive feature was placed in a geometrically incorrect position (Affine, Reflection and One Wall Switch Transformation tests) the distribution of responses made by the two groups were systematically different. When presented with conflicting information, the birds in Group Geometric shared their responses between the geometrically correct corners and the featurally correct corner. In contrast, Group Feature demonstrated primary stimulus control by the feature itself. Thus, initial training with geometric information as the single reliable cue seems to have reduced the relative control by featural information. Features did exert some control in Group Geometric, however. It seems reasonable to attribute this to the necessity of using featural information to discriminate which of the two geometrically correct corners was the goal.

The Transfer tests were conducted to investigate which properties of the features exerted the most stimulus control. These tests revealed that pigeons were able to transfer accurately between 2-D panels and 3-D landmarks and vice versa. This transfer, together with the lack of consistent differences between birds trained with landmarks and birds trained with panels, appears to contrast with results by Chappell and Guilford (1997). They found that pigeons were unable to accurately locate a goal using two-dimensional cues affixed to the walls of an enclosure, but that they were able to locate the goal using a three dimensional landmark placed on the floor of the enclosure. However, their panels were located on walls on either side of the goal rather than being located directly behind the goal. An interesting future experiment will be to compare directly control by panels on the side walls (as in Chappel and Guilford) with control by a panel placed in the corner behind the goal (as in our experiment).

Separation of the two dominant properties of the features, color and shape, revealed color to be encoded predominately for both groups of subjects. It is interesting that although the groups differed in the encoding of feature versus geometry, both groups encoded the same dimension of featural information. The finding that color was the dominant featural property encoded is consistent with the finding by Spetch and Mondloch (1993) that pigeons' spatial search in a touch-screen task was controlled more by the color of a landmark than by the shape of a landmark.

The New Wall test investigated a very interesting aspect of the metric frame. This test showed that when the dimensions of the environment were altered quite radically, both groups of birds relied on the positive feature. The responses of utmost interest are those by Group Geometric. The New Wall test is essentially an affine with a contraction of the search space: The positive feature is now located at a geometrically incorrect corner according to relative geometry (i.e., geometry that is invariant to contraction). Therefore, if pigeons were sensitive to relative geometry, they should respond in the same way to this test as they did to the Affine transformation tests. During Affine tests, birds in Group Geometric showed partial control by the environmental geometry and, in contrast to the birds in Group Feature, they did not show a significant preference for the corner containing the positive feature. During the New Wall test, however, birds in Group Geometric responded in the same way as did birds in Group Feature: They showed primary control by the feature. This suggests that the geometric information was probably encoded according to absolute metrics rather than relative geometry. If the birds encoded the geometry in terms of absolute metrics (e.g., the absolute lengths of the walls on either side of the positive corner), the New Wall manipulation would distort the environment sufficiently that none of the corners would be geometrically correct (i.e., there is no longer a 190 cm wall). In such a case, the birds in both groups would be expected to use featural cues, which is consistent with the results we obtained. In retrospect, an interesting manipulation would have been to combine the New Wall test with removal of all featural information from the environment. If encoding of geometry is indeed absolute, the distribution of responses should be random during such a test.

Our suggestion that the pigeons probably encoded the geometric information in terms of absolute rather than relative metrics seems consistent with results of recent experiments in which pigeons were trained to find a goal in the center of a landmark array and then were tested with expansions of the landmark array (Spetch, Cheng and MacDonald, 1996; Spetch et al, 1997). In tasks conducted both on the monitor screen and on the laboratory floor, pigeons responded to the expansions of the landmark array by maintaining the correct absolute distance from individual landmarks, rather than by responding to the correct relative location in the array (i.e., they rarely searched at the center of the expanded array). Interestingly, a recent study conducted with young chickens (Tommasi, Vallortigara, & Zanforlin, 1997) obtained somewhat different results. The chickens were trained to find food hidden in the center of an enclosure and then the size or shape of the enclosure was varied on tests. Although the chickens sometimes searched at the absolute training distance from the walls of the enclosure, they more often searched at the center of new enclosures. Determining the nature of these contrasting results for pigeons and young chickens is an interesting topic for future research.

In summary, our results suggest two main conclusions. First, we have shown that pigeons, like rats, chicks and young children, encode the geometric shape of an environment, even when the presence of featural cues makes encoding of geometry unnecessary. Cheng's (1986) research suggested that rats primarily use a purely geometric module for navigation. Although rats could use features to distinguish the correct corner from its geometric equivalent, they did not follow the correct feature when it was placed in a geometrically incorrect corner. Consequently, Cheng suggested that rats do not encode features independently of the geometry, but instead "paste the requisite features onto the requisite frame" (p. 176). In contrast, chicks in the study by Vallortigara et al. (1990), and pigeons in Group Feature of the present study appeared to encode features independently of geometry because they followed the correct feature when it was placed in a geometrically incorrect corner. These comparisons suggest that encoding of geometric information may be quite general, but the primacy of geometric information appears to vary across species.

Second, our research revealed that the primacy of control by geometric and featural cues is determined not only by species dispositions, but also by experiential factors. Pigeons that were trained without features before being trained with features responded to tests that pit geometry against featural information in a manner similar to that of rats and different from that of pigeons trained with features from the outset. That is, pigeons in Group Geometric did not show significant choice of the positive feature when it was moved to a geometrically incorrect corner. Instead, they distributed their responses among the corner containing the positive feature and the two geometrically correct corners. Thus, at least for pigeons, initial experiences can alter the primacy of control by geometric and featural information.

Figure 6-1. The top illustration shows the dimensions of the experimental apparatus. The bottom illustrations show the dimensions of the landmarks and panels used for training and testing. The training landmark and panels labeled A were pink with black stripes, those labeled B were green, those labeled C were blue, and those labeled D were red with orange circles. The test landmarks and panels labeled I were used for the identical features tests and were all yellow with a brown stripe. Test landmarks or panels labeled CT were the novel shapes used for the color transfer tests and were presented in the colors of the training landmarks panels.

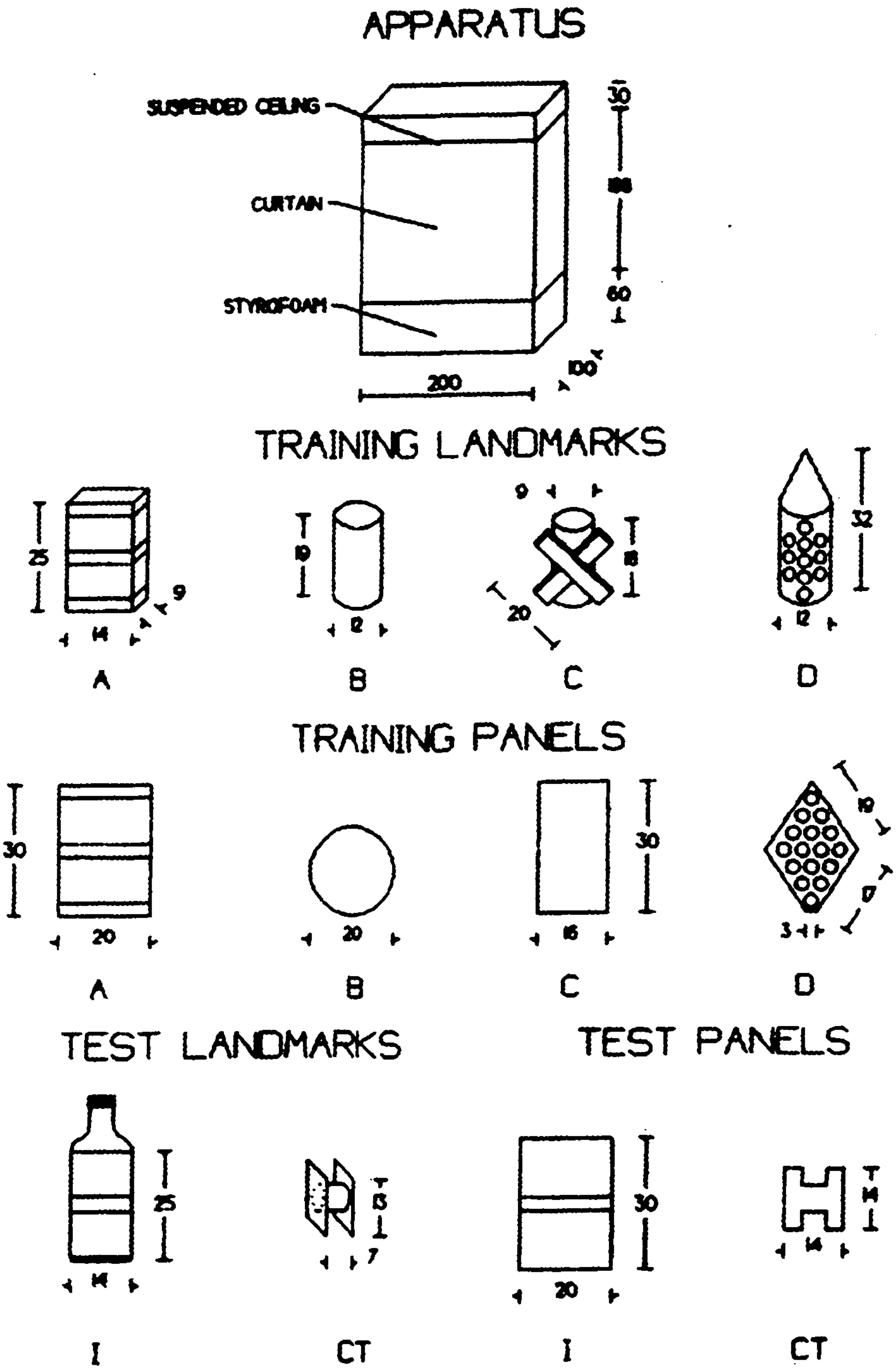
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Figure 6-2. Proportion of choices (rounded to 2 decimal places) to each corner during Control, No Feature and Identical Features tests for Group Feature and during Geometric Only tests for Group Geometric. Data for the No Feature and Identical Feature tests are collapsed and for all graphs, data are averaged across the four birds. Data are shown with the positive corner being in the top left; however, the actual positive corner was counterbalanced across birds.

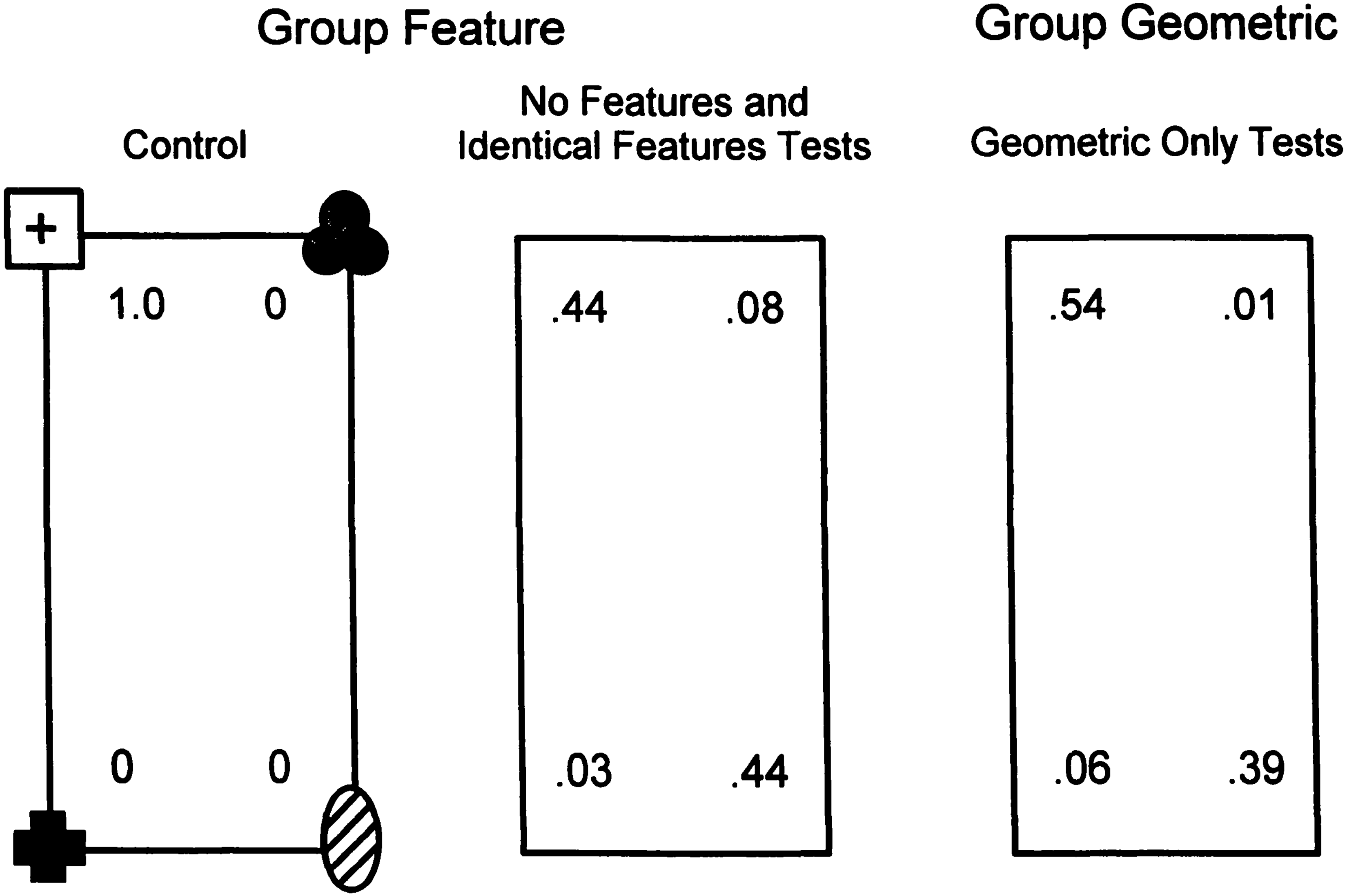
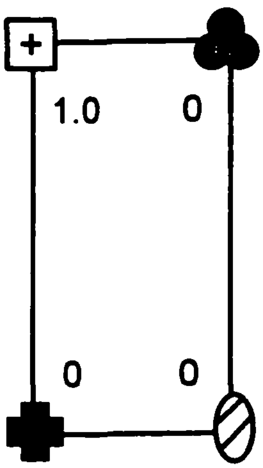

Group Feature
Group Geometric
Control
No Features and Identical Features Tests
Geometric Only Tests
1.0
0
0
0
.44
.08
.03
.44
.54
.01
.06
.39

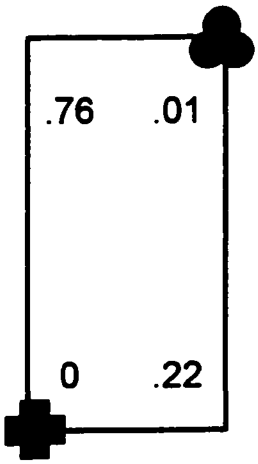
Figure 6-3. Proportion of choices (rounded to 2 decimal places) to each corner during Control and Distant Features Only tests (top panel), and during Control, Rotational and Diagonal Transformation tests (bottom panel). In all graphs, the data are averaged across birds in both groups. The corner containing the positive feature is represented by the square symbol with a + in the center; however, the actual positive corner was counterbalanced across birds.

## Both Groups Combined

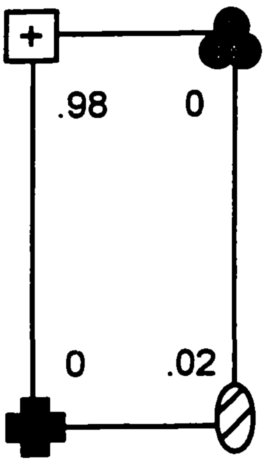
Control



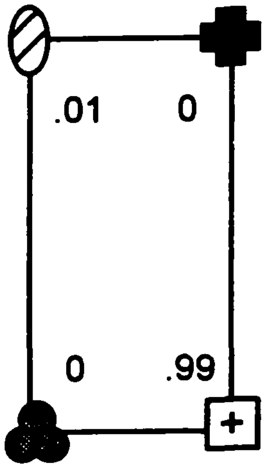
Distant Features Only



Control



Rotational



Diagonal

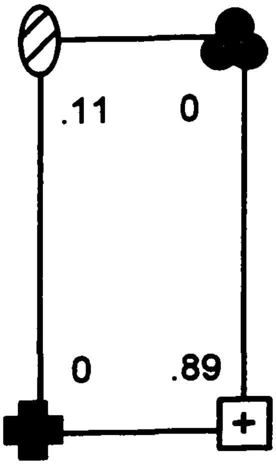


Figure 6-4. Proportion of choices (rounded to 2 decimal places) during Control tests and during the three transformation tests that pitted features against geometry, averaged across the four birds in Group Geometric (top panel) and the four birds in Group Feature (bottom panel). The corner containing the positive feature is represented by the square symbol with a + in the center; however, the actual positive corner was counterbalanced across birds.

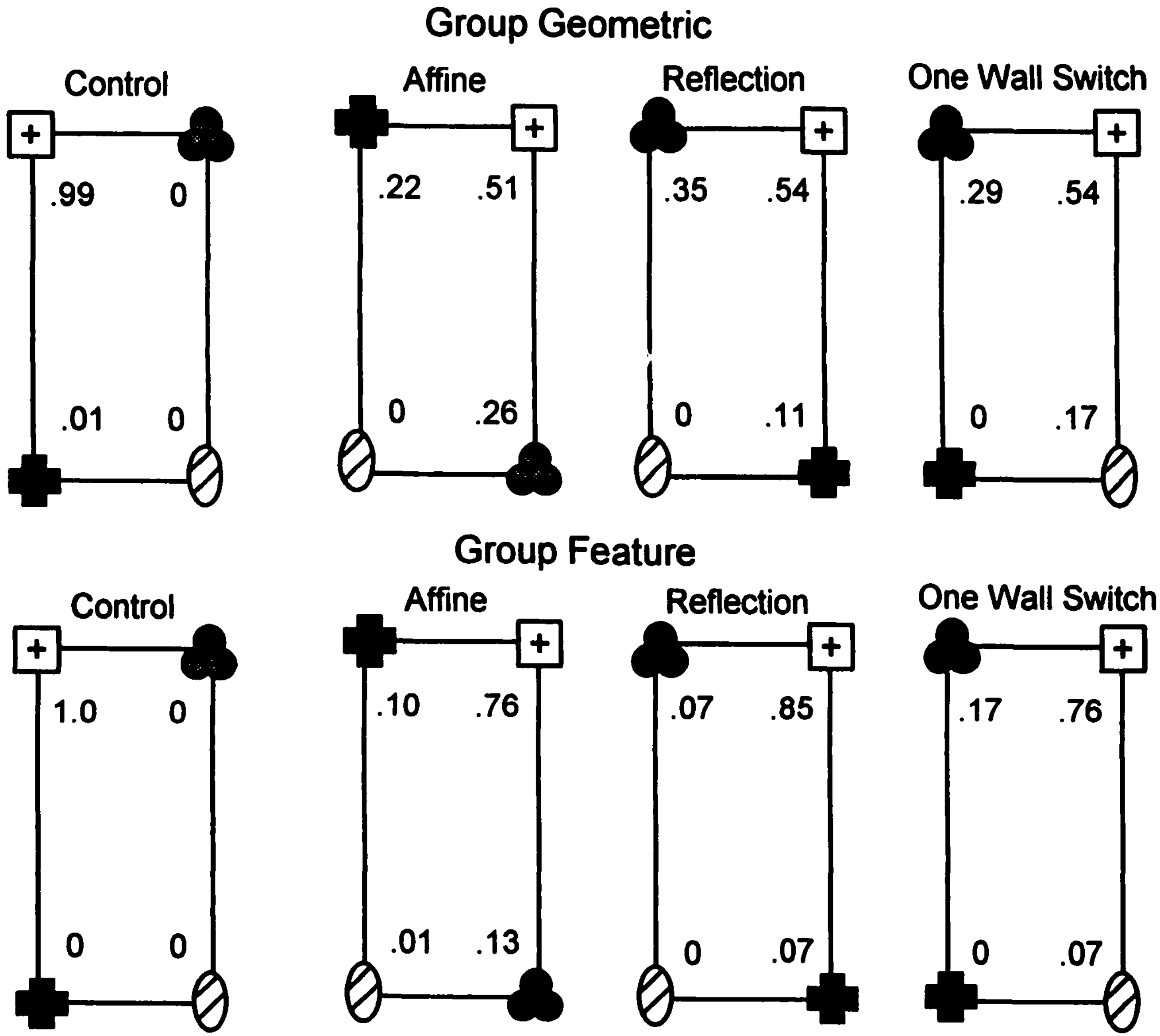

Group Geometric
Control
.99
0
.01
0
Affine
.22
.51
0
.26
Reflection
.35
.54
0
.11
One Wall Switch
.29
.54
0
.17
Group Feature
Control
1.0
0
0
0
Affine
.10
.76
.01
.13
Reflection
.07
.85
0
.07
One Wall Switch
.17
.76
0
.07

Figure 6-5. Proportion of choices (rounded to 2 decimal places) to each corner during Control and Feature Transfer tests (top panel), and during Color tests and Shape tests (bottom panel). In all graphs, the data are averaged across birds in both groups. The corner containing the positive feature is shown in the top left; however, the actual positive corner was counterbalanced across birds.

## Both Groups Combined

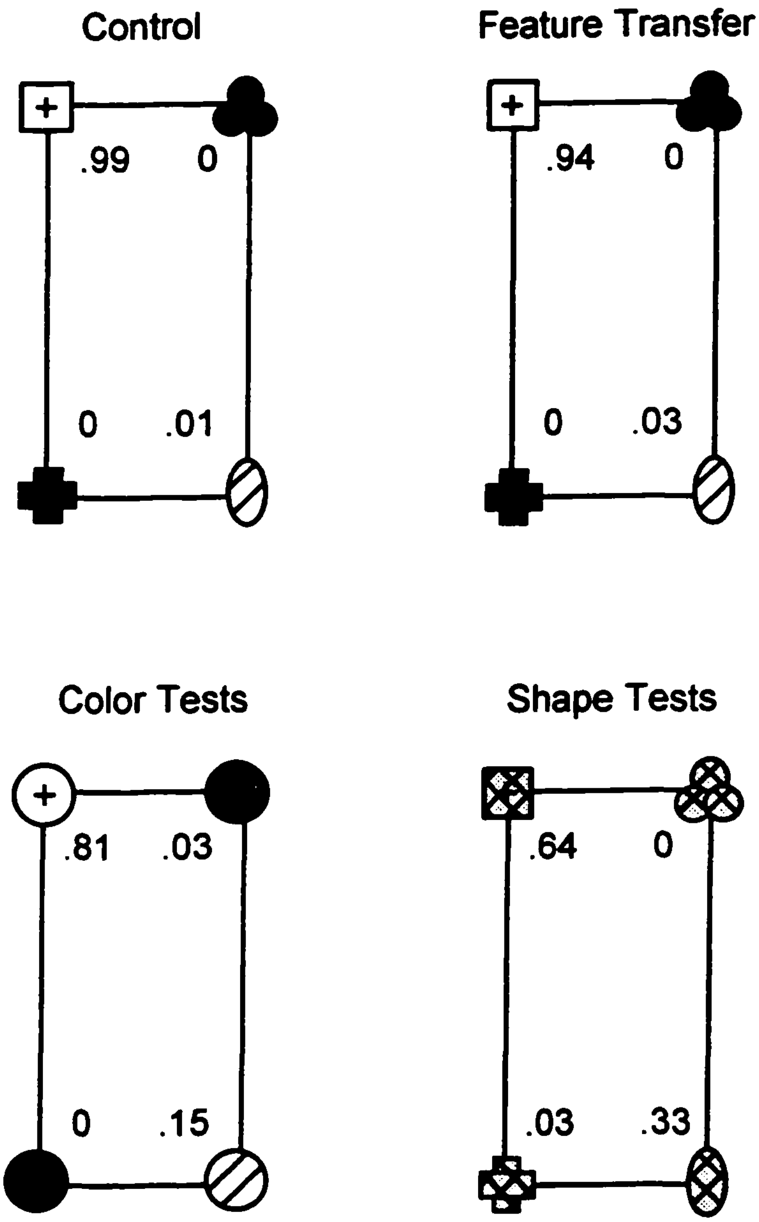
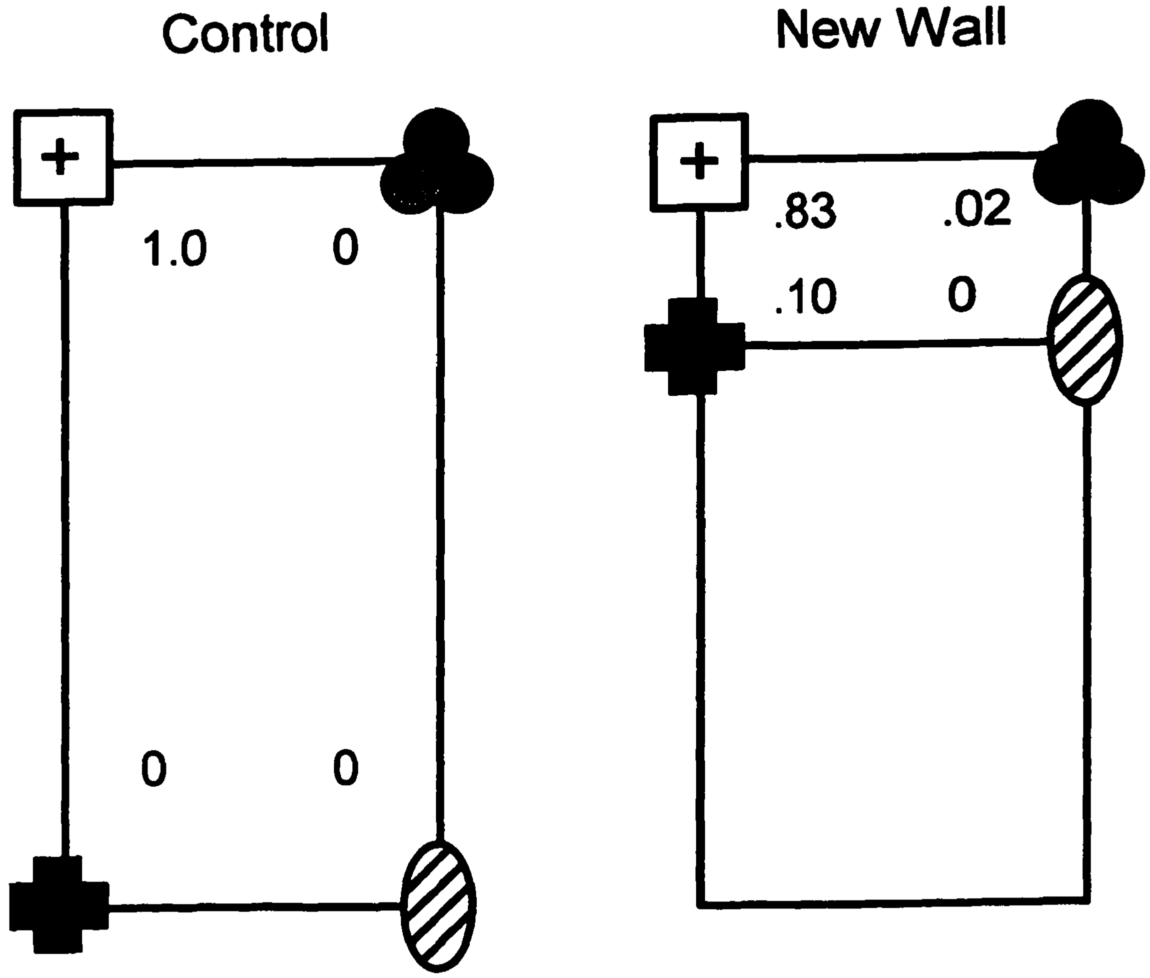


Figure 6-6. Proportion of choices (rounded to 2 decimal places) to each corner during Control and New Wall tests, averaged across birds in both groups. The corner containing the positive feature is shown in the top left; however, the actual positive corner was counterbalanced across birds.

## Both Groups Combined



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# CHAPTER 7

# VISUALLY GUIDED PREDATORY BEHAVIOR IN OWLS

Birds must be able to accurately and economically locate food items. To achieve this they rely on different sensory systems for food detection (e.g., visual, Goldsmith & Goldsmith, 1979; auditory, Konishi, 1973; Montgomerie & Weatherhead, 1997; or pressure gradients, Piersma, van Aelst, Kurk, Berkhoudt & Maas, 1998). In fact, many bird species rely simultaneously on a combination of information received across several sensory systems while foraging. This integration of multiple sensory cues may be particularly important for predatory birds. These birds hunt moving prey items which may occur quite infrequently in the environment, and it is thus important to accurately locate and capture a prey item when it becomes available.

Owls are thought to rely strongly on prey-generated auditory cues. Using binaural cues, such as interaural time differences (ITD's) and interaural intensity differences (IID; also known as interaural level differences), owls are able to accurately localize a sound source (e.g., Frost, Baldwin & Ciszy, 1989; Knudsen, 1980; Konishi, 1973). However, many owls hunt under conditions in which sufficient light is available to use both visual and auditory information (Dice, 1945; Martin, 1986). Integration of the visual and auditory information for recognition and localization of a prey item would allow for a more accurate and successful attack. Integration of auditory and visual cues assist in increasing accuracy for target localization has been shown for humans (Stein, Meredith, Huneycutt & McDade, 1989). Owls use both auditory and visual cues in calculating target direction and distance (Frost, Baldwin & Ciszy, 1989; Konishi, 1973; Payne, 1971; Pettigrew & Konishi, 1976; Wagner & Frost, 1994). Further, visual experience is important for the calibration of the auditory space map (Gold & Knudsen, 2000; Feldman

& Knudsen, 1997; Knudsen & Brainard, 1991; 1995; also see Stein & Meredith, 1994). It is thus, quite likely that these birds also use the combination of auditory and visual information for localizing targets, i.e., when hunting.

Owls may use several different visual cues to locate a target item. Given that owls have eyes that are positioned more frontally than granivorous birds it is clear that these birds may rely more strongly on binocular cues for estimating distance to a desired object. Van der Willigen, Frost and Wagner (1998) have examined stereoscopic depth perception in the barn owl (*Tyto alba*). The results of this study show similar stereoscopic processing in barn owls as has been reported in humans. Furthermore, Pettigrew and colleagues have shown that the barn owl has neurons in the visual Wulst that are sensitive to variations in binocular disparity and direction of motion (Pettigrew & Konishi, 1976; Pettigrew, 1979). Parallels have been drawn regarding the similarity in the topographic organization of these neurons to that found in several visually oriented mammals (cats and primates; Knudsen & Brainard, 1995; Pettigrew & Konishi, 1976). Although studies examining visual processing in owls imply that visual cues, in addition to auditory cues, may play a role in prey localization, few studies have directly examined if visually-based cues are important to a hunting owl.

Previous studies have shown that when visual and auditory cues provide contradictory information the visual system is predominantly used for target localization (Knudsen & Brainard, 1995; Knudsen & Knudsen, 1989). For example, developmental studies of barn owls raised with prisms displacing visual stimulation, while leaving auditory cues unaltered, have shown that it is the auditory localization that is altered to compensate for the discrepancy (Knudsen & Knudsen, 1989). This further emphasizes the importance of vision for target localization.

The current study is the first systematic investigation to examine the relationship between visual prey cues and the initiation of a predatory attack by two species of owls. Short-eared owls (*Asio flammeus*) hunt for small mammals (e.g., voles or mice) by flying low over open habitat such as grassland, marshes, and agricultural fields. This "on-the-wing" predatory behavior is quite different from the perch-and-pounce method used by many other owl species, including the Northern saw-whet owl (*Aegolius acadicus*), that hunt in forested habitats. In addition, the activity or diel patterns of the two species are quite different, with Short-eared owls being crepuscular and Saw-whet owls being nocturnal. If predatory behavior in owls is strongly linked to ecological or activity patterns, one might expect selective differences in the reliance on visual and auditory cues during predatory attacks. However, given that both species are faced with similar selective pressures (i.e., accuracy and economy) in hunting moving prey, the two species may show similar use of available prey-based cues. In the present study, the role of static (physical prey characteristics) and dynamic (prey movement cues) prey characteristics will be examined.

## EXPERIMENT 1

The crepuscular Short-eared owl is active when light levels are sufficient for using visual cues for hunting. To investigate what role vision plays in the foraging strategies of Short-eared owls, dynamic and static prey-based characteristics were manipulated under different lighting conditions.

## Method

### Subjects

Two Short-eared owls (*Aegolius acadicus*) were the subjects of study. Their sex and exact age could not be determined, however both had adult plumage. The owls were housed in an outdoor aviary during the summer months and an indoor aviary during the winter months at a rehabilitation shelter outside of Edmonton (Alberta, Canada). Both owls were housed at the shelter for approximately 2 years due to injuries they obtained in the wild. The injuries had healed prior to the beginning of the study and the owls were being tested to determine if they could be successfully released. The owls were provided with laboratory mice for approximately 3 months prior to the beginning of study. Laboratory mice were fed during all experimental sessions and in supplemental feedings.

### Apparatus & Procedures

The testing enclosure was 3.5 x 2 x 4 meters with walls of black plastic sheeting secured to the flooring with duct tape. A zipper entrance was located on one side of the front wall. Inside the enclosure was a 1.5 m tall cabinet upon which a 60 cm tall straw bale was placed which served as a perch for the owls during experimental sessions. A 60 x 60 x 60 cm table was located 1.8 m from the perch. During testing, a single mouse was placed randomly on this table. Directly behind the table, a Sony Hi-8 video camera was placed on a 120 cm high tripod. The camera was connected to a monitor outside the enclosure to allow viewing of experimental sessions. Owls were caught in their home aviaries and carried to the experimental room. Once in this room, they were given approximately 30 minutes to adjust to the handling (and to dark adapt in some experimental conditions). The owls were tested either in the morning or evening, but were always food deprived for 24 hours prior to testing. They were tested individually approximately once per week, with each session lasting for a maximum of 20 minutes. Ten minutes after the completion of a session the owl was returned to its home aviary.

### Conditions

The owls were tested under two different light levels: In the Light condition, the experimental room was lit with a 60 watt incandescent bulb hung from the center of the room, and the light level in the room ranged from 31 lux (lowest reading at table) to 55 lux (highest reading at perch). In the Dark condition, light levels ranged from 0.2 to 0.5 lux. In every session, either a live or a dead mouse was presented. In the Live condition, a mouse was randomly positioned on the experimental table, and it was able to freely move around the table top. In the Dead condition, a dead mouse was randomly positioned on the table and body orientation was randomly selected from eight orientations. The order of Light and Dark sessions, as well as the Live and Dead sessions was randomized.

### Scoring Procedures

The video tape of each session was analyzed by two researchers to ensure reliability in scoring of the mouse's head orientation and latency of attack. The orientation of the mouse's head was recorded with respect to the midpoint of the bale perch. Since the owls did not attack the mice from any other point in the room, this measurement accurately represented the owl's position. A transparent polar plot was placed on the still image of the mouse on the monitor with the axis of the plot on the midpoint of the mouse's body, keeping the 0-180 line parallel to the bale perch. The segment containing the mouse's eyes and nose was recorded as the orientation of the mouse. For analysis, the head orientation was categorized as either facing "Toward" the perch or facing "Away".

## Results

### Light Levels

The relative frequency of attacks made in the Light condition (83%) was not significantly different from the relative frequency of attacks made in the Dark condition (74%; Fisher's Exact Test; $p > 0.2$). The owl data were also examined for attack latency, latency being defined as the interval from the beginning of the session to the initiation of an attack. Because the latency distributions were highly skewed the median latencies (RT) are reported below. Median latency in the Light condition (RT = 69.2 s) was significantly shorter than median latency in the Dark condition (RT = 198.4 s; $t = -16.8$; $p<0.001$). Therefore, although lighting condition did not systematically affect whether the owls engaged in a predatory attack, it did influence how quickly an attack was initiated.

### Dead versus Live Mice

No significant difference was found for the relative frequency of attacks in the Live (78.7%) and Dead (84.2%) conditions (Fisher's Exact Test; $p > 0.2$). Furthermore, no significant difference was found for the median latency to attack between Live (RT =

93.6 s) and Dead (RT = 114.9 s) conditions ($t$ = -1.63; $p$>0.10). This indicates that the owls did not attack one prey type more often or more quickly than the other.

Mouse Orientation

The influence of the mouse's orientation was examined for both Live and Dead mice. The number of attacks made on mice facing the owl (Toward condition) was compared to the number of attacks made to mice facing away from the owl (Away condition). Fisher's Exact Test (2x4) revealed a significant interaction ($p$< 0.001) of mouse orientation (Toward and Away) and condition (Live and Dead). Further analysis showed that the owls were attacking the Live mice significantly more often when the mice were oriented away (83.8%) from the perch (and the owl) than towards (16.2% ; Binomial $p$<0.0001). On the other hand, the owls attacked Dead mice regardless of their orientation (away = 45.8% and toward = 54.2 %; Binomial $p$>0.3; see Figure 7-1). This result indicates that owls attacked the live mice more often when they were facing away, but orientation had no effect when the mice were dead.

## Discussion

Results show that light level did not affect attack frequency, but attack latencies were shorter in the light. Second, attacks on dead and live mice were equally likely and equally fast. Third, live mice were preferably attacked from behind, whereas orientation did not affect attacks on dead mice.

Could the owls have relied on auditory cues alone? In light of their strong visual capabilities (Pettigrew & Konishi, 1976; Nieder & Wagner, 1999; Wagner & Frost, 1994;

Wagner & Schaeffel, 1991) and dominance of vision over audition (Knudsen & Brainard, 1995; Knudsen & Knudsen, 1989) this is unlikely. In the present experiment, visual cues were always available, given that light levels in the Dark condition were sufficient for rod-based vision. Specific auditory cues for localizing and identifying prey were not available with dead mice. The orientation effect seen when owls attacked live mice, but not dead, is also likely to be visually guided. With live mice, owls are at risk of being injured (e.g., bitten by the mouse); however, no such risk occurs with dead mice. Therefore, the owls may initiate an attack on a live mouse when the risk is lowest. Furthermore, in the case of a dead mouse, there is no chance for escape, thus the mouse's orientation is irrelevant. Quite the opposite is true when owls are hunting live (or moving) mice. It may be easier for an owl to make a surprise attack, with a higher likelihood of success, if it approaches a mouse from behind. Further, it is easier for an owl to make flight corrections when it is attacking a mouse from behind. If a mouse makes a quick change in direction or speed the owl can easily adjust its flight if it is following behind the mouse but not if it is approaching the mouse head on.

## EXPERIMENT 2

Experiment 1 showed that Short-eared owls use visual cues when initiating a predatory attack. Short-eared owls, being a crepuscular species with symmetrical ear openings, may be more likely to use visual cues when hunting than a nocturnal species. To investigate this possibility, we conducted an investigation similar to Experiment 1 using a nocturnal species, Northern saw-whet owls. Although the two species may share similar visual capabilities the saw-whet owl may rely more strongly on its ability to locate mice using auditory cues since this species has asymmetrical ears openings and is generally considered to be nocturnal (Frost, Baldwin & Csizy, 1989). Furthermore, since Saw-whet owls are most active during reduced lighting conditions, variations in illumination may be more influential for this species than the Short-eared owls.

## Methods

### Subjects

Four Northern saw-whet owls (*Aegolius acadicus*) were the subjects of study. The owls were housed in a large open flight room (7 x 3.1 x 2.8 m; length, width, height) in the University of Alberta. The owls were obtained as pre-fledglings (approximately 3 weeks old) from different nest sites around the Edmonton area (collection permit no. 1851). At the beginning of the study the owls were approximately 7 months old. Although the sex of the owls was not known, morphological measurements suggested that three were female and one was male (Buckholtz, 1984). The owls were successfully capturing prey (laboratory raised mice) prior to the beginning of the study.

### Apparatus

Approximately half of a large free flight room was used as the testing area (4 x 3.1 x 2.8 m; length, width, height). The room was divided by a series of large opaque plastic curtains hung from a metal rod flush with the ceiling. The plastic curtains were taped together along the seams with clear plastic tape. The center of the curtains was joined by a series of Velcro® strips. These strips allowed for easy access to the experimental area. Approximately in the center of the testing area was a table (60 x 60 x 60 cm). An individual mouse was randomly positioned on this table during testing. A Sony Hi-8 video camera with infra-red capabilities was placed directly in front of the table on a tripod 95 cm high. The video camera was situated such that when the curtain was closed, only the lens of the camera was visible from the experimental area. The video camera was connected to a monitor outside the room to allow viewing of the experimental sessions. In addition to the experimental equipment, foliage of various types was present behind the table in the experimental area to be used as perches by the owls.

All owls were dark adapted for a minimum of 30 min prior to testing in the Dark conditions. Prior to the start of a trial, an individual owl was isolated in the testing side of the room. Approximately 1 min after the owl was isolated, an experimenter entered the room with an opaque plastic cage containing a single mouse. The experimenter placed the mouse on the table, with the mouse's orientation being either determined randomly (Live conditions) or predetermined according to a randomization scheme (Dead conditions). Once the mouse was on the table, the experimenter left the experimental area and the room.

## Conditions

The four experimental conditions were the same as used in Experiment 1. The light level in the room ranged from 49 lux (lowest reading at table) to 57 lux (highest reading at table directly under fluorescent light) in the Light conditions, and from 0.1 to 0.2 lux in the Dark conditions. The method of positioning live mice, and of positioning and orienting dead mice was the same as Experiment 1.

### Scoring Procedures

Scoring procedures were identical to Experiment 1 except that instead of the mouse's orientation was scored relative to the midpoint of the owl's chest. This scoring procedure was used because several perch sites were available to the owl.

## Results

### Light Levels

The relative frequency of attacks made during the Light condition (43%) was significantly lower than the relative frequency of attacks made in the Dark condition (89%; Fisher's Exact Test; $p < 0.001$). A significant effect of light level was also found when the latency to initiate an attack was examined ($t = 10.6$; $p<0.001$). The owls initiated an attack more quickly in the Dark conditions (RT = 52.0 s) than in the Light conditions (RT = 173.3 s).

### Dead versus Live Mice

No significant difference was found between the relative frequency of attacks in the Live (65%) and Dead (92%) conditions (Fisher's Exact Test; $p > 0.05$). Furthermore, no significant difference was found in latency to attack under the Live (RT = 95.3 s) versus the Dead (RT = 76.6 s) conditions ($t=1.0$; $p>.5$). This indicates that the owls did not attack one prey type more often or more quickly than the other.

### Mouse Orientation

The influence of mouse orientation was examined for both Live and Dead mice.

The number of attacks made on mice facing the owl (Toward condition) was compared to the number of attacks made on mice facing away from the owl (Away condition). Fisher's Exact Test (2x4) revealed a significant interaction ($p < 0.05$) of mouse orientation (Toward and Away) and condition (Live and Dead). Further analysis showed that the owls were attacking the live mice significantly more often when the mice were oriented away from the perch (87.7%) than towards (12.3%; Binomial $p < 0.0001$). On the other hand, the owls attacked the dead mice without regard to orientation (away = 50%; Binomial $p > 0.2$; see Figure 7-2). This result indicates that owls attacked the live mice more often from behind, but orientation had no effect when the mice were dead.

## Discussion

For Saw-whet owls attacks were more frequent, and attack latencies were shorter, under low versus high light levels. Second, attacks on dead and live mice were equally frequent and occurred at a similar point in the trial. Third, live mice were preferably attacked from behind, but orientation of dead mice did not affect the owl behavior.

Saw-whet owls in Experiment 2 displayed predatory patterns similar to the Short-eared owls in Experiment 1, with one exception: Short-eared owls attacked more readily in the light, whereas Saw-whet owls attacked more frequently and sooner in the dark. This can be directly explained by the natural habitat of the two owl species. The Short-eared owl is a crepuscular species and therefore hunts during times of increased light. The opposite is true of the nocturnal Saw-whet owl. Expression of this natural hunting preference in a laboratory setting shows that the owls were indeed demonstrating naturalistic hunting behaviors.

Both owl species showed similar response to mouse orientation, i.e., mouse orientation did not matter for dead mice, but live mice were preferentially attacked from behind. This result suggests that prey orientation may be an important feature influencing when an owl, specializing on small mammals, initiates an attack. The two species of owls studied here differ not only in their preferred hunting strategy, but also in their diel activity patterns. Thus, the similarity seen in preference for attacking live mice from behind seems to be a general predatory characteristic for owls, and cannot be attributed to species-specific characteristics.

The results of Experiments 1 and 2 provide substantial evidence that visual cues play an important role in the predatory behavior of owls. In addition, predatory behavior is dependent on static, physical prey cues as indicated by the effect of mouse orientation on attack frequency and latency. But other static visual characteristics, such as shape, color, or size may play a role, as well as dynamic visual characteristics, such as movement patterns. The role of these cues is further investigated in the next experiment.

## EXPERIMENT 3

Owls may rely on both, dynamic and static prey cues for initiating an attack. In Experiments 1 and 2, mice moved naturally, and their movement patterns were not manipulated. It is not clear from these experiments whether natural movement of the prey is an important cue or whether any movement is sufficient to elicit an attack. For example, would an owl attack an item the size of a mouse moving in a constant direction at a fixed speed? This artificial movement is quite different from the natural movement of a mouse. If owls are using specific movement patterns as a cue to engage in an attack, objects that move in an unnatural pattern should be ignored. On the other hand, if arbitrary movement cues are sufficient for the initiation of an attack, the artificial movement should be sufficient to elicit an attack.

Predatory behavior is also dependent on static, physical prey cues. This was supported by the results on the effect of mouse orientation of attack frequency and latency. But other characteristics, such as shape, color, or size may also play a role. Owls may integrate both movement and physical prey characteristics, and use this combined information to determine whether to attack. So, if for example an item is moving in an appropriate fashion, but is the wrong shape, the owl might be less likely to attack it. Likewise, if the object has the correct physical characteristics, but is moving in an artificial way, the owls might also not attack. But if the two cues are combined in an object with the correct movement and correct physical characteristics, then an owl is very likely to initiate a predatory attack. To examine these questions, Saw-whet owls were presented with potential prey items that had either artificial or natural movement patterns, and had either artificial or natural physical characteristics.

## Methods

### Subjects

Three owls from Experiment 2 were used as subjects in this study. The housing conditions were identical to Experiment 2. The owls were approximately 14 months old at the beginning of the experiment.

## Apparatus

The experimental setup remained the same as in Experiment 2, with the exception of the table. The small table used in Experiment 2 was replaced with a much larger table (115 x 90 x 65 cm; length, width, height). The top of the table was constructed such that it was hollow and approximately 6 cm deep. Recessed within the table top was circular track (circumference 298 cm) complete with a small model train. The track was completely covered except for a narrow circular strip which allowed for two small metal rods to protrude and move smoothly around the track. Powered by the model train, the rods moved at a constant speed of 0.4 m/s in a clockwise direction. A small plastic platform could be attached to the rods. The rods and the plastic platform were only present during the Artificial movement sessions (see below).

## Conditions and Procedures

Owls were tested, under low light levels, with several different conditions. Mice were presented either live or dead. The dead mice could be either moving in one of several ways, or be stationary oriented in several ways. The owls were also presented with an artificial object which was either moving or stationary. Finally, the owls were also presented with an empty table. The combinations of these conditions are described in detail below. The order in which the conditions were tested, and order in which the individual owls were tested, were randomized.

A monitor located outside of the owl room was again used to view all experimental sessions. Prior to the beginning of an experimental session the model train was started (with the exception of No Sound sessions). For each trial the owl to be tested was isolated in the experimental side of the room. One minute after the owl was isolated, an experimenter entered the room with an opaque plastic cage. The cage contained either a mouse, an object or was empty depending upon the experimental condition. The experimenter positioned either the opaque cage or herself between the table and the owl. The two rods and platform were always attached to the train to keep the set-up time and experimenter movements similar across all conditions. If the platform was not needed, it was set-up and promptly disassembled before the prey item was placed on the table. The experimenter quietly and quickly left the room and viewed the remainder of the session from outside the testing room. Each session lasted until an attack was initiated or a maximum of 15 min.

### Live Mouse Conditions

A live mouse was randomly oriented and positioned on the experimental table. To investigate if the sound of the train moving along the tracks would influence either the frequency or latency of the attacks, these sessions were conducted with the train running (Live-Sound sessions) or without (Live-No Sound sessions). Since the train offered no visual cues during these conditions, the only difference between the two conditions was the presence of the train sound.

### Dead Mouse Conditions

Movement Conditions. The experimenter placed a dead mouse on the plastic platform attached to the train. The mouse was oriented such that the mouse's head was positioned forward (Head-First sessions) or backward (Tail-First sessions). During the

Head-First sessions the mouse moved along the circular track with its body oriented correctly. The mouse's body was oriented in the reverse orientation during the Tail-First conditions, as if the mouse were moving backwards. Since these sessions required the train to move the prey, No-Sound conditions were not possible.

Stationary Conditions. A dead mouse was randomly placed on the table. The orientation of the mouse was such that half of the sessions had the mouse oriented toward the camera (Head-Toward) and half of the sessions the mouse was oriented away from the camera (Head-Away). To keep these sessions as similar as possible to the conditions with prey movement, all of the sessions were conducted with the train running.

### Object Conditions

A yellow cylinder (4 x 4 cm; diameter, length) was either positioned and oriented randomly on the table (Object-Stationary) or placed on the small plastic platform attached to the train (Object-Movement). All of the sessions using the artificial object were conducted with the train running.

### Control Conditions

After extended experience of finding food on the table, the owls might have learned to land on the table and search the surface for food. Therefore, control sessions with nothing placed on the table were used to determine how often the owls simply landed on the table. The control sessions were conducted with the train running (Sound sessions) and with the train shut off (No Sound).

## Results

Two measurements were used to examine how the various conditions affected the owls' predatory behavior. First, the number of sessions in which an attack occurred was compared to the number of sessions in which an attack did not occur. Second, the latency to initiate an attack was measured. In addition, the mouse orientation associated with an attack was again recorded to allow a comparison with Experiment 2. With the exception of the Sound/No Sound comparison, all conditions were examined with Sound present.

### Effect of the Train Sound

To determine whether the sound of the train had an effect on the attack behavior of the owls, the Sound and No Sound conditions of the Live sessions were compared. No significant difference was found between the frequency of attacks in the Sound conditions (78%) and the No-Sound conditions (58%, Fisher's Exact Test $p>0.2$). Furthermore, no significant difference was found between attack latencies in the Sound (RT = 168.9 s) and No Sound (RT = 181.4 s) conditions ($t = -2.06$; $p>0.8$).

### Prey Movement

To examine the role of prey movement in the initiation of an attack, the three different movement conditions (natural movement, artificial movement and no movement) were compared for the sessions in which a natural prey item was used. The owls initiated an attack more frequently when a natural prey item was presented either with natural movement (78%; Live Sound) or no movement (81%) than if the natural prey item moved artificially (41%; Fisher's Exact test $p>0.01$; see Figure 7-3). A significant effect was also found for the latency to attack ($F(2,42) = 12.0$; $p<0.001$), with median latency for natural movement (RT=150.2 s) and no movement (RT= 223.7 s) being shorter than for artificial movement (RT= 290.7 s; see Figure 7-3).

### Prey Characteristics

To examine the role of visual prey characteristics in the initiation of a predatory attack, the three different prey conditions (natural prey, artificial object and no prey) were compared under conditions in which no movement was present. The owls initiated significantly more attacks when the prey item was natural (81%) than if the item was artificial (0%) or when no item was available (15%; Fisher's Exact test $\underline{p}>0.01$; see Figure 7-4).

### Mouse Orientation

Similar to Experiment 2, the owls tended to attack live prey more frequently when the prey item was directed away (71%) than when it was facing the owl (29%), but this difference was not significant due to the small sample size (Binomial $\underline{p}>0.1$). This difference was once again not found with the dead mice (53% towards and 47% away; Binomial $\underline{p}> 0.1$). Furthermore, with artificial movement there was no effect of orientation on attack frequency (42% head-first and 58% tail-first; Binomial $\underline{p}>0.1$).

## Discussion

Saw-whet owls attacked artificially moving prey less frequently on than naturally moving or static prey, and attack latencies for moving prey were shorter than for static prey. Attacks on natural prey were more frequent than attacks on artificial objects, with attack latencies being shorter for natural prey than for artificial objects (or the absence of prey). Finally, the effect of prey orientation on attack frequency was the same as in the previous experiments.

Owls do not attack items based simply on the presence of motion; attacks were initiated more often when the movement pattern fell within the parameters of natural movement. Since pauses in motion is also part of a mouse's natural movement repertoire, it is not inconsistent that the owls respond similarly to moving and stationary mice. This is also consistent with the fact that, on several occasions during the Live mouse sessions, the mouse remained stationary for several seconds to several minutes between bouts of movement.

The visual characteristics of the prey also played an important role in the initiation of a predatory attack. The Control conditions showed that the owls had not simply learned to land on the table to search for food. Furthermore, when the owls were presented with an artificial item of similar shape and size to a natural prey item they rarely initiated an attack. This result strongly supports the view that Saw-whet owls respond visually to the presence of specific natural prey characteristics.

Predatory attacks seem to be guided by at least two prey-based characteristics: natural movement patterns and natural static prey characteristics. Further, the combined presence of these two features seem to be necessary for the initiation of an attack: presentation of natural prey items with artificial movement was not sufficient to elicit an attack, nor was the presence of an artificial object without movement.

# GENERAL DISCUSSION

Predatory birds must develop behavior that allows for quick prey detection. By incorporating information from more than one sensory system an individual may more accurately locate a target item. Although many studies have shown that owls are quite adept at localizing prey-generated sound, many species of owls hunt when sufficient lighting is available to permit the use of visual cues. Given the more frontally positioned eyes of owls, many studies of owl vision have focused on the use of binocular cues. Several of these studies report similarities in the visual processing of barn owls and visually oriented mammals (Knudsen & Brainard, 1995; Pettigrew & Konishi, 1976). Although these studies imply that vision provides an important source of information for owls, the present study is, to our knowledge, the first to investigate the role of visual cues for prey localization. The results indicate that owls indeed use a combination of dynamic (motion) and static (shape or orientation) visual cues in localizing prey items.

Motion cues are important for determining if the object is an appropriate prey item. In this situation the owl might attend to specific motion cues, such as pattern of movement. The particular pattern of movement made by a prey item (e.g., a mouse) may be sufficiently different from that made by a non-prey item, such as wind-blown debris, allowing owls to use the motion pattern to determine whether to attack the object. Along with motion, static prey cues may be used for prey detection. Small rodents (as hunted by the owls in these experiments) have similar body shapes, size and color. Owls may use several of these characteristics while hunting. Given that owls need to quickly and accurately determine whether an object is a prey item, integrating several dynamic and static cues may provide more information than either of these cue types alone.

Experimental results also showed that static and dynamic cues must be compatible with natural cues in order to elicit an attack. Movements that occur naturally in a mouse's locomotor repertoire (i.e., the Natural and No movement conditions) elicited more predatory attacks than artificial prey movements. A similar pattern of results was also seen with static prey characteristics. Natural prey characteristics elicited more attacks than artificial characteristics. Further, when the owls were presented with live and dead mice, neither species showed differences in attack frequency or latency. However, both species attacked live mice more often from behind than from the front, whereas an orientation bias was not seen for dead mice. Together, these results show that owls are using a combination of visually-based, naturally occurring prey cues to initiate a predatory attack.

The two species of owls studied here showed diel hunting patterns that are representative of their natural behavioral ecology. This was shown by the differences in attack latency dependent on lighting conditions by the two species of owls. The crepuscular Short-eared owls had shorter latencies to initiate an attack in the light, whereas the Saw-whet owls had shorter latencies in the dark mirroring what would be encountered in natural conditions.

In summary, owls are able to use static and dynamic visual cues in localizing prey items. The current investigations show that owls use a combination of these cues during predation. The motion pattern of the target item must be compatible with the natural movement of a prey item to elicit an attack. Furthermore, the static prey characteristics must also be representative of a natural prey item. These experiments clearly show that vision provides important information to a hunting owl. Thus, further investigations of owl predatory behavior must consider the importance of visually-based prey cues.

Figure 7-1. Percentage of attacks to Live (left) and Dead (right) mice facing away (empty bars) and towards (filled bars) from the perch for Experiment 1.

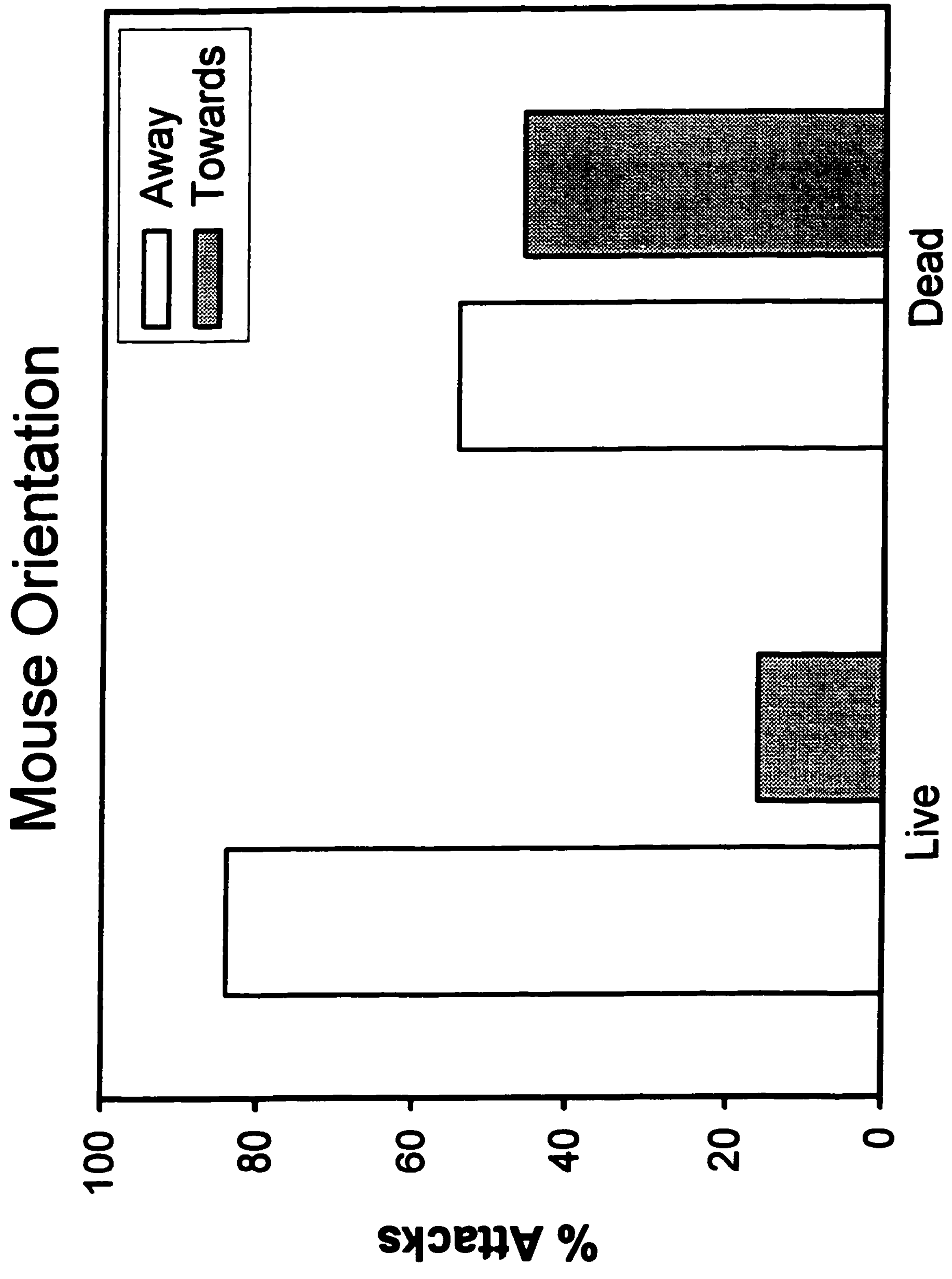

Mouse Orientation
Away
Towards
% Attacks
0
20
40
60
80
100
Live
Dead

Figure 7-2. Percentage of attacks to Live (left) and Dead (right) mice facing away (empty bars) and towards (filled bars) from the owl for Experiment 2.

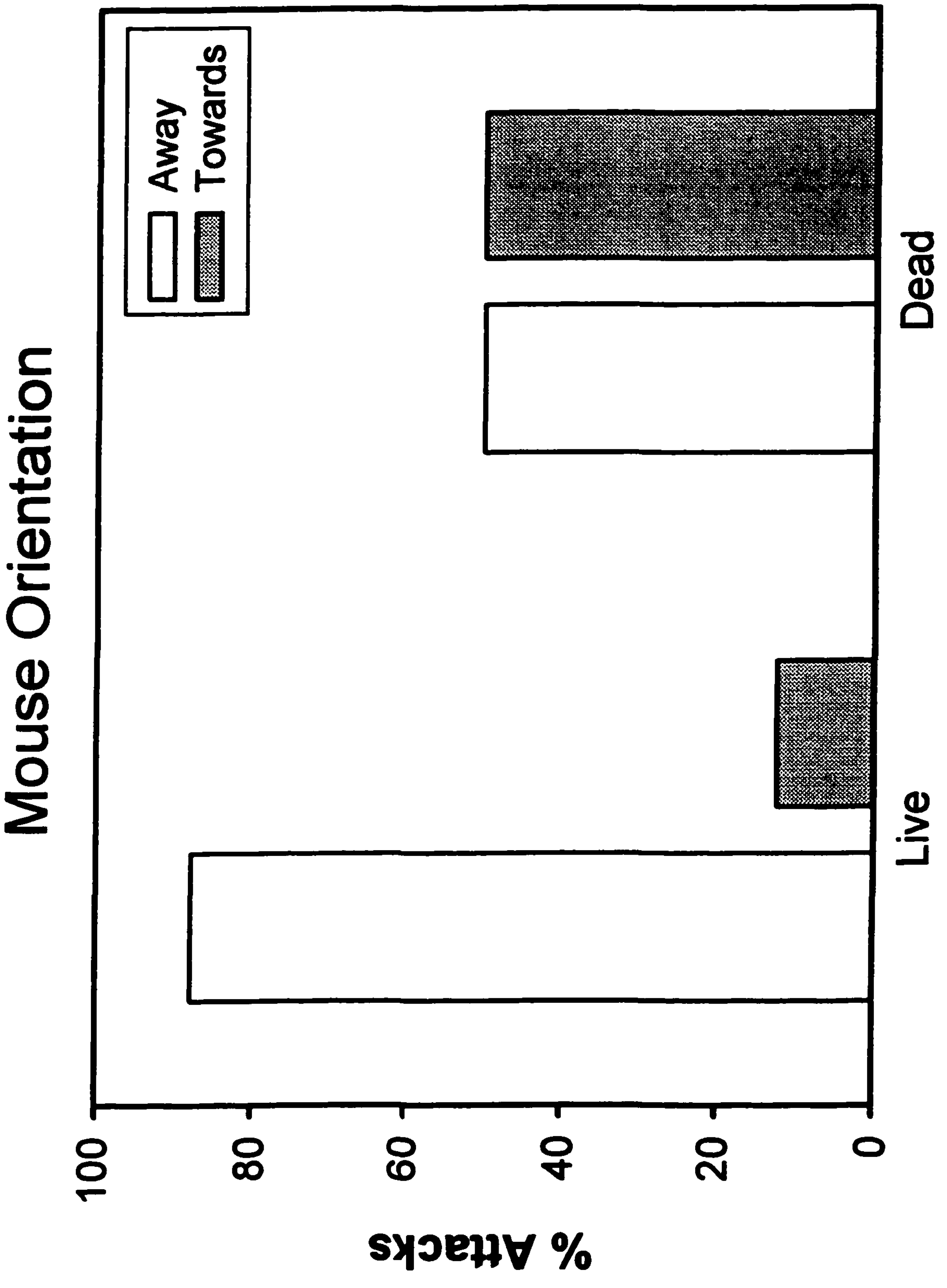
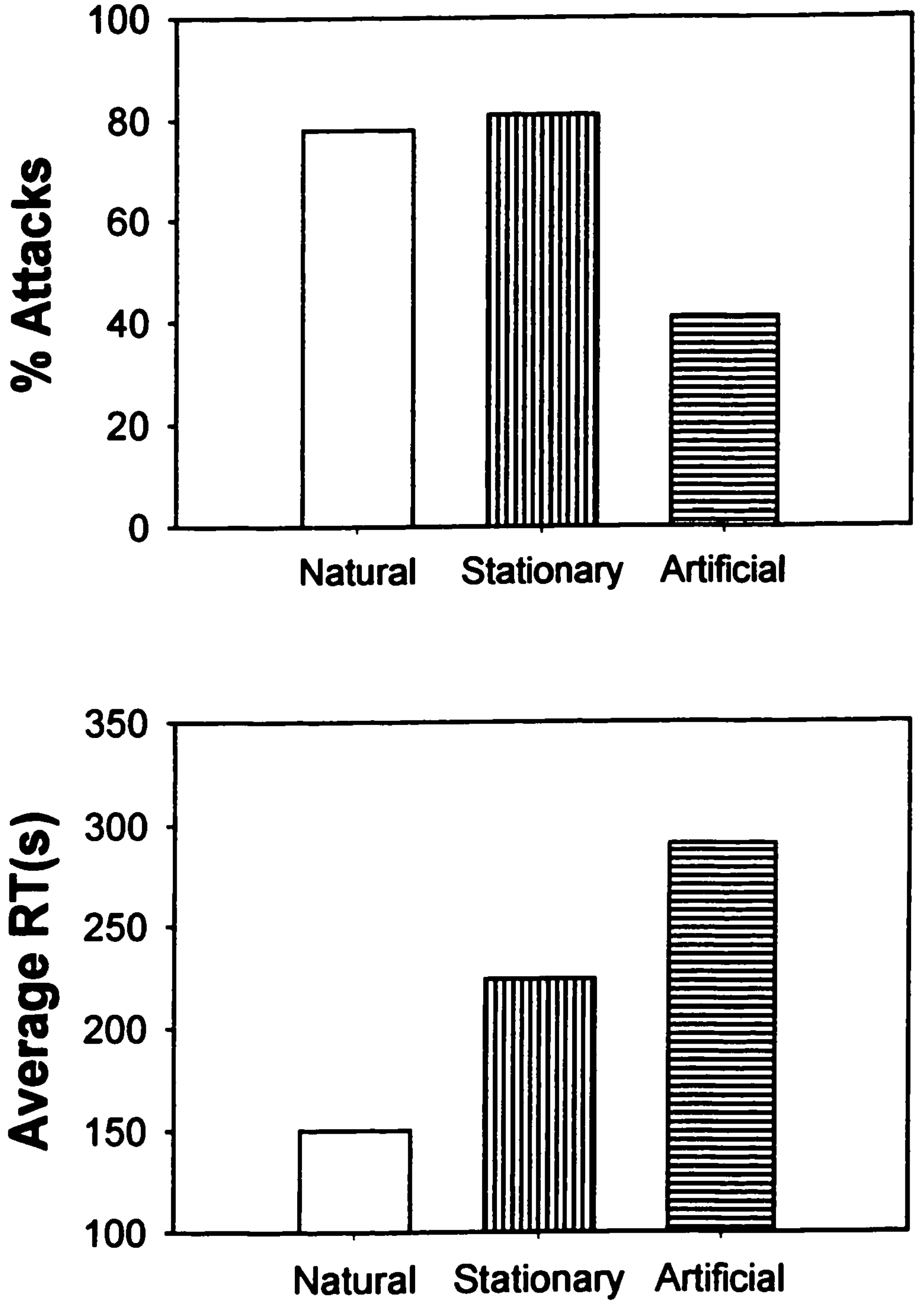
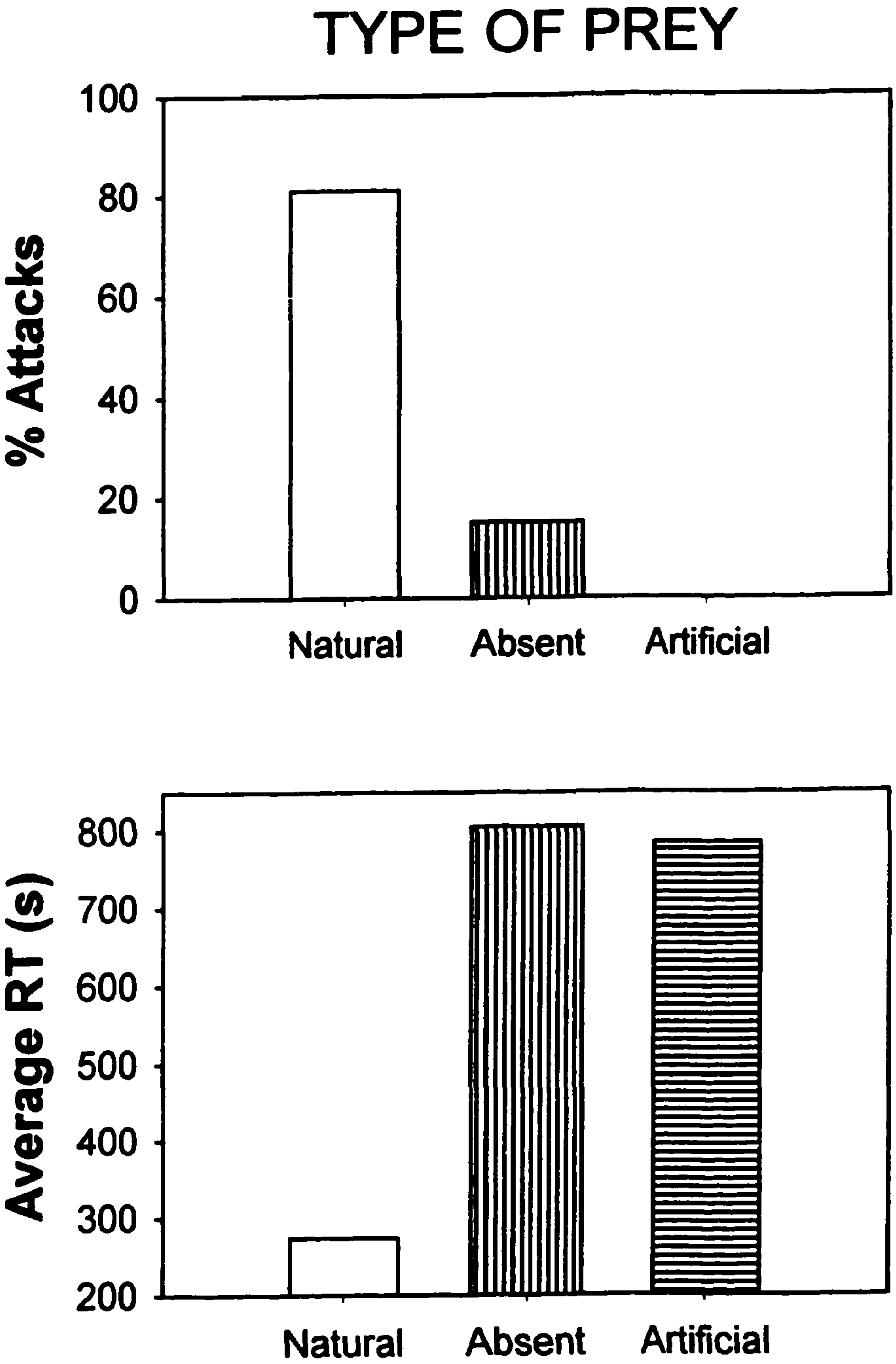

Mouse Orientation
Away
Towards
% Attacks
100
80
60
40
20
0
Live
Dead

Figure 7-3. Influence of prey movement type on attack frequency and reaction time. The upper panel shows average percent of attacks made by the owls in the three prey movement conditions. The lower panel shows the average reaction time for the owls to initiate an attack.



TYPE OF MOVEMENT

Figure 7-4. Influence of type of static prey on attack frequency and reaction time. The upper panel shows average percent of attacks made by the owls in the three static prey type conditions. The lower panel shows average reaction time for the owls to initiate an attack.


TYPE OF PREY
% Attacks
100
80
60
40
20
0
Natural
Absent
Artificial
Average RT (s)
800
700
600
500
400
300
200
Natural
Absent
Artificial

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# CHAPTER 8

# CONCLUSIONS AND GENERAL DISCUSSION

Humans and birds recognize objects and scenes readily, so one tends to believe that the perceptual mechanisms are the same. Recent research shows substantial species differences in the architecture of the perceptual systems. Indeed, birds may not perceive objects in a similar manner as humans. Several experiments have shown that pigeons encode objects presented in images not as complex objects, but in terms of local or elemental properties (Cerella, 1980; Donis & Heinemann, 1993; Kirkpatrick-Steger, Wasserman and Biederman, 1996). This type of elemental encoding would not seem to provide the flexibility needed to recognize dynamic objects in a naturalistic environment. Recognition of complex environmental objects must occur at a global level. Information about elemental stimulus properties must be pooled such that objects are seen as wholes. Investigations showing global processing in birds suggest that birds may selectively rely on local or global cues depending upon the context of the discrimination or the task requirements.

## Local and Global Processing

An initial step in examining complex object discrimination in natural situations is to investigate how birds encode and use simple patterns. Discrimination of line stimuli based on orientation or position differences (as in Chapter 2) provide a simple visual environment to study how birds encode local and global stimulus properties. Previous research has shown that the accuracy of a discrimination may be altered by the presenting the line stimuli embedded within a redundant or seemingly uninformative context. In addition, pigeons and humans have been shown to be differentially affected by the addition of contextual information. Humans have been shown to benefit from the addition of contextual information (Enns & Prinzmetal, 1984; Pomerantz, 1991; Pomerantz & Pristach, 1989; Pomerantz, Sager & Stoever, 1977). Pigeons, on the other hand, have been shown to be significantly less accurate at discriminating line orientation when the lines were presented with a context (Donis & Heinemann, 1993). The investigations in Chapter 2 substantially further our knowledge of the extent to which these species differences exist. Pigeons and humans were required to discriminate between lines that differed in either orientation or absolute position. The lines were presented either in isolation or embedded in a uninformative context. Pigeons were differentially influenced by the contextual information by showing enhanced performance with the contextual stimuli in the line position discrimination (at least in Experiment 1) but not in the line orientation discrimination. This difference was not shown by the human subjects, suggesting that humans use the emergent features of contextual stimuli to enhance discrimination. These results clearly support differences in featural processing between pigeons and humans.

The use of local and global cues by pigeons and humans was further examined in a more complex pattern recognition task. In Chapter 3 pigeons and humans were required to discriminate one of four different Glass patterns from a noise pattern. At higher coherence levels the pigeons were able to accurately discriminate the pattern from the noise display. However, the pigeons did not show threshold differences with the different pattern types. This result suggests that the pigeons were using local pattern information. Responses to all of the patterns showed similar discrimination thresholds. Our results, and those of Wilson and colleagues (1997, 1998), showed that humans globally pool across local elements when processing concentric and radial patterns, but only use elemental processing when processing vertical and horizontal patterns. The experimental evidence shown in Chapters 2 and 3 suggests that the processes underlying form perception are organized differently in pigeons than in humans.

### Scene Perception

Birds have been shown to use both local and global level processing in pattern and object perception. Object recognition requires that the viewer use global information (e.g., surface texture or edges) to discriminate one object when presented among several objects or when discriminating an object from the background. Many investigations of avian object perception have used images of environmental scenes to examine if birds perceive a 2-D image as representative of 3-D space. Many studies have used transfer experiments where birds were trained with one medium (e.g., 2-D pictorial scene) and tested with another (e.g., the actual 3-D environment), to examine whether accurate performance transfers across the two media. In Chapter 4 we used a technique developed by Spetch, Kelly and Lechelt (1998) to measure more directly whether pigeons encode the spatial properties of an image in 2-D or 3-D coordinates. When pigeons were presented with unreinforced novel images of the same scene as in training, the pigeons accurately searched at a target location suggestive of 3-D spatial encoding. Further tests, which manipulated the position of a dominant visual feature in the images, showed that the pigeons did not fully shift their responses in the direction of manipulated structure. Thus, the pigeons were likely relying on several visual properties of the images to locate the target position.

The results of Chapter 4 show that pigeons were using the contextual information available in the pictorial scene to identify or recognize visual properties of the images that may have changed substantially with different viewpoints. The complex scenic images presented provided the pigeons with several cues (e.g., depth cues) not available in more simple stimulus discriminations. Furthermore, when a bird locomotes within a natural environment it views objects from many different viewpoints. Much of the previous research investigating avian object perception only provided a single image or a very small set of images (e.g., Spetch, Kelly & Lechelt, 1998). The experiment in Chapter 4 shows that providing many viewpoints may be an important aspect of encoding a static 2-D scene as representative of a 3-D space.

## Dynamic Object Perception

Several stimulus features of an object may be encoded as a bird moves through its environment. Motion, either on the part of the observer or the object, may provide important discriminative cues that are not available when an object is viewed statically. Indeed motion would appear to be a very important cue in the avian world. Birds must be able to respond to self-motion (e.g., during flight) and to object-motion (e.g., predator detection). In the final three chapters dynamic object discrimination was examined using self-motion (chapters 5 and 6) and object-motion (Chapter 7). Chapters 5 and 6 examined what stimulus properties are encoded as a bird locomotes through a 3-D environment. Chapter 7 examined what properties birds, owls in particular, encode when localizing dynamic prey during hunting.

The pigeons in Chapter 5 learned to locate hidden food based only on the geometric properties of a 3-D environment. When the size of the environment was reduced such that the absolute length of the long walls were made closer to that of short walls used in training the birds continued to search in corners that were correct according to relative geometry. Previous studies using pigeons and chicks (Kelly, Spetch & Heth, 1998; Vallortigara, Zanforlin, & Pasti, 1990) have shown that these birds encode geometric properties of an environment. Yet, the question of how this information is encoded (absolute or relative geometry) has not previously been addressed. From a human perspective it seems reasonable that metric information would be encoded using relative metrics. Pigeons, however, do not always use a relational encoding rule (e.g., Pearce, 1991; Spetch et al., 1996; 1997).

Encoding of relative geometry for directional determination, as used in Chapter 5, might be favored because it allows for the calculation of distance to any of the environmental surfaces regardless of ones position. Using calculations based on absolute geometry would require one to travel to each corner in order to obtain a distance calculation that is then matched to a remembered vector. Thus, directional determination may support the use of relational metrics, whereas when one is determining a specific goal position (as in Spetch et al.,1996; 1997), absolute metrics may be more important. This experiment thus shows the important relationship between the type of task that is being engaged in and what environmental properties are relied upon to solve the task.

The previous chapters have shown that animals can encode and use multiple sources of information to locate a goal, and that the primacy of control may differ according to context (Chapter 5). In Chapter 6 pigeons were tested to determine their reliance on featural information when provided with geometric information only or with geometric and featural information combined. Following training, the birds were tested with non-reinforced transformation tests which altered the featural properties of the environment. The results of this experiment showed that even when provided with distinct featural information, pigeons still encoded the geometric properties of the environment. Furthermore, initial experience with an environment strongly affected what properties pigeons used as primary cues to locate a target position. This was seen during transformation tests which pitted featural and geometric cues against each other. The birds in the group initially trained with features and geometry showed strong control by featural information. The pigeons in this group continued to choose a corner containing the featurally correct cue, even when the corner was geometrically incorrect. Interestingly, the group initially trained with geometric information only (and retrained with features) showed shared control by the correct featural information and the correct geometric information. Chapter 6 showed that pigeons' use of environmental information is strongly influenced by experiential factors.

Chapters 5 and 6 showed that several factors influence how environmental information is encoded as a bird locomotes through an environment. Although the subject was free to view environmental information from several different vantage points, the object or targets within the environment remained stationary at all times. For many bird species important objects do not remain static but move about the environment. An example of such a situation occurs when predatory birds hunt moving prey items. In this context both self-motion and object-motion co-occur.

In chapter 7, we examined how owls use static and dynamic cues in discriminating appropriate and inappropriate prey items. Owls' ability to localize target items using auditory cues has been well established, but less is known about how owls use visual cues when hunting. In the experiments presented in chapter 7, we investigated how owls use visual prey cues when hunting. These investigations showed that owls use a combination of dynamic and static prey cues during predation. It was shown that the motion pattern of the target item must be compatible with the natural movement of a prey item in order to elicit an attack by the owls. Furthermore, the static prey characteristics must also be representative of a natural prey item. These experiments clearly show the importance of vision and movement cues in owl predatory behavior. Furthermore, owls rely not only on the presence or absence of motion but rather on the quality of the motion.

## Summary

The series of experiments presented in this thesis clearly demonstrate the diversity of approaches used to investigate pattern and object recognition in birds. Each of these approaches provides important insights to further our understanding of how birds perceive visual information. Examining avian pattern and object perception requires that one evaluate how birds respond to a series of diverse stimuli. An important initial step is to examine how birds encode simple stimulus patterns. It is only at this level that one can easily manipulate the properties of the visual stimuli to examine how subtle changes in stimulus properties can influence behavioral responses. Understanding avian pattern perception at this level provides a foundation upon which one can further investigate more complex object perception. Objects must be recognized within a visually rich context in a bird's natural environment. Further, different views of a single object are provided as a bird moves. Thus, the role of movement, on the part of the observer as well as the object, must be considered when investigating object perception and recognition. The research presented here investigated avian pattern and object perception at each of these levels. Each experiment provided a new and better understanding of avian visual perception.

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