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The role of edges in object recognition by pigeons

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Abstract. In three experiments, we explored how pigeons use edges, corresponding to orientation and depth discontinuities, in visual recognition tasks. In experiment 1, we compared the pigeon's ability to recognize line drawings of four different geons when trained with shaded images. The birds were trained with either a single view or five different views of each object. Because the five training views had markedly different appearances and locations of shaded surfaces, reflectance edges, etc, the pigeons might have been expected to rely more on the orientation and depth discontinuities that were preserved over rotation and in the line drawings. In neither condition, however, was there any transfer from the rendered images to the outline drawings. In experiment 2, some pigeons were trained with line drawings and shaded images of the same objects associated with the same response (consistent condition), whereas other pigeons were trained with a line drawing and a shaded image of two different objects associated with the same response (inconsistent condition). If the pigeons perceived any correspondence between the stimulus types, then birds in the consistent condition should have learned the discrimination more quickly than birds in the inconsistent condition. But, there was no difference in performance between birds in the consistent and inconsistent conditions. In experiment 3, we explored pigeons' processing of edges by comparing their discrimination of shaded images or line drawings of four objects. Once trained, the pigeons were tested with planar rotations of those objects. The pigeons exhibited different patterns of generalization depending on whether they were trained with line drawings or shaded images. The results of these three experiments suggest that pigeons may place greater importance on surface features indicating materials, such as food or water. Such substances do not have definite boundaries—cued by edges—which are thought to be central to human recognition.

1 Introduction

The role of edges in marking orientation and depth discontinuities has important theoretical implications for theories of object recognition.(1) Some theories propose that such edges and vertices of an image are vital in determining the representation of an object (Biederman 1987; Marr and Nishihara 1978). These contours determine the basic parts of the object, which, along with spatial relationships, can be matched to the appropriate object representation. Many computer models of object recognition also rely on edge extraction as an initial stage in the recognition process (Bergevin and Levine 1993; Brooks 1981; Lowe 1987).

Object edges are typically operationalized as line drawings. So, if object edges are the primary input for recognition mechanisms, then a line drawing of an object should be recognized just as quickly and easily as the fully shaded image of the same object. Biederman and Ju (1988) reported that people were as proficient at recognizing line

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(1) There are many sources of contrast variation in an image of a real-world object. Sharp changes in contrast often correspond to 'edges', which can be produced by a variety of sources, such as shadows, albedo variations, reflectance highlights, texture differences, as well as orientation and depth discontinuities. In this paper, edges refer to orientation and depth discontinuities, although such discontinuities do not always project a sharp change in contrast.

drawings as they were at recognizing color photographs of the same objects. In a naming task with familiar objects, these researchers found no difference between reaction times and accuracies for naming line drawings and photographs. This study thus provides support for the proposal that edges alone are sufficient for real-time object recognition (for the kinds of objects they studied consisting of two or more parts with definite boundaries).

If edge detection is an important part of a general recognition process, then we would expect that other nonhuman primates would be capable of using line drawings in recognition tasks. Kovács et al (2003) tested generalization to line drawings in the rhesus macaque monkey (*Macaca mulatta*) by measuring cellular responses in visual areas of the brain to photographs and line drawings of the same objects. Kovács et al found that, for cells that responded to fully shaded, color images of objects, the response decreased only slightly when the monkey was shown a line drawing of the same object (although some part of this decline could be attributed to regression effects in that the search for responsive cells was performed with the color images). Importantly, the preference of a cell for one object over another was maintained when the objects were shown as line drawings. In addition to recording from cells, Kovács et al tested a monkey in a behavioral task to see if it could generalize discriminative responding from photographs to line drawings. They trained the monkey to discriminate eight different color pictures of objects. Once the animal reached 90% correct, it was shown probe trials with line drawings of the same objects. The monkey exhibited significant stimulus generalization to the line drawings. Thus, at both behavioral and cellular levels, monkeys exhibited significant discrimination transfer from fully shaded images to line drawings.

There is some evidence that the perceived equivalence of line drawings and shaded images may be automatic in primates and does not require explicit associative learning. Hochberg and Brooks (1962) conducted a developmental study using a single child in which the child's exposure to pictorial representations was limited. When the child did encounter images of objects, great care was taken to refrain from naming the objects in the images. Consequently, the child's vocabulary was learned solely with real objects. At 19 months of age, the child was tested for generalization to line drawings and photographs of familiar objects; Hochberg and Brooks recorded the naming response of the child for each of the images. Two independent judges were then given a list of the names of the object images shown to the subject and were required to determine the order of presentation (including repetitions) during the testing session using an auditory tape of the subject's verbal responses for each trial. Based on the predictions of the judges, the child was significantly above chance for naming both photographs and line drawings of familiar objects. Although this study is limited by its use of a single subject and by the difficulty in constraining the subject's exposure to pictorial images, it does suggest that generalization to line drawings does not require explicit associative learning.

1.1 *Pigeon vision research with the use of line drawings*

Previous tests of the ability of pigeons to generalize discriminative responding from shaded images to line drawings have yielded mixed results (Cabe 1976; Cerella 1977; Cook et al 1990; Lombardi and Delius 1988; Lumsden 1977). In one of the few successful demonstrations of transfer, Lombardi and Delius (1988) trained pigeons with novel two-dimensional (planar) geometric shapes and reported significant generalization to line drawings of the outside edges of the same objects. This positive result, however, must be qualified, because the training stimuli were two-dimensional images with a uniform black interior. Thus, the original training objects differed only in terms of the shape of their outlines, ie their silhouettes, with none of the three-legged vertices such as arrows, forks (or Ys), and tangent Ys, that convey the three-dimensionality of a line drawing.

Several studies have explored the pigeon's ability to generalize from complex stimuli to line drawings of those stimuli. Cook et al (1990) trained pigeons with shaded pencil drawings of objects; these stimuli included details such as shading and internal features. The researchers tested pigeons' discriminative responding to silhouettes and outlines of these objects and found that pigeons generalized to the silhouettes, but not to the outlines. In another study, Cabe (1976) used real objects that pigeons viewed through a Plexiglas panel. Cabe tested for transfer to photographs, silhouettes, and line drawings of the objects. He reported statistically significant generalization to photographs and silhouettes, but not to line drawings.

In a more recent study, Young et al (2001, experiment 1) trained pigeons with computer renderings of single-part objects and tested for generalization to other renditions (including line drawings) of the same objects. In the line drawings, all visible edges of the objects were drawn, but the remaining internal information was deleted. Young et al found that the pigeons generalized discriminative responding to silhouettes and to changes in the direction of lighting, but not to line drawings of the objects.

Before one can conclude that pigeons do not perceive line drawings as equivalent either to realistic computer renderings or to the actual objects themselves, simpler explanations must be considered. The training used in earlier studies may not have resulted in the type of general representation that is thought to underlie object recognition. Training pigeons with a single view of a static image is very different from the birds' experiences with objects in the natural environment. In previous studies, they may have attended as much or more to stimulus characteristics, such as internal features and shading, than to the overall shape of the object. In support of this possibility, Young et al (2001) reported that pigeons exhibited a significant performance decrement when the direction of illumination was changed, which minimally altered the visual appearance of the internal features of the objects. Alternatively, previous tests may not have been sufficiently sensitive to detect any perceived correspondence between line drawings and shaded images of the same objects. In experiments 1 and 2 of the present study, we tested whether training or testing sensitivity play important roles in the pigeon's ability to generalize to line drawings.

In experiment 1, we explored whether training with additional views would improve generalization to line drawings of those images. Previous studies have shown that training with more than one view increases generalization to additional views of the object (Wasserman et al 1996), even if those views are in an axis of rotation that is different from training (Peissig et al 2002). Therefore, we investigated whether a more general object representation, formed following training with multiple views of the objects, might lead to above-chance performance with the line drawings of those same objects.

In experiment 2, we used a different behavioral paradigm than that of Young et al (2001) to see whether pigeons behave in a manner consistent with their perceiving similarities between shaded images and line drawings. Here, treating such stimuli as equivalent should give the birds a significant problem-solving advantage. This result would suggest that pigeons do indeed perceive a correspondence between line drawings and shaded images, as well as suggest that edges are important for avian object recognition.

Assuming that pigeons use edge extraction to determine the general shape of an object, one would expect that a line drawing and a shaded image of the same object should lead to similar representations. So, any stimulus translations of line drawings and shaded images should lead to similar response patterns. Any qualitative difference in responding to image translations would suggest that the underlying representations were not equivalent. To explore this idea, in experiment 3 we trained pigeons with either line drawings or shaded images of objects, and then tested the birds with planar rotations of the same objects.

1.2 *Pigeon vision research and planar rotation*

In previous studies exploring the effects of planar rotation on the pigeon's visual discrimination behavior, mixed data have been reported. Hollard and Delius (1982) and Delius and Hollard (1995) have reported invariance to planar rotations of stimuli. These researchers trained pigeons with both matching-to-sample and non-matching-to-sample tasks, in which the comparison stimuli were an exact match to the sample and a mirror image of the sample. All of the stimuli were simple, two-dimensional objects, similar to filled squares and circles, and the pigeons were familiarized with planar rotations before testing for generalization. In the mirror-image discrimination task, pigeons exhibited no performance decrement when the sample and comparison stimuli were shown at different planar rotations.

In contrast to the findings of Hollard and Delius (1982) and Delius and Hollard (1995), Hamm et al (1997) used a go/no-go paradigm to test whether pigeons' behavior was invariant to planar rotations of objects. The stimuli were line drawings of objects taken from Snodgrass and Vanderwart (1980). Once the pigeons had learned to discriminate S+ from S− stimuli, the birds received probe trials in which the original stimuli were rotated within the plane. These researchers found that pigeons exhibited a systematic drop in discrimination performance as stimuli were rotated away from the original training orientation.

In experiment 3 of the present study, we tested whether pigeons that were trained with line drawings form a distinctly different object representation than pigeons trained with shaded images, by probing their ability to generalize to a stimulus transformation. Young et al (2001) proposed that pigeons trained with shaded images formed a representation that heavily weighted the absolute spatial relationships of the light and dark patches in the stimuli. This type of information is significantly disrupted by planar rotation. In contrast, pigeons trained with line drawings should not have this information available to store as part of the representation. So, a planar rotation should be less disruptive for pigeons trained with line drawings.

Any disruption in the pigeon's performance to planar rotations would suggest that pigeons do not automatically generalize to planar rotations, as suggested by Hollard and Delius (1982) and Delius and Hollard (1995). Thus, we sought to explain some of the inconsistencies among previous studies of planar rotation, in addition to testing the processing of line drawings and shaded images. It is possible that the types of stimuli used in previous studies might have biased pigeons to respond invariantly to rotation in some cases and to respond in a more rotation-specific fashion in others.

2 Experiment 1

In experiment 1, we trained pigeons to make a distinctive button response to shaded images of each of four objects. One group of birds was trained with only a single view of each object. A second group of birds was trained with five views of each object. Our objective was to compare how well pigeons generalized their discriminative responding from shaded images to line drawings of the trained images. The data from the one-view group are a subset of the data originally published in experiment 1 of Young et al (2001), in which pigeons were trained with a single view only. It is possible that training with a single view biased pigeons to attend to diagnostic features, such as the patterns of light and dark on the stimuli, rather than to attend to the general shapes of the objects. There is evidence that training pigeons with several views results in the formation of a more general representation (Peissig et al 2002). Consequently, pigeons may be more likely to generalize from shaded images to line drawings of objects with which they have had multiple-view training.

2.1 *Method*

2.1.1 *Participants.* Eight feral pigeons served as subjects. They were kept at 85% of their free-feeding weight and given free access to water and grit. The pigeons were on a 14-h light/10-h dark schedule throughout the experiment.

2.1.2 *Apparatus.* The pigeons were trained in four specially constructed plywood chambers. One side of each chamber consisted of a large opening with an aluminum frame attached to the outside of the box. Inside the frame was a clear touch screen (Accutouch model #002744-FTM-K1; Elographics, Oak Ridge, TN, USA) that was coated with Mylar for durability. The pigeons' pecks on the touch screen were processed by a serial controller board (model #E271-2210, Elographics). A brushed aluminum panel was placed directly in front of the screen to allow pigeons access to limited portions of the video monitor. There were five openings in the aluminum panel. The center of the panel contained a 7-cm × 7-cm square opening in which the stimuli were presented. The remaining four openings were circular, 1.9 cm in diameter, and were located 2.3 cm from each corner of the center display opening, and served as response buttons. In the rear of the chamber, a clear Plexiglas food container was placed level with a wire-mesh floor, to prevent pigeons from perching on the food cup. Noyes 45-mg pigeon pellets were delivered through a vinyl tube into the food cup by a rotary pellet dispenser (model #ENV-203M; MED Associates, Lafayette, IN, USA). Figure 1 shows the configuration of the food cup, center opening, and corner response buttons within the experimental chamber. During experimental sessions, a house light mounted on the upper rear wall of the chamber provided constant illumination. The house light was a 6 W, 125 V incandescent bulb, housed within a Plexiglas cover to diffuse

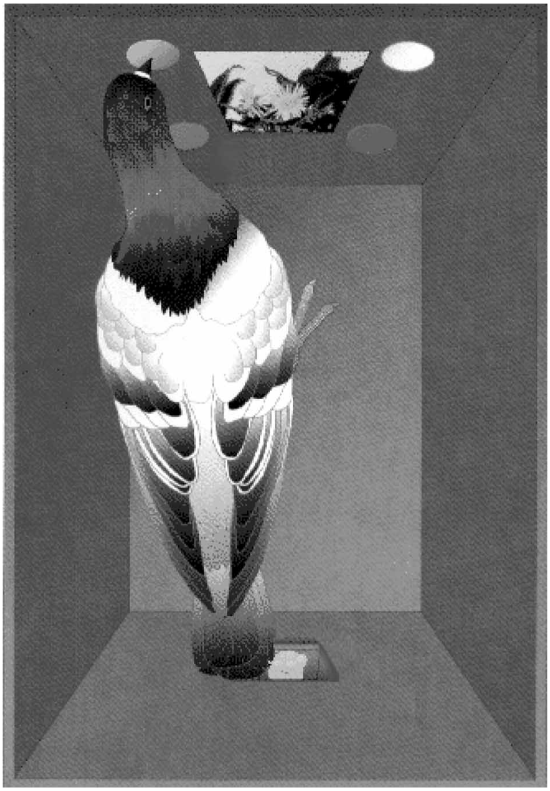


Figure 1. The configuration of the experimental chamber used in all three experiments. The approximate placement of the center opening, corner response buttons, and food cup are shown.

the light. The luminance of the chamber with the house light on was 0.32 lux. A digital I/O interface board (National Instruments model #NB-DIO-24, Austin, TX, USA) controlled the pallet dispenser and the house light.

Control of house light, feeder, and touchscreen (via the I/O interface) and recording of pigeons' responses (via the serial controller board) was accomplished by four Apple Macintosh 7100/66 Power PC computers. The pigeon's monitor was an Apple Multiple Scan 15-inch (model M2943) with a refresh rate of 60 – 75 Hz. The pigeon's monitor and an identical monitor located in an adjacent room were connected by a distribution amplifier (model #MAC/2 DA2; Extron Electronics, Santa Fe Springs, CA, USA). The programs were developed in Hypercard version 2.3.

2.1.3 *Stimuli.* The stimuli consisted of four geons: an arch, a barrel, a brick, and a wedge, that varied from one another by a variety of non-accidental properties (see figure 2; Biederman 1987). All stimuli were shown in grayscale (achromatic); based on an estimated viewing distance of 6.66 cm (Macko and Hodos 1985), the stimuli subtended a maximum visual angle of 34 deg and a minimum visual angle of 17 deg. The shaded stimuli were rendered in Raydream Designer 4.0 at 300 dots per inch resolution. For the shaded images, there were five views created by rotating the objects in depth by 72° intervals (see figure 2). The line drawings were prepared in Adobe Photoshop 4.0 and were created by tracing the edges of each shaded stimulus at the 0° view (see figure 3).

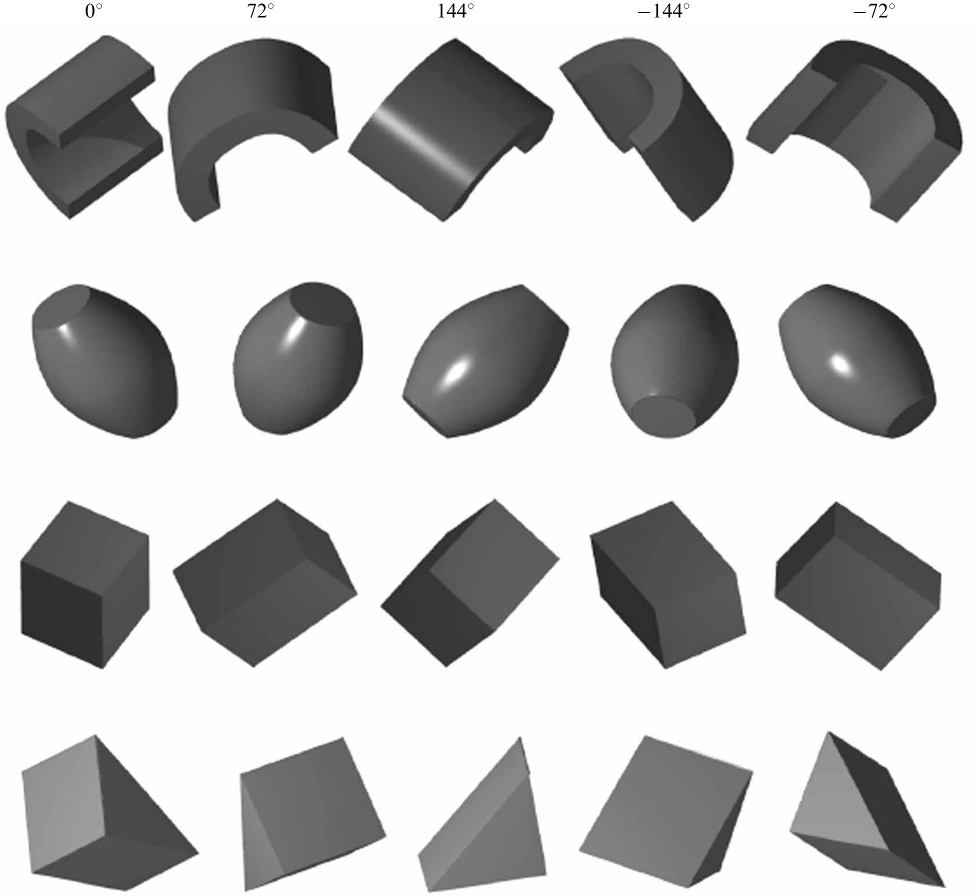


Figure 2. The 0°, 72°, 144°, −144°, and −72° views of the arch, barrel, brick, and wedge. The five-views group was trained with all these views and the single-view group was trained with only the 0° view.

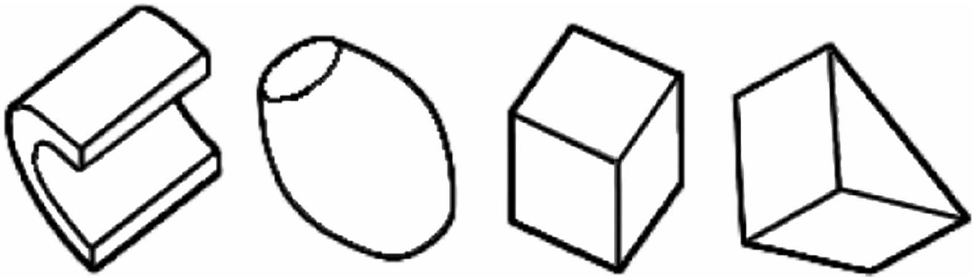


Figure 3. Line drawings of the four geons that served as testing stimuli in experiment 1 and training stimuli in experiment 2. The geons were: arch, barrel, brick, and wedge.

We used Adobe Photoshop (version 4.0) to determine the brightness of each stimulus. Brightness was measured on a scale ranging from 0 (black) to 255 (white). The stimuli were presented on a solid white background (255). Table 1 shows the contrast proportion and mean brightness for all five views of the four shaded images used for training (the contrast proportion is the difference between the highest and lowest luminance regions divided by their sum). Table 2 shows the accuracy scores, contrast proportion, and mean brightness for the 0° view of the line drawings given during the generalization tests. The line drawings always have a contrast proportion of 1.0, because the lines comprising the edges are black (0), and the inside space is white (255); thus, the calculation for line drawings is $(255 - 0)/255 = 1$.

Table 1. The contrast proportion (the difference between the highest and lowest luminance regions divided by their sum) and the mean brightness (black = 0 and white = 255) for the shaded-image stimuli used in experiments 1 and 2.

Geon	Angle of rotation/°				
	0	72	144	−144	−72
Contrast proportion					
Arch	0.41	0.48	0.70	0.48	0.47
Barrel	0.75	0.68	0.68	0.60	0.74
Brick	0.44	0.23	0.41	0.44	0.39
Wedge	0.44	0.37	0.25	0.39	0.55
Mean brightness					
Arch	73.00	74.37	81.89	69.33	75.51
Barrel	82.71	90.08	92.81	91.53	82.47
Brick	69.90	73.08	75.98	73.70	76.02
Wedge	109.38	108.11	124.32	115.52	101.48

Table 2. The accuracy scores for the five-views group and one-view group in experiment 1, and the mean brightness and contrast proportion for the line-drawing stimuli used in experiments 1 and 2.

Geon	Accuracy/%		Brightness data	
	five-views group	one-view group	contrast proportion	mean brightness
Arch	1	8	1.00	192.14
Barrel	5	45	1.00	219.63
Brick	21	51	1.00	205.34
Wedge	74	5	1.00	205.76

2.1.4 *Procedure.* At the beginning of a trial, the central display area was illuminated with a black cross centered on a white background. A single peck anywhere within that display area turned on a single-geon stimulus in the center. The pigeons were required to peck the central screen a fixed number of times; the number of required pecks was individually adjusted for each bird, depending on its level of performance. Completing the final peck illuminated the four corner response buttons. After a correct choice, the stimulus was removed from the display area, the response buttons were darkened, and a food pellet reinforcer was delivered. After an incorrect choice, the stimulus was turned off for 1 s, the response buttons were darkened, and the house light was turned off for 4 to 6 s ($M = 5$ s). The pigeon then proceeded through one or more correction trials (repeating the incorrect trial until a correct choice was made); correction trials were not scored for data analysis. Intertrial intervals randomly ranged from 6 to 10 s ($M = 8$ s).

The pigeons were trained with either one view or five views of each of the four objects. The assignment of correct-response buttons to the four different geons was counterbalanced across birds by a Latin-square design. We used a randomized-block training design. For the one-view group, each block consisted of five presentations of each of the shaded images of the four geons, for a total of 20 trials in a single block. For the five-views group, each block consisted of one presentation of each of the five views of the four different objects, for a total of 20 trials in a block. For both groups, daily sessions comprised ten blocks for a total of 200 trials per day. Before testing with the line drawings, the pigeons were required to meet a criterion of at least 85% accuracy overall and 80% accuracy for each geon ('85/80' criterion). The pigeons were required to maintain this 85/80 criterion throughout the testing phase as well. If a pigeon did not meet the criterion, it was required to return to training sessions until it had once again done so.

During the testing phase, the pigeons continued to receive training trials with the training stimuli. In addition, they received non-differential reinforcement on trials with the line-drawing test stimuli; this procedure was adopted to prevent the pigeons' pecks from extinguishing (if they were given no reinforcement) and to prevent the pigeons from learning which responses to make to the testing stimuli (if they were given differential reinforcement). During testing, the pigeons were given 40 warm-up trials. For the one-view group, the warm-up trials consisted of the four different geons at the 0° view, each repeated ten times. For the five-views group, the warm-up trials consisted of the five views of each of the four objects each repeated two times. Following the warm-up trials, the testing trials began. Blocks during testing comprised 20 training stimuli (five repetitions of four objects or one viewing of four objects shown at the five views). In addition, each testing block also included three testing stimuli. The testing stimuli were line drawings of the four objects at the 0° view. Thus, pigeons in both the one-view and five-views groups were tested with only the 0° view of each object. The pigeons also experienced two additional stimulus manipulations which were not related to the current study (changes in lighting direction and silhouettes of the objects). These three manipulations across the four objects resulted in 12 testing stimuli. The 12 testing stimuli were each presented twice within a session. The pigeons were shown eight repetitions of each 23-trial testing block, resulting in 224 total trials (40 warm-ups, 160 training trials, and 24 testing trials).

2.2 *Results and discussion*

The pigeons trained with one view took a mean of 30 days to meet the criterion in the training phase. The pigeons in the five-views group took a mean of 28 days to meet the criterion. Thus, there appeared to be no learning advantage to pigeons that were given fewer views.

Figure 4 shows the results for the one-view and five-views groups. Performance with line drawings was very similar for both groups. To confirm these observations, we

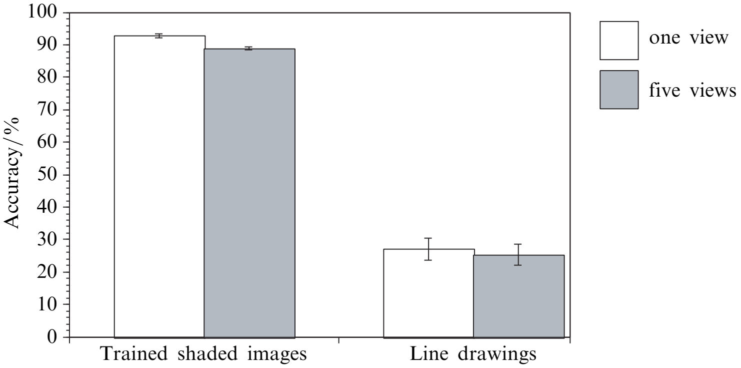


Figure 4. Experiment 1. Accuracy scores for pigeons for the one-view group (solid bar) and the five-views group (patterned bar) plotted for the trained shaded images and tested line drawings. Vertical lines indicate standard error of the mean (here and elsewhere, standard error was calculated by dividing the standard deviation by the square root of N).

analyzed the pigeons' choice accuracies using a repeated-measures, full-factorial ANOVA of group (one-view and five-views) and stimulus type (shaded image and line drawing). The main effect of group was not significant ($F_{1,6} = 3.11$, $p > 0.05$), indicating that there were no overall differences between the birds trained with one view and those trained with five views. The main effect of stimulus type was significant ($F_{1,6} = 2457.93$, $p < 0.0001$). This result confirms previous findings that pigeons do not generalize to line drawings, of objects (Cabe 1976; Cook et al 1990; Young et al 2001). The interaction between condition and stimulus type was not significant ($F_{1,6} = 0.66$, $p > 0.05$).

We also analyzed whether the pigeons responded significantly above chance to the line drawings. A one-tailed binomial ($p > 0.05$) indicated that neither the one-view nor the five-views group responded significantly above chance.

The results of experiment 1 show that training pigeons with multiple views of shaded object images does increase generalization to line drawings of the same objects. This result is especially interesting because training with multiple views does improve performance to novel views along an orthogonal axis of rotation (Peissig et al 2002). Thus, these data suggest that, although pigeons trained with five views may attend more to general shape than those trained with a single view, they still did not perceive the line drawings of those objects as equivalent to the shaded images with which they were trained.

3 Experiment 2

In experiment 2, we expanded on the results of experiment 1 by seeing if pigeons perceive line drawings and shaded images as equivalent, using another testing method. Pigeons were trained to respond to shaded images and line drawings of four objects (2 depictions × 4 objects = 8 stimuli). One group of birds was trained to make the same response to a shaded image and its corresponding line drawing (consistent condition). A second group of birds was trained to make the same response to a shaded image of an object and a line drawing of a different object (inconsistent condition).

The pigeons in the inconsistent condition had no other option but to memorize the responses associated with each specific stimulus. In the consistent condition, if the pigeons did not perceive the line drawings and shaded images as at all equivalent, then they too would have to memorize the specific response associated with each individual stimulus and, thereby, exhibit learning rates similar to birds in the inconsistent condition. If, however, pigeons perceived some correspondence between the object depictions, then learning should proceed more rapidly in the consistent condition than in the inconsistent condition.

3.1 *Method*

3.1.1 *Participants.* The participants were eight feral pigeons, different from those used in experiment 1. They were kept at 85% of their free-feeding weight and given free access to water and grit. The pigeons were on a 14-h light/10-h dark schedule throughout the experiment.

3.1.2 *Apparatus.* The apparatus was identical to that used in experiment 1.

3.1.3 *Stimuli.* The stimuli were line drawings (see figure 3) and shaded images (see figure 5) of the arch, barrel, brick, and wedge single geons used in experiment 1. We used Adobe Photoshop (version 4.0) to determine the brightness of each stimulus. Brightness was measured on a scale ranging from 0 (black) to 255 (white). The stimuli were presented on a solid white background (255). Table 1 shows the contrast proportion and mean brightness for the 0° view of the shaded images used in experiment 2 (the contrast proportion is the difference between the highest and lowest luminance regions divided by their sum). The contrast proportion and mean brightness for the line drawings are shown in table 2. The line drawings always had a contrast proportion of 1.0, because the lines constituting the edges are black (0) and the inside space is white (255); thus, the calculation for line drawings is $(255 - 0)/255 = 1$.

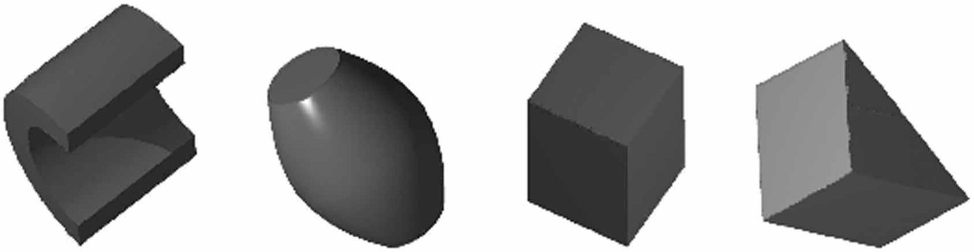


Figure 5. Shaded images of the four geons that served as training stimuli in experiment 2. The geons were: arch, barrel, brick, and wedge.

3.1.4 *Procedure.* Individual trials proceeded the same way as in experiment 1. The pigeons were randomly assigned to one of two different conditions, with four pigeons serving in each. In the consistent condition, the line drawing and the shaded image of an object were associated with the same response button. For example, the line drawing and the shaded image of the arch were associated with the upper-left button for one of the pigeons. The assignment of correct-response buttons to the four different geons was counterbalanced across birds by a Latin-square design. In the inconsistent condition, the line drawing of an object and the shaded image of a different object were assigned to the same response button. For example, the line drawing of the brick and the shaded image of the wedge were associated with the upper-left button for one of the pigeons. There were three completely independent pairings of objects and shaded image/line drawing combinations (the first three birds in table 3). The pairings of the fourth bird were randomly assigned (fourth bird in table 3). The assignment of correct-response buttons to the paired stimuli was counterbalanced by a Latin-square design (see table 3).

We used a randomized-block training design. Each block consisted of four presentations of each of the shaded images of the four geons and four presentations of each of the line drawings of the four geons, for a total of 32 trials in a single block. Daily sessions comprised five blocks for a total of 160 trials per day. Only sessions in which a bird had completed all 160 trials were used for statistical analysis. Each pigeon completed a total of forty-five daily sessions.

Table 3. Response button assignments for pigeons in inconsistent condition of experiment 2.

Bird	Response key			
	key 1	key 2	key 3	key 4
37B	barrel-shaded image wedge-line drawing	wedge-shaded image barrel-line drawing	arch-shaded image brick-line drawing	brick-shaded image arch-line drawing
39R	arch-shaded image barrel-line drawing	barrel-shaded image brick-line drawing	brick-shaded image wedge-line drawing	wedge-shaded image arch-line drawing
2B	brick-shaded image barrel-line drawing	arch-shaded image wedge-line drawing	wedge-shaded image brick-line drawing	barrel-shaded image arch-line drawing
27R	wedge-shaded image barrel-line drawing	brick-shaded image wedge-line drawing	barrel-shaded image arch-line drawing	arch-shaded image brick-line drawing

3.2 *Results and discussion*

The pigeons in the consistent condition attained a mean accuracy of 66% correct and the pigeons in the inconsistent condition attained a mean accuracy of 70% correct over the forty-five sessions. Both of these means are significantly above chance (one-tailed binomial, $p < 0.05$). Numerically, pigeons in the inconsistent condition had a higher mean accuracy than pigeons in the consistent condition; this difference is in the direction opposite to that predicted if the pigeons perceived any similarity between the line drawing and the shaded image of the same object. Figure 6 shows the accuracies of each condition throughout the nine 5-day blocks of training. The pigeons in each condition appeared to learn at approximately the same rate, suggesting no learning advantage for the pigeons in the consistent condition.

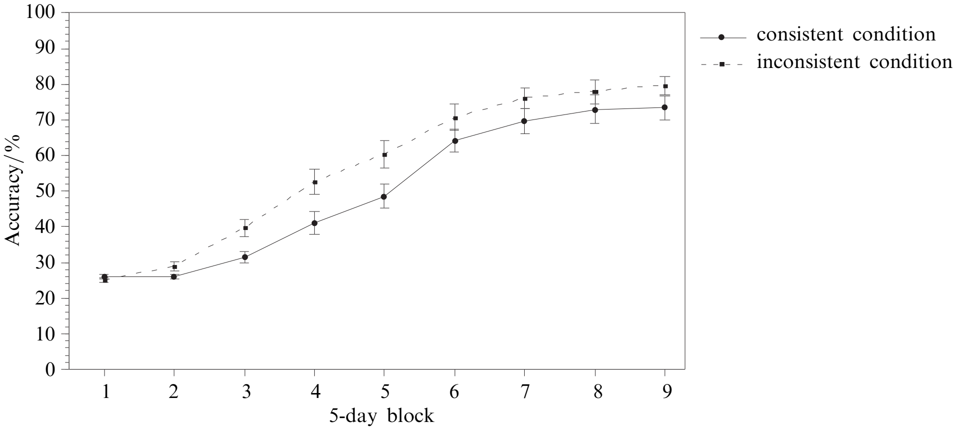


Figure 6. Experiment 2. Accuracy scores for pigeons in the consistent condition (solid line) and the inconsistent condition (dashed line) plotted in 5-day blocks. Vertical lines indicate standard error of the mean.

To confirm these observations, we analyzed pigeons' choice accuracies using a repeated-measures, full-factorial ANOVA of condition (consistent and inconsistent) and 5-day training block (1 to 9). The main effect of 5-day block was significant ($F_{8,48} = 15.41$, $p < 0.0001$), indicating that the pigeons exhibited reliable discrimination learning over the course of the experiment. Neither the main effect of condition ($F_{1,6} = 0.62$, $p > 0.05$) nor the condition × block interaction ($F_{8,48} = 0.47$, $p > 0.05$) was significant, indicating that there were no notable differences between the conditions.

The results of experiment 2 suggest that pigeons perceived no correspondence between a shaded image and its equivalent line drawing. The pigeons in the consistent condition could have solved the task more easily by attending to any perceptual similarities between the stimuli. If they had, they would have learned more quickly than the pigeons in the inconsistent condition. The pigeons trained with consistent associations, however, actually exhibited slightly slower learning than the pigeons trained with inconsistent associations. Although this difference was not significant in our ANOVA, a sign test does yield a significant difference (one-tailed binomial, $p < 0.05$). This difference is in the opposite direction to that predicted if the pigeons in the consistent condition were able to use the consistent object identity assigned to each key to solve the task.

Despite this evident failure to generalize between the different kinds of pictorial stimuli, pigeons may nevertheless process these stimuli in the same general way. Alternatively, pigeons may process the two types of images in distinctly different ways; a difference in how pigeons process these images may be the underlying cause of their inability to see any correspondence between shaded images and their line drawings.

4 Experiment 3

The pigeons' failure to perceive any equivalence between shaded images and their line-drawing variants implies that edges may not be critical for pigeons' mastery of some visual-recognition tasks. Consequently, pigeons may process line drawings in a way that is distinctly different from the way they process shaded objects; the birds may thus form distinctly different representations for each type of stimulus. In contrast, the primate data suggest that a line drawing and a shaded image of the same object activate a similar neural representation (Kovács et al 2003).

There is some evidence that pigeons trained with shaded images form a representation that preferentially encodes the global shading properties of the stimulus. Thus, surface and depth information may play a larger role than object edges in avian recognition when that information is available. Young et al (2001) reported that pigeons preferentially attended to the spatial locations of light and dark areas in a recognition task using shaded images. In Young et al's study, a small change in the lighting direction—which changed the locations of the areas of light and dark within the stimuli—caused a significant performance decrement. However, when the contrast between light-shaded and dark-shaded areas was increased—a change in relative shading information—the pigeons exhibited very little or no performance decrement.

On the basis of their findings, Young et al (2001) predicted that any significant change in shading information should produce a large decrement in recognition performance. Pigeons should thus exhibit large decrements for rotation of the objects in the picture plane, which disrupts the absolute location of shading information yet maintains the relative brightness relationships.

The results of experiments 1 and 2 clearly show that pigeons do not see a perceptual correspondence between line drawings and shaded images; this failure may be due to the lack of shading information in line drawings. Training with line drawings or shaded images may thus lead to different representations. If so, then pigeons trained with line drawings may exhibit a different pattern of generalization for planar rotations than pigeons trained with shaded images.

In experiment 3, we explored whether pigeons trained with line drawings or shaded images would form similar representations. If the patterns of responding to object translations differ depending on the original training stimulus, then we have convergent evidence that pigeons do not automatically use the edges of objects in discrimination tasks.

We tested two groups of pigeons: one trained with line drawings and the second trained with shaded images. Both groups initially learned to discriminate among the same four single-geon objects used in experiment 2. They were then tested with the training stimuli rotated in the picture plane by 90°, 180°, and 270°. Pigeons' performance on these rotated stimuli allowed us to infer the nature of the object recognition process(es) deployed with shaded and line-drawing stimuli.

4.1 *Method*

4.1.1 *Participants.* Seven feral pigeons, different from those in experiments 1 and 2, were used for experiment 3. An eighth bird was omitted because of failure to learn the discrimination task. Birds were kept at 85% of their free-feeding weight and given free access to water and grit. The birds were on a 14-h light/10-h dark schedule throughout the project.

4.1.2 *Apparatus.* The apparatus was identical to that used in experiments 1 and 2.

4.1.3 *Stimuli.* The stimuli were the four geons used in experiments 1 and 2. Here, the geons were somewhat smaller than in experiments 1 and 2;(2) at an estimated viewing distance of 6.66 cm (Macko and Hodos 1985), the stimuli subtended a maximum of 23 deg of visual angle and a minimum of 17 deg. The testing stimuli involved planar rotations of the training stimuli rotated 90°, 180°, and 270° in the picture plane (see figure 7). The images were rendered in Adobe Photoshop 4.0.

We used Adobe Photoshop (version 4.0) to determine the brightness of each stimulus. Brightness was measured on a scale ranging from 0 (black) to 255 (white). The stimuli were presented on a solid white background (255). The two leftmost columns of table 4 show the contrast proportion of the four shaded images and the four line drawings (the contrast proportion is the difference between the highest and lowest luminance regions divided by their sum). The line drawings always have a contrast proportion of 1.0, because the lines comprising the edges are black (0), and the inside space is white (255); thus, the calculation for line drawings is $(255-0)/255 = 1$. The two rightmost columns of table 4 show the mean brightness value for each stimulus.

Table 4. Contrast proportion (difference between highest and lowest luminance regions divided by their sum) and mean brightness (black = 0 and white = 255) for stimuli in experiment 3.

Geon	Contrast proportion		Mean brightness	
	shaded images	line drawings	shaded images	line drawings
Arch	0.39	1.00	76.81	197.62
Barrel	0.74	1.00	82.81	230.44
Brick	0.39	1.00	74.98	211.36
Wedge	0.46	1.00	109.22	211.56

4.1.4 *Procedure.* Individual trials were identical to those in experiments 1 and 2. The pigeons were randomly assigned to one of two conditions: the line-drawing (four pigeons) and shaded-image (three pigeons) conditions. Experiment 3 proceeded in two phases: training and testing. In the training phase, the pigeons' pecks were reinforced after correct choices. Correction trials were given after incorrect choices. We used a randomized block design in which each block consisted of five presentations of each of the four training stimuli, for a total of 20 trials in a single block. Sessions comprised eight blocks resulting in 160 trials per day. Each pigeon remained in training until it had reached a criterion of at least 85% correct overall and 80% correct to each of the individual geons for one session (85/80 criterion).

During testing, the pigeons continued to receive differential reinforcement on the training trials. In addition to the training trials, the pigeons were given testing trials on which they received non-differential reinforcement (eg, they were reinforced for any choice response).

(2) These pigeons were also tested in separate testing phases with several other types of stimulus changes unrelated to the current study. The nature of the tests required that we train the pigeons with smaller versions of the original training stimuli used in experiment 1.

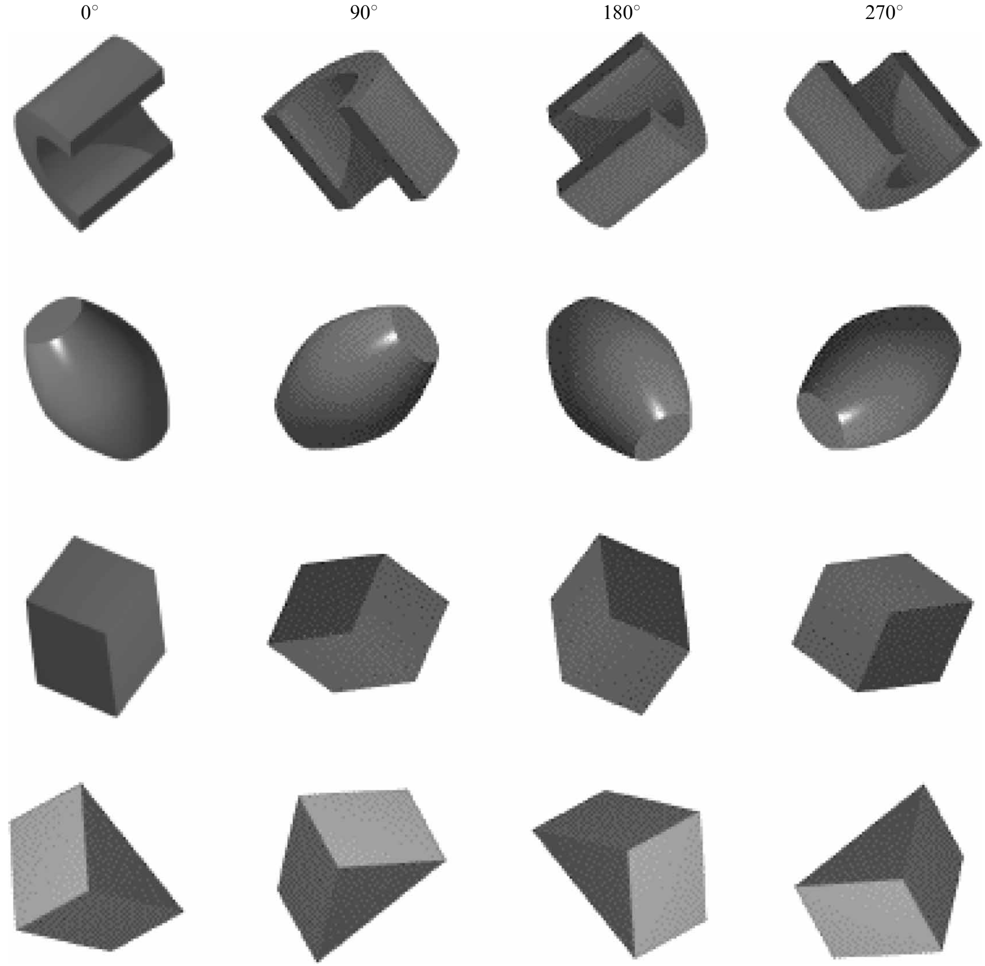
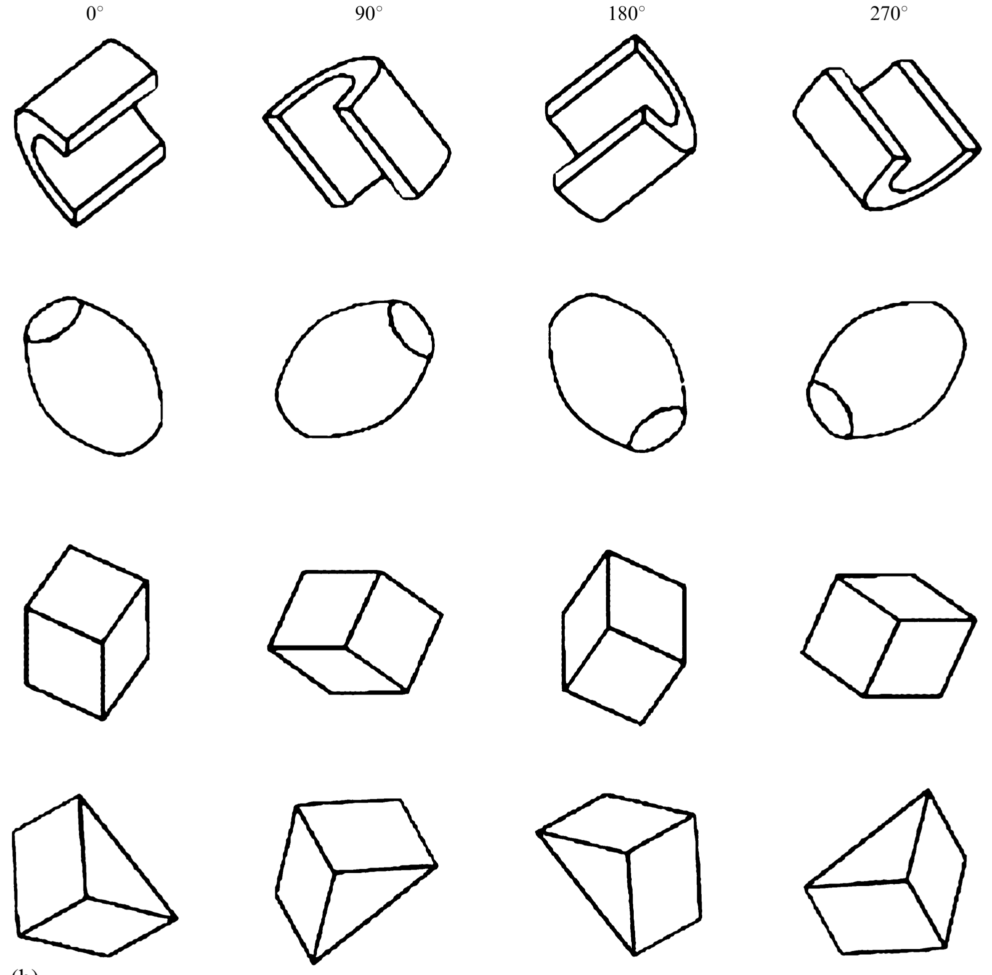


Figure 7. (a) Shaded images of the four geons at the training view and at 90°, 180°, and 270° rotations within the plane used in experiment 3.

We used a randomized-block design. Sessions began with 12 warm-up trials comprising 3 of each of the four training stimuli. For the remainder of the session, blocks contained 35 trials: eight presentations of each of the four training stimuli plus 3 testing stimuli chosen without replacement from the pool of 12 (each of the four objects shown at three planar rotations). Pigeons received four blocks during a session for a total of 152 trials (12 warm-up training trials, 128 training trials, and 12 testing trials). Pigeons were required to meet the 85/80 criterion to the training stimuli for each testing session. If a bird failed to meet the criterion, it was given training sessions until it had again met the 85/80 criterion in one session.

4.2 *Results and discussion*

The pigeons in the shaded-image condition spent a mean of 25 days in training; the pigeons in the line-drawing condition spent a mean of 50 days in training. The pigeons trained with shaded images required 0 days of additional training during the testing phase; the pigeons trained with line drawings required a mean of 5 additional training sessions during the testing phase. Thus, reaching the same level of discrimination took longer for pigeons trained with line drawings, and the line drawing discrimination was more difficult to maintain during the testing phase.



(b)

Figure 7. (b) Line drawings of the four geons at the training view and at 90°, 180°, and 270° rotations within the plane used in experiment 3.

Figure 8 shows the recognition performance of the pigeons in both conditions for the training stimuli and for the 90°, 180°, and 270° planar-rotation testing stimuli. The pigeons in both groups exhibited decrements in recognition performance for the planar-rotation stimuli. For pigeons in the shaded-image condition, the accuracies showed a progressive decrement, falling from 97% correct at the 0° training view to 45% and 50% at the 90° and 270° rotations, respectively, and to 35% at the 180° rotation. Pigeons in the line-drawing condition exhibited a decrement from the training view to the planar rotations, but the decrement was larger at the 90° rotations than at the 180° rotation; for the line-drawing condition, accuracy at the 0° training view was 94%, it was 51% and 52% at the 90° and 270° rotations, respectively, and it was 73% at the 180° rotation. The pigeons in both conditions discriminated reliably above chance (25%) all planar rotations (one-tailed binomial, $p < 0.001$).

To test the significance of these initial observations, the data were analyzed with a repeated-measures ANOVA with rotation (0°, 90°, 180°, and 270°) and geon (arch, barrel, brick, and wedge) as within-subjects variables, and condition (shaded-image versus line-drawing) as a between-subjects variable. The main effect of rotation was significant ($F_{3,15} = 44.11$, $p < 0.0001$), indicating that pigeons exhibited a change in recognition

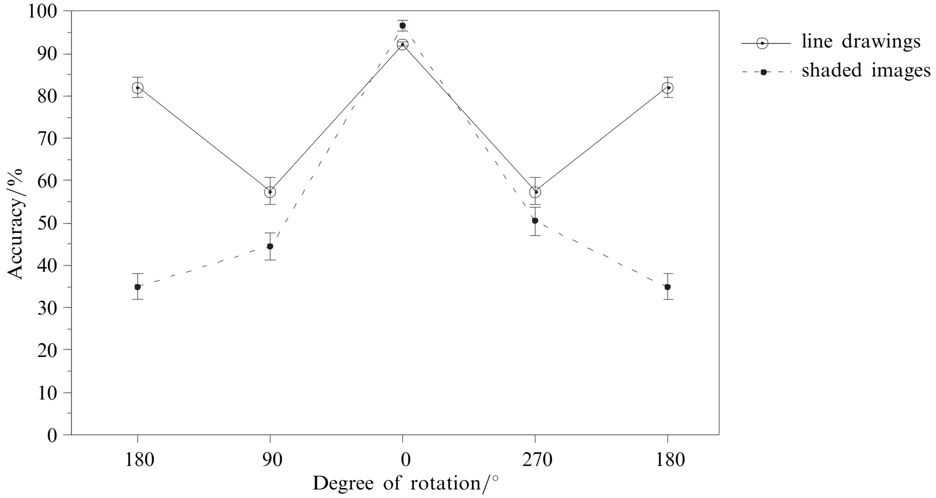


Figure 8. Experiment 3. Accuracy scores at the training view and at the tested 90°, 180°, and 270° planar rotations for the pigeons in the line-drawing condition (solid line) and the shaded-image condition (dashed line). Vertical lines indicate standard error of the mean.

accuracy when the objects were rotated in the picture plane. The main effect of geon was not significant ($F_{3,15} = 0.91$, $p > 0.05$), suggesting that the pigeons showed no difference in their discrimination of the four objects. The main effect of condition was also not significant ($F_{1,5} = 2.00$, $p > 0.05$), indicating that the pigeons in each condition exhibited similar performance overall. The rotation-by-condition interaction was significant ($F_{3,15} = 3.36$, $p < 0.05$), suggesting that the pigeons in the two conditions did not respond similarly at each of the rotations. All other interactions were not significant.

To look more closely at the rotation-by-condition interaction, we performed planned comparisons between the shaded-image and line-drawing conditions at each rotation. The differences were not significant at the 0°, 90°, and 270° rotations ($t = -1.23$, $t = 0.49$, $t = 0.09$, respectively, $p > 0.05$); however, there was a significant difference at the 180° rotation ($t = 2.95$, $p < 0.01$), indicating that pigeons in the line-drawing condition did perform significantly better than pigeons in the shaded-image condition at the 180° rotation.

Pigeons trained with line drawings were better able to generalize to 180° planar rotations than pigeons trained with shaded images. The pigeons in the shaded-image condition exhibited a large recognition decrement for all three planar rotations, with the largest decrement for the 180° rotation. Thus, the pigeons trained with shaded images showed a linear generalization gradient, with accuracy decreasing as the objects were rotated farther from the original trained rotation. The pigeons in the line-drawing condition, however, exhibited a smaller recognition decrement for the 180° rotation than would be expected if the generalization gradient were linear. Reynolds (1961) reported a similar result with pigeons trained with an isosceles triangle. He found that when pigeons were reinforced for two rotations 36° apart, they exhibited more generalization to the inverted version of the reinforced rotation than to the nearest rotations.

These data again suggest that pigeons do not automatically rely on edges in a visual-recognition task involving shaded images. For pigeons trained with shaded images, the evidence suggests that they attend to surface properties of the objects and do not place much importance on object edges. In contrast, pigeons trained with line drawings must attend exclusively to the edges, as this is all they are shown. Indeed, the markedly faster learning of the pigeons in the shaded-image condition attests to the advantage of the cues available in shaded images.

This experiment may also help to explain the inconsistent results reported in the literature for the pigeons' recognition performance when they are shown planar rotations of stimuli. The data reported here do not accord with those of Hollard and Delius (1982), and Delius and Hollard (1995); these authors reported that pigeons exhibited no decrease in accuracy for planar rotations of two-dimensional objects. However, their objects were simple silhouettes with no internal structure. In contrast, Hamm et al (1997) found a significant decrement for the planar rotation of line drawings of three-dimensional objects. Similar to Hamm et al, we found a significant reduction in accuracy for planar rotations of both line drawings and shaded images, although this decrease was not identical across stimulus types. Our findings suggest that the type of stimulus biases the pigeon to attend to different properties of the objects, which can lead to performance differences when the objects are rotated. It is also likely that the nature of the discrimination task influences the visual properties to which the birds attend. Evidently, the combination of these factors can produce disparate results.

5 General discussion

In this study, we explored the possibility that pigeons similarly process line drawings and shaded images of the same objects. In experiment 1, pigeons trained with five views of each object did not show any greater generalization to line drawings than pigeons trained with only a single view. Thus, the formation of a more general representation did not help the pigeons see the line drawings as similar to the shaded images of the same objects.

In experiment 2, the pigeons' ability to perceive any correspondence between line drawing and shaded image of the same object was tested. Despite the potential advantage of processing these two stimulus types as perceptually equivalent, the pigeons treated the line drawing and shaded image as completely independent representations.

In experiment 3, pigeons were first trained with either line drawings or shaded images and they were later tested with planar rotations of the original stimuli. The pigeons exhibited a systematic, linear decrease in accuracy to the shaded images. The pigeons trained with line drawings showed a decrease in accuracy to the 90° and 270° rotations similar to the birds trained with shaded images; but, the birds trained with line drawings performed significantly more accurately than the birds trained with shaded images at the 180° rotation.

The nonlinear generalization to 180° planar rotations that we found in experiment 3 has been reported in human studies as well. In several experiments with line drawings of objects, researchers have reported faster reaction times for a 180° rotation than would be expected if the subjects were using a linear transformation, such as mental rotation (Jolicoeur 1985; Kanamori and Yagi 2002; Murray 1997). To explain this improved performance at the farthest rotation, Murray (1997) proposed that, for 180° rotations, people used a flipping strategy to mentally rotate the objects in depth, rather than mentally rotating the objects in the plane. Murray hypothesized that the flipping strategy was more efficient than rotating in the plane, thus leading to decreased reaction times at 180°. At rotations other than the 180°, it is not possible to easily rotate the object in depth to transform it; consequently, in order to maximise efficiency, people should continue to use mental rotation in the plane at other rotations. As evidence for this hypothesis, Murray reported that, when people were explicitly instructed to mentally rotate objects in depth (flipping), they responded significantly faster than when they were instructed to rotate the objects in the plane.

An alternative view why a 180° planar rotation enjoys an advantage over nearby lesser rotations, eg 135°, was proposed by Hummel and Biederman (1992). They argued that the two-dimensional orientation of features (eg, vertical, horizontal, or diagonal) disrupted at lesser rotations, is restored at 180°; thus, a vertical geon or contour becomes vertical again.

To our knowledge, no one has looked at the 180°-rotation effect by directly comparing line drawings to other types of representations. Most researchers examining this phenomenon in humans and nonhumans have used line drawings of objects. Interestingly, we found that pigeons trained with shaded images did not exhibit increased generalization to the 180° rotation. So, for pigeons at least, increased generalization at 180° appears to be specific to impoverished representations, such as line drawings and other clearly two-dimensional stimuli.

It is unclear whether this disparity in 180° recognition performance is specific to pigeons or if it holds true for other organisms as well. In one suggestive study, Jolicoeur (1985, experiment 1) tested humans with line drawings that had been hand-colored by an artist; he did not find the typical decrease in reaction times at 180°; instead, he found a small decrease at 240°. Jolicoeur's results suggest that organisms may use different strategies for planar rotation of images that are more complex than line drawings. Additional comparative research is necessary to address this question.

Our finding of a nonlinear effect of planar rotation for line drawings and a linear effect of planar rotation for shaded images is not easily explained by Murray's theory of flipping in depth (1997). Flipping the object in depth should be equally efficient for line drawings and shaded images. Indeed, one might argue that the pigeons should be more likely to flip objects in depth when they are shown fully-shaded images because of the enhanced three-dimensional appearance of these stimuli.

The Hummel and Biederman (1992) account would appear to be more compatible with our results. With crude line-orientation detectors, there should be more similarities between the original and the 180° rotation than any other rotation. However, the shaded images contain considerable visual information in addition to line segments, such as shading and texture, to which the pigeons might have preferentially attended. These surface features are not necessarily strongly oriented, so the restoration of their orientation might not be sufficient to affect discriminative performance.

In support of a simple perceptual account, Vetter and Hearst (1968) studied the effects of planar rotation using parallelograms. They trained one group of pigeons with the parallelogram oriented so that it resembled a diamond shape (the diagonals parallel to the horizontal or vertical plane; see the stimulus in figure 9a for an example) and a second group of pigeons with the parallelogram oriented so that it more closely resembled a rectangle (two of the four sides parallel with the horizontal or vertical plane; see the stimulus in figure 9b for an example). Vetter and Hearst found that birds trained with diamond-shaped stimuli generalized more to rotations that also had parallel diagonals, whereas birds trained with stimuli resembling rectangles generalized more to other rotations in which the sides were parallel. This occurred even though the similarly shaped parallelograms were farther from the trained view (90° planar rotation) than the other tested rotations (40° to 50° from the trained view). Thus, in Vetter and Hearst's study, the pigeons exhibited better generalization to rotations in which the

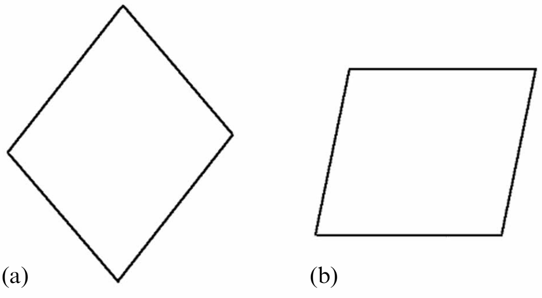


Figure 9. Examples of stimuli similar to those used by Vetter and Hearst (1968). (a) Parallelogram with the diagonals parallel. (b) Parallelogram with the sides parallel.

orientation of the edges aligned with the training stimulus, rather than to those which were closer rotations to the training stimulus.

We can also assess an account of edge orientation rather than mental flipping by comparing response accuracy to the line drawings and shaded images of the different objects used in experiment 3. Although these stimuli were not designed to explicitly test a perceptual account of the 180° performance difference, they can be informally compared. Because the barrel and the brick are bilaterally symmetrical, they are likely to have line segments that align at the 0° and 180° viewpoints. The wedge and the arch, however, are both asymmetrical for one axis, and consequently should involve fewer line segments that align. Thus, we should see a greater performance disparity between the line drawings and the shaded images at 180° for the barrel and brick stimuli. In our analysis of the data from experiment 3, the interaction of geon and rotation was not significant ($F_{9,45} = 1.64$, $p = 0.13$). However, the data do suggest a trend in the predicted direction. Figure 10 shows the disparities in accuracy scores between the line drawings and shaded images at 180° for all 4 geons; clearly, the greatest disparities are for the barrel and brick (50% and 60%, respectively). The disparity at 180° is smallest for the arch (4%) and somewhat greater for the wedge (37%). These data suggest that there may be a relationship between the alignment of contours or line segments and performance at the 180° rotation.

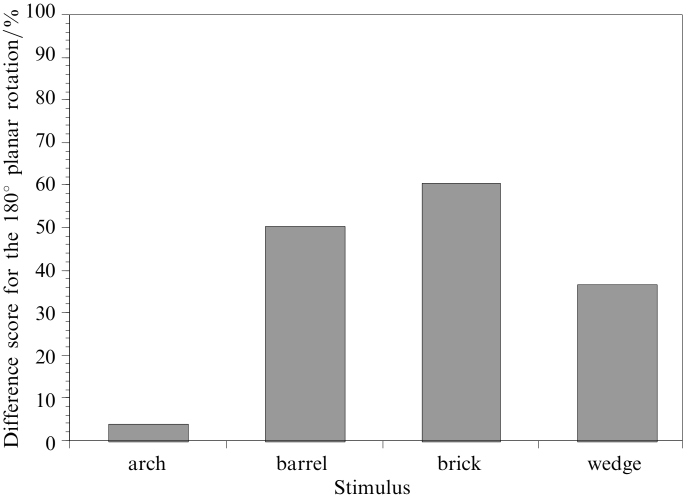


Figure 10. The difference score for the 180° planar rotation (the accuracy for the line-drawing condition minus the accuracy for the shaded-image condition) for the four different geons in experiment 3.

It has been found earlier that the pigeon is capable of generalizing performance across depth-rotated views in an object-recognition task (Cook and Katz 1998; Peissig et al 1999, 2000; Spetch et al 2001; Wasserman et al 1996). Peissig et al (2002) reported that this generalization even extends to views in a rotational axis that is orthogonal to the training axis. As well as pigeons transferring across depth rotations, Young et al (2001) found that pigeons generalize recognition performance to silhouettes of objects and across changes in lighting direction and contrast. It is clear from the present study, however, that the pigeon's talent for pictorial generalization does not extend to line drawings (also see Wasserman et al 1996).

Previous researchers using various types of stimuli and procedures have reported that pigeons do not readily treat line drawings as equivalent to real objects or to realistic-looking depictions of objects (Cabe 1976; Cabe and Healey 1979; Cerella 1977; Cook et al 1990; Lombardi and Delius 1988; Lumsden 1977; Young et al 2001). The measures used in these past studies, however, may not have been adequate for detecting subtle effects.

In experiment 1, we trained pigeons with multiple views to help them form a more general object representation; nevertheless, the pigeons still did not exhibit significant generalization to line drawings. In experiment 2, we used a different task, which did not test for stimulus equivalence; instead, we explored whether pigeons perceived any similarity between the line drawings and the shaded images. It is clear from the results that they did not. Additionally, in experiment 3, we demonstrated that pigeons trained with line drawings form a different type of visual representation than pigeons trained with shaded images, indicating that pigeons do not preferentially process object edges.

One explanation for these data is that, given the availability of surface cues, pigeons do not employ the edges in great enough detail to see that they are similar to the corresponding line drawings. It is not that the pigeon lacks the resolution to perceive the lines; pigeons manifest very high acuity (Hodos et al 1976; Nye 1968). So, the pigeon should be capable of perceiving the line drawings in enough detail to respond accurately. This conclusion is also supported by previous studies in which pigeons discriminated among several different line drawings (Wasserman et al 1993, 1996) as they did in this study.

Investigations testing contrast sensitivity in pigeons have shown that pigeons are quite good at detecting high-contrast stimuli, but that they are much poorer than humans at detecting low-contrast stimuli (Hodos 1993; Hodos et al 2002; Jassik-Gerschenfeld and Hardy 1979). Pigeons have greater difficulty perceiving the differences between areas of similar contrast. One explanation for our data is that the birds used the overall level of brightness to discriminate individual stimuli. Consequently, when they were shown line drawings, which contain very different mean brightness levels than shaded images (see tables 1 and 2), they were unable to accurately respond. To test this hypothesis, we performed a logistic regression using the brightness data of the five views of each object used in experiment 1 (see table 1) to predict whether the views were classified as arch, barrel, brick, or wedge. Brightness could be used as an accurate predictor of class ($\chi^2_{3,20} = 4666.29$, $p < 0.01$): all five wedges were correctly classified, all five arches and all five bricks were classified as bricks, and three barrels were correctly classified (-144, 144, and 72) whereas two others (0 and -72) were classified as bricks.

We examined the first 20 days of training for three of the four birds in the five-views group in experiment 1 to determine the most likely choice for each stimulus type for each pigeon.(3) For the pigeons, all five wedges, all five bricks, and all five barrels were correctly classified by all three birds. The arch proved the most problematic, but it was more likely to be confused with the much brighter wedge than with the more similar brick. A logistic regression of the birds' choice behavior as a function of brightness confirmed the low agreement ($R^2 = 0.085$). These data suggest that pigeons were not performing the discrimination using only overall stimulus brightness, and therefore brightness differences cannot explain the pigeons' inability to generalize to line drawings.

Further evidence that overall stimulus brightness was not responsible for the pigeons' behavior is the response observed in experiment 3, when pigeons were shown planar rotations of the stimuli. Planar rotations do not alter stimulus brightness; however, the pigeons exhibited significant decreases in response accuracy as the objects were rotated away from the 0° orientation (see figure 8).

Another explanation for these findings is that, when available, pigeons used the patterns of shading within the image, rather than edges, to perform the recognition task. In shaded images, the internal edges are defined by slight variations in contrast. Thus, owing to the pigeons' greater difficulty in perceiving the edges within these objects, they instead used the locations of the light and dark areas to solve the task. In the case of line drawings, however, pigeons are unable to use shading information, so they must rely on information about the locations of the line segments. This task

(3) The training data for the fourth bird were lost owing to a technical error.

is aided by the increased contrast between the line segments and the internal space. The longer learning period required by pigeons trained with line drawings suggests that the available cues were less salient for the pigeons' visual-discrimination system than those present in shaded images.

5.1 *Concluding comments*

The primary goal of our study was to determine whether pigeons might use edges to perform object recognition tasks, by investigating whether pigeons similarly process line drawings and shaded images. As noted in the introduction, many theories of object recognition propose that edge detection is essential for recognition in primates (Biederman 1987; Marr and Nishihara 1978). Both human and nonhuman primates generalize from real objects or photographs of real objects to line drawings of objects. It is possible that, for pigeons and other non-primate species, surface characteristics are more important than shape for object recognition. Pecking at a food morsel, determining that a surface is a liquid, or finding nesting material are tasks which may place greater importance on surface and/or material properties than on the edges that provide definite boundaries for these entities. Biederman (1987) noted that the linguistic distinction between count and mass concrete nouns generally indicates whether the entity can be distinguished by its boundaries, such as 'chairs' or 'elephants', or by its surface properties (ie, color and texture), such as 'snow' or 'grass'. Pigeons may live in a world where the entities denoted by mass nouns assume center stage.

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References

Bergevin R, Levine M D, 1993 "Generic object recognition: Building and matching coarse descriptions from line drawings" *IEEE Transactions on Pattern Analysis and Machine Intelligence* **15** 19 – 36

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

Biederman I, Ju G, 1988 "Surface versus edge-based determinants of visual recognition" *Cognitive Psychology* **20** 38 – 64

Brooks R A, 1981 "Symbolic reasoning among 3-D models and 2-D images" *Artificial Intelligence* **17** 285 – 348

Cabe P A, 1976 "Transfer of discrimination from solid objects to pictures by pigeons: A test of theoretical models of pictorial perception" *Perception & Psychophysics* **19** 545 – 550

Cabe P A, Healey M L, 1979 "Figure – background color differences and transfer of discrimination from objects to line drawings with pigeons" *Bulletin of the Psychonomic Society* **13** 124 – 126

Cerella J, 1977 "Absence of perspective processing in pigeons" *Pattern Recognition* **9** 66 – 68

Cook R G, Katz J S, 1998 "Dynamic object perception by pigeons" *Journal of Experimental Psychology: Animal Behavior Processes* **25** 194 – 210

Cook R G, Wright A A, Kendrick D F, 1990 "Visual categorization by pigeons", in *Behavioral Approaches to Pattern Recognition and Concept Formation* Eds M L Commons, R J Herrnstein (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 187 – 214

Delius J D, Hollard V D, 1995 "Orientation invariant pattern recognition by pigeons (*Columba livia*) and humans (*Homo sapiens*)" *Journal of Comparative Psychology* **109** 278 – 290

Hamm J, Matheson W R, Honig W K, 1997 "Mental rotation in pigeons (*Columba livia*)?" *Journal of Comparative Psychology* **111** 76 – 81

Hochberg J, Brooks V, 1962 "Pictorial recognition as an unlearned ability: A study of one child's performance" *American Journal of Psychology* **75** 624 – 628

Hodos W, 1993 "The visual capabilities of birds", in *Vision, Brain, and Behavior in Birds* Eds H P Zeigler, H J Bischof (Cambridge, MA: MIT Press) pp 25 – 46

Hodos W, Ghim M M, Potocki A, Fields J N, Storm T, 2002 "Contrast sensitivity in pigeons: a comparison of behavioral and pattern ERG methods" *Documenta Ophthalmologica* **104** 107 – 118

Hodos W, Leibowitz R W, Bonbright J C Jr, 1976 "Near-field visual acuity of pigeons: Effects of head position and luminance" *Journal of the Experimental Analysis of Behavior* **25** 129 – 141

Hollard V D, Delius J D, 1982 "Rotational invariance in visual pattern recognition by pigeons and humans" *Science* **218** 804 – 806

Hummel J E, Biederman I, 1992 "Dynamic binding in a neural network for shape recognition" *Psychological Review* **99** 480 – 517

Jassik-Gerschenfeld D, Hardy O, 1979 "Single-neuron responses to moving sine-wave gratings in the pigeons optic tectum" *Vision Research* **19** 993 – 999

Jolicoeur P, 1985 "The time to name disoriented natural objects" *Memory & Cognition* **13** 289 – 303

Kanamori N, Yagi A, 2002 "The difference between flipping strategy and spinning strategy in mental rotation" *Perception* **31** 1459 – 1466

Kovács G, Sáry G, Köteles K, Chadaide Z, Tompa T, Vogels R, Benedek G, 2003 "Effects of surface cues on macaque inferior temporal cortical responses" *Cerebral Cortex* **13** 178 – 188

Lombardi C M, Delius J D, 1988 "Pattern recognition invariance in pigeons (*Columba livia*)" *International Journal of Comparative Psychology* **2** 83 – 102

Lowe D G, 1987 "Three-dimensional object recognition from two-dimensional images" *Artificial Intelligence* **31** 355 – 395

Lumsden E A, 1977 "Generalization of an operant response to photographs and drawings/silhouettes of a three-dimensional object at various orientations" *Bulletin of the Psychonomic Society* **10** 405 – 407

Macko K A, Hodos W, 1985 "Near point of accommodation in pigeons" *Vision Research* **25** 1529 – 1530

Marr D, Nishihara H K, 1978 "Representation and recognition of the spatial organization of three-dimensional shapes" *Proceedings of the Royal Society of London, Series B* **200** 269 – 294

Murray J, 1997 "Flipping and spinning: Spatial transformation procedures in the identification of rotated natural objects" *Memory & Cognition* **25** 96 – 105

Nye P, 1968 "The binocular acuity of the pigeon measured in terms of the modulation transfer function" *Vision Research* **8** 1041 – 1053

Peissig J J, Wasserman E A, Young M E, Biederman I, 2002 "Learning an object from multiple views enhances its recognition in an orthogonal rotational axis in pigeons" *Vision Research* **42** 2051 – 2062

Peissig J J, Young M E, Wasserman E A, Biederman I, 1999 "The pigeon's perception of depth-rotated shapes" *Current Psychology of Cognition* **18** 657 – 690

Peissig J J, Young M E, Wasserman E A, Biederman I, 2000 "Seeing things from a different angle: The pigeon's recognition of single geons rotated in depth" *Journal of Experimental Psychology: Animal Behavior Processes* **26** 115 – 132

Reynolds G S, 1961 "Contrast, generalization, and the process of discrimination" *Journal of the Experimental Analysis of Behavior* **4** 289 – 294

Snodgrass J G, Vanderwart M, 1980 "A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity" *Journal of Experimental Psychology: Human Learning and Memory* **6** 174 – 215

Spaetch M L, Friedman A, Reid S L, 2001 "The effect of distinctive parts of recognition of depth-rotated objects by pigeons (*Columba livia*) and humans" *Journal of Experimental Psychology: General* **130** 238 – 255

Vetter G H, Hearst E, 1968 "Generalization and discrimination of shape and orientation in the pigeon" *Journal of the Experimental Analysis of Behavior* **11** 753 – 765

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

Wasserman E A, Kirkpatrick-Steger K, Van Hamme L J, Biederman I, 1993 "Pigeons are sensitive to the spatial organization of complex visual stimuli" *Psychological Science* **4** 336 – 341

Young M E, Peissig J J, Wasserman E A, Biederman I, 2001 "Discrimination of geons by pigeons: The effect of variation in surface depiction" *Animal Learning & Behavior* **29** 97 – 106

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