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*Research Article*

# The Contribution of Monocular Depth Cues to Scene Perception by Pigeons

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ABSTRACT—*The contributions of different monocular depth cues to performance of a scene perception task were investigated in 4 pigeons. They discriminated the sequential depth ordering of three geometric objects in computer-rendered scenes. The orderings of these objects were specified by the combined presence or absence of the pictorial cues of relative density, occlusion, and relative size. In Phase 1, the pigeons learned the task as a direct function of the number of cues present. The three monocular cues contributed equally to the discrimination. Phase 2 established that differential shading on the objects provided an additional discriminative cue. These results suggest that the pigeon visual system is sensitive to many of the same monocular depth cues that are known to be used by humans. The theoretical implications for a comparative psychology of picture processing are considered.*

Large moving animals, such as birds or mammals, need an accurate perception of the 3-D world and the layout of its objects. Given the efficiency of the human visual system's computation of such relations, the complexities of reconstructing 3-D depth relations from a 2-D retinal image are easily overlooked. Although space and depth perception have been investigated in humans and nonhuman primates, they are still poorly understood in birds—despite their obvious survival value when flying amid the branches of a forest, nesting on cliffs, or avoiding man-made obstacles. Birds of prey have frontally placed eyes that permit the use of binocular depth cues, but most birds have laterally placed eyes with only limited degrees of binocular overlap and eye movement (McFadden, 1993). Thus, monocular depth cues are far more likely to be important for these birds. The current experiments examined how pigeons (*Columba livia*) discriminated the organization of object-based, 3-D pictorial scenes.

In addition to examining depth perception in a nonmammalian system, these experiments were intended to contribute to the ongoing debate over animal picture perception (Bovet & Vauclair, 2000; Cerella, 1980; Fagot, 2000; Miller, 1973). Since the research of Herrnstein and Loveland (1964), pictures have been increasingly used to investigate perceptual and cognitive issues in animals (Cook, 2001). Nevertheless, what animals understand about pictures is still not well understood. This is reflected in researchers' inability to predict how any animal will react to a picture, short of empirically testing it. A number of studies have suggested that pictures have some correspondence to or contain key features of the real world, because animals often show appropriate spontaneous or learned reactions to pictures (see Bovet & Vauclair, 2000). It is often difficult, however, to tell whether only a few features are mediating the observed equivalence (when it occurs) or whether the animal is experiencing a more "complete" representation of the picture's content (Fagot, Martin-Malivel, & Depy, 1999). Other research has indicated that pictures sometimes produce responses that do not correspond to their veridical perception (e.g., Aust & Huber, 2001; Cerella, 1990; D'Amato & Van Sant, 1988; Jitsumori, 1991; Ryan & Lea, 1994). For instance, Aust and Huber (2001) found that pigeons easily learn a human/nonhuman categorization, but tests revealed that this achievement does not require the pictures to be correctly organized—the pigeons continued to discriminate the pictures even after they had been scrambled into smaller fragments.

Previous studies have also painted a mixed picture regarding the contribution of monocular cues to avian picture perception. Cerella (1977, 1990) found that pigeons failed to discriminate

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perspective in line drawings. In contrast, pigeons have been shown to be sensitive to the Ponzo illusion, which is presumably based on such perspective processing (Fujita, Blough, & Blough, 1991, 1993). Several studies have examined whether pigeons are sensitive to the monocular cue of occlusion. These studies have looked for evidence of amodal completion behind an occluder. Although there is some positive evidence of such completion in some types of birds (Forkman, 1998; Forkman & Vallortigara, 1999; Lea, Slater, & Ryan, 1996; Regolin & Vallortigara, 1995), pigeons have consistently not shown this effect (Cerella, 1980; Fujita, 2001; Fujita & Ushitani, 2005; Sekuler, Lee, & Shettleworth, 1996; Ushitani & Fujita, 2005; Watanabe & Furuya, 1997). Of course, any failure to amodally complete hidden contours does not necessarily mean that occlusion is not an important cue for depth in other settings. In the most detailed study so far, Reid and Spetch (1998) examined if pigeons could discriminate pictures of intact objects from pictures of objects in which the depth cues of shading and perspective had been altered. They found that both cues could serve as the basis for such discrimination using both familiar and novel objects. Finally, a subset of Cook and Katz's (1999) experiments examined if pigeons are sensitive to the recovery of 3-D structure from motion. They found a weak structure-from-motion effect for a majority of the birds, which suggests that object recovery might be possible from motion in the absence of other depth cues.

Using a new approach, the current experiments examined whether pigeons are able to extract the 3-D layout of objects as specified by different combinations of monocular pictorial cues. We used computer graphics to create controlled, semirealistic scenes, and the discrimination required the pigeons to "describe" the scenes' contents by responding differentially to the arrangement of the pictured objects. The task was to discriminate the spatial ordering of three different objects as determined by the presence or absence of three classic monocular cues: occlusion, relative density, and relative size. These are three of the most powerful cues for humans (Cutting, 1997; Cutting & Vishton, 1995) and would likely be the most salient for birds in interacting with their spatial environment. The task required a go/no-go discrimination: The pigeons had to learn to peck a stimulus showing the correct sequence of objects in depth (ABC) and not to peck stimuli showing the remaining five possible configurations of the same objects (e.g., CBA or BAC). In the displays, each of the pictorial depth cues was rendered independently with respect to the other cues, and each possible combination of the cues was tested. Examples of the resulting one-cue, two-cue, three-cue, and control displays appear in Figure 1. Additional manipulations were specifically included to prevent other cues, such as height in field, from controlling behavior. We expected that if the different cues promoted the perception of depth in these scenes, the discrimination would be learned most readily in the three-cue condition, followed by the two-cue, one-cue, and control conditions, respectively.

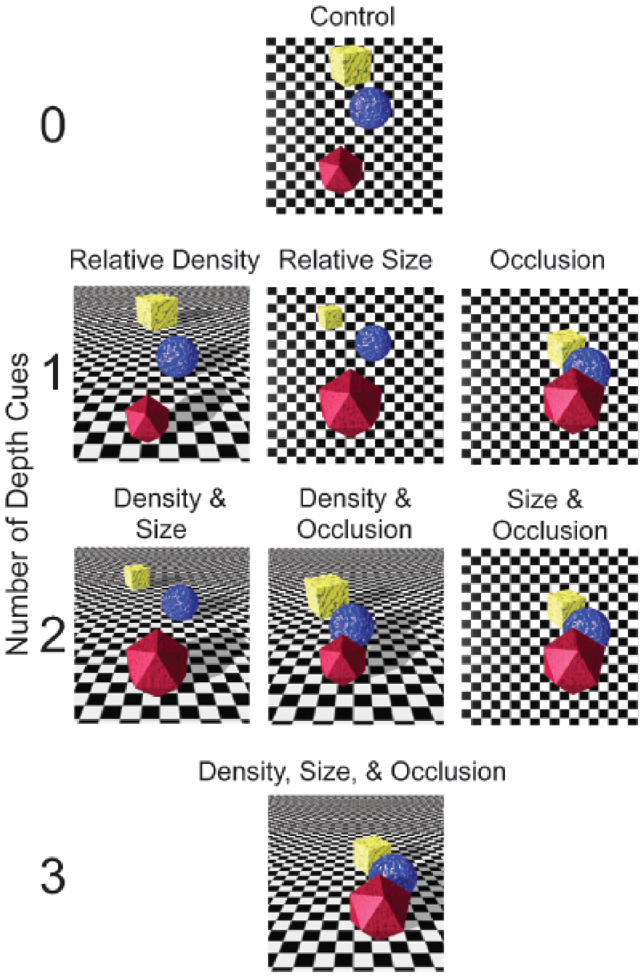

**Fig. 1.** Examples of the displays in Phase 1. Each illustrates a different combination of the monocular cues tested. In total, 768 such stimuli were used to train and test the pigeons in Phase 1 (see the text for details).

## METHOD

### Animals

Four naive male White Carneaux pigeons maintained at 80 to 85% of their free-feeding weight were tested.

### Apparatus

Testing was done in a black chamber (38 × 36 × 38 cm) controlled by a microcomputer. Stimuli were presented on a color monitor (NEC MultiSync II; 800 × 600 pixels) and were visible through a 25-cm × 17-cm touch-screen window in the middle of the chamber's front panel. Stimuli were located 20 cm beyond the window. Pecks were detected by an infrared LED touch screen (EMS Systems, Champaign, IL) surrounding this window. A house light was located in the ceiling and was illuminated at all times, except during time-outs. A centrally located food hopper below the window delivered reinforcement.

### Stimuli

All stimuli were created with Dream3D (Corel, Dallas, TX) and rendered as 13-cm × 13-cm, 256-color bitmaps. Three objects, approximately 3.5 cm in size, appeared in each scene (a blue sphere, yellow cube, and red icosahedron, each with a different surface texture). For each pigeon, a different ordering of the objects was designated as the S+ stimulus (e.g., ABC). Pecks to this stimulus were reinforced on a variable-interval 15-s (VI-15) schedule. Hopper presentations were 4 s in duration. The remaining five orders (e.g., ACB, BAC, BCA, CBA, and CAB) were designated as S− stimuli and never reinforced.

Within each scene, the apparent depth of the three objects was altered by independently manipulating three pictorial depth cues. The first cue consisted of the presence of depth as provided by *relative density* and was imparted by a texture gradient composed of a black-and-white or green-and-white checkerboard. This texture was slanted at 55° from the picture plane and was consistent with a receding surface, with the size of the squares decreasing from 14 to 1 mm from front to back (mean size = 7 mm). In displays without this cue, the nonreceding texture was behind the objects and parallel to the picture plane. It provided no depth and was composed of 7-mm squares. The second cue consisted of the presence of depth as provided by *occlusion*. Occlusion was created by partial overlap of the sequenced objects (overlap ranged from about 10 to 30% across examples). Occlusion was removed by eliminating this overlap. The third cue consisted of the presence of *relative size*. This cue was created by rendering each object in a size corresponding to its depth in the scene and was removed by making all three objects the same size. These three monocular cues were independently combined in eight ways (see Phase 1 Procedure).

The stimuli varied in three other significant ways. First, the objects within the scenes varied in their right to left position and relative distance from each other. These irrelevant factors did not change the objects' order, but created variety among the stimuli. Second, the orientation of the entire scene was rotated 0°, 90°, 180°, or 270°. Thus, the textured surface, when present, appeared as a "floor," "ceiling," or right or left "wall." This created further variety and discouraged the use of height in field as a cue. Finally, all scenes were illuminated by ambient light and one point source positioned above the surface and to one side. Half the scenes that involved a receding texture were rendered with object shadows, and half were rendered without these shadows. One camera position was used for all scenes. Altogether, 768 unique scenes were created.

### Phase 1 Procedure

Following training to peck all displays, which took fewer than five sessions, discrimination training began. Each trial started with a peck to a centrally presented 2.5-cm white signal. This signal was then replaced by a stimulus scene, which was presented for 30 s. If the scene showed the correct depth ordering of the objects (S+), it was reinforced on the VI-15 schedule. Presentations of any of the five S− orders were not reinforced. The intertrial interval was 5 s.

Daily sessions consisted of 112 trials (32 S+ and 80 S− scenes). Disregarding the variation in texture color, the left/right and close/far arrangement of the objects, and the orientation of the scenes, there were eight conditions, defined by the depth cues that were present: three one-cue conditions (relative density, relative size, occlusion); three two-cue conditions (relative density and size, relative density and occlusion, relative size and occlusion); one three-cue condition (all three cues combined); plus one control condition, in which the three cues were absent, preventing the impression of depth (see Fig. 1). For the purposes of scoring performance in the control condition, S+ and S− assignments were determined by the original scenes from which the cues were removed. The 80 daily S− scenes tested each of the five nonreinforced orders in each of the eight conditions. The 32 S+ stimuli tested four scenes for each of the eight conditions. Two different randomly selected picture orientations were tested in each session (56 trials each). The displays tested in each session were selected without replacement from the entire set of stimuli with these orientations. Following 36 sessions of training (except for 1 bird; see Results), nonreinforced probe trials were added to each session to measure peck rates on S+ trials without the involvement of effects of reinforcement. Eight randomly selected S+ trials (one per condition; 25% of S+ trials) were presented for 30 s without any consequence. Seven such probe sessions were tested to complete Phase 1.

### Phase 2 Procedure

As described later, the control condition, in which the three manipulated cues were absent, was found to support a poor, but above-chance level of discrimination. In the second phase of the experiment, we explored why. One possibility seemed to be the differential lighting and shading reflected off the objects from the point light source illuminating the scenes. Therefore, we tested a new condition in which we made the lighting more uniform by reducing the intensity of the point light source by 60% across each scene. We were also interested in the role of the foremost object, and thus included probe scenes in which only the front object was rendered.

Only the 3 pigeons that successfully mastered the discrimination in Phase 1 were tested. In Phase 2, we implemented three procedural changes: We increased the number of orientations tested per session (three, rather than two) and reduced both the intertrial interval and the hopper interval to 3 s. Daily sessions consisted of 186 trials: 162 trials testing the same conditions as constructed in Phase 1 and 24 trials testing four new conditions (6 trials per condition). The scenes in the uniform-light control condition were rendered with the density, size, occlusion, and lighting cues removed. The other three test conditions involved scenes with just the front object present. The back two objects were removed from each of the six different orderings of the objects, and each scene was rendered with just the relative size, density, or relative size and density of the front object present (occlusion not being possible). For each condition, trials were scored by treating the display with a front object consistent with a pigeon's S+ sequence as "correct" and treating the remaining two object displays as "incorrect." All test trials were conducted as nonreinforced probe trials. Eight test sessions were conducted.

## RESULTS

### Phase 1

Three of the 4 birds readily learned the discrimination, showing strong indications of learning in the multiple-cue conditions within 10 sessions. Figure 2 describes the performance of these 3 pigeons in the one-, two-, and three-cue and control conditions by graphing mean discrimination ratio (DR; number of S+ pecks/number of S+ pecks plus number of S− pecks) as a function of training block. Overall, the discrimination was strongly dependent on the number of monocular cues present in the scenes, with the three-cue condition supporting the best discrimination, followed in order by the two-cue, one-cue, and control conditions. Each pigeon benefited in the same way from increasing the number of cues. A repeated measures analysis of variance (ANOVA; Number of Cues × Session) revealed significant main effects of both number of cues, $F(3, 6) = 39.5$, $\eta_p^2 = .95$, and session, $F(8, 16) = 18.6$, $\eta_p^2 = .9$, and a significant interaction, $F(24, 48) = 2.1$, $\eta_p^2 = .52$ (in all analyses, an alpha level of $p < .05$ was used to judge statistical significance). To investigate the effect of cue number and type, we examined the steady-state performance of these pigeons in the seven probe sessions. Mean DR again varied significantly as a function of number of cues in the scene: three cues = .83, two cues = .79, one cue = .71, control condition = .64. A repeated measures ANOVA (Number of Cues × Session) confirmed the presence of a significant main effect of cue number over these sessions, $F(3, 6) = 6.4$, $\eta_p^2 = .76$.

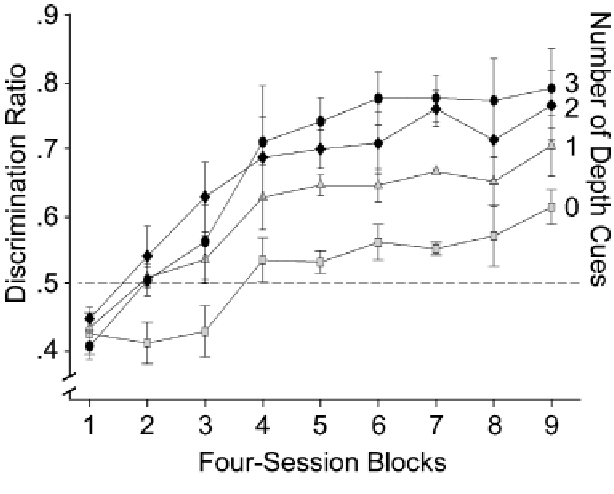

**Fig. 2.** Mean discrimination ratios for the 3 successful pigeons as a function of block in Phase 1. Results are shown separately for one-cue, two-cue, and three-cue conditions and for the control condition. The dotted reference line depicts chance responding in the task. Error bars show standard errors of the means.

The 4th pigeon took much longer to learn the discrimination (more than 70 sessions) and never performed well in some of the conditions. Although this pigeon's performance was much poorer than the other birds', its DRs showed the same pattern of discrimination. Mean DRs over the last 10 sessions of its Phase 1 testing were .57, .54, .49, and .46 for the three-cue, two-cue, one-cue, and control conditions, respectively. Single-mean *t* tests confirmed that performance in the three-cue and two-cue conditions was significantly above chance, $ts(9) > 2.2$.

We next examined the 3 successful birds' discrimination with the different combinations of pictorial cues in the seven probe sessions (see Fig. 3). Across conditions, no type of pictorial cue (relative density, occlusion, or relative size) appeared to be more salient than the others; a Cue Type × Session ANOVA examining DR showed no statistically significant effect of cue type, $F(2, 4) = 1.2$. Each bird's performance was statistically above chance with each cue type, $ts(6) > 2.44$. Examination of the different combinations of cue types revealed no systematic or significant interactions. Finally, results from the seven probe sessions showed that the presence or absence of shadows, the orientation of the scene (up, down, left, or right), and the color of the textured ground (black vs. green) had no significant impact on responding.

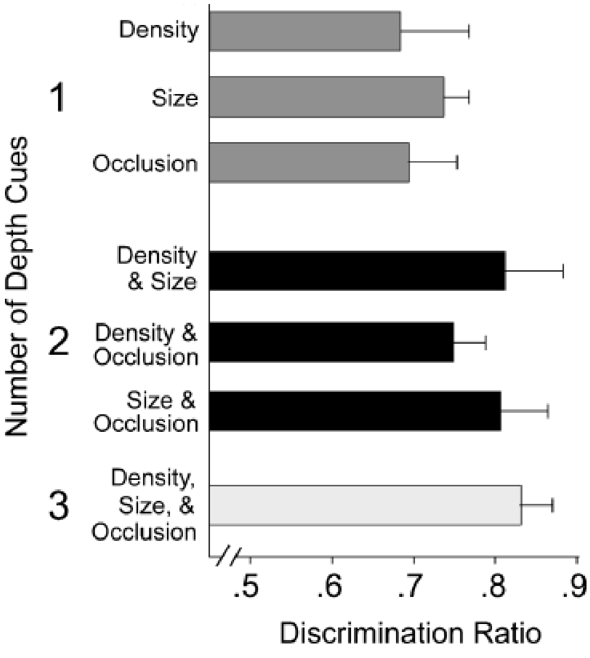

**Fig. 3.** Mean discrimination ratio for the 3 successful pigeons as a function of the specific depth cues present in the display during the seven steady-state probe sessions in Phase 1. Error bars show standard errors of the means.

We also examined the pigeons' sensitivity to the six ordinal sequences. For purposes of analysis, we divided the one-, two-, and three-cue conditions into those with occlusion present among the objects and those without such occlusion. The results were adjusted to accommodate the different S+ sequences tested with different birds, so that order "ABC" represented the standardized S+ display. The mean number of pecks for each sequence when occlusion was present was as follows—ABC+: 35.9, ACB−: 17.5, CAB−: 9.5, BAC−: 8.9, BCA−: 7.7, CBA−: 5.3 (mean SEM = 3.5). The mean number of pecks when occlusion was absent was as follows—ABC+: 36.4, ACB−: 34, CAB−: 13.2, BAC−: 10.9, BCA−: 5.1, CBA−: 4.2 (mean SEM = 2.3). A repeated measures ANOVA (Session × Ordinal Sequence × Occlusion Presence/Absence) on the number of pecks to each display revealed both a significant main effect of sequence, $F(5, 10) = 30.0$, $\eta_p^2 = .94$, and a significant interaction of sequence and occlusion presence/absence, $F(5, 10) = 7.1$, $\eta_p^2 = .78$. This interaction was primarily due to the fact that the pigeons discriminated the ACB sequence significantly better when occlusion was present than when it was absent.

Finally, performance in the control condition was above chance (mean DR = .64), despite the absence of the three manipulated cues. Single-mean *t* tests revealed that 2 pigeons performed significantly above chance in this condition, $ts(6) > 2.44$, and the performance of the 3rd was numerically (mean DR = .64) above chance. The 4th pigeon's performance was not above chance. Despite the mixed statistical results, this surprising outcome prompted us to conduct Phase 2 of the experiment.

### Phase 2

In this phase, the differential-light control condition (formerly the control condition in Phase 1) still supported above-chance discrimination (mean DR = .68) in all 3 pigeons, $ts(5) > 2.44$. More important, discrimination in the uniform-light control condition (mean DR = .53) was significantly poorer than performance in the differential-light control condition, $F(1, 2) = 32.5$ $\eta_p^2 = .94$, and was not significantly different from chance in separate tests for each bird, $ts(5) < 2.44$. In the conditions involving presentation of only the front object, discrimination was above chance (mean DR = .68), suggesting that the apparent depth positioning of the foremost object was an important factor in the discrimination. Nevertheless, discrimination in the one-object conditions was significantly reduced relative to discrimination in the three-object conditions in Phase 1 (mean DR = .77), $F(1, 2) = 50.1$, indicating that the presence of all the objects improved performance and that the pigeons used all the objects in making their discrimination.

## GENERAL DISCUSSION

These experiments demonstrate that pigeons are sensitive to the pictorial depth cues of relative density, occlusion, relative size, and differential object shading. As these cues were additively combined, they provided an increasingly veridical perception of the ordinal depth of objects in computer-generated scenes. Without these cues, the pigeons were incapable of discriminating the objects' arrangements during Phase 2. Presumably, these same perceptual mechanisms would be equally functional in more natural settings. These results indicate that birds share some of mammals' monocular roads to seeing and locating objects in visual space. The value of such depth information for a rapidly flying animal requires little comment.

Like the human visual system, the visual system of these birds seems to take advantage of the multiple cues inherent in spatial layouts. One important question for future investigations will be to examine how these independent cues are combined by the avian visual system and how these depth-constructing mechanisms compare with those in primates (Cutting & Vishton, 1995; Hillis, Ernst, Banks, & Landy, 2002). All the cues seemed about equally effective when tested in isolation, with each producing approximately the same level of discrimination in the one-cue condition. Given previous failures to find amodal completion in pigeons, it is interesting that occlusion proved to be an important depth cue, facilitating the discrimination whenever it was present. Thus, although pigeons may not complete the hidden contours of an object located behind an occluder in some settings, this occlusion information can be easily used to determine the ordinal position of objects with respect to one another. It may be that in some simple situations, pigeons are too detail or part oriented to see the sets of relations necessary for completing hidden contours. Of course, it is possible that the pigeons in the present experiment did recognize the entire and "complete" objects, and this might have been promoted by the use of semirealistic scenes.

There is debate about whether brightness and shaping are true depth cues or simply help the observer to recover object shape. Nevertheless, our results are in agreement with those of Reid and Spetch (1998): Pigeons are more sensitive to depth when provided with appropriate lighting and shading information. Only when we controlled for this factor by making the lighting more uniform across the scene did the pigeons drop to chance performance. Despite the subtle nature of these lighting cues, it is perhaps not too surprising that diurnal birds are sensitive to this lighting information, as it would provide not only perspective, shape, and depth information, but also direct information for orientation during flight.

As in humans, the closest or foremost objects seemed to exert the greatest control over the discrimination. As long as depth context allowed the closest object to appear to be toward the front of the scene, the pigeons were capable of above-chance discrimination. The importance of the front position is further reflected by the fact that the pigeons' discrimination decreased as the front object in their S+ sequence was positioned further back in the scene. Nevertheless, the other objects played their role: Performance was better when all three objects were present in the scenes, and the ACB sequence was successfully discriminated, at least when occlusion was present.

Turning to the issue of picture perception, its apparent duality has been a long-standing theoretical issue. Humans recognize that pictures are flat, lack motion, and are objects themselves, but humans are also simultaneously able to extract the perceptual content in pictures as if they were the real world. It is not clear if pigeons experience this simultaneous conflict between a 2-D image and its 3-D content. In part, this potential difference between pigeons and humans may help to explain the mixed results of picture perception experiments with pigeons.

The small, efficient visual system of pigeons has been uncompromisingly sculpted by the demands of perceiving their natural world. Thus, when presented with pictures, pigeons may be able to bring to bear only those perceptual mechanisms evolved for those functions. In the case of depth processing, if the image is rich in relevant 3-D cues capable of activating these mechanisms, and if attention is drawn to these cues by the contingencies of the task, then the pigeons react in a manner consistent with the picture's representation of the real world, much as if looking through a window. This is likely what happened in the present experiment, because both of these requirements (highly relevant cues, directed attention) were intentionally part of the design. When the 3-D perceptual cues are weak or ambiguous, such as in line drawings, or when attention is not specifically directed to such 3-D features, pigeons' perceptual mechanisms may allow them to react to an image only as a flat pattern of colors and shapes. Even when images are treated as nonrepresentational, however, pigeons can often do remarkably well in making visual discriminations simply because of their substantial capacity to memorize large numbers of images regardless of their content (Cook, Levison, Gillet, & Blaisdell, 2005; Vaughan & Greene, 1984).

Two other factors are also likely to influence the representational outcome of pigeons' picture processing. First, if the demands of the situation require spatial attention to be deployed over a substantial area, the likelihood that they will react to a 2-D image as a representation of the real world is increased. Pigeons, at least in their frontal visual fields, tend to be locally dominant animals in operant chambers—looking first at small or local details before processing larger perceptual structures (Cavoto & Cook, 2001). Although larger areas can be integrated (Cook, Kaz, & Brooks, 2005; Wasserman, Kirkpatrick-Steger, Van Hamme, & Biederman, 1993), this is apparently not the first priority of pigeons. In the present case, we specifically attempted to promote more global processing of the scenes by moving the screen back from the pecking surface to decrease visual angle.

Second, pigeons may lack the mechanisms for processing all of the same visual information as primates or may possess alternative mechanisms for processing it. Although for certain visual functions, such as perceptual grouping, pigeon and human performance appears to be similar (Cook, 1992; Cook, Cavoto, Katz, & Cavoto, 1997), in several studies these two species have reacted differently to the same stimuli, suggesting that some of the underlying visual mechanisms may function differently (e.g., DiPietro, Wasserman, & Young, 2002; Hollard & Delius, 1982; Kelly & Cook, 2003; Sekuler et al., 1996). Such comparative differences may also interact importantly with picture processing.

In conclusion, this experiment indicates that pigeons rely on many of the same monocular cues as humans for seeing pictorial depth. The results suggest that the pigeons perceived and represented the content of these images much as intended—as three spatially arranged objects on a receding surface. This suggests that, at least under the circumstances tested here, pigeons' picture perception can be realistic. The contribution of the various factors just discussed needs to be better understood, however, before researchers can confidently predict how any animal will respond to a picture. The current results provide an important new anchor point for such explorations.

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