Dynamic Object Perception by Pigeons

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Three experiments examined pigeon discrimination of computer-generated three-dimensional (3-D) projections of cube and pyramid objects. Four pigeons were tested using a go/no-go procedure involving static and dynamically rotating presentations of these stimuli. Transfer tests with different types of rotational and featural transformations suggested the pigeons may have used a 3-D representation of the objects as their primary means of performing the discrimination. The comparative implications for object and motion perception in animals are considered.

When we open our eyes, we see a world that consists of stable, meaningful, and unified objects that move in spatially and temporally predictable ways. We are readily able to visually detect, grasp, catch, and avoid these objects both effortlessly and efficiently. Such observations naturally raise the question of what constitutes the functional unit of perception and action mediating our dynamic, visually guided interactions with the world. One popular answer has been the object (e.g., Gibson, 1966, 1979; Johansson, 1975), a representation in which the structured spatial and temporal properties of the optic array are encoded, organized, and acted on as a higher order structure of unified surfaces and events. How such stable three-dimensional (3-D) representations might be created by the brain from the ambiguous two-dimensional (2-D) retinal images that are their source is one of the enduring puzzles of cognitive science.

There is no doubt that birds are equally as visual and mobile as we are. Their rapid avoidance of obstacles during flight (e.g., flying through the gaps of chain-link fences), detection of small cryptic insects, and pinpoint landings on wind-blown limbs all point to a rich and accurate perception of the surrounding visual environment. These casual observations of bird behavior suggest these animals may experience an object-filled world like our own. Do they? If not, then what are the mechanisms of perception and action mediating their highly active visually guided behavior? This article begins to explore these difficult questions by examining how pigeons discriminate dynamically moving and static computer-generated projections of 3-D objects.

In these experiments, pigeons were trained and tested in a

discrete trial go/no-go discrimination with cube and pyramid object stimuli (see Figure 1). Because they directly pertain to the larger issue of whether these complex stimuli were viewed as "objects" by the pigeons, we were interested in understanding the following characteristics of this discrimination. The first issue concerned identifying the means by which the pigeons learned to discriminate between these two kinds of object-like stimuli. The critical question was whether discrimination was based on the simple 2-D local features of the images or the higher order representation of them as 3-D objects. The second issue of interest was how the addition of motion in the presentation of these stimuli would influence the discrimination. That is, would the rotation of these stimuli around their different axes facilitate, interfere, or have no effect on their discrimination of the displays? The third issue concerned how the pigeons would perform with different types of rotational and featural transformations of the stimuli. These latter manipulations were important because of their connections to the major perceptual issues of viewpoint invariance in object recognition (Beiderman, 1987; Bulthoff & Edelman, 1992; Marr & Nishihara, 1978; Palmer, 1977; Poggio & Edelman, 1990; Rock, 1973; Tarr, 1995) and the perception of object structure from motion (Johansson, 1975; Rogers & Graham, 1982; Ullman, 1979; Wallach & O'Connell, 1953). Collectively, the determination of these characteristics contributes to answering the far more difficult and slippery question of greatest interest—did the pigeons perceive, represent, and act on these stimuli as if they were 3-D objects?

How pigeons react to stimuli that dynamically change in perspective has not been extensively explored. As such, the experimental literature is not very helpful in predicting what to expect with our stimuli. Consider first the mixed results concerning how changes in perspective have influenced visual discriminations of static displays by pigeons. The most widely known of these experiments are those conducted by Cerella (1977, 1982, 1990a, and 1990b). Over a number of tests with different types of stimuli, he consistently failed to find evidence that pigeons generalize to x-, y-, or z-axis rotations or size-transformed variations of previously discriminated stimuli. Of most interest to us was Cerella's (1977) report that pigeons failed to generalize to any greater degree to changes in perspectives with a 3-D
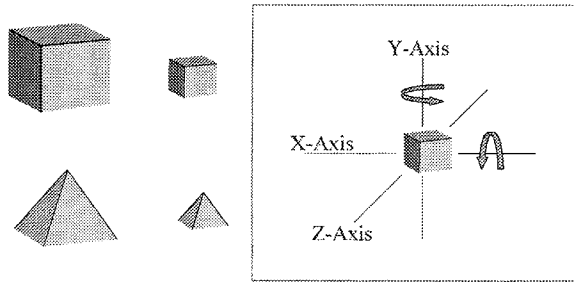
Figure 1. Examples of the two sizes of cube and pyramid object stimuli used in these experiments. The diagram on the right shows the coordinate system used in these experiments. Experiment 1 involved rotations around the y-axis. Experiment 2 involved rotations around the x-axis. Experiment 3 involved rotations simultaneously around both the x- and y-axes. Colors are shown as different gray levels. The contour lines are more noticeable in this diagram than in the actual displays.

wire-frame cube than to a 2-D control condition. Such results led him to argue that pigeons learned to recognize and discriminate stimuli on the basis of a local feature detection as encoded by viewer-centered 2-D templates of the training stimuli (Cerella, 1986). In this regard, his results are in good company with the many other findings, indicating these animals frequently learn discriminations by memorizing the specific training exemplars (Berrymàn, Cumming, Cohen, & Johnson, 1965; Carter & Werner, 1978; Cumming & Berryman, 1961; Cumming, Berryman, & Cohen, 1965; Edwards & Honig, 1987; Farthing & Opuda, 1974; Heinemann & Chase, 1989; Holmes, 1979; Santi, 1978, 1982; Vaughan & Green, 1984; Wright, 1997).

Recently, results more indicative of an object-like perception of complex visual images by pigeons have been reported by Wasserman et al. (1996). They found above-chance generalization to transformations of complex line drawings of objects rotated in the y-axis or depth plane of the image. In their experiments, pigeons were trained with single views of four objects in a four-alternative choice task. When tested with depth-rotated pictures of these objects, the pigeons showed complete generalization over a range of ±33°C with systematically decreasing, but above-chance, discrimination over a range of ±133°. These results suggest that birds might be capable of using object-based structural descriptions of images when responding to them.

In the real world, such perspective changes are typically induced by the motion of objects relative to the observer or vice versa. As such, a key idea in many theories of object perception is that motion provides additional information not available in a single static snapshot or view about an object's structure and its position in space. The contributions of these kinematic factors to object perception have been widely considered in humans (e.g., Cutting, 1986; Gibson, 1966, 1979; Johansson, 1975; Kellman, 1993; Ullman, 1979; Wallach & O'Connell, 1953).

This has not been the case for birds, despite the obvious ecological validity of motion discrimination and the physiological evidence that motion is of exceptional importance in the pigeon nervous system (see Frost, Wylie, & Wang,

1994, for a review). Those behavioral studies that have been conducted have concentrated on the basic abilities of pigeons to discriminate stimulus velocity (Hodos, Smith, & Bonbright, 1975; Mulvanny, 1978; Siegel, 1970; Stenhouwer & Denny, 1975), track stimulus movement (Pisacreta, 1982; Rilling & LaClaire, 1989; Wilkie, 1986), see apparent motion, (Siegel, 1970, 1971) or detect the presence or absence of motion in general (Dittrich & Lea, 1993).

The one of most relevance to the current research is an important study by Emmerton (1986). She trained pigeons in a go/no-go procedure to discriminate between Lissajous figures, created by combining sine-wave functions on an oscilloscope. These stimuli consisted of either dynamically rotating shape outlines or a single dot that traced out over time the contour of these same outline patterns. She found that pigeons could learn both types of discriminations with the outline patterns supporting faster learning than the moving dot patterns. The eventual discrimination of the moving dot patterns suggested that pigeons are capable of temporally integrating a path of motion as a discriminative cue per se.

The following studies begin filling in this obvious and large gap in our knowledge about avian object and motion perception. Four pigeons were trained and tested in a modified go/no-go discrimination with computer-generated 3-D projections of cubes and pyramids. Two methods of presentation were used within a session. On half of the trials, the stimuli were presented statically on the display at a randomly selected orientation. On the other half of the trials, the stimuli were presented dynamically, with the objects appearing to rotate in depth on the display. Experiment 1 examined the acquisition of this object discrimination as implemented by dynamic and static rotations around the y-axis (see Figure 1 for the coordinate system used in this article). Experiment 2 examined the transfer of this discrimination to novel conditions involving the static and dynamic rotation of the objects in the x-axis. Experiment 3 examined the transfer of this discrimination to novel conditions involving the simultaneous static and dynamic rotation of the objects in both of these axes. Within each experiment, different featural transformations to the objects designed to clarify the basis of the pigeons' discrimination of these stimuli were also conducted. To anticipate our major conclusion, we believe the results of these experiments suggest the pigeons are capable of experiencing and using object-like 3-D descriptions of such images as the primary means of their discrimination.

Experiment 1

We started by choosing to implement a relatively simple axis of rotation for the purposes of training. During static trials, the object stimuli were presented at randomly selected orientations around the y-axis of each object. During dynamic trials, the object stimuli were started at a randomly selected orientation and then put in apparent motion around the y-axis by continually updating successive 3-D projections of the objects on the display. For 2 pigeons, a cube of any size was the S+ cue, whereas a pyramid of any size

served as the S− cue. This assignment was reversed for the other 2 pigeons.

Beside the traditional measures of peck rate to the S+ and S− stimuli, we were also interested in determining how quickly the birds recognized these stimuli. To collect this temporal information, we modified our procedure to encourage rapid initial responding to the S+ stimuli. This was done by using a FR-15 schedule of reinforcement on the S+ trials. Because of this response contingency, rapidly processing and responding to the S+ displays reduced the time to reward. From these S+ response times, we could then derive how long it took the pigeons to process positive from negative displays. Would the pigeons take a longer or a shorter time to respond to the dynamic stimuli in comparison with the static ones? Longer times would suggest they needed more time to integrate the multiple views presented on dynamic trials or had to wait for a particular view to come around before responding. Shorter times to the dynamic displays, on the other hand, would suggest the presence of beneficial kinematic information in such displays.

Following the successful completion of discrimination training, we conducted three transfer tests to examine how the pigeons would generalize to various transformations of the stimuli. The first tested three new sizes of the objects. The second test examined how changes in the rate of object rotation influenced the discrimination. In the third transfer test, we examined how the pigeons performed with stimuli in which all of the surface and contour cues were eliminated. These "featureless" object stimuli, best described as monochromatic polygonal blobs, were then either statically presented or dynamically put in motion in accordance with the rigid projective structure of a cube or pyramid.

This latter transformation is interesting because it tests whether pigeons can extract stimulus structure from motion-based information, much like Wallach and O'Connell's (1953) classic experiment on the kinetic depth effect (KDE). In their study, they tested human observers with 3-D wire-frame objects that were back projected onto a translucent screen. Humans reported viewing 2-D patterns when these stimuli were stationary, but quickly perceived 3-D figures when the objects were dynamically rotating behind the screen. We were interested in knowing whether pigeons, too, could similarly recover the identity of a display on the basis of coherent 3-D structure present in its moving 2-D pattern.

Method

Subjects

Four male White Carneaux pigeons (*Columba livia;* Palmetto Pigeon Plant, Sumter, SC) were tested. No training to peck the displays was needed because of their prior experience in learning a same–different discrimination involving small textured stimuli. They were maintained at 80% of their free-feeding weights during testing, with free access to water and grit in their home cages.

Apparatus

Testing was done in two flat-black Plexiglas chambers (38 cm wide × 36 cm deep × 38 cm high). Two birds, Columbus and Spike, were tested in one chamber and 2 birds, Hawkeye and PW, were tested in the other. Stimuli were presented on computer monitors (NEC MultiSync 2A; Wooddale, IL) visible through a 26- × 18-cm viewing window located in the middle of the front panel of each chamber. These were controlled by video cards (VGA Wonder; ATI Technologies, Scarborough, Ontario) set in the EGA graphics mode (640 × 350 pixels). The viewing window's bottom edge was 20 cm above the chamber floor. A thin piece of glass mounted in this window protected the monitor. Pecks were detected by an infrared touch screen (resolution of 80 × 48 locations; EMS Systems, Champaign, IL) mounted behind a 40 mm wide Plexiglas ledge around the inside edge of the viewing window. A 28-v houselight was located in the ceiling and illuminated at all times. A food hopper was located in the lower middle of the front panel. Experimental events were controlled and recorded by identical 386-class computers.

Procedure

Stimulus conditions. The pigeons were trained and tested with orthographic 3-D projections of the cube and pyramid objects. For Columbus and Hawkeye, the S+ stimulus was the cube, and the S− stimulus was the pyramid. For Spike and PW, this was reversed. The viewer's perspective of these objects was elevated 15° above the object's transecting horizontal plane. This enhanced the appearance of depth in the display (to the human eye). Six colors (blue, gray, green, purple, red, and yellow) were used in creating the different surfaces of the objects. These six colors were randomly assigned without replacement on each trial to one of the cube's six surfaces and the pyramid's five surfaces, resulting in 720 total examples of each object. Thin black contour lines were drawn at the intersection of each surface. Each object was tested at two different sizes, 2.0 cm³ and 4.4 cm³, to help eliminate absolute screen position as a contributing feature.

During training, object stimuli were tested as both static and dynamic stimuli. On static trials, an object was presented for its duration at one of 360 angular orientations around the object's *y*-axis. This orientation was randomly determined on each trial. On dynamic trials, the object appeared to revolve around its *y*-axis during its presentation. Dynamic objects revolved at either 12 revolutions per minute (rpm) or 60 rpms around this axis. The starting orientation for this movement was randomly determined on each trial.

Discrimination training procedures. Training was conducted using a discrete trial procedure. Each trial started with the presentation of a 2.5-cm white, circular warning signal in the center of the display. A single peck caused the warning signal to be replaced by one of the object stimuli. On S+ trials, the pigeons had to peck the display 15 times (FR-15). On completion of this peck requirement, the display was turned off, and 3 s of access to mixed grain was allowed. On S− trials, the display remained visible for 15 s (FT-15) and then was turned off with the trial ending in extinction. A 5-s intertrial interval separated each trial. Each daily session consisted of 48 randomly ordered S+ and S− trials (96 total trials). For each trial type, there were 24 static (12 at each size) and 24 dynamic presentations (6 at each combination of rate and size). The pigeons learned the basic discrimination rapidly and seemed to reach a performance asymptote by the 20th session. Ten sessions after this, a partial reinforcement schedule was introduced where a random 12.5% of S+ trials ended with no reward after the 15th peck.

Finally, two adjustments were made in scoring the results in order to compare performance on these different response schedules. In theory, if a pigeon did not peck 15 times within 15 s on an S+ trial, it could have known that a reinforcement was scheduled

for trial. Similarly on S− trials, once a pigeon pecked more than 15 times it could have known that it would never obtain food on this trial as well. In reality, such behavioral sequences were rare. Nonetheless, this possibility was taken into account by using only the first 15 pecks on S− trials and those pecks that occurred prior to 15 s on S+ trials when computing response rates.

Transfer Test 1: Novel rates of rotation. Test 1 was conducted 10 sessions after the introduction of the partial reinforcement schedule. It lasted 8 sessions. The first 4 sessions consisted of 112 randomly ordered trials. These sessions were composed of the 96 training trials and 8 additional dynamic trials (four S+/four S−), testing equal numbers of two novel rates of rotation (2 rpms and 40 rpms), and 8 additional static trials were included to keep the number of dynamic and static trials equated within a session. Only the large object size was tested on the novel rotation trials. The last 4 sessions comprised 128 randomly ordered trials. The 16 new test trials in these sessions additionally tested the small object size in the same manner as just described. Pecking behavior on training and test trials was reinforced according to the same partial reinforcement and extinction contingencies used at the end of acquisition training.

Transfer Test 2: Novel object sizes. Test 2 consisted of six 140-trial sessions. In addition to the 128 trials just described for Test 1, 12 additional trials were incorporated into each session, testing three new object sizes. One of these was larger (5.4 cm³), one was in between (3.4 cm³), and one was smaller (1 cm³) than the two familiar training values. Each size was tested four times in a session, appearing twice as static and dynamic S− and S+ displays. Only the 12 rpm rate was used with the novel object sizes. Pecking behavior on bóth training and size transfer trials was partially reinforced according to the same contingencies used at the end of acquisition.

Transfer Test 3: Elimination of surface and contour cues. Test 3 consisted of three 144-trial sessions. Beside the 128 trials described in Test 1, 16 additional trials tested variations of the cube and pyramid stimuli in which either (a) the surface cues or (b) both the surface and contour cues were eliminated. Surface cues were eliminated by making all of the object's surfaces the same color. In the eight test stimuli with contour cues (four S+/four S−), the thin black contour lines separating the different surfaces of the objects were retained. In the eight test stimuli without contour cues (four S+/four S−), the thin black contour lines were colored the same as the surfaces (see upper panel of Figure 2). Each session tested two of the six training surface colors. All test trials were tested only at the large training size, with half of the stimuli presented statically and half dynamically (12-rpm rate only). The transfer trials were conducted in extinction.

Results

Acquisition

The pigeons learned to discriminate between the S+ and S− objects in only a few sessions. They began to differentiate the two objects by the second session, quickly increasing discrimination between Sessions 4 and 10 and leveling off after that. This can be seen in Figure 3, which shows the mean discrimination ratio {DR = [adjusted S+ response rate/(adjusted S+ response rate + adjusted S− response rate)] × 100} over the first 20 training sessions for the static and dynamic conditions (rates combined).

This figure also shows that the kinematic status of the displays had little effect, with static and dynamic presentations supporting equivalent rates of discrimination learning.
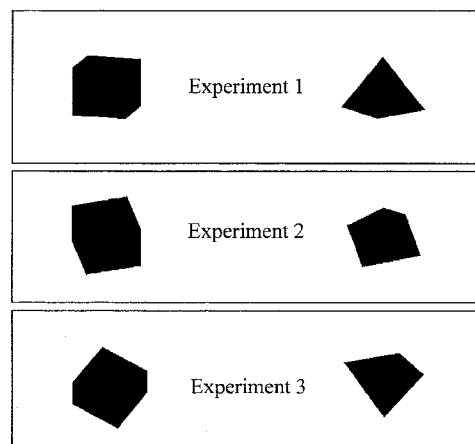

Figure 2. Examples of static cube (left column) and pyramid (right column) objects in which the surface and contour features have been removed as tested in each experiment.

A repeated measures analysis of variance (ANOVA; Sessions × Presentation Condition × Size) of DR for these data revealed a significant main effect for sessions, $F(19, 57) = 9.0$ (all reported statistical tests were evaluated using an alpha level of $p \le .05$), but no significant main effects or interactions involving the dynamic and static status of the displays. There was a significant effect of stimulus size, $F(1, 3) = 31.1$, with discrimination of the larger objects being slightly better than smaller ones.

Postacquisition Performance

The pigeons improved little after the 10th session of training. As such, we used Sessions 11–20 to judge the effects of the different stimulus conditions on postacquisition performance. A repeated measures ANOVA (Sessions × Presentation Condition × Size) of DR revealed no main effect or interactions with sessions, $Fs < 1$. As mentioned, the pigeons reliably discriminated the larger objects (M DR = 86.6) better than the smaller ones [M DR = 81.4; $F(1, 3) = 19.1$]. Although all 4 birds showed a numerical superiority in mean performance with the dynamic stimuli (M DR = 84.6) over the static one (M DR = 82.7), this difference was not significant. No other main effects or interactions were significant in this analysis. A separate analysis comparing DR for the two rates of rotation in the dynamic condition found no significant differences between these conditions (12 rpm = 84.6; 60 rpm = 84.5).

We next looked at the time to first peck to the S+ and S− displays, using these same postacquisition sessions. On S+ trials, the pigeons pecked in an average time of 1,120 ms of an object's appearance (Columbus, 1,239 ms; Hawkeye, 1,430 ms; PW, 996 ms; Spike, 821 ms). A repeated measures ANOVA revealed no significant difference among the time to first peck for the dynamic and static stimuli (12 rpm = 1,073 ms; 60 rpm = 1,233 ms; static = 1,057 ms). In comparison on S− trials, the pigeons significantly delayed
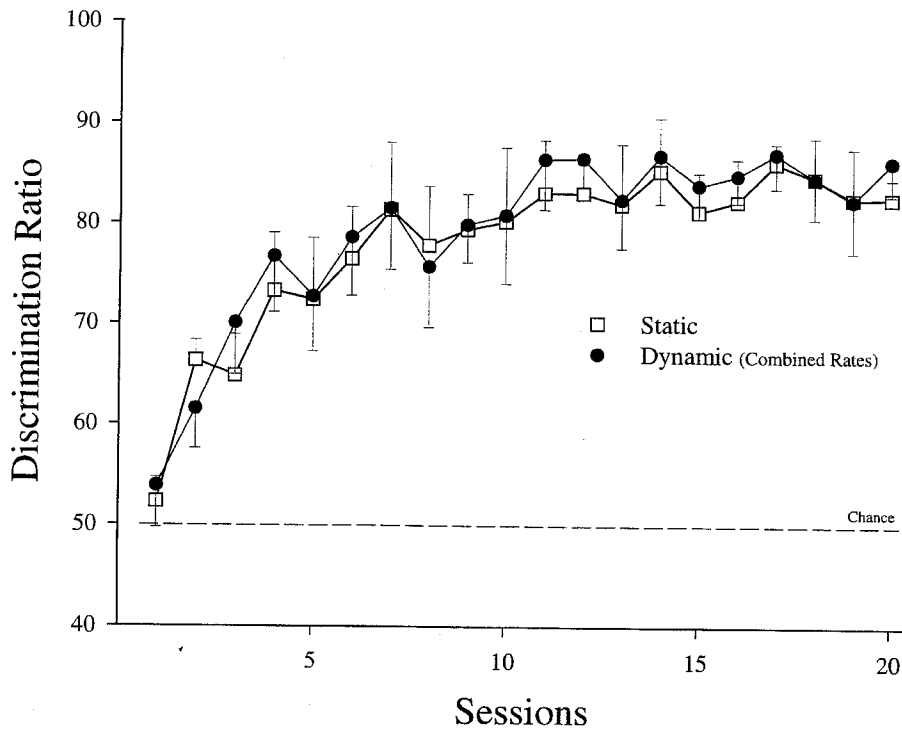
Figure 3. Mean discrimination ratios for the static and dynamic presentation conditions during acquisition in Experiment 1. The dotted reference line depicts chance performance in the task.

their first peck until about a third of the way through the presentation interval [mean time to first peck = 5,601 ms; $F(1, 3) = 16.9$]. There was no significant difference in the capacity of the static and dynamic displays to promote this S− response suppression (12 rpm = 5,749 ms; 60 rpm = 5,757 ms; static = 5,298 ms).

Transfer Test 1: Variation in Rate

There was no significant effect of varying the rate of object rotation as tested by repeated measures ANOVAs. The two new rates supported the same level of discrimination performance as the three training values. This was true for both the first test session and for all eight test sessions combined. During the critical first transfer session, DRs on the two new test rates (2 rpm = 93; 40 rpm = 87.3) were not significantly different from performance on the three training values (12 rpm = 89.1; 60 rpm = 89.4; static = 89.4). Over all eight test sessions, the DRs on the two test rates (2 rpm = 88; 40 rpm = 88.1) were also not significantly different from performance on the training values (12 rpm = 84.3; 60 rpm = 86.7; static = 89.5).

Transfer Test 2: Variation in Object Size

There were no significant effects related to varying object size. The three novel object sizes supported equivalent levels of performance as the two training sizes. In the first transfer session, mean DRs for the three novel sizes were 1 cm³ = 77.9; 3.4 cm³ = 80.1; and 5.4 cm³ = 78.9. In the same

session, performance on the two training sizes were 2 cm³ = 81 and 4 cm³ = 80.5. There was no change over the six test sessions, with mean DRs on the three new sizes, being 1 cm³ = 78.6; 3.4 cm³ = 77.3; and 5.4 cm³ = 81.3. Performance over all six sessions for the two training sizes was 2 cm³ = 83.1 and 4 cm³ = 78.6. Two-way repeated measures ANOVAs (Object Size × Presentation Condition) conducted on DR scores from the first session and for all six sessions revealed no significant effects of object size.

Transfer Test 3: Surface and Contour Cue Removal

In the first transfer session of this test, the birds significantly transferred to the entire set of KDE test stimuli at above chance levels [M DR = 86.1; single M t test, $t(3) = 13.2$]. Further, all 4 birds showed better transfer in the dynamic condition than in the static condition. For those test stimuli having no surface or contour information, mean DR was 93.3 for dynamic trials and 84.5 for static trials in the first session. For those stimuli with contour information, mean DR was 85.7 for dynamic trials and 80.9 for static trials. A two way repeated measures ANOVA [Contour (Presence vs. Absence) × Presentation Condition] of these first session DR scores confirmed there was a significant main effect of presentation condition, $F(1, 3) = 30.9$, but no main effect or interaction with the presence or absence of the contour information. This difference between the dynamic and static presentation conditions grew smaller and unreliable over the next two sessions. Mean DR over all three sessions for KDE stimuli, having no surface or contour

information, was 83.6 for the dynamic trials and 84.2 for static trials. For those KDE stimuli with contour information, mean DR was 77.9 for dynamic trials and 80.9 for static trials. Finally, there was no significant change in overall S+ response rate to the monochromatic displays during the four sessions (Baseline S+ trials = 1.3 pecks per s; KDE trials = 1.3 pecks per s).

Discussion

Experiment 1 revealed that both the dynamic and static object stimuli were easily discriminated by the pigeons. This discrimination transferred with little or no significant loss in performance to objects of novel sizes or moving at novel rates of rotation. On the basis of earlier studies examining simpler size (Lombardi & Delius, 1990) and movement discriminations (Mulvanny, 1978; Stenhouwer & Denny, 1975), these transfer values should have been readily discriminable from the training values. If so, then this complete generalization represents the true invariant transfer of the learned discrimination, and not just simple perceptual discrimination failure. Finally, the viewing time to decide whether it was a cube or pyramid was just around 1 s in duration.

Because of the objects' numerous examples and variable irrelevant features (i.e., surface color, rate, and size), we had anticipated the pigeons' discrimination might be flexible, especially given previous research on the effects of exemplar number on concept formation (Kendrick, Wright, & Cook, 1990; Wasserman, 1995; Wright, Cook, Rivera, Sands, & Delius, 1988). The pigeons' continued discrimination over the different transformations tested indicates that responding was being controlled by invariant components that were consistently recognized across these changes. What was the nature of this invariance? One possibility is that the pigeons indeed experienced the stimuli as 3-D objects, encoding their structural relations as unified objects akin to "cubes" and "pyramids." This certainly was the powerful perception invoked by these visual stimuli in the human brain.

A second and simpler possibility, however, is that the pigeons may have learned only a 2-D discrimination of the objects. For instance, they might have only learned to discriminate between stimuli that were flat on top or came to a point, or whose forms were roughly square or triangular in outline. These 2-D invariants account for the majority of obtained results. We had expressly included objects of different sizes and rates to prevent the birds from using simple absolute features, templates, screen locations, or patterns of color change from mediating the discrimination, but the pointed and flat natures of the pyramid or triangle and cube or square were consistently visible to the human eye and likely so for the pigeons as well.

The best evidence against such a 2-D account of the discrimination was the brief inferiority of the static condition in the KDE transfer test. If the pigeons were simply looking for a flat or pointed top of a 2-D image, then the static condition should have supported equal, if not better, performance than the dynamic condition. On initial exposure, however, that was not the case for the pigeons as the projective motion of these monochromatic images added information not present in the static displays. The additional implication of this result is that pigeons, much like humans and other nonhuman primates (Siegel & Anderson, 1988), may be able to recover object structure from motion.

Nonetheless, the conservative opening gambit of using a single simple type of motion that provided a continuous and unambiguous view of the objects' most distinguishing features was not the theoretically most revealing option. Beside the difficulty of distinguishing between 2-D and 3-D accounts of the discrimination, this tactic also likely reduced any kinematic advantages contributed by the objects' motion as well. To amend these limitations, we increased the complexity of the objects' motion in the next experiment.

Experiment 2

Experiment 2 introduced a new type of rotational motion that increased the psychological demands and theoretical utility of the discrimination. Specifically, we added tests of the objects as if they were being rotated around their x-axis. On dynamic trials, the objects appeared to rotate away from the viewer and come back up from the bottom. This type of rotation visually distorts the overall shape and features of the objects as they move toward and away from the viewer's perspective. If the pigeons had just learned to discriminate the simple 2-D features or square and triangular shapes of the objects, then discriminating the objects when rotated along a new axis should be difficult. If the pigeons had learned a more flexible 3-D representation of the objects, on the other hand, then transfer to this novel discrimination should be easy. We also predicted that the distortions introduced by this type of rotation should correspondingly increase the benefits of an object's movement during its presentation.

Experiment 2 had three separate phases. The first phase tested the pigeons' reactions to changes in the observer's viewpoint. New viewpoints ranging from looking directly up from the bottom to looking down from the top and four additional points in between were tested with the same objects as used in Experiment 1. Phase 2 then tested the entire range of static x-axis rotations and introduced for the first time dynamic displays that revolve around the x-axis. Phase 2 had two parts. The first part tested unreinforced static and dynamic objects as rotated around the x-axis. On these trials, the objects were presented for 20 s and then turned off. In the second part, the static and dynamic x-axis displays were added to the pigeons' daily training regime using the same response schedules and reinforcement contingencies as in Experiment 1. The third phase of the experiment examined static and dynamic KDE displays along this new axis of rotation.

Method

Subjects

The same pigeons as used in Experiment 1 were used in Experiment 2.

Apparatus

We used the same chambers in this experiment as in Experiment 1.

Procedure

Phase 1: Novel perspectives. Phase 1 lasted for 10 sessions. Each session comprised 152 randomly ordered trials. One hundred twenty-eight of these trials were identical to those used in Experiment 1. Each object and size was tested equally often in the two presentation conditions, with the dynamic trials divided equally among four rates of rotation (2, 12, 40, and 60 rpms). The 24 remaining trials of each session tested each object twice from six novel viewpoints. These novel viewpoints were made by either increasing (45°, 90°) or decreasing (0°, −15°, −45°, −90°) the height of the viewing angle as referenced from the horizontal plane of the objects. From each perspective, each object was tested once as a static and dynamic display (12-rpm rate only). It should be noted that in this first phase only the viewpoint's angle of elevation changed and that the axis of rotation for the static and dynamic displays still remained the y-axis. For the test trials, the small and large object sizes were tested on alternative sessions. The timing and reinforcement parameters were the same as used in Experiment 1.

Phase 2: Transfer to novel x-axis rotation-extinction testing. Part 1 consisted of four 140-trial sessions. In addition to the 128 y-axis baseline trials, 12 additional trials (6 S+ and 6 S−) tested dynamic and static presentations of the objects as rotated around the x-axis. Each object on these x-axis transfer trials was tested three times (randomly oriented static display, 12 and 40 rpm rate of rotation) at each of the two object sizes. All of these x-axis test trials were conducted in extinction with each stimulus simply presented for 20 s and then turned off.

Phase 2: Transfer to novel x-axis Rotation-reinforced testing. Static and dynamic x-axis rotation trials were integrated into the daily sessions in this second part. These sessions consisted of 112 trials. The 64 y-axis baseline trials (32 S+ and 32 S−) were organized in the same way as phase 1, but their number reduced by half. The remaining 48 trials (24 S+ and 24 S−) consisted of x-axis rotation trials. These trials were divided equally between static (randomly chosen orientation) and dynamic conditions (12 and 40 rpm) and the two object sizes. This part of the experiment lasted 18 sessions.

Phase 3: Surface and contour cue removal. Phase 3 consisted of four 128-trial sessions. In addition to the 112 baseline trials (64 y-axis and 48 x-axis trials) just described, 16 test trials (8 S+ and 8 S−) in which both surface and contour cues were eliminated were tested (see middle panel of Figure 2 for examples). Surface and contour cues were again eliminated by making all these features the same color (cyan, green, purple, or red in a randomized order across sessions for each bird). Eight of these trials tested stimuli rotated around the x-axis, with half of them presented in the static condition and half of them in the dynamic condition (12-rpm rate only). The remaining eight test trials tested stimuli as rotated around the y-axis (four dynamic and four static). Pecking behavior on test trials was partially reinforced as on the baseline trials to avoid the birds extinguishing their responding to this particular type of test stimulus.

Results

Phase 1: Novel Perspectives

The pigeons' performance systematically varied with objects' angle of elevation. Displayed in Figure 4 is mean DR for both the dynamic and static presentation conditions as a function of the viewer's elevation. The pigeons did quite well from viewpoints within 30° of the training value. They continued to perform accurately, but showed a clear dropoff, at values between 30° and 60° from the training perspective.
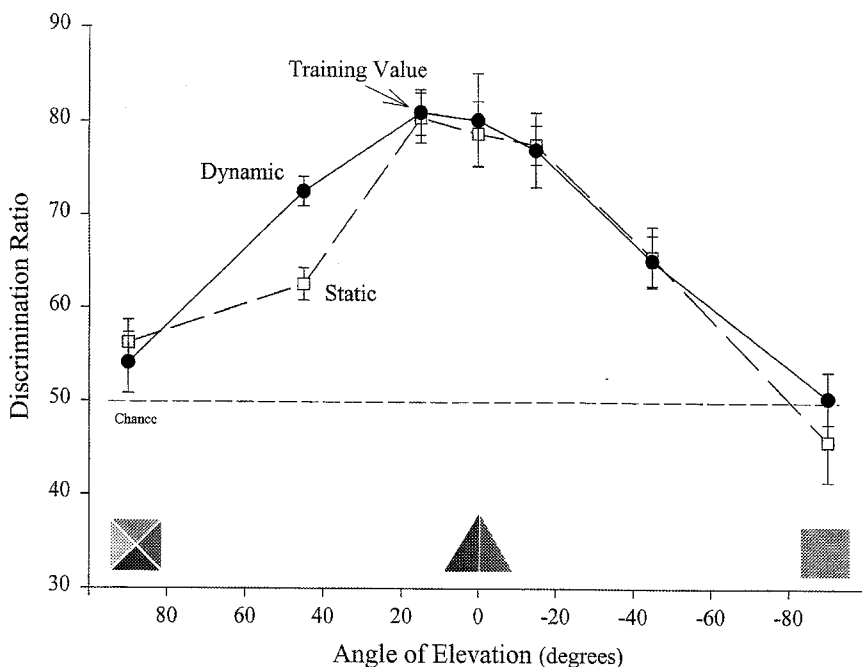

Figure 4. Mean discrimination ratios for object stimuli presented from different viewpoints in Phase 1 of Experiment 2.

A repeated measures ANOVA (Elevation × Presentation Condition × Size) of DR confirmed the significant effect of elevation, $F(6, 18) = 16.2$. The same analysis revealed no main effects or interactions among either presentation condition or size. Subsequent statistical comparisons revealed that discrimination was significantly above chance from all viewpoints, all $ts(3) > 4.36$, except when the objects were viewed as if from directly above (90°) or below (−90°).

Phase 2: Transfer to Novel x-Axis Rotation-Extinction Testing

Phase 2 found significant above chance transfer of the discrimination to objects oriented or rotating around the novel x-axis. Over all four sessions of extinction testing, the 4 birds showed significantly better performance with the dynamic x-axis stimuli (12 rpm = 70.2; 60 rpm = 72.8) than with the static versions (67.3), $F(1, 3) = 15.9$. There was no reliable effect of session in this analysis. There was no reliable difference between dynamic (81.1 for all four rates) and static (80.6) presentation conditions for the baseline y-axis stimuli over these same sessions. Further, there was no significant change in overall S+ response rate to the transfer stimuli (baseline y-axis trials = 1.3 pecks per s, novel x-axis trials = 1.5 pecks per s).

Phase 2: Transfer to Novel x-Axis Rotation-Reinforced Testing

This test revealed that the dynamic superiority effect for x-axis stimuli revealed in the extinction test persisted even when correct responding in each condition was reinforced (see Figure 5). Like in the prior test, discrimination performance in the x-axis conditions was significantly poorer than in the y-axis conditions, especially over the first half of the experiment as confirmed by a significant Condition × Session interaction, $F(5, 15) = 4.23$, in a two-way repeated measures ANOVA. Second, there was a consistent and significant difference in DR between the x-axis static and dynamic presentation conditions (combined rates), $F(1, 3) = 17.9$, in a second repeated measures ANOVA comparing just these conditions. A separate repeated measures ANOVA of the x-axis dynamic condition's two rotation rates found no reliable difference between them. As in Experiment 1, there was no reliable difference between static and dynamic y-axis performance. Finally, the difference between the x- and y-axis dynamic conditions diminished more quickly with training than it did for the static displays. By the end of testing, both dynamic conditions were supporting equivalent levels of performance. Discrimination in the static x-axis condition did improve slightly, but even after 18 sessions, performance in this condition was consistently the poorest.

Why was performance in the static presentation condition so much poorer than the dynamic condition for the novel x-axis rotations? Whereas y-axis rotations maintained a relatively constant view of the critical portion of the two objects, the x-axis conditions introduced a large set of more ambiguous projections of the objects. As the objects rotated away from the viewer's perspective, many of the features were distorted or disappeared from sight and then reappeared at the bottom of the display. How did these different views influence the pigeons' discrimination?

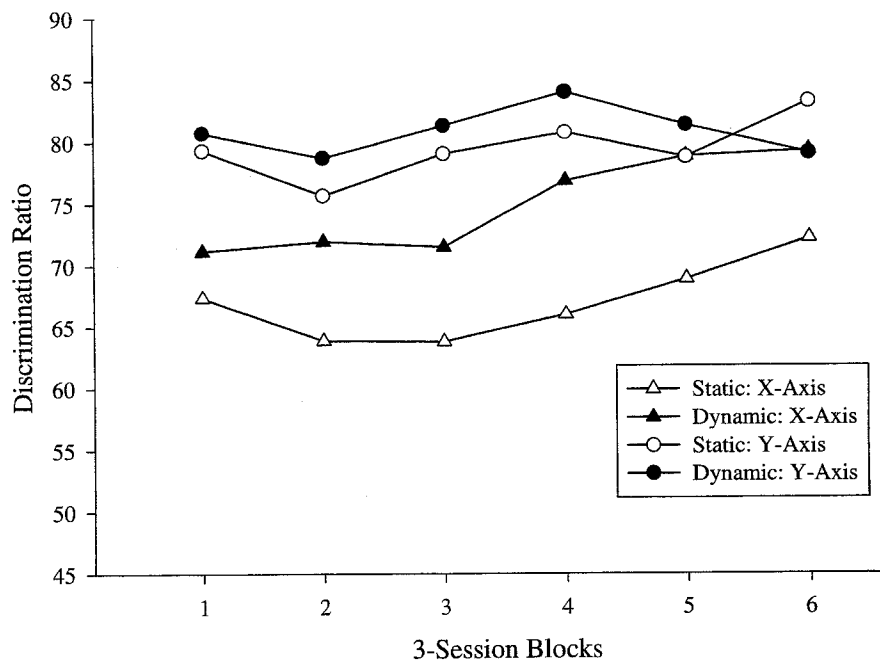To answer this question, the data from all static trials over

Figure 5. Mean discrimination ratios for dynamic and static S+ and S− object stimuli as rotated around different axes over the 18 reinforced sessions of Experiment 2.

the 18 sessions were divided up according to their angle of presentation. The resulting 360 perspectives were then grouped into twelve 30° bins. Figure 6 shows these data in polar coordinates. These radial plots show DR as a function of each 30° bin with increasingly better discrimination performance depicted as being farther away from the center of the plot (point of origin = chance). The left panel shows performance for each of the angular orientations tested on the static y-axis trials. The reference line depicts average dynamic performance over these same sessions. The circular nature of the static presentation data shows there were no consistent effect of orientation, with each supporting equally good performance.

The right panel shows static performance for each of the angular orientations tested on x-axis trials (the reference line is mean dynamic performance). The noncircular nature of these static presentation data indicates that the pigeons' were not equally good with each point of view. When the objects appeared upright (i.e., near the training view), performance was generally equivalent to dynamic performance. As the objects rotated away from the pigeons, increasingly showing the highly ambiguous base of each object, their DR decreased. When the objects were presented upside-down, performance was above chance, but overall poorer than when they appeared upright. When views of the tops of the objects were presented, performance again declined.

In the last analysis of these data, we again looked at the initial response times to the displays averaged over the 18 sessions. On familiar y-axis trials, the pigeons first pecked in a mean time of 1,389 ms on S+ trials (static = 1,341 ms; dynamic [rates combined] = 1,437 ms) and a mean time of 4,751 ms on S− trials (static = 4,698 ms; dynamic [rates combined] = 4,804 ms). On x-axis trials, the pigeons first pecked in a mean time of 1,433 ms on S+ trials (static = 1,450 ms; dynamic [rates combined] = 1,416 ms) and a mean time of 3,492 ms on S− trials (static = 3,006 ms; dynamic [rates combined] = 3,979 ms). A repeated measures ANOVA (S+ vs. S− × Rotation × Static/Dynamic [rates combined]) found that S+ displays were responded to significantly faster than S− displays, $F(1, 3) = 14.6$, but no other significant main effects or higher order interactions were found among these factors. A second repeated measure ANOVA (Rotation × Static/Dynamic [rates combined] × Sessions), which used just the response times to S+ displays, revealed no significant differences for any of these factors.

Phase 3: Surface and Contour Cue Removal

Our primary interest was with performance on the new x-axis rotation trials. In the critical first transfer session, 3 of the 4 birds showed better performance with the dynamic KDE test stimuli (DR = 90.0) than with the static versions (DR = 62.7) of these displays (Columbus dynamic = 94.3, static = 81.7; Hawkeye dynamic = 87.5, static = 57.4; PW dynamic = 88.3, static = 48.9). The fourth bird (Spike) showed no discrimination or difference between the two conditions (dynamic = 43.3; static = 43.6). Turning to the y-axis KDE trials, in the first test session, the same 3 birds

again showed superior performance with the dynamic KDE test stimuli (M DR = 75.6) than with the static versions (M DR = 49.9). The 4th bird (Spike) again performed poorly (dynamic = 40.9, static = 54.3). A repeated measures ANOVA (Presentation Condition × Axis of Rotation) of these first session DRs for the 3 birds showing a dynamic superiority effect revealed a significant main effect of presentation condition, $F(1, 2) = 195.7$, and a significant main effect of axis of rotation, $F(1, 2) = 24.1$, but no interaction between them. There was no significant change in overall S+ response rate to the KDE stimuli (baseline trials = 1.5 pecks per s, KDE trials = 1.5 pecks per s).

Averaged across all four sessions, Columbus and Hawkeye continued to show better performance with both x-axis dynamic stimuli (dynamic = 85.1, static = 52.4) and y-axis dynamic stimuli (dynamic = 88.1, static = 58.6). PW's dynamic performance generally declined for both types of rotation (dynamic = 55.9, static = 48.2), and Spike showed, if anything, the opposite effect (dynamic = 43.9, static = 60.4).
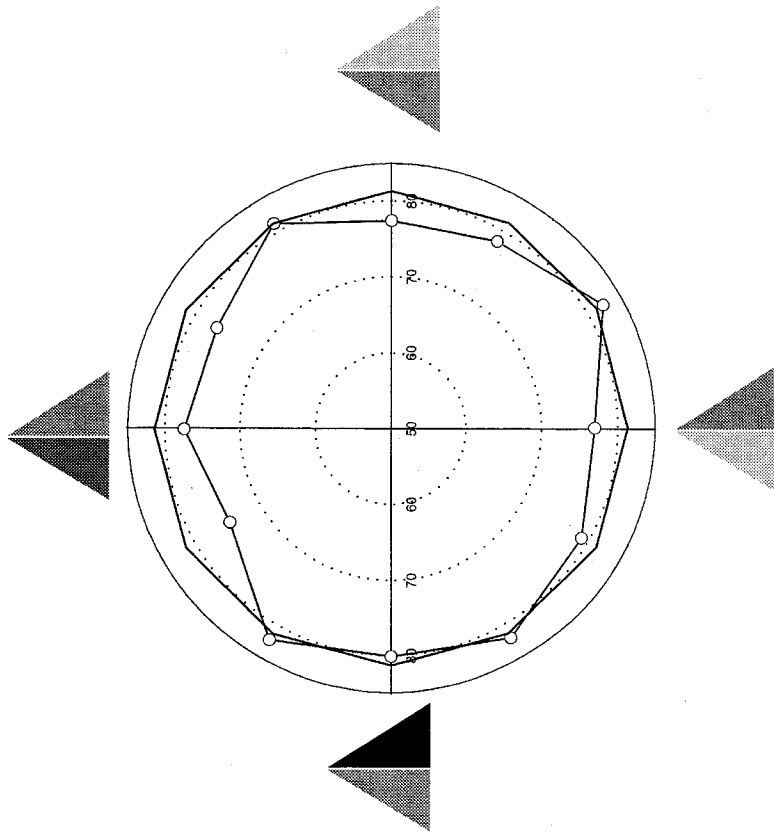
Discussion

When tested with the original stimuli from different viewpoints, the pigeons showed good generalization to these novel perspectives, showing perfect transfer over a range of ±30° from the training perspective and above chance discrimination over a range of ±60°. When transfer tested with a novel axis of rotation, the pigeons showed evidence of discrimination transfer to both static and dynamic views of the objects, with the latter supporting significantly higher levels of performance. Finally, 3 of the 4 birds showed a dynamic superiority effect initially in their discrimination of the KDE stimuli, and 2 of them showed this effect consistently.

These results suggest the pigeons had a more elaborated representation of these stimuli than did the results of Experiment 1. For instance, the birds' very good transfer to perspectives created from a new axis of rotation strongly supports the idea that their performance was not mediated by a simple 2-D representation of the objects. The birds continued to discriminate between the objects despite the presence of 2-D visual distortions caused by the accretion and occlusion of objects' surfaces by this particular axis of rotation. The significant dynamic superiority found for the KDE test stimuli in 3 of the birds supports this conclusion as well. As a whole, the pattern of data from Experiment 2 is more consistent with the hypothesis that the pigeons represented these stimuli as 3-D objects, in which the structural position of the surfaces and corners were the critical discriminative features, rather than as simple 2-D images.

Consistent with this interpretation is the generalization shown by the pigeons over a wide range of x-axis viewpoints. This generalization indicates that their performance was not dependent on a particular viewpoint. In spite of this, there was evidence of generalization decrement for those perspectives that did vary greatly from the familiar upright training value. This does suggest that certain viewpoints were more important or informative than others. Such
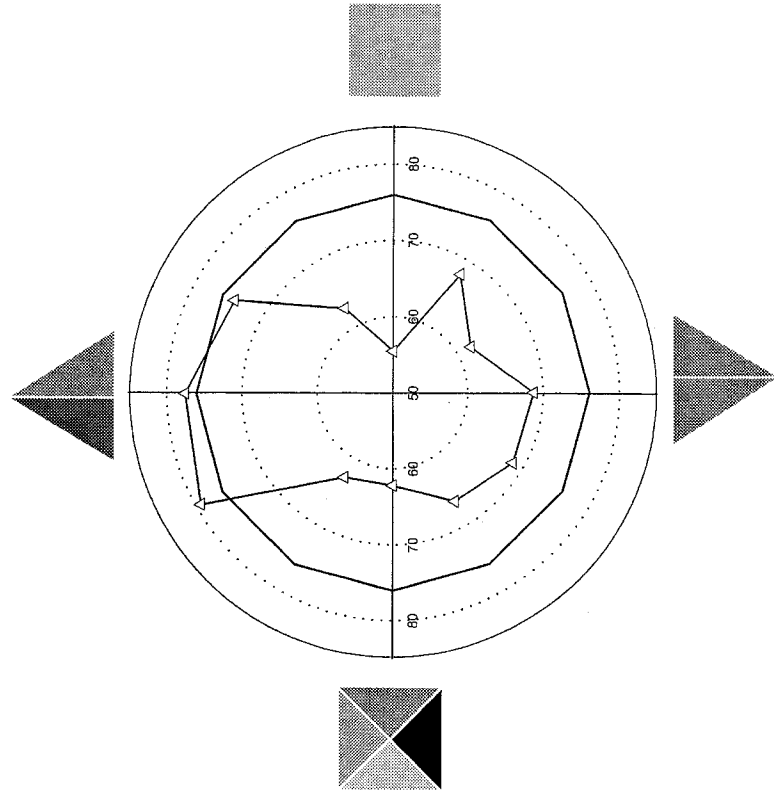
X-Axis Orientation

Y-Axis Orientation

Figure 6. Polar plots of discrimination performance for static trials (unfilled circles) during Experiment 2. The left panel shows performance in 30° divisions for static trials as oriented around the training *y*-axis. The right panel shows performance in 30° divisions for static trials as oriented around the *x*-axis. The pyramid stimuli represent the observer's view at the corresponding orientation for the adjacent data points. The black reference line in each plot represents mean performance on dynamic trials.

results are generally in keeping with Wasserman et al.'s (1996) recent results with static depth-rotated (y-axis) line stimuli. They found that pigeons transferred above chance over a range of ±133° in perspective change as well, but also found that performance declined systematically with distance from the training viewpoint. Thus, both studies contained a mixture of evidence that both viewpoint independent (evidenced by above chance discrimination transfer) and viewpoint dependent (evidenced by the systematic decline with changes in perspective) factors influence the discrimination of depth-rotated stimuli by pigeons. This mixture of results suggests the pigeons may simultaneously encode both relative and absolute attributes of 3-D objects and their projections in learning these types of discriminations (see Logothetis, Pauls, Bulthoff, & Poggio, 1994, for a similar result in monkey). Nonetheless, our results and Wasserman et al.'s indicate that Cerella's (1977, 1982, 1986, 1990a, 1990b) earlier work had underestimated the pigeon's capacity to recognize objects from new perspectives.

Finally, this experiment revealed that dynamic stimuli consistently supported better discrimination than their static cousins, especially for x-axis rotations. Although performance with the static x-axis conditions improved slightly with experience, even this increased familiarity was not sufficient to overcome this dynamic superiority effect. One possible model of dynamic performance rejected by these data might be called the momentary view integration model. It suggests that the birds' moment-to-moment pecking behavior is based on the current view of the display and an associated response strength for that specific view (as derived by its similarity to a training view or its own independent training history), and that the overall peck rate on dynamic trials is the simple accumulation of these viewpoint-based peck rates integrated over the object's exposure time. This model predicts that dynamic performance should be equivalent to mean static performance and that this dynamic value should fall between the highest and lowest peck rates associated with different static orientations. Neither of these predictions was affirmed. Dynamic conditions were always discriminated better than the static condition. Moreover, our more detailed analysis of static performance as a function of orientation indicated that dynamic performance was equal to that associated with the best static perspective. Clearly, dynamic performance was more than the simple serial concatenation of responding as derived from a set of discrete object views. In fact, these results suggest that the most poorly discriminated object perspectives did not interfere with the general recognition of the dynamic objects, despite their presence on every dynamic trial.

Might it be possible that dynamic superiority effect just reflects the pigeons obtaining one of the discriminable 2-D view of the objects from a subset of the dynamic trials? This seems unlikely. Given that the best level of static performance (presumably the best 2-D view) was equivalent to the average of the dynamic trials, this would imply, on the basis of the above hypothesis that this view occurred on each dynamic trial. Given that about .5 s is required for the motor act of pecking itself, the response times recorded in Experi-

ment 2 suggest the birds only needed about 1 s to decide the identity of the objects (i.e., the initial response inhibition shown to the S− stimulus strongly indicates that these S+ responses were already under appropriate stimulus control when first emitted). On the basis of this decision time, the objects had typically revolved about 72° on average at the slowest rotation rate when the pigeons started to respond accurately. This would suggest that the dynamic objects were being discriminated without going through a complete revolution and without regularly passing through the least ambiguous 2-D views. Note also that the stimuli revolved about 240° prior to the first response when presented the faster rotation rate. Despite the best 2-D view's greater frequency in the latter dynamic condition, there was no measurable difference in response accuracy with the two rates, suggesting also that no particular view was critical to superior discrimination of the dynamic displays. A closely related notion is that the birds simply waited for this distinctive viewpoint to come around on dynamic trials before making a response. There is no direct evidence supporting this kind of waiting hypothesis, however, as the birds responded to both the static and dynamic stimuli in the same amount of time. Collectively, these results suggest that despite being present during some portions of the dynamic displays, the best 2-D view of the objects as judged from static performance seemed to play little role in directly producing the dynamic superiority effect. Rather this effect seems due to the possibility that even slight changes in an object's perspective enhances a pigeon's capacity to distinguish its structure.

Experiment 3

Experiment 3 had the following goals. The first was to add yet more complexity to the orientations experienced on static trials and the pattern of movements experienced on dynamic trials. This was done by introducing displays in which the y- and x-axes were both simultaneously varied for each object. This operation resulted in displays quite different in appearance from those previously tested. For instance, dynamic objects appeared to "tumble," "roll," or "spin" in 3-D space, depending on the rates used. These more complex trials were introduced in two phases. In Phase 1, the rate of rotation in each axis was set at the same value during each presentation. In Phase 2, the rate of rotation in each axis was varied independently, further increasing the complexity and types of motion experienced on each presentation. In addition, between these two phases, the simple trials testing motion and orientations in just the x- or y-axis were eliminated, removing all trials with a direct resemblance to the training experiences of Experiments 1 and 2. Just how well would the pigeons do with this third, more complex type of object motion and how would they be affected by the elimination of the familiar simple displays? If the birds were relying on 2-D features or the most familiar training views, then the answer should be badly. If, on the other hand, they had encoded a 3-D structural description of the objects, then they should again easily accommodate to these changes.

The second part of this experiment tested two additional

variations of the objects. The first of these introduced new directions of motion to the stimuli. Prior to this point, all of the objects' motions had moved either right to left or back to front, depending on the axis of rotation. In this test, the object stimuli were moved for the first time in the opposite of these trained directions. The second test examined how the pigeons performed when the objects were made from an entirely new set of six colors. If the birds were encoding the generalized shape of the objects, then again these changes in surface appearance should have had little effect on the basic discrimination.

Method

Subjects

We tested the same pigeons as in Experiments 1 and 2.

Apparatus

In this experiment, we used only a single chamber. The 2 birds from the second chamber were transferred to the first chamber without problem, 3 weeks prior to Experiment 3.

Procedure

Transfer to combined xy-*axes rotations.* Each session in this phase consisted of 120 trials: 48 trials testing x-axis rotations, 48 trials testing y-axis rotations, and 24 new trials testing objects simultaneously moving or rotated around both x- and y-axes. For all three types, displays were presented equally often as S+ and S− trials, large and small sizes, and static and dynamic trials (2, 12, and 40 rpm). For the dynamic trials involving simultaneous x and y rotations, the rate of rotation in both axes was the same for any given trial. This phase of the experiment lasted 18 sessions. From sessions 15 on, the number of xy trials was doubled to 48 (144 total trials). Because of a computer malfunction, data from Sessions 5 through 8 were lost. Reinforcement contingencies for pecking behavior on all transfer trials of Experiment 3 were the same as for baseline trials.

Surface and contour cue removal. This test consisted of four 168-trial sessions. In addition to the 144 trials (48 y-axis, 48 x-axis, 48 xy trials) just described, 24 KDE test trials (12 S+ and 12 S−; see bottom panel of Figure 2 for static examples) having no surface and contour cues were tested (cyan, green, purple, or red in a randomized order across sessions for each bird). Eight of these trials tested stimuli simultaneously rotated around both x and y axes, half presented in the static condition and half in the dynamic condition (12-rpm rate only). The remaining 16 test trials tested the same type of y-axis and x-axis KDE stimuli as in Experiment 2.

Transfer to the novel combinations of rates. After completion of the cue removal test, the x-axis and y-axis trials were eliminated from each daily session. The pigeons were tested for 12 sessions (144 trials each) with the xy rotation trials just described (i.e., equal rates in both axes). Over the next 18 sessions (120 trials each), 30 dynamic and 30 static xy trials were added that involved all possible combinations of the 2, 12, and 40 rpm rates of rotation across the two axes. On the remaining 60 trials (30 static and 30 dynamic), the rotation was the same for both axes.

Transfer to the novel directions of a rotation. Immediately after the above test, the pigeons were tested with objects where the direction of motion around the simple x- and y-axis was reversed. These three test sessions consisted of 144 trials, 48 of which tested y-axis rotations, 48 x-axis rotations, and 48 combined x- and y-axis rotations (different rates for each axis). These trials were counterbalanced in the same way as described in the section on the transfer to combined x- and y-axis rotations, except that in half of the dynamic y-axis and x-axis trials the direction of motion was reversed (right to left and bottom to top) in comparison with that exclusively experienced by the pigeons to that point (left to right and top to bottom).

Transfer to novel surface colors. Next the pigeons were tested for transfer with objects constructed from an entirely new set of surface colors. The test consisted of three 120-trial sessions (60 S+ and 60 S−). All trials consisted of only static and dynamic xy trials (i.e., there were no x-axis or y-axis trials). Ninety-six of these trials used the same colors as used throughout the experiment. The remaining 24 trials, divided equally between dynamic (2, 12, and 40 rpm) and static presentations, tested the objects as composed from six new colors (baby blue, brown, lime green, orange, pink, cyan [used in one session of each KDE test in Experiments 2 and 3]). The procedure for randomizing these novel colors among the different surfaces was the same as normally used (i.e., there were 720 possible combinations for each object).

Results

Transfer to Combined xy Axes Rotations

The pigeons transferred well to the novel combination of simultaneous rotation or motion of the objects in the x- and y-axes. During the first session with this type of combined motion, mean DR on dynamic xy trials (81.3, combined across rates) was significantly better than for its comparable static condition (67.6), $F(1, 3) = 19.2$. Thus, despite being tested with three new patterns of motion never seen before, the pigeons continued to better discriminate the objects when they were in motion.

Shown in Figure 7 is the mean discrimination ratio for each type of rotation as a function of dynamic and static presentation conditions over the 14 recorded sessions of the experiment. This figure shows the significant interaction between type of rotation and the effect of object motion, $F(6, 18) = 4.3$ as found by repeated measures ANOVA. The interaction was due in part to the differential effects of motion on xy and x-axis trials in comparison to y-axis rotation trials. During static presentations, all 4 birds showed significantly poorer performance on combined xy trials and x-axis trials than on static y-axis trials. For dynamic conditions, it appeared that the faster rates of rotation generally supported better discrimination than the slower ones, but this difference was not significant. Finally, there were no significant differences in level of performance for the different types of axis motion as well (mean DR averaged across all rates y-axis = 79.6; x-axis = 77.3; xy axes = 80.2). As in Experiment 2, these results for the combined xy condition indicate that the objects' motion compensated for the ambiguous views that repeatedly occurred during any presentation. Finally, for each of these types of motion, the mean time to first peck the S+ displays in the static and dynamic conditions (combined rates) were: y-axis static = 693 ms; y-axis dynamic = 653 ms; x-axis static = 791 ms; x-axis dynamic = 718 ms; xy static = 892 ms; xy dynamic = 710 ms. A repeated measure ANOVA
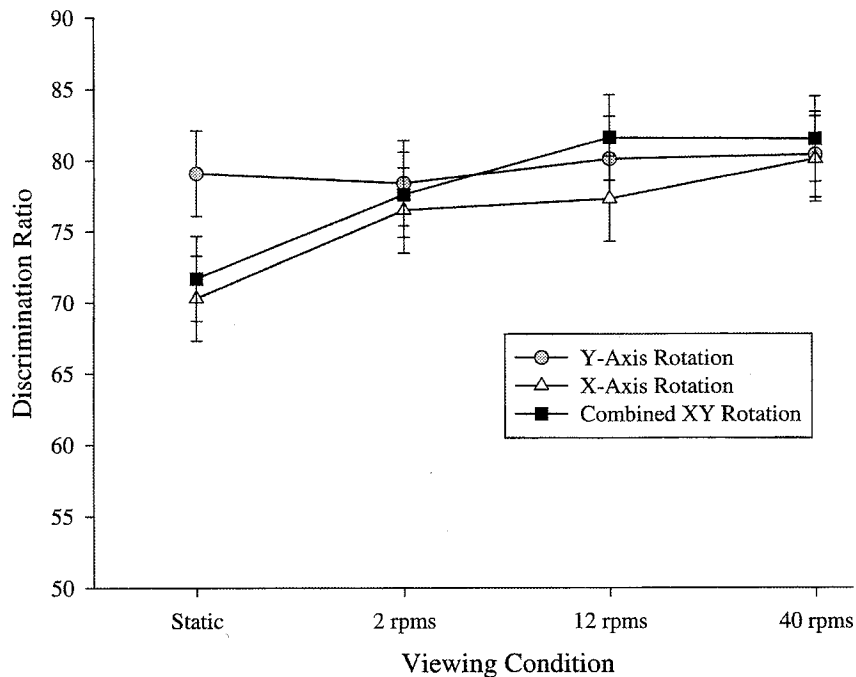
Figure 7. Mean discrimination ratios for dynamic and static S+ and S− object stimuli for different types of rotations over the 14 recorded transfer sessions of Experiment 3.

(Axis × Size × Presentation Type) revealed no significant differences among these values.

Surface and Contour Cue Removal

The same 3 birds (Hawkeye, Columbus, and PW) as in Experiment 2 again showed positive evidence of deriving more discriminative information from the dynamic than static KDE displays. Averaged across all four sessions, these birds discriminated dynamic *xy* presentations (*M* DR = 71.1) better than static ones (*M* DR = 58.3). Spike showed no difference between the two KDE conditions (dynamic = 72.1; static = 73.5). The pattern of results for *x*-axis test trials was similar with the same 3 birds discriminating dynamic trials (*M* DR = 72.9) better than static trials (*M* DR = 66.1), and Spike showed no difference between the displays (dynamic = 71.5, static = 69.8). The pattern of results for *y*-axis test trials was essentially similar, with these same 3 birds discriminating dynamic trials (*M* DR = 67.1) better than static trials (*M* DR = 64.8): Spike showed the opposite effect (dynamic = 72.6, static = 78.9).

Tests With Novel Combinations of Rates

The results for this phase of the experiment were essentially identical to the first phase, testing equal rates of rotation. The birds experienced no drop in performance with these more variable novel stimuli. Across all 18 sessions, performance with dynamic displays (*M* DR = 78.2, rates combined) was significantly better than with the comparable static displays (*M* DR = 67.5), $F(1, 3) = 10.2$. There were no differences attributable to which of the two axes revolved

faster. Performance with dynamic displays having equal rates of rotation around each axis (*M* DR = 77.1 across all three rates) was still significantly better than with their comparable static displays (*M* DR = 67.4), $F(1, 3) = 9.5$. The results from the first session were not different from the average values reported above. There were no significant effects or interactions with the factor of sessions in any of the analyses.

Transfer to the Novel Directions of a Rotation

The pigeons transferred to the novel directions with little drop in performance. For the *x*-axis dynamic condition there was a significant difference between baseline trials (*M* DR = 77.9) and novel direction test trials (*M* DR = 71.7), $F(1, 3) = 10.6$, but this difference essentially disappeared by the third session (baseline = 78.2; novel direction = 75.3). For the *y*-axis dynamic trials, there was no significant difference between baseline trials (DR = 81.3) and the novel direction test trials (*M* DR = 78.3), $F(1, 3) < 1$. In neither of these analyses were there any effect of session.

Transfer Tests With Novel Surface Colors

Shown in Figure 8 is discrimination performance with the novel color displays averaged across the three test sessions. It shows that the pigeons transferred without a problem to the novel objects when presented in motion, but showed significant decrements in performance when presented statically. Separate repeated-measures ANOVAs, comparing training with novel color displays DRs at each presentation condition, revealed that the only significant difference was
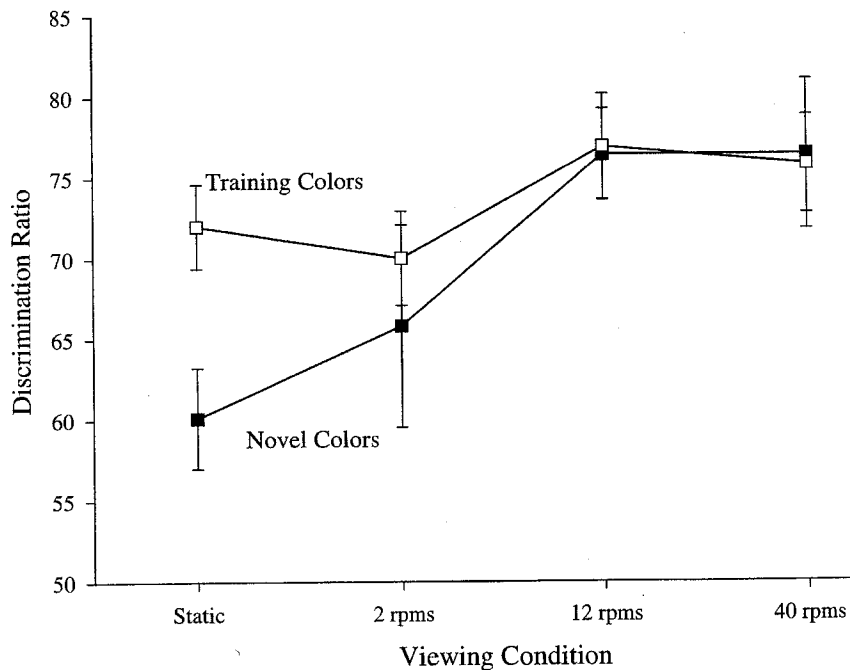
Figure 8. Mean discrimination ratios for dynamic and static S+ and S− object stimuli composed from training and novel surface colors in Experiment 3.

in the static condition, $F(1, 3) = 39.7$. No significant differences in DR existed between the training and novel color dynamic displays whether examined at each rate or averaged across rates. It did appear, however, that at the slowest rate of rotation, the level of novel color transfer was intermediate to that of the static and faster rotation conditions. There were no significant effects of session or its interaction with the various conditions revealed by these analyses.

Discussion

Experiment 3 revealed that pigeons easily transferred to object stimuli using a combination of motion in two axes. Further, the presence of the single axis rotations were not required for maintaining performance with these more complex displays. The pigeons also showed robust directional invariance, exhibiting little evidence that the absolute direction of motion was critically involved in the discrimination. Three of the 4 pigeons again showed positive evidence of a dynamic superiority effect with the KDE stimuli. Finally, all birds showed evidence of transferring their discrimination to objects created from novel colors. Of most interest, the dynamic presentation of these novel objects resulted in no drop in performance, whereas their static presentation resulted in poorer discrimination than in its control condition. These latter facts again suggest that the objects' motion contributed information about their structure that was not obtainable from the static views.

General Discussion

These experiments contain evidence that the birds discriminated these objects by experiencing a generalized 3-D representation of them. Evidence for the generalized nature of this discrimination came in many forms. The most prominent was the limited drop in performance whenever they were tested alterations of the stimuli. This discrimination invariance was found across variations in stimulus size (Experiment 1), rate of motion (Experiment 1), combinations of different motions and rates (Experiment 3), direction of motion (Experiment 3), and changes in surface color (at least when presented dynamically, as in Experiment 3). The pigeons also showed clear above chance, but not perfect, transfer when tested with a new axis of rotation (Experiment 2) and changes in surface colors when presented statically (Experiment 3). Clearly, whatever aspect of the stimuli the birds were discriminating, it was readily recognized across a wide variety of transformations. This type of robust stimulus invariance is infrequently found and interesting in its own right, but is only a foundation for answering the more provocative question of whether the pigeons saw these stimuli as invariant coherent 3-D objects or as collections of flat 2-D features.

Consider first the simpler and noncontroversial hypothesis that the birds memorized a set of specific 2-D features, without seeing the stimuli as object-like wholes. Such a simple coding mechanism can be very effective as long as the critical feature retains its identity across all transformations. Given the structural similarity of the object stimuli and procedures used in the experiments, the list of candidate

features available for this function would be limited to looking for the presence and absence of a sharp acute angle at the top of the image. Because of the type of rotation tested in Experiment 1, for instance, this critical feature approach would have worked effectively in learning the discrimination. Nevertheless as the complexity of motion and the variability of the stimuli increased over the experiments, this approach becomes increasingly untenable as a strategy. This was especially the case by the end of Experiment 3, where the variety and complexity of the objects' orientations in the static displays and their differing rates of motion in two dimensions in the dynamic displays continually distorted the angular and surface features of the objects' appearances. Despite these deformations in the 2-D features, the pigeons nevertheless continued to discriminate the objects without difficulty.

Nor does a 2-D interpretation effectively explain the pigeons' superior discrimination of the dynamic stimuli in the experiment. Dynamic stimulus presentations supported better performance than equivalent sets of static ones when tested with a new axis of rotation (Experiment 2), with new complex paths of motion (Experiment 3), with changes in surface color (Experiment 3), and during the elimination of surface and contour information (Experiments 1, 2, and 3). Each of these results indicates that more discriminative information was present from a successive of dynamic images displayed within a trial than from the same set of images presented statically across trials. Why did the pigeons do decidedly better at discriminating the dynamic displays? Given the absence of evidence that the birds engaged in any form of speed/accuracy trade-off with such displays, we suggest the reason is that even briefly viewed movements of the objects resulted in a superior 3-D perception of their structure (see also the discussion of Experiment 2).

Further evidence for this conclusion comes from two other important results from these experiments. The first is associated with the KDE stimuli in which all contour and surface information were eliminated, and the second is the differential transfer with dynamic and static objects constructed from novel colors. Both of these results suggest the birds were recovering more than the 2-D qualities of these stimuli. Consider first the results from the different KDE tests. Three of the 4 pigeons consistently showed superior performance with dynamic stimuli in comparison with the static stimuli. In this case, additional information must have come from the dynamic changes in the projective geometry of the image as it transformed on the display. These KDE results offer the first substantive, appropriately qualified, evidence that pigeons are able to recover 3-D object structure from rigid projective motion. It is likely that it is this same capacity that is also responsible for the corresponding dynamic superiority effect found with novel colored objects. Although differences in the color of the surfaces were present in this case, allowing the pigeons to partially recognize the static images, they again had an easier time recognizing these "novel" objects when in motion. Collectively, both of these results suggest that the birds benefited

from being able to use the 3-D information present in the projective geometry created from the motion of the objects.

The evidence as a whole suggests that any type of 2-D feature-based explanation of the current discrimination is difficult to sustain after Experiment 1, whereas a 3-D object-based account is not. Given the dynamic perceptual demands taken on by an animal designed to use rapid flight as its primary means of transportation, this outcome may be not too surprising. Numerous human studies verified a similar capacity to recognize 3-D objects across large changes in an optic array such as illumination, motion, perspective, size, and positional translations. The mechanism underlying such object constancy remains one of the central problems in human perceptual research. Recent theories of human pattern recognition have generally fallen into two groups on this issue. Although the current experiments were not specifically designed to discriminate between these theories, it is instructive to examine briefly some of our results in their context.

The first group of theories has focused on the role of object-centered representations in visual recognition. These theories are based around the encoding and use of generalized structural descriptions of an object's properties and hierarchical relations as the functional representational unit of object perception (Biederman, 1987; Marr & Nishihara, 1978; Palmer, 1977). In contrast, the other major class of object recognition theories is viewer centered. These latter theories propose that the functional unit is a particular 3-D view or a sample of multiple views of the object as experienced by the observer (Bulthoff & Edelman, 1992; Poggio & Edelman, 1990; Rock, 1973; Tarr, 1995). The effects of how perspective transformations in the X, Y, and Z axes influence recognition performance has become a key testing ground to these accounts. View-centered theories predict that projective changes in viewpoint should systematically interfere with recognition performance as a direct function of the difference between the current view of the object's features and the set of stored views. Object-centered theories predict, on the other hand, that performance should be viewpoint invariant as long as the same set of configural information is present.

Overall, our results seem most consistent with the predictions of viewer-centered theories. The most critical result in this regard comes from the viewpoint analysis of performance done in Experiment 2. This analysis revealed that when noncanonical views of the objects' distinguishing features were provided, the birds generally performed poorly, a fact accommodated by both types of theories. It also revealed, however, that performance with the objects when they appeared upside down (only meaningful for the pyramid) was poorer than when tested in their upright training position. Because the structure of the objects is the same in these two orientations, object-centered theories have a harder time accounting for this decrement than do viewer-centered theories. This result is perhaps mitigated by the fact that this superiority with the training viewpoint may be due to the much greater experience that the birds had with this particular view. Such overtraining may have promoted the birds to encode and use this particular view of the objects as

"special." Seeing this particular view of the displays was not essential for accurate performance, however. First, as discussed previously, the pigeons on the dynamic trials did not seem to wait to see any particular view. Second, in Experiment 3 where the motion was most complex and the two simple x-axis and y-axis rotations had been eliminated, the birds continued to respond accurately. It will be interesting in future experiments to see if pigeons can perform this object discrimination when only the most complex motions are used from the beginning and no particular viewpoint is overtrained (as may have been the case here). Given the present data, we speculate this will be an easy discrimination for the pigeons to master.

In sum, these results add considerably to our very limited knowledge about how pigeons perceive objects and how motion is involved in their perception. The apparent ease and flexibility of the current object discrimination is in keeping with the general propositions that birds are (a) adept at the processing of motion information and (b) that they see the world as composed of unified objects much like we do. The current results join our earlier research on early visual processing in birds (Cook, 1992a; 1992b; Cook, Cavoto, & Cavoto, 1996; Cook, Cavoto, Katz, & Cavoto, 1997), which has found that human and avian visual cognition may share more similarities than differences. Although much remains to be done in specifying the mechanisms of higher order object perception in pigeons, and its relation to human object processing, these experiments are a promising start. If the speculative conclusion that human and avian visual cognition are similar both in the operation of their lower order registration process and higher order object-related processes, it raises the following interesting question. Why is there such a huge difference in the absolute size of the visually active parts of the human and pigeon brain? This simple difference in size clearly suggests we are doing something more than the pigeons, but what those adjunctive visual functions are has yet to be established. What is likely is that these functions are not critically tied to the visual demands of being a highly mobile organism in an object-filled world. For solving that problem, a brain the size of a thumb seems to be sufficient.

References

Berryman, R., Cumming, W. W., Cohen, L. R., & Johnson, D. F. (1965). Acquisition and transfer of simultaneous oddity. *Psychological Reports, 17,* 767–775.

Biederman, I. (1987). Recognition by components: A theory of human image understanding. *Psychological Review, 94,* 115–147.

Bulthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences, USA, 89,* 60–64.

Carter, D. E., & Werner, J. T. (1978). Complex learning and information processing in pigeons: A critical analysis. *Journal of the Experimental Analysis of Behavior, 29,* 565–601.

Cerella, J. (1977). Absence of perspective processing in the pigeon. *Pattern Recognition, 9,* 65–68.

Cerella, J. (1982). Mechanisms of concept formation in the pigeon.

In D. J. Ingel, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 241–260). Cambridge, MA: MIT Press.

Cerella, J. (1986). Pigeons and perceptrons. *Pattern Recognition, 19,* 431–438.

Cerella, J. (1990a). Pigeon pattern perception: Limits on perspective invariance. *Perception, 19,* 141–159.

Cerella, J. (1990b). Shape constancy in the pigeon: The perspective transformations decomposed. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn, & D. B. Mumford (Eds.), *Quantitative analyses of behavior: Behavioral approaches to pattern recognition and concept formation* (Vol. 8, pp. 145–163). Hillsdale, NJ: Erlbaum.

Cook, R. G. (1992a). Dimensional organization and texture discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 18,* 354–363.

Cook, R. G. (1992b). The acquisition and transfer of texture visual discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 18,* 341–353.

Cook, R. G., Cavoto, K. K., & Cavoto, B. R. (1996). Mechanisms of multidimensional grouping, fusion, and search in avian texture discrimination. *Animal Learning & Behavior, 24,* 150–167.

Cook, R. G., Cavoto, B. R., Katz, J. S., & Cavoto, K. K. (1997). Pigeon perception and discrimination of rapidly changing texture stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 23,* 390–400.

Cumming, W. W., & Berryman, R. (1961). Some data on matching behavior in the pigeon. *Journal of the Experimental Analysis of Behavior, 4,* 281–284.

Cumming, W. W., Berryman, R., & Cohen, L. R. (1965). Acquisition and transfer of zero-delay matching. *Psychological Reports, 17,* 435–445.

Cutting, J. E. (1986). *Perception with an eye for motion.* Cambridge, MA: MIT Press.

Dittrich, W. H., & Lea, S. E. G. (1993). Motion as a natural category for pigeons: Generalization and a feature-positive effect. *Journal of the Experimental Analysis of Behavior, 59,* 115–129.

Edwards, C. A., & Honig, W. K. (1987). Memorization and "feature selection" in the acquisition of natural concepts in pigeons. *Learning and Motivation, 18,* 235–260.

Emmerton, J. (1986). The pigeon's discrimination of movement patterns (Lissajous figures) and contour-dependent rotational invariance. *Perception, 15,* 573–588.

Farthing, G. W., & Opuda, M. J. (1974). Transfer of matching-to-sample in pigeons. *Journal of the Experimental Analysis of Behavior, 21,* 199–213.

Frost, B. J., Wylie, D. R., & Wang, Y. C. (1994). The analysis of motion in the visual systems of birds. In P. R. Green & M. N. O. Davies (Eds.), *Perception and Motor Control in Birds* (pp. 248–269). Berlin: Springer-Verlag.

Gibson, J. J. (1966). *The senses considered as perceptual systems.* Boston: Houghton Mifflin.

Gibson, J. J. (1979). *The ecological approach to visual perception.* Boston: Houghton Mifflin.

Heinemann, E. G., & Chase, S. (1989). A quantitative model for pattern recognition. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn, & D. B. Mumford (Eds.), *Computational and clinical approaches to pattern recognition and concept formation. Quantitative analyses of behavior* (Vol. 9, pp. 109–126). Hillsdale, NJ: Erlbaum.

Hodos, W., Smith, L., & Bonbright, J. C., Jr. (1975). Detection of the velocity of movement of visual stimuli by pigeons. *Journal of the Experimental Analysis of Behavior, 25,* 143–156.

Holmes, P. W. (1979). Transfer of matching performance in pigeons. *Journal of the Experimental Analysis of Behavior, 31,* 103–114.

Johansson, G. (1975). Visual motion perception. *Scientific American, 232,* 76–89.

Kellman, P. J. (1993). Kinematic foundations of infant visual perception. In C. Granrud (Ed.), *Visual perception and cognition in infancy. Carnegie Mellon symposia on cognition* (pp. 121–173). Hillsdale, NJ: Erlbaum.

Kendrick, D. F., Wright, A. A., & Cook, R. G. (1990). On the role of memory in concept learning by pigeons. *Psychological Record, 40,* 359–371.

Logothetis, N. K., Pauls, J., Bulthoff, H. H., & Poggio, T. (1994). View-dependent object recognition by monkeys. *Current Biology, 4,* 401–414.

Lombardi, C. M., & Delius, J. D. (1990). Size invariance in visual pattern recognition by pigeons. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn, & D. B. Mumford (Eds.), *Behavioral approaches to pattern recognition and concept formation. Quantitative analyses of behavior.* (Vol. 8, pp. 41–65). Hillsdale, NJ: Erlbaum.

Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Philosophical Transactions of the Royal Society of London, B, 200,* 269–294.

Mulvanny, P. (1978). Velocity discrimination by pigeons. *Vision Research, 18,* 531–536.

Palmer, S. E. (1977). Hierarchical structure in perceptual representation. *Cognitive Science, 9,* 441–474.

Pisacreta, R. (1982). Stimulus control of the pigeon's ability to peck a moving target. *Journal of the Experimental Analysis of Behavior, 37,* 301–309.

Poggio, T., & Edelman, S. (1990). A network that learns to recognize three-dimensional objects. *Nature, 343,* 263–266.

Rilling, M. E., & LaClaire, T. L. (1989). Visually guided catching and tracking skills in pigeons: A preliminary analysis. *Journal of the Experimental Analysis of Behavior, 52,* 377–385.

Rock, I. (1973). *Orientation and form.* New York: Academic Press.

Rogers, B., & Graham, M. (1982). Similarities between motion parallax and stereopsis in human depth perception. *Vision Research, 22,* 261–270.

Santi, A. (1978). The role of physical identity of the sample and correct comparison stimulus in matching-to-sample paradigms. *Journal of the Experimental Analysis of Behavior, 29,* 511–516.

Santi, A. (1982). Hue matching and hue oddity in pigeons: Is explicit training not to peck incorrect hue combinations a sufficient condition for transfer? *Psychological Record, 32,* 61–73.

Siegel, R. K. (1970). Apparent movement detection in the pigeon. *Journal of the Experimental Analysis of Behavior, 14,* 93–97.

Siegel, R. K. (1971). Apparent movement and real movement detection in pigeons: Stimulus generalization. *Journal of the Experimental Analysis of Behavior, 16,* 189–192.

Siegel, R. M., & Anderson, R. A. (1988). Perception of three-dimensional structure from motion in monkey and man. *Nature, 331,* 259–261.

Stenhouwer, D. J., & Denny, M. R. (1975). Discrimination of speed and direction of rotation in the pigeon: A mirror-image effect. *Bulletin of the Psychonomic Society, 5,* 101–104.

Tarr, M. J. (1995). Rotating objects to recognize them: A case study of the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin & Review, 2,* 55–82.

Ullman, S. (1979). *The interpretation of visual motion.* Cambridge, MA: MIT Press.

Vaughan, W., Jr., & Green, S. L. (1984). Pigeon visual memory capacity. *Journal of Experimental Psychology: Animal Behavior Processes, 10,* 256–271.

Wallach, H., & O'Connell, D. N. (1953). The kinetic depth effect. *Journal of Experimental Psychology, 45,* 205–217.

Wasserman, E. A. (1995). The conceptual abilities of pigeons. *American Scientist, 83,* 246–255.

Wasserman, E. A., Gagliardi, J. L., Cook, B. R., Kirkpatrick-Steger, K., Astley, S. L., & Biederman, I. (1996). The pigeon's recognition of drawings of depth-rotated stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 22,* 205–221.

Wilkie, D. M. (1986). Some factors affecting pigeon's visual tracking behavior. *Behavioural Processes, 12,* 287–297.

Wright, A. A. (1997). Concept learning and learning strategies. *Psychological Science, 8,* 119–123.

Wright, A. A., Cook, R. G., Rivera, J., Sands, S. F., & Delius, J. (1988). Concept learning by pigeons: Matching to sample with trial-unique video picture stimuli. *Animal Learning & Behavior, 16,* 436–444.