Rotational Object Discrimination by Pigeons

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Four experiments examined the discrimination of directional object motion by pigeons. Four pigeons were tested in a go/no-go procedure with video stimuli of geons rotating right or left around their central *y*-axis. This directional discrimination was learned in 7 to 12 sessions and was not affected by changes in object starting orientation, but did require the coherent ordering of the videos' successive frames. Subsequent experiments found no or little transfer of this motion discrimination to novel objects. Experiments varying the speed of rotation and degrees of apparent motion per frame revealed that both factors strongly affected the discrimination. Finally, tests with partial occlusion of different portions of a rotating object suggested that the majority of the object was likely involved in determining rotational direction. These experiments indicate that pigeons can exclusively use motion cues to judge relative object motion. They also suggest the pigeons may have used a specific representation of the motion sequences of each object to make the discrimination.

Keywords: pigeon, motion, object motion, motion discrimination, motion perception

Many animals, much like humans, respond to the world as if they are perceiving and reacting directly to the visual objects surrounding them. Because many mammals and birds share the world at approximately the same spatial scale as humans, it makes good sense that these objects might comprise the fundamental unit of perception and action for these animals. If so, it is important to establish that "objects" exist as separate psychological entities for animals and understand how they are processed and represented by their nervous systems. This information is not only important for understanding the mechanisms of animal behavior, but contributes fundamental insights into the basis of visual cognition more generally (Biederman, 1987; Cook, 2001; Marr, 1982; Zeigler & Bischof, 1993). Because birds regularly engage in visually demanding behavior, but do so with a small central nervous system, our lab has been particularly interested in how pigeons process visual objects and whether this processing is similar to human object processing (Cook & Katz, 1999; Cook, Riley, & Brown, 1992; Cook & Roberts, 2007; Cook, Shaw, & Blaisdell, 2001).

Past research on object perception has primarily focused on investigating static stimuli (Kirkpatrick-Steger, Wasserman, & Biederman, 1996; Kirkpatrick, 2001; Spetch & Friedman, 2003; Spetch, Friedman, & Reid, 2001). Either because of the observer's self-motion or the motion of the object itself, however, few objects in the world are ever experienced statically. The information derived from an object's motion helps in detecting and

recognizing objects, separating them from their background, contributes to their perceived unity, generates depth information, and reveals how these objects might potentially interact with the perceiver (e.g., collision, avoidance, predator, prey). Concentrating on the role of motion in animal object perception is therefore a critical issue, but is one largely unexplored or producing conflicting results. It is this empirical and theoretical gap that motivated the current research. In this paper, we report four experiments examining the mechanisms of dynamic information processing with object-based stimuli. Using the direction of object's rotation as the mediating discrimination, we present new evidence concerning the perception, discrimination, and representation of moving objects by pigeons.

For some time, it has been established that pigeons can discriminate between static and moving images (Dittrich & Lea, 1993; Goto & Lea, 2003; Hodos, Smith, & Bonbright, 1976; Siegel, 1970, 1971). For example, Siegel (1970, 1971) determined that pigeons could perceive apparent motion and its absence in a variety of displays as produced by a rotating polarized disk. Dittrich and Lea (1993) used video stimuli to train pigeons successfully to discriminate between moving and static images of other pigeons (see also Goto & Lea, 2003).

Movement also seems to contribute to the discrimination of an object's shape. Testing pigeons, Cook and Katz (1999) examined the contribution of rotational motion to the discrimination of three-dimensional (3D) cubes and pyramids. As revealed by transfer to different types of changes in rotation and object manipulations, the pigeons showed a dynamic superiority effect in which moving objects consistently supported better discrimination than did static presentations of the same objects. In contrast, however, Jitsumori and Makino (2004) found that dynamic 3D rotations of faces in depth contributed little beyond what would be expected from the additional views provided by the motion component but not the motion per se (see also Loidolt, Aust, Steurer, Troje, & Huber, 2006).

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Of most direct relevance to the current studies are those experiments that have examined if and how pigeons discriminate between different types of motion. Emmerton (1986) was the first to examine if pigeons can discriminate conditions based on a particular pattern of motion. Using Lissajous figures, she trained pigeons to differentiate between different trajectories of a single dot on an oscilloscope (see also Goto, Lea, & Dittrich, 2002). Using far more dots, Bischof, Reid, Wylie, and Spetch (1999) were able to train pigeons to discriminate between large groups of randomly moving dots from groups of dots moving coherently in a common direction. Dittrich, Lea, Barrett, and Gurr (1998) successfully trained pigeons to distinguish between videos of conspecifics either walking or directing pecks at the ground. Goto and Lea (2003) were able to train pigeons to discriminate rightward from leftward moving backgrounds after first training them with moving and static images, but were not able to obtain this discrimination with moving foreground objects with or without additional training. Jitsumori, Natori, and Okuyama (1999) trained pigeons to discriminate among moving images of different pigeons acting in different ways. Cook et al. (2001) investigated how pigeons discriminated video stimuli that portrayed the actions of "through" and "around" relative to a number of different objects to examine whether they could discriminate different types of motion with respect to a specific object. Video stimuli were computer-generated to create a semi-realistic landscape over which different objects (arches, doughnuts, etc.) appeared to be approached from the camera's perspective. Near the end of the video, the camera's point of view either veered off to the left of the display, creating the impression of going "around" the object, or passed "through" the object's central interior opening. It was found that pigeons could learn this type of motion discrimination and transfer it to novel objects not previously discriminated before.

As a group, the above studies suggest that different types of motions are potentially distinguishable to pigeons. The overarching and consistent problem with the majority of these studies, however, is that each one retains simple featural cues that may have mediated the discriminations independent of the perception and discrimination of different types of motion. For instance, in Emmerton (1986) unique spatial cues were present that could have distinguished the different motion paths, as the moving dot appeared only in certain areas of the screen for each path. In Dittrich et al., (1998) the salient motions of their pigeons' different behavior occurred at different points in space, with the heads of the pigeons in predominately different spatial locations depending upon whether they were walking upright or pecking at the ground. Jitsumori et al., (1999) concluded that their discrimination was based on invariant spatial features that were shared in common between their static and dynamic conditions. Similarly in Cook et al. (2001) the position of the approaching object was in spatially different positions during the critical frames illustrating the around/through paths. Thus, it was possible to make the discrimination based on any one of the last 10 frames of the video without necessarily seeing the integrated motion related to the object or its approach before that.

The consistent presence of simpler spatial cues in these earlier approaches to studying object-based motion is both theoretically and empirically troublesome. The more successful studies of this group have not been object-based, but instead have relied on very large changes in the overall display to mediate motion (Bischof et al., 1999; Goto & Lea, 2003). The solution to this problem is to test a motion discrimination in which such differential spatial cues are entirely removed as a possible source of discrimination and no single static frame or moment reveals the trajectory of the constituent object.

One motion of exactly this type is object rotation. In this paper we report four experiments in which pigeons were taught to discriminate the direction of rotation of different 3D rendered objects (tube, prism, cone, torus) using video stimuli. These objects were either rotated leftward or rightward around their central axis (see Figure 1). This type of discrimination allowed us to examine the issue of motion discrimination without the previous confounds of differential spatial cues across time. In Experiment 1, pigeons were successfully trained to discriminate this rotational motion with a single object. To explore further the interaction between this motion and its meditating object, three additional experiments were conducted. Experiment 2 examined whether this motion discrimination would transfer to new objects as a test of generalized motion categorization (Cook et al., 2001; Dittrich et al., 1998). Experiment 3 examined the contributions of rotation rate and change in angular perspective per frame to the discrimination. Experiment 4 examined how different arrangements of an occluding object interfered with this discrimination to investigate which part of the object was critical to detecting its directional rotation.
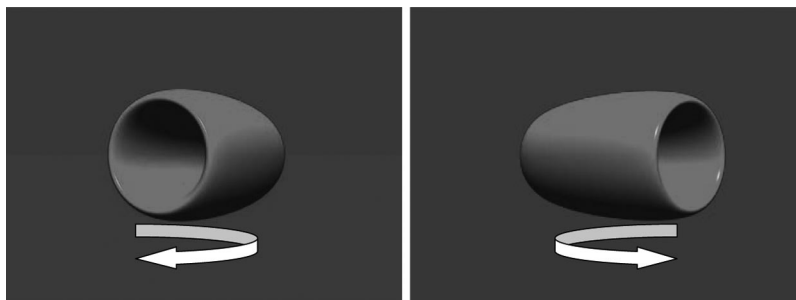

Figure 1.   Single frame examples of the rotating tube object used in Experiment 1. The motion arrows depict the right/left rotation, but were not part of the video. Each example is a single frame from a 60 frame video depicting one 360° rotation.

Experiment 1: Acquisition of Rotational Discrimination

The goal of Experiment 1 was to examine if the pigeons could acquire an object-based rotational discrimination using video stimuli. The objects used to mediate the motion in these experiments were rendered by animation software to appear 3D to the human eye. Using a go/no-go procedure, the pigeons were differentially reinforced for pecking when the object rotated in depth around its central *y*-axis in one direction (S+), but not when it rotated in the opposite direction (S−).

Upon acquiring this rotational discrimination, we conducted two tests to examine the basis of the discrimination. The first test examined the effect of randomizing the initial orientation of the object. During training, the rotating object was always started from the same perspective to make the discrimination potentially easier to learn. This raised the possibility that only the first few frames of the video might be critical to the discrimination rather than recognizing the entire rotational movement of the object. If the pigeons were responding based on the object's rotational direction, it was predicted that randomizing the point of view at which the object started would have no effect. The second test involved presenting randomized orderings of the 60 frames used to make each video. This test was to ensure further that the pigeons were truly integrating the object's motion over the separate frames of the video. Without the properly ordered, coherent, and successive sequences of frames to judge the relative rotation of the object, these randomly ordered video presentations should result in chance levels of discrimination.

Method

Animals

Three male White Carneaux and one Silver King pigeon (*Columba livia*) were tested. These pigeons were previously in a motion discrimination task investigating an around versus through object discrimination (Cook & Roberts, 2007). All pigeons were maintained at 80% to 85% of their free-feeding weight during testing, with free access to water and grit in their home cages.

Apparatus

Testing was done in a flat-black Plexiglas chamber (38 cm wide × 36 cm deep × 38 cm high). The stimuli were presented on a color computer monitor (800 × 600 pixels, ViewSonic E55, Walnut, CA) visible through a 28.5 cm wide by 21 cm high viewing window located in the middle of the front panel of the chamber. The viewing window's bottom edge was 16 cm above the chamber floor. Pecks were detected by an infrared LED touch screen (Carroll Touch; distributed by EloTouch Systems) in the front panel. The monitor was recessed 7 cm back from the glass of the touch screen to reduce the visual angle of the video stimuli. A house light was located in the chamber's ceiling and was illuminated at all times, except during timeouts. A food hopper was located in the middle of the front panel with its access hole flush to the floor. All programming was done in Visual Basic (Microsoft, Redmond, WA) using the FX Tools video control component (Pegasus Software, Tampa, FL).

The stimulus videos (13.5 × 10 cm) were created and rendered in the AVI format (384 × 288 pixels; Cinepak Codec compres-

sion) using the Bryce 5 animation package (MetaCreations Corporation, Carpinteria, CA). Each video consisted of 60 frames. The central object was a hollow red tube that was 9.5 cm in length and 5.75 cm in diameter (see Figure 1). It was centrally placed on a uniform blue background. The tube rotated right or left around its central *y*-axis at 6° per frame and rotated at a rate of 105° per sec. As it rotated, this object subtended a maximum visual angle of 69° and minimum visual angle of 39°.

Procedure

Discrimination training. Because the pigeons were experienced, training to peck the displays was not required. A trial began with the presentation of a 2.5 cm white warning signal in the center of the computer display. A single peck to this signal caused it to be replaced with a video stimulus. Each video started with the tube positioned with its end (0°) facing the pigeon and then rotated in depth either rightward or leftward. Each trial consisted of 10 rotations of the object and lasted 34.2-s. On positive S+ trials, all pigeons were reinforced on a VI-10 schedule; two birds for pecking at the rightward rotation and two for pecking the leftward rotation of the object. On negative S− trials when the object rotated in the opposite direction, reinforcement never occurred (extinction) and each bird was punished with an 8-s dark timeout after the termination of the video. A small percentage of S+ trials were tested as *probe trials* in which no reinforcement occurred, allowing for the uncontaminated measurement of peck rate without the presence of food presentations. All reported dependent measures were calculated using these probe trials. Daily sessions consisted of 96 trials (48 right/48 left rotations), with 12 of the S+ trials conducted as probe trials. Training was conducted until each pigeon was consistently performing above chance for at least three sessions. At this point, two tests were conducted.

Test 1-randomized starting viewpoint. The purpose of this test was to see if the pigeons depended on the first few frames involving the initial deviation of the object to either the right or left of the screen from the 0° end view. In this test, the videos now started with the object orientated at a random angle in 6° increments around its *y*-axis, rather than the 0° view exclusively used during acquisition. Twelve randomly chosen orientation trials (6 right/6 left) were tested as probes in each session. These were randomly inserted among the 96 baseline trials tested each session (108 total trials). Three test sessions were conducted. After these test sessions, all subsequent training and testing was conducted using randomized object starting orientations.

Test 2-randomized sequencing. This test involved adding probe trials that presented the video's frames in randomized sequences. Its purpose was to determine if ordered coherency was required for the discrimination. Twelve randomly ordered videos were tested as probe trials (6 right/6 left). A different randomized order was used on each trial. These were randomly inserted among the 96 baseline trials in each session (108 total trials). Three test sessions were conducted.

Results

Acquisition. All four pigeons easily acquired the rotation discrimination within 12 sessions. The left half of Figure 2 shows the acquisition as a function of 2-session blocks as measured by
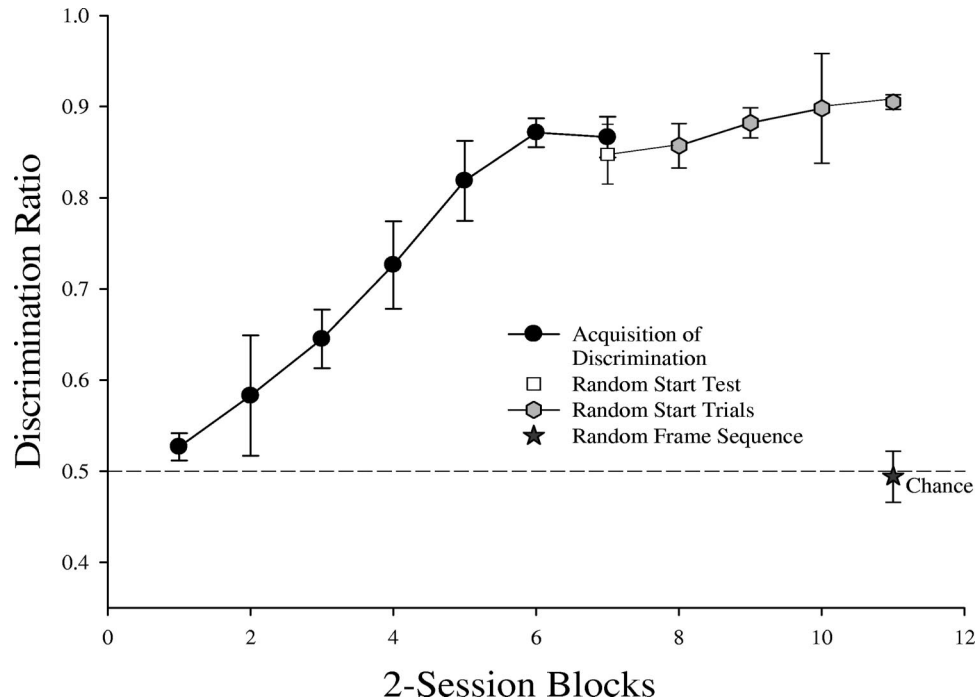
Figure 2. Mean discrimination ratio across two-session blocks for all four pigeons during acquisition of the rotation discrimination. The white square shows test performance with randomized starting points, gray hexagons show subsequent training performance with randomized starting points and the star shows test performance with randomized sequences. The dashed line depicts chance discrimination. The error bars represent *SEM*.

discrimination ratio (DR = S + probe peck rate/[S + probe peck rate + S– peck rate]). A one-way repeated measure analysis of variance (ANOVA) using DR confirmed this significant improvement across sessions, $F(5, 5) = 16.4$ (an alpha level of .05 was used for all statistical tests). By the last session of acquisition, all pigeons (mean DR = .87) were significantly above chance (DR = .5) as measured during the 12th session, $t(3) = 23.3$.

Test 1-randomized starting viewpoint. All pigeons easily accommodated to changes in the initial object viewpoint, showing little decline in performance when tested with probe trials or introduced as a regular part of each trial. The second group of points in Figure 2 shows mean DR for the baseline condition (DR = .87) in black, and the randomized viewpoint test condition (DR = .81) in white. A repeated measures ANOVA (Sessions × Condition) using DR revealed no significant main effect between the baseline and randomized viewpoint condition or their interaction across sessions. The next set of points in Figure 2 (gray points) shows the result of the immediately subsequent sessions in which randomized viewpoints were exclusively used. This change in presentation procedure had little impact on their level of discrimination.

Test 2-randomized sequencing. Randomizing the order of the frames within the video caused a dramatic and significant drop in discrimination in all pigeons. The last point (star) on the right side of Figure 2 shows the mean DR for the randomized sequence test trials (DR = .49). This can be compared with their excellent baseline performance (DR = .90). A comparison of the random-

ized sequence condition against chance revealed no significant difference, $t(3) = .21$.

Discussion

Experiment 1 revealed that pigeons could easily learn this rotational discrimination within a few sessions. Test 1 revealed that changes in the initial viewpoint had little measurable impact on performance. This indicates that the initial frames of the object were not important in mediating this rotational discrimination. Test 2 confirmed that randomizing the sequence of the video's frames dropped discrimination to chance levels. This indicates that a coherent and orderly sequence in the object's successive transformations were essential to the discrimination. Together, these results suggest the birds were making the discrimination based on the detection of sequential motion cues associated with the object's apparent rotation in depth.

These results offer the first strong evidence that pigeons can perceive object-based motion when all momentary spatial two-dimensional cues have been eliminated. Unlike the majority of previous motion studies, the current rotational discrimination could not have been based on any individual frame or moment or a unique spatial position occupied during its different types of motion. This is because identical frames are used in each direction with the only difference being the order in which they appear. This result has some similarities to Goto and Lea's (2003) finding that the direction of large scale background cues could be discrimi-

nated after special training. Unlike Goto and Lea (2003), however, we were able to successfully train the birds to discriminate the direction of movement simply based on the foreground object. Further, no special or preliminary training was needed as our birds quickly learned the discrimination.

Experiment 2: Introduction of Novel Objects

The next three experiments were aimed at better understanding how the pigeons processed rotational motion and the object that instantiated that motion. Two prevailing questions over these experiments concerned whether the sequences of images were perceived as motion by the pigeons and what contribution did the object's 3D appearance make to this motion discrimination.

Experiment 2 examined if the pigeons had learned to discriminate the rotation of the object based on a generalized concept of this motion or were they relying instead on cues tied specifically to the training object. Several authors have suggested that pigeons may be able to form motion or verb-like categories similar to that found frequently with noun categories (Cook et al., 2001; Dittrich & Lea, 1993). To determine whether these pigeons were using generalized rotational motion, we successively introduced three novel objects during Experiment 2. If the pigeons were making the discrimination based on a generalized concept of rotation independent of the object's shape, then they should show discrimination transfer at the introduction of the new objects. This result would suggest they had learned a generalized rotational concept. If, on the other hand, their recognition of the rotational motion involved object-specific cues, then transfer to these new objects should be limited or not occur.

Three novel objects were added in succession. Those objects consisted of a prism, cone, and torus (see Figure 3). Each object was selected so as to differ in overall shape, symmetry, size, and how it transformed during rotation from the other objects. To test

for transfer, each new object was initially presented for three sessions as a series of probe trials. After transfer testing, each new object was added into the pigeons' baseline daily training trials and differentially reinforced based on its direction of rotation. Increasing the number of objects in the baseline training set might serve to promote the formation of a generalized concept. Once they acquired the discrimination with each introduced new object, the next novel object was introduced and tested and trained in the same way.

Method

Animals and Apparatus

The pigeons and apparatus were the same as in Experiment 1.

Procedure

This experiment involved adding three new objects: a prism, cone, and torus. The prism consisted of a rectangular solid, 12.5 × 4.25 × 4.25 cm in length, height, and width. As it rotated, this object subtended a maximum visual angle of 76° and minimum visual angle of 29°. The cone was 7.5 cm in height and 7.75 cm in diameter at its base. As it rotated, this object subtended a maximum visual angle of 50° and minimum visual angle of 47°. The torus was 7.25 in its outer diameter, 3.5 in its inner diameter, and 1.87 cm thick. As it rotated, this object subtended a maximum visual angle of 49° and minimum visual angle of 13.3°. All objects were colored red. Each video consisted of 60 frames and used the same rendering parameters as for the tube.

The objects were added in successive blocks in the following order: prism, cone, torus. During a block, each object was initially tested using nonreinforced probe trials to test for discrimination transfer. There were 12 probe trials (6 left/6 right), with each new object randomly mixed among the 96 baseline trials to form a
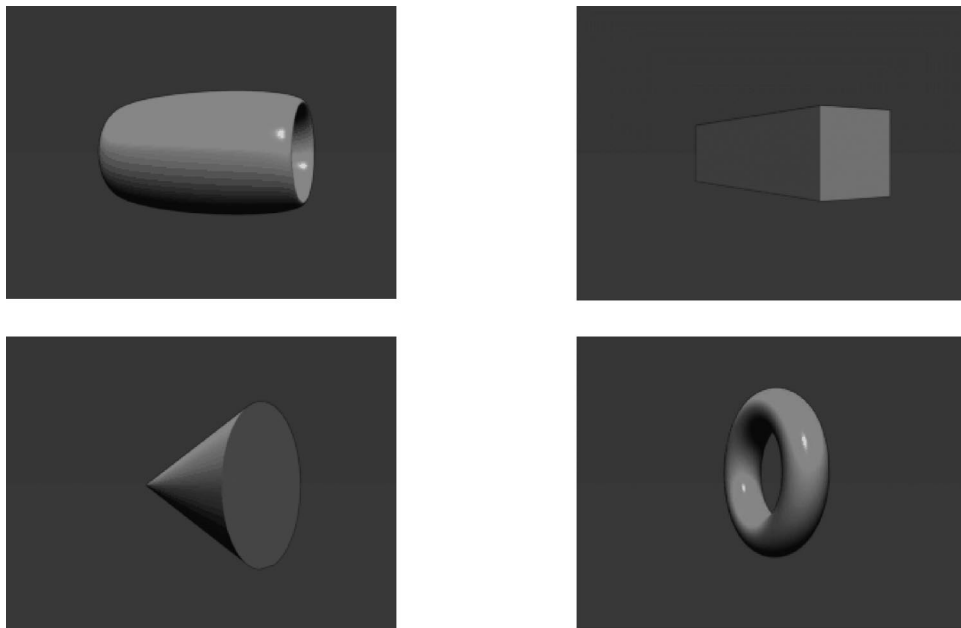

Figure 3. Single frame examples from the tube, prism, cone, and torus video stimuli tested in Experiment 2.
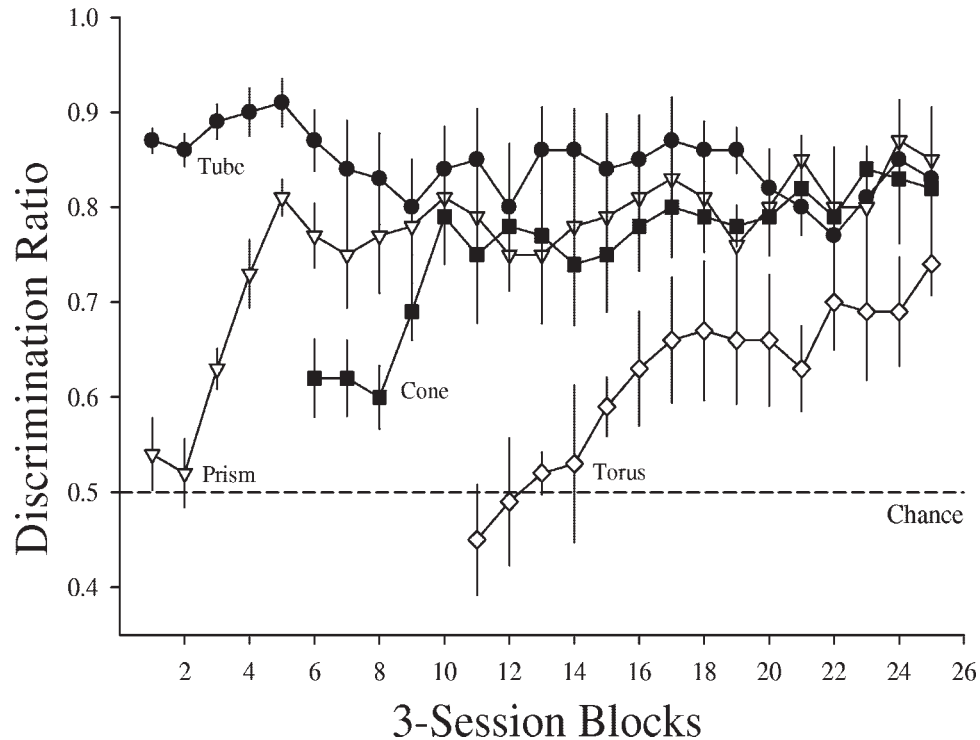
Figure 4. Mean discrimination ratio across transfer (first point in each curve) and training sessions for the three novel objects introduced in Experiment 2. The dashed line depicts chance discrimination. The error bars represent *SEM*.

session of 108 total trials. Three such transfer sessions were conducted. Following transfer testing, the new object was added to the daily training regime and these trials were now differentially reinforced depending on the direction of object's rotation. Over these subsequent training sessions, the number of trials conducted with each object was equated and counterbalanced and their order of presentation within a session randomized. Once the new object supported a mean discrimination ratio of .65 or higher for at least four sessions for each individual pigeon, the next transfer test was conducted using the next object. This incremental procedure was used until all three objects were tested and added to the discrimination.

Results

Shown in Figure 4 are the mean results for the transfer and subsequent training of the three novel objects. The first point in each curve represents the mean of the three probe transfer tests, with the successive points showing the results from the later differential training sessions. Overall, the pigeons showed little evidence of transfer. Mean performance with all three objects during the initial transfer tests was (DR = .54) with performance with the cone being slightly better than with either the prism or torus. Single mean *t* tests against chance for each object revealed no significant transfer (prism − *t*(3) = .9; cone − *t*(3) = 2.6; torus − *t*(3) = 1.8).

When each object was subsequently added into the daily reinforced training trials, discrimination of the objects' directional

rotation was acquired fairly quickly. The prism and cone were learned by all of the pigeons within three to nine sessions. Acquisition with the torus was slower, with all pigeons taking at least 13 sessions to reach criteria with the torus. Discrimination involving the torus also reached a generally lower asymptotic level in comparison to the other three objects by the end of the experiment.

Discussion

This experiment revealed little evidence for a generalized rotational concept. The pigeons showed little immediate transfer to new objects, although initial performance with the cone was marginally better than either of the other two objects. The discrimination of each new object was gradually learned with relative ease in all birds, albeit the torus took longer. There might be some savings here in comparison to initial learning, but this is speculative without a proper control comparison and a counterbalancing of the order in which the objects were introduced. Thus, the appropriately conservative conclusion is that the pigeons had not learned a rotational concept. Their increasing experience with up to four objects did not seem to help. Instead the pattern of gradual and repeated learning with each object looked more like the pigeons were learning to use object-specific motion cues to perform the discrimination.

Experiment 3: Manipulation of Rate and Angular Change

In Experiment 3, we examined how the speed of object's rotation and the degree of change in apparent motion across successive

views influenced this rotational discrimination. These key variables help to reveal the basic properties of the avian motion system responsible for this rotational discrimination. The experiment was conducted in two parts.

Experiment 3A varied the rotational velocity of the object as it spun around its central axis. In the preceding experiments, the objects rotated around their central axis at a rate of 105° per second. This rate was selected because it produced coherent motion to the human eye and was above previous estimates for movement thresholds for pigeons (Bischof et al., 1999; Hodos et al., 1976). In the experiment, we tested rates of rotation that were faster and slower than the original training rate to investigate how it affected the discrimination. We were particularly interested in determining the rate of rotation producing the best discrimination and the threshold rate of rotation needed to minimally determine the direction of motion. Experiment 3A consisted of two phases testing different combinations of rotation rates ranging from 13° per sec to 222° per sec. These different rates were added to their daily sessions and reinforced in the same manner as baseline trials.

Experiment 3B varied the amount of apparent motion between frames of the video by changing the degree of angular change across successive views of the object. This proximity factor is important to producing smooth apparent motion in humans (Palmer, 1999). In the pigeons' baseline training the objects were rotated by 6° between successive frames of the video. To the human eye, the missing views between these orientations go unnoticed and produce smooth apparent motion. Here we tested how the pigeons would react to differences in this property of the videos. In this experiment, we held the rate of rotation constant at 105° per second and varied the amount of angular displacement between successive views of the objects across frames. The angular changes tested were 6, 12, 18, 24, 30, 36, 60, 72, 90, and 120° per frame. To hold rate of rotation constant, the time to view each frame was adjusted depending on the angular displacement tested. We were interested in determining how well the pigeons could detect the direction of rotation as the amount of angular displacement per view changed. To the human eye, the larger displacements tested here became increasingly more difficult to integrate into a coherently and smoothly rotating object as there was increasingly greater demands on the motion system to successfully establish the correspondences between different portions of the objects as they appeared across these disjoint views.

Method

Animals and Apparatus

The pigeons and the chamber were the same as in the first two experiments.

Procedure

Experiment 3A: Manipulation of rate. The experiment had two blocks of testing that examined combinations of different rates of object rotation. The first block lasted 24 sessions and tested the following rates: 43°, 51° 62°, 78°, 105°, 127°, 162°, and 222° per sec. The second block lasted 20 sessions and tested the following rates: 13°, 16° 20°, 29°, 38°, 43°, 51°, and 105° per sec. Each video was presented for a fixed period of 30-s, rather than 10 rotations as

done in the first two experiments, otherwise the experimental parameters were the same. Each session consisted of 128 trials (64 right/64 left). The tube and cone or the prism and torus were tested on alternative sessions. Within a session, each of the eight rates in a block was tested eight times (4 right/4 left) with each of the session's two objects. One positive trial for each rate was tested as a probe trial.

Experiment 3B: Angular change. This experiment tested the four objects over a range of changes in the degree of angular distant traveled between successive frames. Thus, rather than show a view every 6°, successive frames showed a greater angle traveled. The following angular distances were tested: 12°, 18°, 24°, 30°, 36°, 60°, 72°, 90°, and 120° between frames. This was done by not showing intermediate frames of the video. Because there were fewer frames per object rotation, the duration of the frames was adjusted to keep the overall rate of apparent rotation the same across the different conditions.

Initially, these different angular conditions were introduced in daily training sessions as probe trials. The tube and cone or the prism and torus were tested on alternative sessions. Sessions consisted of 80 baseline trials and 36 randomly intermixed nonreinforced probe trials (2 objects × 9 angles × right/left rotation). This probe testing was conducted for four sessions. Next, the angular distance conditions were differentially reinforced. This test lasted 20 sessions, with the tube and cone or the prism and torus tested on alternative sessions. Sessions consisted of 120 trials. Within these sessions, the 10 angles were tested six times (3 right/3 left) with each of the session's two objects. One positive trial for each rate was tested as a probe trial.

Results

Experiment 3A. Figure 5 shows mean DR as a function of the rate of object rotation combined across the two test blocks. Overall, the pigeons discriminated the direction of rotation at near or above baseline levels for all rates greater than 100° per sec. As rotation rate slowed down relative to the training value discrimination systematically declined for all objects. A repeated measures ANOVA (Rate × Object) using DR revealed significant main effects of rate, $F(12, 36) = 33.5$, and object, $F(3, 9) = 13.5$ and their interaction, $F(36, 108) = 3.4$. The latter interaction was because of object differences at the faster rates, with the torus consistently being the most poorly discriminated object for each pigeon regardless of rate. These object differences gradually converged at the slower rates of rotation.

In the next analysis we examined how the pigeons' discrimination changed over the presentation of an object within a trial. Besides revealing details of how behavior unfolds over time with dynamic stimulation, it also allowed us to investigate how much each object had rotated before it established discriminative control. For these analyses, we divided each stimulus presentation into a series of 200 millisecond bins and summed the number of pecks occurring in each bin over all trials. The results for seven representative rates from across the range of all tested values are displayed in Figure 6 (we examined all 13 rates, but these seven nicely represent the family of curves that emerged). To best compare peck rates, we normalized each curve relative to the maximum number of pecks recorded in any bin for a particular curve. We collapsed these data across the different objects, as each
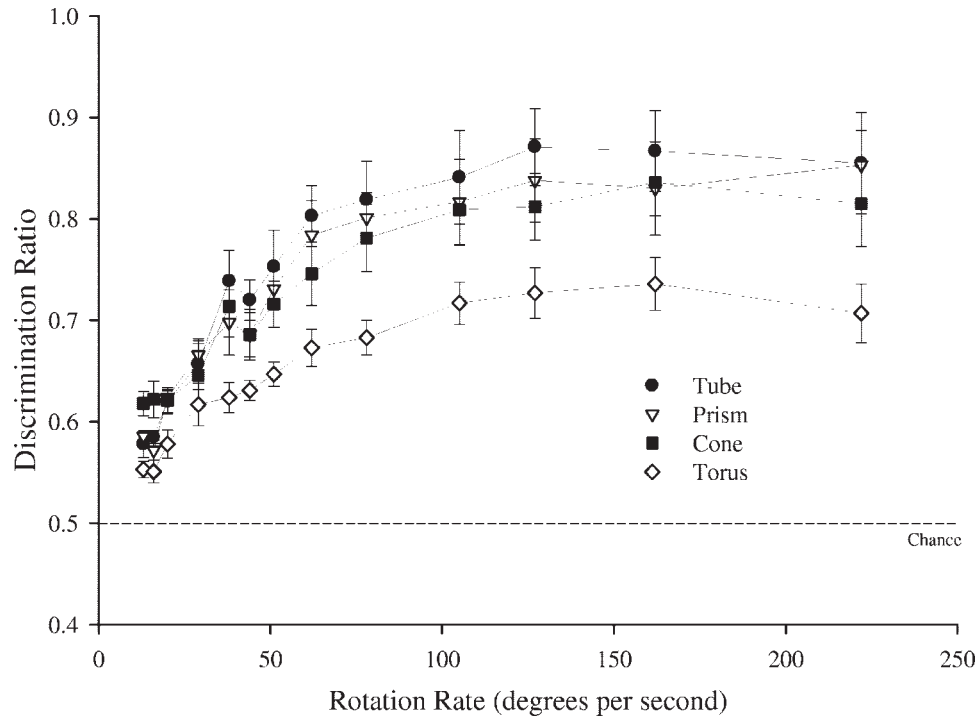
Figure 5. Mean discrimination ratio for the four objects rotating at different rates during Experiment 3A. The arrow points to 120° per second condition that the pigeons were trained with originally. The dashed line depicts chance discrimination. The error bars represent *SEM*.

object showed the same general form. We then smoothed each curve using the method of running means. The top curve shows the mean peck rate for the positive trials across all seven rates. These data were combined because there were no significant temporal differences in peck rate across rate for positive trials. These S− data show that the birds started each positive trial by pecking vigorously at the display and then gradually slowing down over the duration of the trial. The remaining seven curves show normalized peck rates for the S- trials at the different rates of rotation. Again, they start by vigorously pecking the video, but here they reduce their peck rate depending on the rate of rotation. For the faster rates of rotation, the pigeons rather dramatically decrease their peck rate after only two or three seconds of seeing the objects rotate on the screen. This rapid development of stimulus control suggests their motion system can detect the direction of motion quickly. As the rate of rotation slows, however, the pigeons take systematically longer to reduce their peck rates and in most cases never reach the same level of suppression by the end of the trial as observed with the higher rotation rates.

To see how much of the object had rotated before the birds showed good stimulus control we further examined these same data. For this analysis, we determined how far the objects had rotated for each rate until the pigeons showed a 65% drop in their normalized peck rate on the negative trials. The results of this analysis for each individual bird are in Figure 7. This figure shows how far these objects had rotated before the emergence of this criterion level of discrimination for the 13 rates tested. Three of the birds were quite similar in their response. Over the vast range of rates over which the object moved slowly to moderately, they

seemed to need a relatively constant percentage of an object's rotation to show the same level of discrimination. This can be seen in the basically flat functions toward the left side of Figure 7. The exceptions for these three birds occurred at the fastest rates toward the right side of the figure. We think this is an artifact of how quickly the objects rotated at these rates in concert with the speed at which the pigeons could suppress pecking to the display. It takes time for the birds to slow down their pecking and while doing so these objects continue to rotate quickly on the display. This likely resulted in an inflated value relative to what the pigeons actually required to begin suppressing their responses and reflected in the upward turn to the curves at the fastest rates. The fourth bird showed a different form of constancy. For this pigeon there was a much greater amount of rotation occurring before criterion was met for most values. Unlike the other birds, its curve suggests it needed less rotation of the object as rotation rate slowed. This analysis seems to suggest that each bird needed to see a fairly characteristic amount of motion from each object regardless of rate to reach the same level of discrimination.

Experiment 3B. Shown in Figure 8 is mean DR as a function of the differences in angular perspective for the different objects tested during the training portion of Experiment 3B. Examination of the first four sessions where these conditions were tested as probe trials revealed no substantive differences from the training phase. These four sessions are not further considered. Overall, discrimination systematically declined as the degree of rotation traveled between successive views increased. When successive object views moved greater than 40°, the pigeons had a difficult time determining an objects' direction of motion as their discrim-
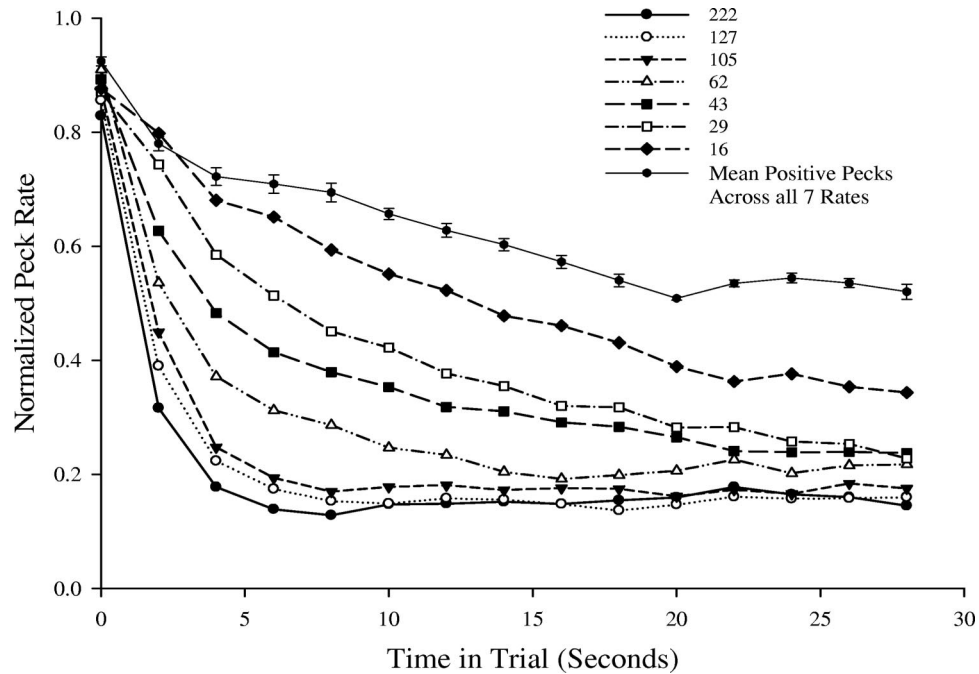
Figure 6. Mean normalized peck rate for positive and negative rotations within a single trial during Experiment 3A. The top solid lines show mean normalized peck rate on positive trials averaged across all rates as there were negligible differences between conditions. The other lines show performance with negative stimuli over a broad range of 7 of the 13 rates tested and which did differ as a function of rate. The rates not graphed fell to the ones shown. Each data point represents successive number of pecks as separated into 200 millisecond bins during a video's presentation and normalized to the highest count within each curve.

ination approached chance levels. A repeated measures ANOVA (Angle × Object × 10-session Block) on DR revealed a significant main effect for angular change, $F(9, 27) = 33.8$, block, $F(1, 3) = 12.9$, and object, $F(3, 9) = 11.2$. The effect of block was because of slight decline in overall performance between the first and second half of the experiment. The main effect of object was again because of the poorer performance with the torus. This ANOVA also revealed a significant Angle × Object interaction, $F(27, 81) = 2.9$. This interaction was because of the same general convergence seen in Experiment 3, although performance with the prism did appear to decline more quickly in comparison to the cone and tube. Further, all four birds showed slightly greater performance with the cone at the largest angular transformations. No other interactions were significant.

Discussion

Experiment 3 established three important results. First, rate of rotation influenced how quickly the pigeons can determine an object's direction of rotation. Faster is better. Second, the amount of apparent rotation traveled between successive views of a dynamic object strongly influenced this directional discrimination. Smaller increments are better. Third, the birds appeared to need a relatively constant amount of rotation to support an equivalent level of discrimination across the different rates.

Together, these results are consistent with the hypothesis that the pigeons are deriving and discriminating the directional motion as embodied by these objects. As the rate of rotation slowed down, the

pigeons had a greater difficulty in detecting this motion. While the general form of this decline did not vary between the objects, the different objects did support different levels of discrimination at the higher rotation rates. Overall, the tube and cone seemed to support the most robust discrimination, followed closely by the prism, and lastly by the torus, which consistently supported the poorest discrimination. Comparing our overall rate results with other experiments that varied the velocity of other types of motions (Bischof et al., 1999; Hodos et al., 1976; Mulvanny, 1978), the current results don't suggest that determining the direction of rotation is particularly harder than other motions. For example, Bischof et al. (1999) examined the velocity required for the discrimination of coherent versus randomly moving displays of dots. They found that pigeons had a higher threshold than humans, and that required a velocity of 28.3 deg/sec to reach a 70% accuracy threshold. Although the response measures are different, rate values around this point did seem critical in the present experiment. Performance was poorer or declined with slower rates around this point and dramatically improved for much faster rates.

The manipulation of angular perspective is also consistent with a motion-based interpretation of the discrimination. As the angular difference between successive frames grew larger, the videos become progressively jumpier and incoherent, which in turn likely disrupted or interfered with the accurate perception of apparent directional rotation. It is therefore reasonable to believe that the pigeons' motion system is combining the resulting transformations of the objects between successive frames to produce a smooth
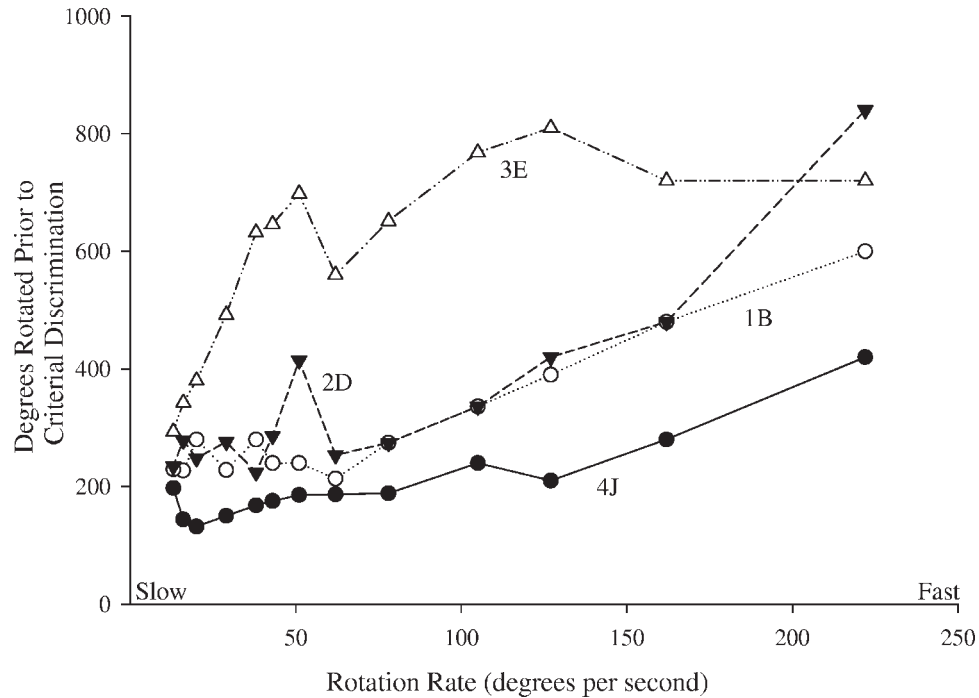
Figure 7. Mean object rotation observed for the 13 rates for each bird before reaching the criterial discrimination of a 65% reduction in peck rate in Experiment 3A.

perception of motion by looking for proximal correspondences between parts of the object (Attneave & Block, 1974; Dawson, 1991).

These latter results are consistent with the coherent superiority effect reported by Cook et al. (2001) and Cook and Roberts (2007). In both of those experiments, pigeons were required to discriminate different types of motion (around vs. through the opening of an object). When coherent versus randomized presentations of the videos were then tested, it was found that the coherent video presentation condition always supported better performance even when equated for experience. When combined with the results of Experiment 3B, the current results are consistent with the general notion that, similar to humans, pigeons experience a smoothly transforming world of objects.

Experiment 4: Analysis of Critical Features

Experiment 4 used an occlusion technique to examine what portions of the objects and their motion were critical to recognizing the direction of rotation. Over three phases, different portions of the tube object were occluded by a gray field placed over the object. This occluder hid a portion of the object and its resulting motion from view to determine whether the hidden portion was critical or not to successful discrimination.

In Experiment 4A, a vertically or horizontally oriented gray field was placed over 50% of the object (see top row of Figure 9). The vertical occluder allowed the left or right end of the object to be seen as it rotated. The horizontal occluder allowed the full extent of the object to be viewed, but restricted it to the top or bottom halves. Besides this occlusion condition, two other conditions were included. These were inspired by recent experiments looking at the effects of occlusion on static geon recognition

(DiPietro, Wasserman, & Young, 2002). Although comparisons to DiPeitro et al.'s experiments will be developed later, these additional conditions included a test in which the gray field was also placed around the object or placed behind the object, but in the same spatial location as in the occlusion condition. These two conditions allow further examination of the effect of the introduced "occluder," as the entire object remained visible in these two conditions. This is of interest because DiPeitro et al. found that brick-like textures placed behind their geons were as disruptive as ones placed in front of the object and which hid a portion of its features. Although the origins of the disruption in this latter behind-the-object interference effect are poorly understood, we decided to include these conditions because they remain logical controls to judge the effects of the occlusion condition and it allowed us the opportunity to judge how object motion might modulate this surprising effect.

In Experiment 4B, we varied the vertical and horizontal percentage of the object occluded from 0% to 100%. This test was to determine how much of the object was required to perform the discrimination. In Experiment 4C, the occluder was vertically located over the central portion of the object or located peripherally to each side of the object (see bottom row of Figure 9). This test was designed to determine how the ends of the object were used and whether their central or peripheral locations were of any greater importance in supporting the discrimination.

Method

Animals and Apparatus

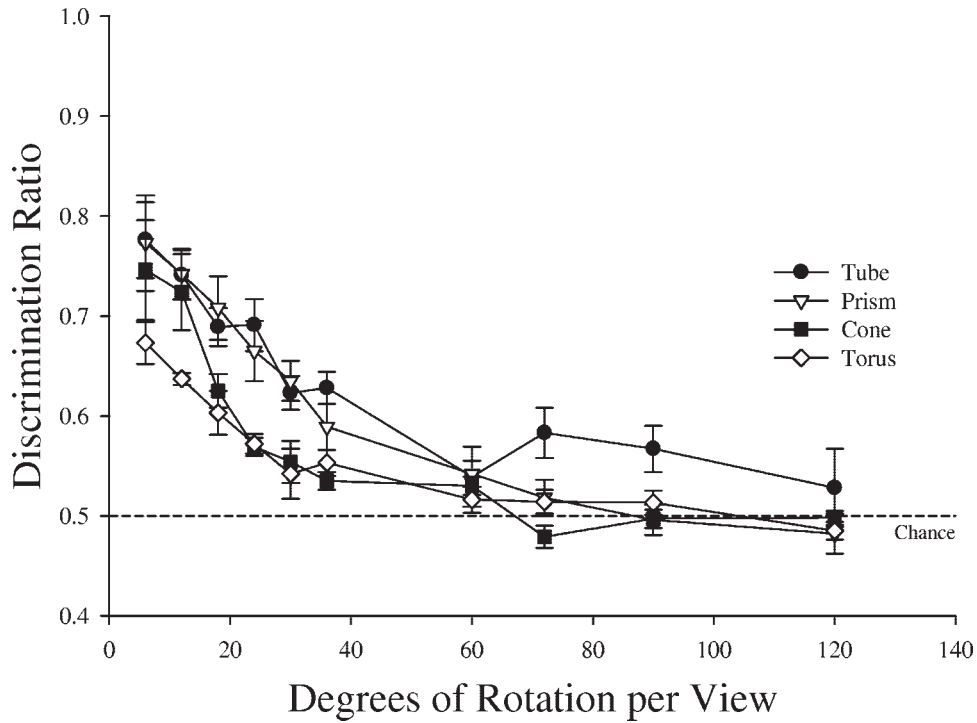The pigeons and the chamber were the same as in earlier experiments.

Figure 8. Mean discrimination ratios for all objects as a function of angular separation between successive views in Experiment 3B. The horizontal dashed line depicts chance discrimination. The error bars represent *SEM*.

Procedure

Experiment 4A: Vertical/horizontal occlusion. Three different test conditions were examined. For all three conditions, only the tube object was tested. In each condition, a solid gray rectangular field was rendered into the video. In the *occluding* condition, the gray field (10 × 6.75 cm) was vertically placed to cover the entire left or right of the video or horizontally (5 × 13.5 cm) placed to cover the entire top or bottom of the video (see leftmost example in Figure 9). In the *behind* condition, the same field was present in the same locations, but was rendered to appear to be behind the

object (centermost example). In the *around* condition, the same gray field and locations were added, but with a small notch (5 × 3.8 cm − right/left, 2.5 × 8 cm − upper/lower) cm removed from around the object (rightmost example).

Daily sessions consisted of 108 trials. Ninety-six were baseline trials testing all four objects with equal numbers of both directions. The remaining 12 trials tested these three conditions (4 trials each—right/left rotation × top/bottom placement or right/left placement) as nonreinforced probe trials and these were randomly inserted among the baseline trials. Vertical or horizontal place-
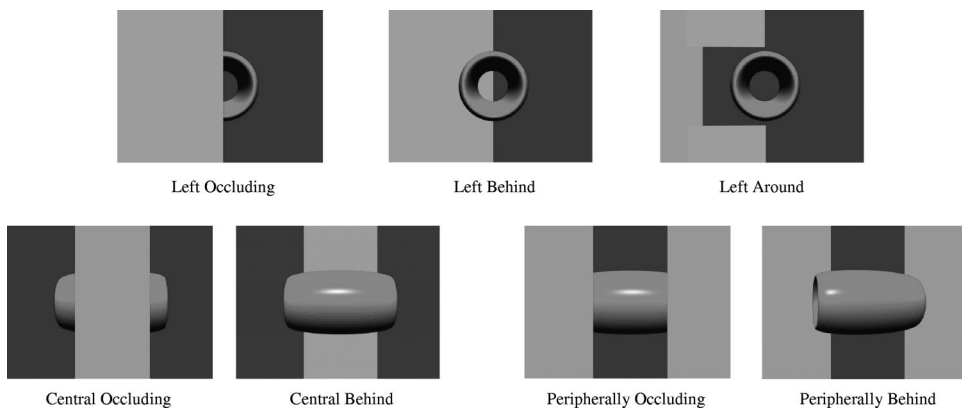

Figure 9. Example frames from conditions tested in Experiment 4A and 4C. Row 1: Conditions from a subset of Experiment 4 A. The objects were occluded from below, above, and the right and left. Those from the left behind, occluding, and around condition are shown. Row 2: Conditions from Experiment 4 C. The occluder was tested in both central and peripheral positions and was either behind or in front of the rotating tube.

ments were tested in alternate sessions. Each pigeon received 12 total test sessions. Eleven baseline sessions occurred between Test Sessions 8 and 9.

Around training. After the above test, the around condition was added to their daily training sessions and pecks to any positive stimuli in this condition were reinforced on a VI-10 schedule. This around training consisted of 16 around trials (8 right/8 left) randomly added to 80 baseline trials. DiPeitro et al., (2002) did the same type of training with their pigeons to examine its affect on their occluding and behind conditions. After the pigeons acquired the around condition to a satisfactory degree (range: 8–12 sessions), the first test described above was conducted again, for a total of four sessions. All conditions were again tested as was done in the Pretraining part of the experiment. Each test condition was administered twice for a total of four sessions in this Posttraining test.

Experiment 4B: Percent occlusion. Experiment 4B varied the percentage of object occluded with the vertical and horizontal oriented fields tested in Experiment 4A. Either 0%, 20%, 40%, 60%, 80%, or 100% of the tube object was covered at the 0° orientation (the end-on view). Daily sessions consisted of 104 trials. Eighty baseline trials testing all four objects were given. The remaining 24 trials tested only the occlusion condition (6 values × right/left rotation × top/bottom or right/left placement) with the tube object as nonreinforced probe trials randomly inserted among the baseline trials. Vertical or horizontal placements were tested in alternate sessions. Each pigeon received eight total sessions.

Experiment 4C: Central and peripheral occlusion. Experiment 4C tested conditions where the gray field was centrally or peripherally located and either occluded the tube object or was placed behind it (see bottom row of Figure 9). During central placements, a 4.5 cm wide gray field was vertically placed down the center of the video. In the *center-occluding* condition it was rendered in front of the tube object and in the *center-behind* condition it was rendered to appear behind the tube object. During peripheral condition, two 10 × 4.5 cm wide gray fields were vertically placed down both the right and left of the video. In the *peripheral-occluding* condition it was rendered in front of the tube and in the *peripheral-behind* condition it was rendered to appear behind the tube. Daily sessions consisted of 96 trials. Eighty baseline trials tested all four objects. The remaining 16 trials tested equal numbers of the center-occluding, center-behind, peripheral occluding, and peripheral behind conditions as nonreinforced probe trials. These were randomly inserted among the baseline trials. Each pigeon received eight sessions.

Results

Experiment 4A: Vertical/horizontal occlusion. Displayed in the top panel of Figure 10 are the results for the pre- and post-around training tests for the around, behind and occlusion test conditions and the baseline condition (tube object only). During this first test before around training the pigeons showed a commonly reduced discrimination in the three test conditions relative to tube-only baseline, $F(3, 9) = 9.2$. A repeated measures ANOVA comparing the three test conditions revealed no significant differences in performance. Following separate training with the around condition, performance in the around condition improved (DR = .81) relative to the first test (DR = .67). This was confirmed by a
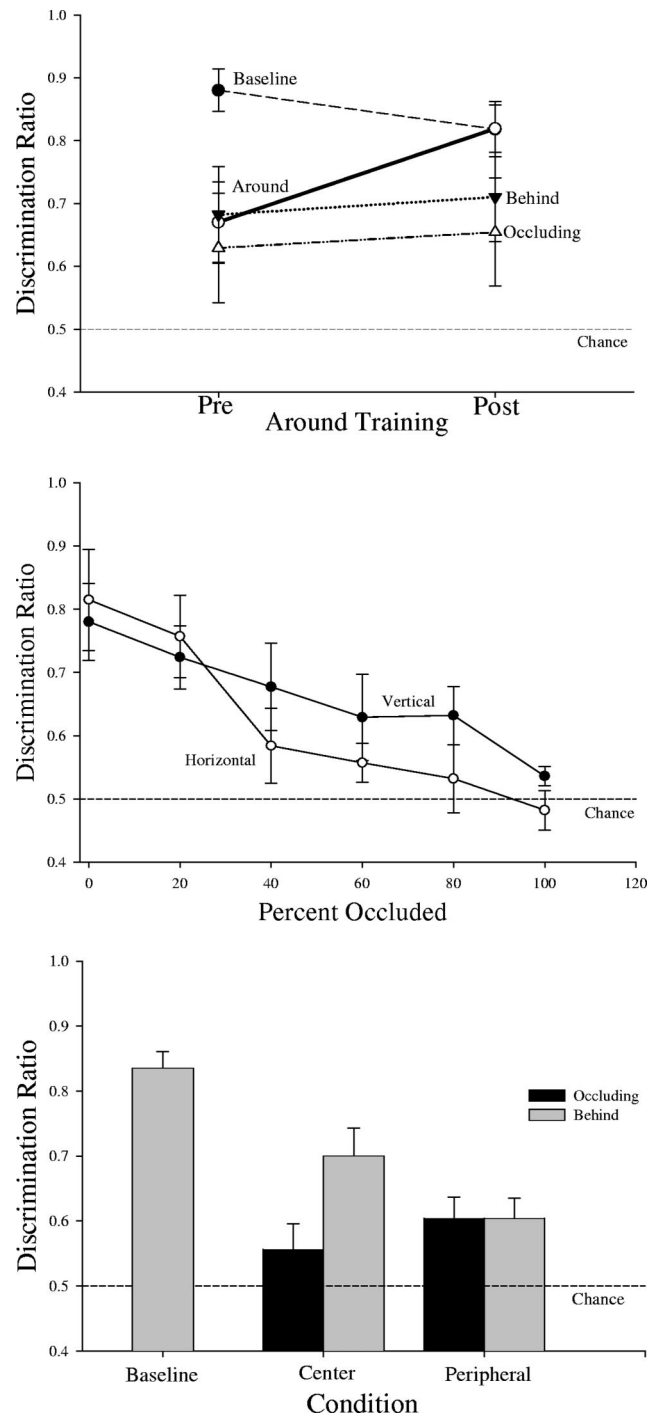

Figure 10. A. Results for Experiments 4A, 4B, and 4C. The top panel shows mean discrimination ratio for all three test conditions from before and after separate reinforced training with the around condition in Experiment 4A. The middle panel shows mean discrimination ratio as a function of the amount of the object occluded vertically and horizontally in Experiment 4B. The bottom panel shows mean discrimination ratio for centrally and peripherally located test conditions in Experiment 4C. The black bars are the occluding conditions, whereas the gray bars are the behind conditions. The horizontal dashed lines depict chance discrimination. The error bars represent *SEM*.

significant Pre/Post Test × Condition interaction in an ANOVA comparing the two tests for the around condition relative to the baseline condition, $F(1, 3) = 38.3$. Despite this increased performance with the around condition, discrimination in the behind and occluding conditions remained degraded relative to baseline. Pairwise comparisons among just the three test conditions across the pre- and postaround training revealed significant Pre/Post Test × Condition interactions between the around and behind conditions, $F(1, 3) = 9.4$, and between the around and occluding conditions, $F(1, 3) = 19.8$, reflecting the relative increase in the around condition between the two tests. An identical comparison of the behind and occluding conditions revealed no similar interaction, but did reveal a significant main effect of condition, $F(1, 3) = 12.2$, reflecting the consistently better discrimination in the behind condition (DR = .7) relative to the occluding condition (DR = .64) across the tests.

Experiment 4B: Percent occlusion. Displayed in the middle panel of Figure 10 are the results for Experiment 4B. This test revealed that as more of the object was covered, discrimination declined. For three of the four birds, it did so more for occluders in the vertical orientation than in the horizontal orientation. A repeated measures ANOVA (Percent × Orientation × Session) using DR that included all four birds confirmed the systematic decrease with increasingly greater coverage, $F(5, 15) = 12.8$. This analysis found no main effect or interaction with orientation. This was because of the fact that one pigeon (#4J) showed no difference as a function of orientation, just a steady decline with increased coverage. Reconducting the analysis with just the three pigeons who did show the pattern displayed in Figure 10 confirmed the significant presence of an orientation effect for them, $F(1, 2) = 21.3$.

Experiment 4C: Central and peripheral occlusion. Displayed in the bottom panel of Figure 10 are the results for Experiment 4C. Compared to baseline (DR = .83) and the around condition (DR = .81), both the behind (DR = .65) and occluding conditions (DR = .58) showed reduced discrimination. A repeated measures ANOVA (Central vs. Peripheral × Behind vs. Occluding × Sessions) revealed a marginal interaction between the location of the field and whether it was in front or behind the object, $F(1, 3) = 6.2, p = .088$), with the effects of occlusion being stronger when centrally located relative to the periphery. The birds showed greater individual differences in this study than in any other test. For instance, the interaction prominent in Figure 10 was strong in two birds, but markedly reduced or absent in the two other birds, accounting for the marginal p value. For these latter two birds, the presence of the gray field, whether behind the object or in front of the object generally reduced performance regardless of spatial position.

Discussion

These stimulus analytic tests revealed the following findings. Introduction of the gray field initially reduced discrimination regardless of its location, whether around, behind or in front of the rotating object. Following subsequent training with the around condition, the difference between baseline and the around condition was eliminated, but a continued interference effect remained for both the occluding and behind test conditions, although the occluding condition produced reliably poorer performance than the behind condition. Further, performance declined as greater portions of the object were covered, with a slightly greater reduction for horizontally oriented occlusion. Finally, both the central and peripheral portions of the object seemed involved with the discrimination as occluding either portion reduced discrimination.

When considered in their entirety, the pattern of these results suggests that a majority of the object's shape was capable of transmitting information about rotational direction. In general, the greater proportion of the object that was visible, the better the pigeons' performance. Reduced, but above chance, discriminations were still consistently observed when more limited or smaller parts of the object were visible. It didn't seem to matter much whether these parts were centrally or peripherally located. For the majority of the birds, seeing the longer and horizontal extent of the tube seemed to be more critical than seeing the smaller end-on view.

Besides revealing what part of the objects were important for performing the rotational discrimination, the present results also add information to the recent and somewhat baffling effects of occlusion reported by DiPeitro et al. (2002). Using four static geons, DiPeitro et al. trained pigeons in an object naming task. After training, they tested the partial occlusion effects of a colored textured brick-like surface covering different parts of the objects. Their testing sessions involved four conditions: an erased, occluded, notched, and on-top condition (the latter three being procedurally equivalent to our occluding, around and behind conditions). Similar to our findings, their initial test revealed poorer choice performance with this additional surface whether the objects were occluded or not. Apparently the introduction of a partial occluder to a static or moving object causes a generalized recognition problem regardless of whether the occluder visibly hides features (the occlusion conditions) or not (the on-top or behind conditions). The latter effect appears to be a form of interference as the features should be visible to the birds. Our results in which the occluding condition was reliably worse than behind suggests there may be two separate effects involved, one tied to the interference effect of adding a new background and a second one tied to the actual elimination of critical features by the occluder. After separate training with the on-top condition (our behind condition), DiPietro et al. found their pigeons generally improved in their ability to recognize partially occluded objects. In contrast to their finding, we found no such facilitation after our separate around training. This difference in the effects of training, suggests that whatever benefits accrued in their study it was not simply because of experience with the occluder, but specifically related to having to process the object in its superimposed position on the occluder. Finally, our results speak to one other aspect of this interesting and still unexplained phenomenon. DiPietro et al. suggested that one source of this generalized interference effect may be related to the difficulty of separating the foreground object from its new background. Although possible because of their use of static pictures, this hypothesis seems less viable given our dynamically rotating objects. These dynamic cues should have helped the birds readily segregate our rotating object from the gray background. This apparently didn't help eliminate the DiPietro et al. interference effect.

General Discussion

These experiments indicate that pigeons can readily discriminate object-based rotational motion under conditions where non-

motion related spatial cues have been eliminated. Experiment 1 revealed the ease of acquiring this type of directional motion discrimination and its dependence on sequential coherency. Experiment 2 found no generalized transfer of this rotational discrimination to other novel objects, suggesting that object-specific motion cues mediated the discrimination. Experiment 3 revealed that faster rotation rates and closely related successive views of the objects supported the best performance. It also suggested that the pigeons may have viewed a relatively constant amount of the rotating object regardless of rate to reach an equivalent level of discrimination. Finally, the occlusion experiments suggested that different portions of the tube object were all capable of mediating some degree of the discrimination.

Given these results, several important questions require discussion. The key questions surround how the pigeons perceived and represented the different moving objects in the present task. The first concentrates on the interpretation of the sequential integration of information required by current discrimination. The second focuses on the nature of the visual cues derived from the mediating object used to instantiate this motion. Each is considered in turn, followed by a representational hypothesis that attempts to integrate these questions.

The original goal of this study was to create a better motion discrimination task that eliminated simple spatial cues as a potential source for discrimination (Cook et al., 2001; Emmerton, 1986; Goto et al., 2002). Because of the use of directional rotation, the current results would seem to offer the strongest evidence yet that object-based motion discriminations can be readily learned by pigeons without confounding spatial cues. It certainly requires that the pigeons be sensitive to the order in which the same sequential information is presented. Thus, in combination with previous motion studies that did not involve object-based motion but similarly controlled for such spatial factors (Bischof et al., 1999; Goto & Lea, 2003), these results indicate that motion is a salient cue of its own for pigeons. The reactions of the pigeons to changes in rotation rate and angular separation are also all consistent with the idea that they were interpreting the videos as depicting something moving. That birds would be sensitive to object motion makes extremely good ecological sense given their natural history and primary mode of locomotion.

An alternative hypothesis is that the birds were simply learning to respond to different sequences of images in which derived motion per se plays no role. Such a sequential hypothesis would handle the rate and angular separation results by suggesting that both resulted from a generalization decrement from a learned sequence of images rather than any successive transformation of them into perceived motion. Such a sequential hypothesis is difficult to discriminate from a motion hypothesis since in essence both are about the reaction to sequential information. One area where they differ is that the sequential hypothesis really says nothing about the order of the sequence or the nature of the content imaged. As a result, any pictorial information presented in any order at comparable rates should make a learnable sequence. Recent results from our lab using a similar object-based discrimination, however, have found that even when experience was equated, smoothly transforming videos of coherently moving objects support faster learning and better performance than arbitrarily randomized sequences of the same information (Cook & Roberts, 2007). Of course, a sequential account could be modified to prefer

orders of similar looking images, but then this essentially becomes the motion account by a different name. Although there is no doubt that animals can learn sequences of separated images that do not portray motion (Terrace, 2001), in the present case the structure and organization of the video's transforming content, their fast rate of presentation, and the pigeons' overall reactions to our different manipulations, especially in Experiment 3, each suggests that the pigeons were experiencing content that was recognized as motion. Consistent with this motion account are the numerous physiological studies that have identified neurons in the pigeon visual system that would be ideal for performing exactly the kind of motion-based perception required of the present task (Frost, 1978; Frost, Scilley, & Wong, 1981; Frost, Wylie, & Wang, 1990).

Given this motion perception, the question arises as to what was perceived as being in motion. One possibility is that pigeons perceived a 3D rendered object rotating in depth. A second possibility is that they were reacting to 2D motion properties in the videos that were correlated with direction of rotation, such as the leftward or rightward sweep of an object's end. Because the experiment was focused on motion perception, rather than the nature of object dimensionality, our evidence speaks less strongly to this issue. We recently established that given strong visual support pigeons can detect the 3D depth relations of objects in pictures using relative size, occlusion and relative density as monocular cues (Cavoto & Cook, 2006). In the current task, the stimuli were specifically designed to capture these properties with the strong use of supporting cues that would promote seeing these videos as objects rotating in depth. Nevertheless, it is possible that the birds could have been responding to the right and left movement of 2D cues associated with each object. It is worth noting on this point that these rotating stimuli do contain an interesting ambiguity. As the front part of an object goes rightward its back portion is going leftward. Because a 2D hypothesis cannot use terms like front and back or foreground and background, this leaves portions of the same object moving in a way that contains conflicting cues about what to do. A 3D hypothesis has no such dilemma. One solution for the 2D hypothesis would be to posit that the features in the front of the object are larger and thus dominate performance. Although not decisive on this point, we think the occlusion results are interesting in suggesting that no one particular part of the display was necessary. This seems more consistent with the idea that the birds were seeing the objects as global units rather than 2D fragments.

Another possibility to be considered is that our pigeons were not processing object-based motion, but instead were simply responding to portions of their visual field moving right or left based on optic flow. We do not think this is the case for several reasons. First, the receptive fields of the cells used to detect optic flow are large and do not respond to movement in small local regions of visual space. Thus, it is unlikely given the size of our objects, that our motion would have driven such cells especially given the static background of the larger screen. Furthermore, these cells are also most sensitive to motion velocities that are much slower than those used here (Morgan & Frost, 1981). Second, if the birds were simply detecting directional optic flow, one would have expected this discrimination to readily transfer to new "objects" because the same directional flow and properties would have been present in each. Behaviorally this was not the case, as each novel object in Experiment 2 seemed to be learned independently, indicating that

the motion cues involved were specific to the perception of each object.

Two classic views of object recognition have received extensive investigation. The structural view has suggested that objects are recognized based on invariant descriptions of the relations among an object's parts or primitives (Biederman, 1987; Marr, 1982). The exemplar view has suggested that objects are recognized based on their similarity to a stored collection of specific views or snapshots of the experienced objects (Edelman & Bülthoff, 1992; Tarr & Pinker, 1989). These theories have generally not specified how motion might be incorporated into these object representations. It has become increasingly recognized in humans, however, that motion is also involved in object recognition (Hill & Johnston, 2001; Matthews, Benjamin, & Osborne, 2007; Newell, Wallraven, & Huber, 2004; Vuong & Tarr, 2004). In these kinds of studies, the addition of characteristic motions to different objects or scenes improves recognition. Such studies suggest that motion and shape are integrated in some manner into a unified object representation. We believe the current results suggest the same may be true for pigeons.

Our hypothesis is that the pigeons represented and recognized our dynamic stimuli as integrated spatiotemporal sequences of the objects dynamically transforming over time. Namely, the pigeons may have learned a set of temporally extended exemplars that consist of separate memorized sequences of how each object appeared and changed as it rotated around its axis. Thus, these temporally extended representations share more properties in common with a short video than an image or snapshot. Thus, we imagine they can capture both the motion-based, 3D attributes of objects that have been repeatedly presented or sequences of 2D images. This hypothesis accounts for the lack of motion transfer between the different objects in Experiment 2 by the fact that each object generates its own independent representation of its transformation over time. These probably have little or no overlap in similarity with the other objects' changes, preventing any generalized recognition of rotation. Perhaps as found with picture categorization, more exemplars might have facilitated such motion categorization. That these object representations were extended in time is suggested by the fact that the birds could quickly recognize the rotation/object within a few hundred milliseconds regardless of starting orientation. This was observed in Experiment 1 and further confirmed by the rapid suppressions in peck rate documented in Experiment 3. The extended nature of the representation is also suggested perhaps by the result that the birds tended to reach the same level of discrimination after seeing approximately the same amount of the object. Our results are not the only ones that have suggested that both object and motion information are stored about dynamic stimuli. Spetch, Friedman, and Vuong (2006) have reported in pigeons that manipulations of characteristic motions with different objects can influence recognition performance, at least for decomposable objects. These sundry pieces of evidence suggest that motion and object information might be simultaneously encoded and tightly linked in memory.

The idea that motion and shape information are integrated into dynamic temporally extended exemplars is a novel and attractive hypothesis. Unlike other exemplar theories (Carter & Werner, 1978; Chase & Heinemann, 2001; Wright, 1997) suggested for pigeons, it suggests that long-term memory representations are not simple collections of static viewpoints or chained groups of sep-

arate associations. Instead, it suggests that memories have a temporal component that can encode sequences or sets of events and actions as single units of information. This would nicely allow motion and the associated object engaged in the motion to be stored together in memory and create the natural substrate for remembering events and the behaviors of other animals and objects as integrated wholes. This latter organization for representations is much more in line with the dynamic structure of an event-filled world than static snapshots or structural description. It is only our historical reliance on testing static stimuli that has tended to make people think that traces are simple and image-based. A temporally extended view of the representational unit transforms how we think about memory and how animals might encode sequences of complex events as unified representations. Besides permitting a new way to think about how dynamic sequential information is encoded, it raises a new group of problems to examine. If memories are extended in time, much like a video, what kind of events or signals start and stop the encoding of such temporal memory units. Clearly, everything is not encoded on a continuous basis, so certain signals and events must dictate or permit the temporal stream of experience to be broken up into these units. Could there be some basic unit of time that characteristically captures a set of actions or scene? One possibility is that species might differ in how they segregate these "temporal" divisions of the world or how long they can capture a particular moment or set of events. It is easy, for example, to remember several entire scenes from a movie, but generally not the complete film. The characteristic length of scenes may reflect something basic about how human memory integrates and divides streams of events. Such event and memory horizons may be shorter for pigeons, for example. Finally, if memories of representations are extended in time, can they be accessed only from the beginning of each complete unit or can they support random access to any point in the memorized sequence? Related to this idea is the possibility that some of the effects in Experiment 3 may represent memory failures in which the altered video stimuli did not well match the representation of object motion already experienced. Future research should begin to concentrate on such possibilities as increasingly more studies with dynamic stimuli begin to challenge the theoretical notions based on static displays.

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