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Figure–ground assignment in pigeons: Evidence for a figural benefit

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Four pigeons discriminated whether a target spot appeared on a colored figural shape or on a differently colored background by first pecking the target and then reporting its location: on the figure or the background. We recorded three dependent variables: target detection time, choice response time, and choice accuracy. The birds were faster to detect the target, to report its location, and to learn the correct response on figure trials than on background trials. Later tests suggested that the pigeons might have attended to the figural region as a whole rather than using local properties in performing the figure–background discrimination. The location of the figural region did not affect figure–ground assignment. Finally, when 4 other pigeons had to detect and peck the target without making a choice report, no figural advantage emerged in target detection time, suggesting that the birds' attention may not have been automatically summoned to the figural region.

Every moment of their lives, organisms from pigeons to people are bombarded by a wide variety of visual stimuli. Some of these stimuli are relevant to current circumstances and goals, whereas others are not. How does the visual system distinguish relevant from irrelevant stimuli? One adaptive strategy may be to establish which visual regions are figures and which are backgrounds. Figures correspond to objects that should be attended to, recognized, and acted on, whereas backgrounds correspond to the spaces between objects and should be ignored. Thus, knowing which regions are figures and which are grounds potentially restricts visual processing to a manageable subset of the full visual field (e.g., Feldman, 2003; Vecera, Flevaris, & Filapek, 2004; Vecera, Vogel, & Woodman, 2002).

Figure–ground segregation was first investigated by Rubin (1915/1958), who found that some visual regions have a strong tendency to be perceived as figures (also see Bahnsen, 1928). Rubin, as well as other Gestalt psychologists, identified a number of cues ("laws") that distinguished figures from grounds. For example, people tend to perceive as figures regions that are small in area, symmetric, convex, and surrounded, to list a few (see Palmer, 1999, 2002, for reviews). Many other cues have been added since this early work, including the following: spatial frequency, in which high-spatial-frequency regions are perceived as figures (Klymenko & Weisstein, 1986); temporal frequency, in which high-temporal-frequency regions are perceived as figures (Klymenko, Weisstein, Topolski, & Hsieh, 1989; Lee & Blake, 1999); top-bottom polarity, in which regions with wide bases are perceived as figures (Hulleman & Humphreys, 2004); and "lower region," in which areas in the lower portion of a stimulus display are perceived as figures (Vecera et al., 2002). Additionally, figure–ground discrimination can be affected by high-level visual processes. Familiar objects tend to be perceived as figures; hence, object recognition processes can influence figure–ground assignment (see Peterson, 1994, 1999; Peterson & Gibson, 1991, 1993; Peterson, Harvey, & Weidenbacher, 1991; Rock, 1975; Vecera & O'Reilly, 1998, 2000). Spatial attention also can influence figure–ground assignment: Regions to which attention is automatically summoned are perceived as figures (Vecera et al., 2004).

Given this extensive research on human figure–ground segregation, the obvious question arises: Are nonhuman animals also able to discriminate figure from ground? Neurobiological evidence suggests that neurons in primate visual cortex may be sensitive to figure–ground status. Lamme and colleagues (Lamme, 1995; Supèr, Spekreijse, & Lamme, 2001) trained rhesus monkeys to identify a figural region (defined by common orientation of line segments or by common motion) by making a saccadic eye movement toward its position. Neurons in primary visual cortex, area V1, were found to fire more rapidly when the element activating their receptive fields was located within a figural region than when it was located within a background region (but see Rossi, Desimone, & Ungerleider, 2001). Moreover, when rhesus monkeys were anesthetized, enhanced responding to the figural region disappeared, whereas the properties of the receptive fields remained unaffected. This pattern of results suggests that sensitivity to figure–ground status may critically depend on integrated visual information that is only available to

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the awake animal (Lamme, Zipser, & Spekreijse, 1998). Other evidence suggests that the responses of edge-sensitive neurons in areas V1 and V2 are determined by the side of the figural region to which this edge belongs, again suggesting that figure–ground assignment occurs relatively early in the course of visual processing (Zhou, Friedman, & von der Heydt, 2000). This evidence is consistent with a model of figure–ground assignment proposed by Vecera and O'Reilly (1998, 2000) that presumes separate processes for edge detection and for figure–ground assignment.

Recent studies suggest that avian and mammalian visual systems are functionally highly similar despite significant anatomical differences (Jarvis et al., 2005; Medina & Reiner, 2000). It is hardly surprising, therefore, that some early visual processes in birds are analogous to those in mammals, at least on the behavioral level. Odd-item search and texture segregation provide particularly good examples. When trained to detect a single odd item among uniform distractors, pigeons' search time and accuracy reflect the similarity of the target and the distractors: If the target is highly discriminable from the distractors, then the pigeons' detection time does not increase with an increase in the number of the distractors (Blough, 1989). Pigeons trained to discriminate the odd region in a texture display do so more accurately when the visual elements come from the same dimension (e.g., color) than when the visual elements are represented by a conjunction of features (e.g., color and shape). Moreover, pigeons were able to detect texture differences within 100 msec, implying that texture discrimination and perceptual grouping are early processes in pigeon vision, just as they are in human vision (Cook, B. R. Cavoto, Katz, & K. K. Cavoto, 1997; Cook, K. K. Cavoto, & B. R. Cavoto, 1996). Although there seem to be differences in later visual processing in pigeons and people (e.g., perception of 2-D occlusion; see DiPietro, Wasserman, & Young, 2002; Fujita, 2001; Sekuler, Lee, & Shettleworth, 1996), we believe that a visual process as fundamental as figure–ground assignment is likely to be similar for pigeons and people.

Unfortunately, little research has directly explored this question. In categorization studies, pigeons have often been found to attend to background regions instead of (or in addition to) the target object (Edwards & Honig, 1987; Goto & Lea, 2003). But, the stimuli in these experiments were photographs of complex visual scenes, in which one object was designated by the experimenter as the target; for example, a person (target object) could be photographed on the street, inside a building, or in the park. Such stimuli contain a large number of potential figural regions, besides the target object.

More closely related to figure–ground segregation was a study by Herrnstein, Vaughan, Mumford, and Kosslyn (1989), who presented pigeons with a closed white outline filled with a bright red interior on a black background. A white dot could be placed either inside or outside the white outline. Pigeons were trained via food reinforcement to peck a response key when the dot fell inside the figure and to withhold pecking when the dot fell outside the figure on the ground (or vice versa for different birds). The pigeons learned the task only when the outline's interior was red and its exterior was black. When the outline's interior and exterior were both black, the pigeons did not learn to discriminate figure from background, suggesting that local color differences—not figure–ground status—supported the pigeons' learning. Additionally, Herrnstein et al.'s go/no-go procedure did not permit direct comparison of figure and ground responses, either in terms of accuracy or response time (RT). Thus, this method cannot fully reveal the behavioral consequences of figure–ground assignment that human observers exhibit, such as an advantage for detecting targets on figures over those on grounds (Nelson, 2003; Palmer, Nelson, & Brooks, 2001).

Thus, our goal was to explore figure–ground assignment in pigeons. If both birds and primates exhibit common figure–ground effects, then figure–ground processes (1) are phylogenetically old, (2) reflect environmental regularities that similarly mold the visual system through experience, or (3) are some combination of the two above processes. Furthermore, a clear behavioral demonstration of figure–ground discrimination in pigeons would provide added support for the idea that nonhuman animals can use objects as units of attention. Obtaining such behavioral evidence was one aim of our study.

A second aim was to train the figure–ground discrimination in such a way as to provide a means for directly comparing "figure" and "background" responses in terms of both accuracy and RT. We taught pigeons in Experiment 1 to discriminate whether a small yellow target was located on the figure or on the background. Two well-known Gestalt cues—area and surroundedness—defined the figure in the displays. The targets were shown equally often on the figure and on the background, so that the location of the figure could not serve as a cue for the location of the target. Furthermore, the colors of the figure and the background were randomly reversed from trial to trial, so that color alone could not serve as the cue for figure or background assignment.

The pigeons were required to peck the target to progress through each trial. This requirement ensured that the birds were attending to the target and provided a first measure of the pigeons' performance—target detection time (TDT). On completion of the target detection response, two choice keys were shown, and the pigeons were required to select one of them on the basis of whether the target was on the figure or on the background. Thus, we obtained two additional performance measures: choice response time (CRT) and choice accuracy.

If pigeons are inclined to attend to the figure rather than to the background, then they ought to be faster to detect the target when it is located on the figure than when it is located on the background. Pigeons might also learn more quickly to make the correct response on figure trials than on background trials. Finally, pigeons might be faster to make a choice response on figure trials than on background trials. Any of these outcomes would suggest that objects may have a special status for avian visual attention, as they do for human visual attention.

EXPERIMENT 1

Method

Subjects

The subjects were 4 feral pigeons (*Columba livia*) maintained at 85% of their free-feeding weights by controlled daily feeding. Grit and water were available ad lib in their home cages. The pigeons had served in unrelated studies prior to the present project.

Apparatus

The experiment used four 36 × 36 × 41 cm operant conditioning chambers detailed by Gibson, Wasserman, Frei, and Miller (2004). The boxes were located in a dark room with continuous white noise. The stimuli were presented on a 15-in. LCD monitor located behind an AccuTouch resistive touchscreen (Elo TouchSystems, Fremont, CA). A food cup was centered on the rear wall level with the floor. A food dispenser delivered 45-mg food pellets through a vinyl tube into the cup. A houselight on the rear wall provided illumination during the session. Each chamber was controlled by an Apple iMac computer. The experimental procedure was programmed in HyperCard (Version 2.4). An 8.5-cm square, or button, in the middle of the screen was used to display the stimuli. Two black Macintosh icons, a palette and a compass, on white backgrounds served as 2.0-cm square report buttons. Four additional 0.9-cm square yellow buttons were used as targets (see below). The rest of the screen was black.

Stimuli and Design

We used stimulus displays similar to those of Vecera et al. (2002). Each display contained a figural region (height = 4.2 cm, width = 6.5 cm, total area = 19.5 cm^2) in the shape of a "cityscape" placed on top of a square background (height = 8.5 cm, total area = 72.3 cm^2). On three sides, the figure was located 1.1 cm from the edge of the display; on the fourth side, it was located 3.2 cm from the edge of the display. Two Gestalt cues—area and surroundedness—thus distinguished the figure from the background. Figure 1A shows that the figural region could be located in the top, bottom, left, or right portion of the square background.

We used four slightly different cityscape figures of the same area to produce 16 unique stimulus displays. For each stimulus display, there were four randomized locations of the target. Finally, the colors of the figure and the background (red or green) were randomly reversed as well. Thus, there were 128 unique combinations of stimulus display and target location in training. Note finally that the target was presented equally often on the figure and on the background; thus, the location of the target was not cued by the location of the figure.

Procedure

Pretraining. After weight reduction, the birds began pretraining, during which they had to peck at a square, 8-cm button colored red, green, yellow, or blue to obtain food. Later, the pigeons were trained to peck at the 1-cm yellow target button that was randomly presented in the center of the screen or in the upper left, upper right, lower left, or lower right corners.

Acquisition. Following pretraining, the birds entered the training phase, in which they were taught to discriminate whether the target appeared on the figure or the background. Figure 1B illustrates the sequence of events in the course of a training trial. At the beginning of a trial, the pigeons were shown a black cross in the center of the white display screen. Following one peck anywhere on the white display, the training stimulus display and the target simultaneously appeared. The pigeons had to satisfy an observing response requirement (from 4 to 10 pecks) to the target button. This requirement was adjusted to the performance of each pigeon. If the bird was consistently pecking, but not meeting the figure–background discrimination criterion (see below) in a timely fashion, then the number of pecks was increased to make incorrect responses more punishing. The time from the onset of the stimulus display to the first peck at the target button (the TDT) was recorded.

On completion of the observing requirement, the two report keys appeared to the left and right of the stimulus display; the pigeon

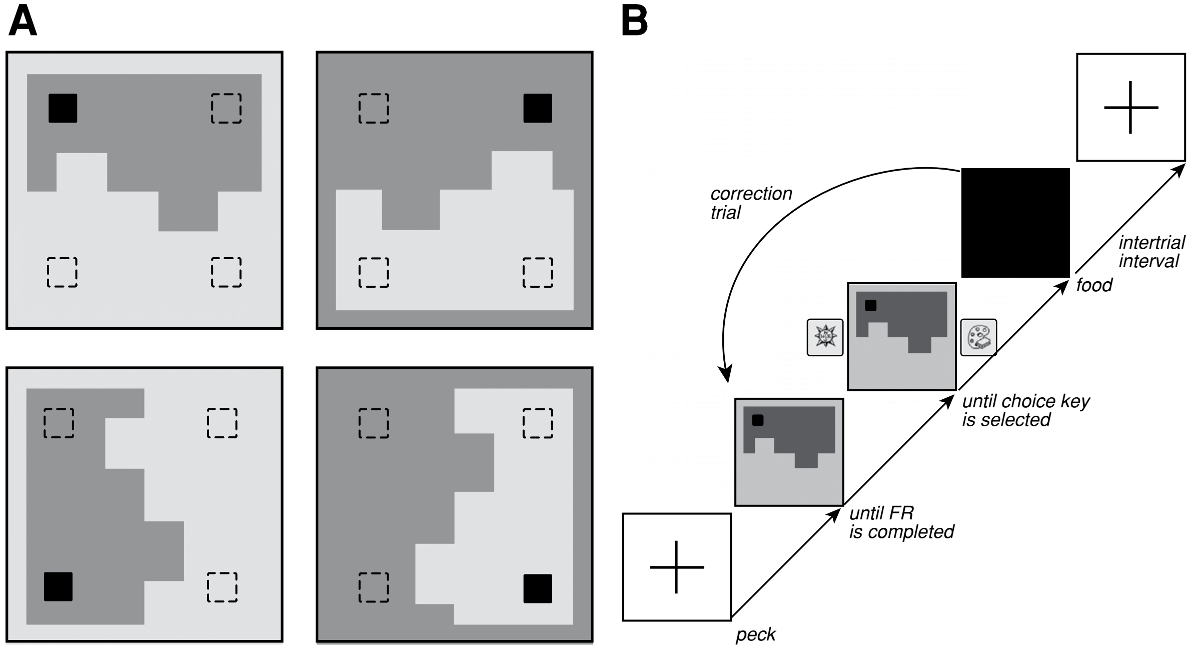

Figure 1. Examples of the stimulus layout (A) and the sequence of events in the course of a training trial (B). Dashed lines in (A) indicate the other potential locations of the yellow target spot. The figure and background colors were randomly red and green.

had to select one of them. The time from the onset of the report keys to the pigeon's first response (the CRT) was recorded. For 2 birds, the left key represented a "figure" response and the right key represented a "background" response; the assignment was reversed for the other 2 birds. If the report response was correct, then food reinforcement was delivered and the intertrial interval (ITI) ensued. The ITI randomly ranged from 18 to 21 sec. If the report response was incorrect, then the houselight darkened and a correction trial was given. On correction trials, the ITI randomly varied from 21 to 24 sec. Correction trials were given until the correct report was made. Only the first report response of a trial was scored and used in data analysis, although correction trials were recorded as well. Occasional incomplete sessions were not used in data analysis; such sessions were most likely at the start of training when errors were most frequent.

In training, each session comprised one block of 128 trials, so that each combination of stimulus display and target location was shown once per session. The pigeons were required to meet an 85/80 criterion: 85% correct overall and 80% correct to each of the eight subgroups of stimuli (four targets located either on the figure or on the background). However, one of the birds failed to reach this criterion in 60 training sessions. So, the criterion level for this pigeon was slightly lowered to 75% correct to each of the eight subgroups of stimuli and 80% correct overall.

Maintenance. After training ended, all 4 birds were exposed to a series of tests (described in the Method sections of Experiments 2 and 3, below) over an average of 90 sessions. Thereafter, the birds were retrained for 35 sessions using the same procedure as during acquisition in order to see whether the differences in performance observed in acquisition were preserved more than 3 months later, after accuracy on both figure and background trials had reached asymptote. (In maintenance, mean accuracy was 94.8% ± 0.2% correct on figure trials and 90.7% ± 0.3% correct on background trials.)

Behavioral measures. We explored differences in responding on figure trials and on background trials by examining three dependent measures: choice accuracy, TDT, and CRT. We analyzed the CRT scores only on correct trials in order to minimize the contribution of any speed–accuracy trade-offs. We included all trials when analyzing the TDT scores, since statistical analysis revealed the same pattern of responding on both correct and incorrect trials. Both TDT and CRT scores were subjected to log-transformation before the statistical analyses. Alpha was then set at .05 for all statistical tests.

Results

The pigeons rapidly acquired the figure–ground discrimination. Training took a mean of 30.0 sessions, with a minimum of 13 sessions and a maximum of 66 sessions. To analyze acquisition, we constructed Vincent learning curves by grouping the training sessions into 6 blocks of 2 sessions (for 2 pigeons), 4 sessions (for 1 pigeon), or 10 sessions (for 1 pigeon) and by placing any remaining sessions into Block 4 (Kling & Riggs, 1971). We then separately calculated the percentage of correct responses on figure and background trials and used these scores for further analysis.

Figure 2 shows that mean discrimination accuracy was higher on figure trials than on background trials, particularly during the first half of training. An ANOVA with trial (figure, background) and block (6) as the independent variables and percentage of correct responses as the dependent variable revealed a significant main effect of trial type [$F(1,3) = 8.65$], indicating that the birds were indeed more accurate on figure trials than on background trials. The ANOVA also revealed a significant main effect of block [$F(5,15) = 79.47$] and a significant trial × block interaction [$F(5,5) = 5.45$], suggesting that the disparity in accuracy between figure and background trials became less pronounced as training proceeded.

At the end of the trial, the pigeon had to report whether the target spot was located on the figure or on the background; but, at the start of the trial, the pigeon simply had to locate and peck the target spot. Because the target was equally often on and off the figure, the location of the

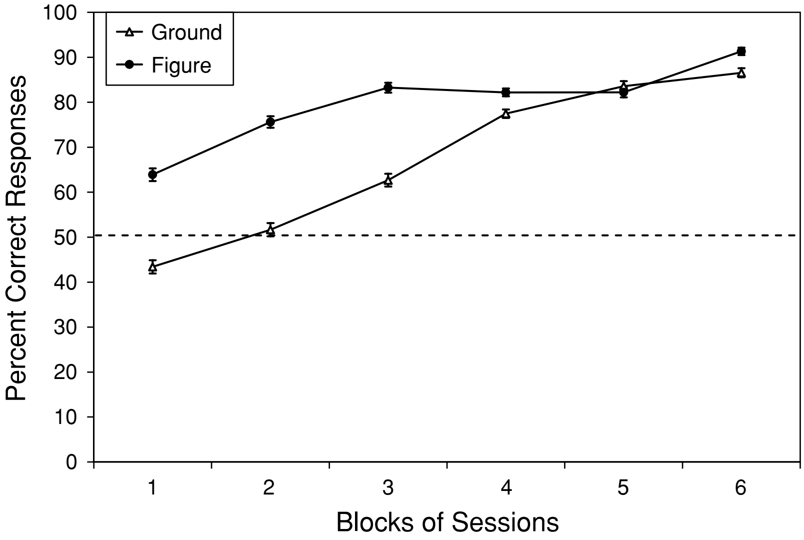

Figure 2. Mean discrimination performance on figure and background trials throughout training. The acquisition curves of the four individual pigeons were divided into six training blocks (see text for details in constructing Vincent learning curves).

target could not be predicted by the location of the figure. Thus, one possible outcome of the TDT analysis is no difference in TDT on figure and background trials. Another possible outcome of the TDT analysis is that TDTs might be shorter on figure trials than on background trials. Why? First, the birds' attention might be automatically summoned to figural regions defined by certain Gestalt cues as soon as those regions appear in visual field. Second, the birds' attention might be directed to the figural region because of its importance to solving the figure–ground discrimination.

Figure 3A shows that the pigeons were indeed faster to peck the target when it appeared on the figure than when it appeared on the background in both acquisition and maintenance, although the disparity was numerically larger in acquisition (*M* = 685 msec) than in maintenance (*M* = 425 msec). An ANOVA with trial and training phase as the independent variables and with log-transformed TDT scores as the dependent variable found a significant main effect of trial [$F(1,3) = 40.87$], confirming that the birds were faster to detect the target on the figure than on the background. The ANOVA also revealed a significant effect of training phase [$F(1,3) = 16.63$] and a significant training phase × trial interaction [$F(1,1) = 9.54$]. Planned comparisons verified that the pigeons were faster to detect the target on the figure than on the background in both acquisition [$t(3) = 2.61$] and maintenance [$t(3) = 7.09$].

Figure 3B shows that a figural advantage was also evident in the CRT scores. The pigeons were faster to select the correct response when the target appeared on the figure than when it appeared on the background in both acquisition and maintenance, although the disparity was numerically smaller in acquisition (*M* = 119 msec) than in maintenance (*M* = 515 msec). An ANOVA with trial and training phase as independent variables and with log-transformed CRT scores as the dependent variable found a significant main effect of type [$F(1,3) = 166.83$], indicating that the birds were faster to select the correct response when the target appeared on the figure than when it appeared on the background. The ANOVA also revealed a significant main effect of training phase [$F(1,3) = 142.37$], as well as a significant type × training phase interaction [$F(1,1) = 243.19$]. Planned comparisons disclosed that the figural benefit in acquisition did not reach significance [$t(3) = 1.63, p = .10$]; however, the figural benefit in maintenance did [$t(3) = 25.15$]. The absence of a significant effect during acquisition might have been due to the relatively small sample of correct trials as the birds were still learning the task. In maintenance, however, most of the trials were correct, thereby providing much greater power for detecting differences in RT.

One possible reason for the differences in accuracy and CRT might have been the different amounts of time that the birds took to complete the response requirement on figure trials and background trials. If, for some reason, the birds took longer to complete the response requirement on figure trials, then they would be exposed to the display longer, resulting in greater accuracy and faster CRT on figure trials. However, statistical analysis found no significant differences in the time to complete the observing response requirement on figure and background trials in acquisition or in maintenance.

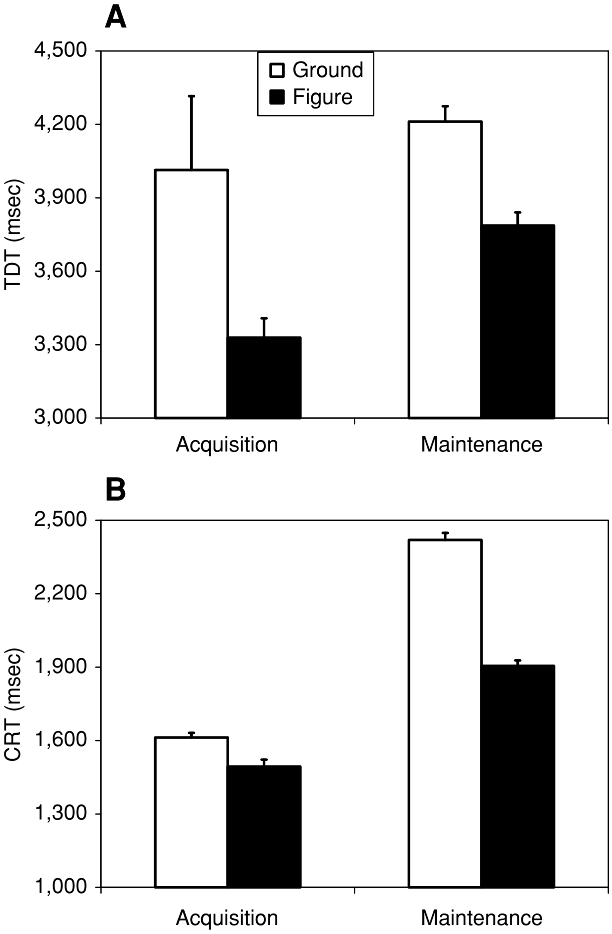

Figure 3. Mean target detection time (TDT) (A) and mean choice response time (CRT) (B) in acquisition and maintenance (Experiment 1). The plotted TDT data included all trials. When only correct trials were considered, mean TDT in acquisition was 4,127.2 ± 428.2 msec on background trials and 3,343.5 ± 90.1 msec on figure trials, whereas mean TDT in maintenance was 4,211.8 ± 66.0 msec on background trials and 3,776.7 ± 55.0 msec on figure trials. The plotted CRT data include correct trials only. When all trials were considered, mean CRT in acquisition was 1,549.8 ± 19.1 msec on background trials and 1,574.3 ± 25.8 msec on figure trials, whereas mean CRT in maintenance was 2,376.7 ± 27.4 msec on background trials and 1,968.3 ± 24.3 msec on figure trials.

Discussion

As in Herrnstein et al. (1989), our pigeons successfully mastered a figure–ground discrimination. But, because we used a two-alternative forced-choice task rather than a go/no-go task, we could directly compare the pigeons' report responses on figure trials and on background trials. Moreover, our training procedure required that the pigeons learn a figure–ground relationship to perform this task, rather than learning an incidental discrimination, such as the color of the region on which the target appeared.

We found that the pigeons more quickly learned to respond correctly on figure trials than on background trials (Figure 2). Although we know of no comparable experiment having been conducted with human participants, such a result with humans is plausible. Prior studies have reported that people are more likely to retain figures than backgrounds, both in short-term and long-term memory (Driver & Baylis, 1996; Rubin, 1915/1958). Although our experiment did not directly evaluate the pigeons' memory for figure and background, it is reasonable to believe that superior figure memory may contribute to faster learning on figure trials. The pigeons were also faster to peck the target when it appeared on the figure than on the background (Figure 3A). Similar results were obtained with human participants by Nelson (2003): When participants were instructed to detect the target, they were faster if the target appeared on a figural shape, which was defined by smaller region, surroundedness, or familiarity. Finally, a figural advantage was also seen in the CRTs: The pigeons were faster to make a correct choice on figure trials than on background trials (Figure 3B).

As Figure 1A demonstrates, during training, the figural region could be presented in the upper, lower, left, or right portions of the display. Vecera et al. (2002) found that people were more inclined to assign figural status to the region shown in the lower portion of the display than in the upper portion of the display. Examining our own training data during both acquisition and maintenance, we found no consistent biases related to the location of the figure in any of the three dependent measures. However, area and surroundedness served as the main cues determining figural status in our training displays; these cues could have overshadowed the possible contribution of the lower region effect. In Experiment 3, we explicitly explored a possible lower region effect in pigeons.

Before we turn to exploring lower region effect, we must answer another important question about pigeons' discrimination performance: Namely, did our pigeons actually learn the intended figure–ground discrimination? It could be hypothesized that the pigeons were using some other incidental cue in our displays as the effective discriminative stimulus—for example, the distance to the nearest colored edge. Specifically, if the target is located in the upper right corner and it is on the figure, then the distance from the target to the nearest colored edge is 0.9 cm; however, if the target is located in upper right corner and it is on the background, then the distance to the nearest colored edge is 2 cm (cf. Figure 1). We examined this possibility in Experiment 2 by modifying this distance on a small proportion of nondifferentially reinforced probe trials.

EXPERIMENT 2

We investigated the role of local edge distances by systematically varying the geometry of specially prepared testing stimuli, as described in the Method section.

Method

Subjects and Apparatus

The subjects and the apparatus were the same as those in Experiment 1.

Stimuli

For training, we continued to use the same stimuli as those in Experiment 1. To obtain the various testing stimuli, we modified the training images by removing one or more rectangular strips (1.1×8.5 cm, total area = 9.35 cm^2) from different locations on the displays. Figure 4 shows examples of the testing stimuli. In the *base cut* test, we removed the rectangular area located below the cityscape figure—a manipulation that did not affect the distance from the target to the nearest colored edge. In the *top cut* test, we removed the area located above the cityscape figure, modifying the distance to the nearest colored edge on background trials. In the *top & base cut* test, both areas were removed simultaneously. In the *one side cut* test, we removed an area either on the left or on the right side of the cityscape figure, which modified the distance to the nearest colored edge on one half of the background trials. Finally, in the *two side cut* test we removed areas on both sides of the figure, modifying the distance to the nearest colored edge on all of the background trials.

Procedure

Training. The training procedure was the same as that used in Experiment 1. Three pigeons were required to meet the 85/80 criterion: 85% correct overall and 80% correct to each of the eight subgroups of stimuli (four targets located either on the figure or on the background). Because the 4th bird failed to reach this criterion in a timely fashion, the criterion level was slightly lowered to 75% correct for each of the eight subgroups of stimuli and 80% correct overall. The selected criterion had to be maintained during testing: If performance to the training trials fell below criterion, then the bird was returned to training until it again reached criterion.

Testing. The birds were successively exposed to each type of tests: top cut, top & base cut, base cut, two side cut, and one side cut. Each testing session comprised 128 training trials and 16 testing trials. On training trials, only the correct response was reinforced, and incorrect responses were followed by correction trials (differential reinforcement). On testing trials, any choice response was reinforced (nondifferential reinforcement). Testing lasted for 8 days for all tests except the one side cut test. The one side cut test lasted for 16 days, in order to accommodate twice as many testing trials. Thus, in all tests, the birds were exposed to each testing stimulus–target combination once.

Behavioral measures. In this experiment, we presented novel displays as infrequent, nondifferentially reinforced probe trials. This procedure permitted the evaluation of accuracy, but it prohibited the analysis of TDT and CRT. Thus, only one dependent measure—accuracy—was analyzed.

Results

If the pigeons did use the distance to the nearest colored edge as a discriminative cue, then how should our manipulations affect their performance? On figure trials, two outcomes were possible. First, because on figure trials the distance from the target to the nearest colored edge never changed, there might have been no change whatsoever in performance on figure testing trials. One could argue, however, that all of the testing images (except for the top cut test) involved unfamiliar red–black or green–black edges instead of the familiar red–green or green–red edges that were seen in training. Therefore, we might expect no change on figure trials in the top cut test and equivalent generalization decrements in all other tests, due to novelty.

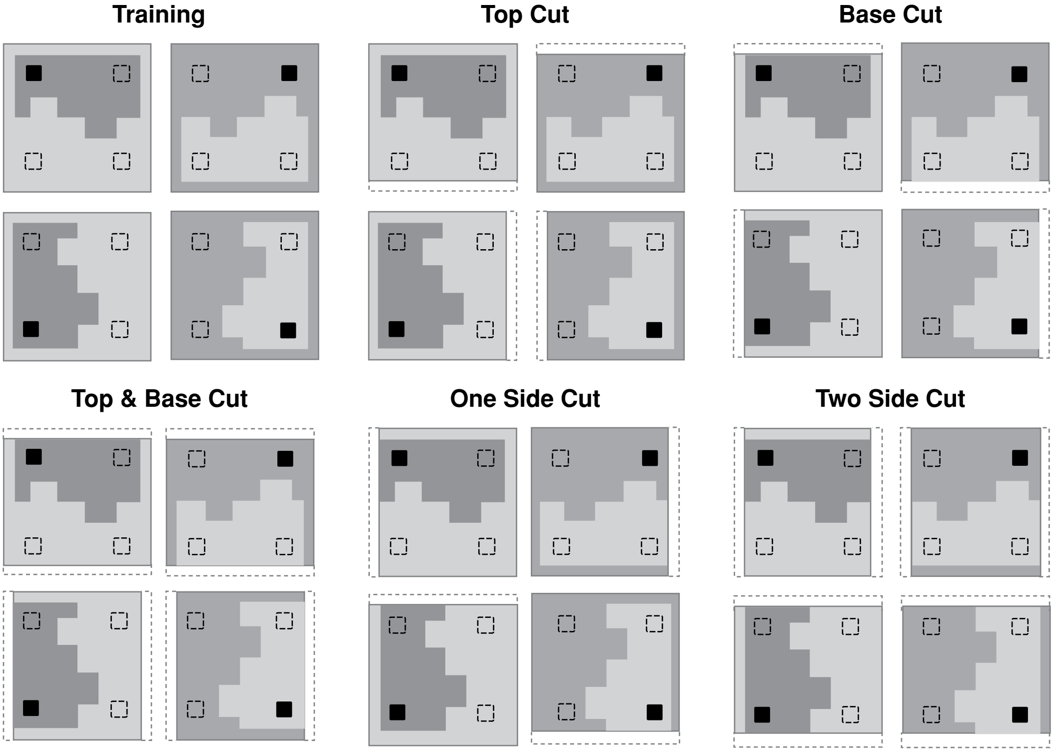

Figure 4. Examples of the training and testing stimuli in Experiment 2. The dashed lines around the outside of the displays show the area that was removed from the training images to prepare the testing stimuli (see text for further details).

With respect to background trials, the base cut test ought to have no effect on the birds' performance, since the distance to the nearest colored edge remained unchanged. In the top cut test, the pigeons ought to respond to background trials as if they were figure trials, because the distance to the nearest colored edge on background testing trials was reduced to the same value as on figure training trials. Moreover, the top & base cut test ought to have the same effect on the pigeons' performance as the top cut test, because the distance was modified in the same fashion. The one side cut test ought to incline the pigeons to respond to half of the background trials as if they were figure trials and to have no effect on the other half of the background trials. Finally, in the two side test, the pigeons again ought to respond to all background trials as if they were figure trials.

The results of testing are illustrated in Figure 5 (also depicted are the uniformly high scores obtained on the training trials that were randomly intermixed with the testing trials). Although some of our image manipulations led to declines in discriminative performance, testing performance on both figure and background trials was at or above 70% correct and always remained significantly above chance (two-tailed t test, $t \geq 6.46$). Contrary to expectations, the pigeons did not respond to background trials as if they were figure trials in the top cut, top & base cut, and two side cut tests; instead, discrimination accuracy on both figure and background trials fell as more area was removed from the display (top & base and two side tests vs. the base, top, and one side tests).

We conducted a repeated measures ANOVA with trial type (figure training, background training, figure testing, and background testing) and test (5) as factors and percentage of correct responses as the dependent variable. The ANOVA found a significant main effect of test [$F(4,12) = 11.31$], indicating that the birds' performance was affected by the different types of testing displays. Although the main effect of trial type failed to reach significance [$F(3,9) = 2.88, p = .095$], a planned linear contrast revealed that mean performance on testing trials was significantly lower than on training trials [$t(3) = 2.67$]. The trial type × test interaction was significant [$F(3,12) = 2.87$], indicating that performance to training and testing stimuli varied across the various different tests. We then conducted a series of planned comparisons designed to estimate the effect of the distance to the nearest colored edge on the birds' performance.

As outlined above, we did not expect systematic changes in accuracy on figure trials if the distance to the nearest colored edge is an effective discriminative cue. Planned contrasts revealed, however, that performance on figure testing trials in the top & base cut test was significantly lower than in the base cut, top cut, and one side cut tests [$t(3) \geq 9.45$]. Performance on figure trials in other tests did not differ significantly.

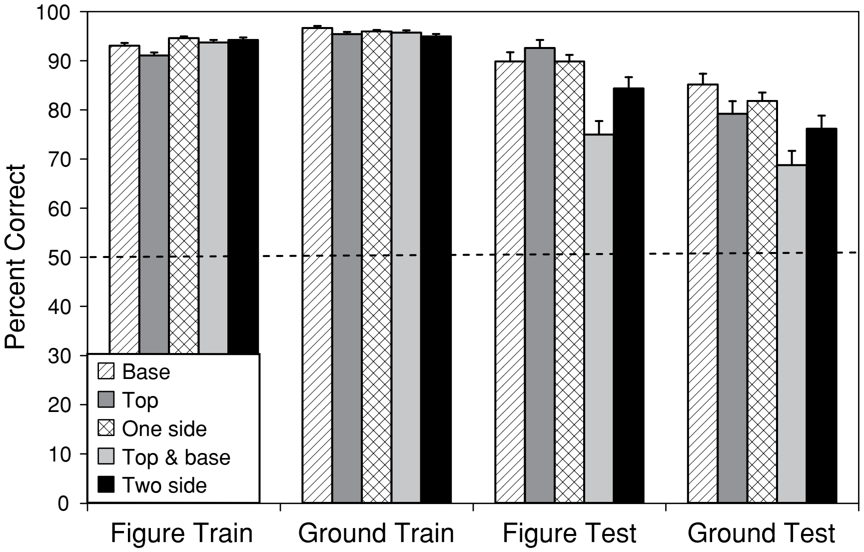

Figure 5. Mean discrimination performance on figure and background trials during base cut, top cut, one side cut, top & base, and two side cut tests (Experiment 2). Accuracy on all trial types was significantly above chance.

As to background trials, we expected a discrimination reversal in the two side cut, top cut, and top & base cut tests, a significant drop of performance in the one side cut test, and no decrement in the base cut test. The pigeons responded least accurately (but significantly above chance) to background testing trials in the top & base cut test, and their performance here was significantly lower than in the top cut, one side cut, and base cut tests [$t(3) \geq 4.94$]. Performance to background trials in the other tests did not differ significantly. Again, these results did not accord with expectations.

Discussion

Because the figure was surrounded by the background in all of our training displays, the distance from the target to the nearest colored edge on background trials had to be larger than on figure trials. Thus, this distance could have provided a potential discriminative cue to our pigeons. Nevertheless, the results of the present series of tests indicated that the distance to the nearest colored edge was unlikely to be the prime mediator of our birds' discrimination performance. Even when that distance on background trials was reduced to match figure trials (top cut, top & base cut, and two side cut tests; cf. Figure 4), the birds maintained their discrimination on background trials well above chance. Thus, it may be more parsimonious to assume that pigeons attend to the same Gestalt figural cues as do humans: smaller size and surroundedness.

The present pattern of results also hints at the importance of smaller size for figure–ground assignment in pigeons. For example, in the top & base cut test, the figural region occupied 36% of the entire display, whereas it occupied 27% on the training images. As illustrated in Figure 5, this condition produced the largest decrease in discrimination performance on both figure and background trials. When the figural region occupied 31% of the display (top cut, base cut, and one side cut tests), the pigeons demonstrated better performance on both figure and background trials. The present series of test did not permit more extensive evaluation of effect of smaller area on the birds' performance; it did suggest, however, that this variable merits further investigation.

In the present series of tests, we removed one or two strips from the display, which still permitted the use of surroundedness and area for figure–ground assignment. If we were to remove all four strips, then the figural region would cease to be surrounded, and it would occupy 50% of the display, thereby producing the displays shown in Figure 6. In those displays, neither surroundedness nor area could be used for figure–ground assignment. But, if the pigeons were sensitive to the lower region cue, then we would expect them to respond "figure" when the target was located in the lower region of the display. This hypothesis was tested in Experiment 3.

EXPERIMENT 3

Method

Subjects and Apparatus

The subjects and the apparatus were the same as those in Experiment 1.

Stimuli

We used the same training stimuli as those in Experiment 1. Recall that for the training stimuli, the background was larger than the figure. We therefore prepared the testing stimuli either by changing the width of the square background to match the width of the figure (Test 1) or by changing the width of the figure to match the width of the background (Test 2). In both cases, this manipulation eliminated surroundedness and area as cues for figure–ground assignment. We

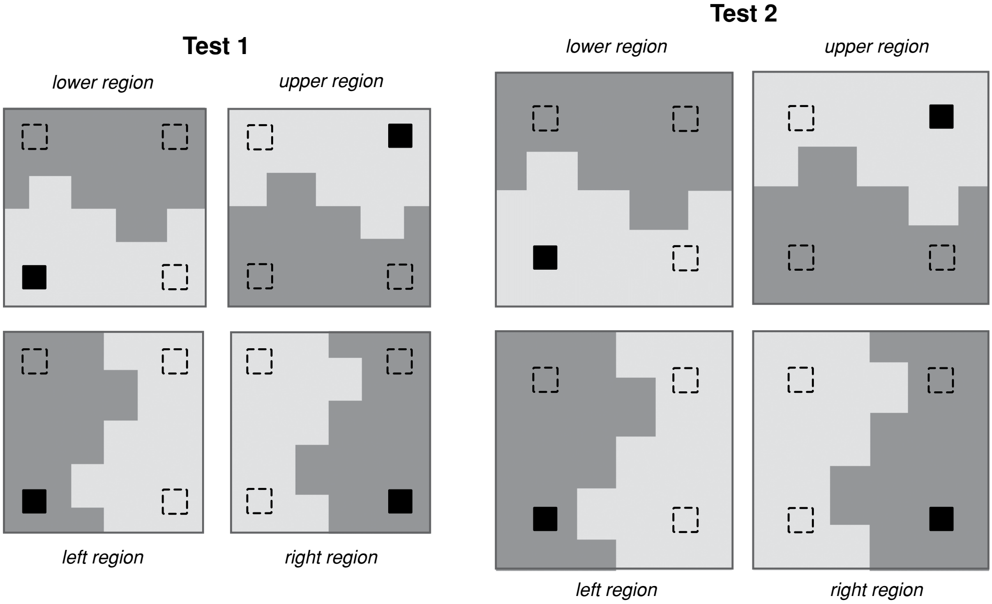

Figure 6. Examples of the testing stimuli in Experiment 3 in both Test 1 and Test 2 (see text for further details about Tests 1 and 2). Dashed lines indicate the other potential locations of the yellow target spot.

divided all testing trials into four groups, with examples shown in Figure 6. When the colored areas were aligned horizontally and the target appeared in either the lower left or the lower right corner, the trial was termed a *lower region* trial; when the target appeared in the other two locations, the trial was termed an *upper region* trial. When the colored areas were aligned vertically and the target appeared in either the upper left or the lower left corner, the trial was termed a *left region* trial; when the target appeared in the other two locations, the trial was termed a *right region* trial. The key choices associated with "figure" and "background" responses on training trials were coded as "figure" and "background" responses, respectively, on testing trials. Because we used four different cityscape figures in training, each test comprised 64 unique stimulus–target combinations.

Procedure

Training. The training procedure was the same as that used in Experiment 1. The birds again were required to maintain high performance to the training stimuli during testing: If performance to the training trials fell below criterion, then the bird was returned to training until it again reached criterion.

Test 1. During Test 1, the pigeons were exposed to the first set of the testing stimuli (Figure 6, left panels). The birds received 144 trials per day, consisting of 128 training trials and 16 testing trials. As in Experiment 2, training stimuli were differentially reinforced, whereas testing trials were nondifferentially reinforced. Testing lasted for 12 days, in order to collect 48 trials with each trial type (lower region, upper region, left region, and right region).

Test 2. Here, the pigeons were exposed to the second set of testing stimuli (Figure 6, right panels). Otherwise, the testing procedure was the same as in Test 1.

Behavioral measures. As in Experiment 2, we presented novel displays as infrequent, nondifferentially reinforced probe trials, which prohibited the analysis of TDT and CRT. Thus, only one dependent measure—accuracy—was analyzed.

Results

Figure 7 illustrates the results of Tests 1 and 2, with behavior plotted as percentage of "figure" responses. The pigeons continued to discriminate the training stimuli at a very high level of accuracy as documented by a high percentage of "figure" responses on figure trials and by a low percentage of "figure" responses on background trials. The pigeons' responses to all types of testing trials in both tests were significantly below chance (two-tailed t test, $t \leq -2.34, p \leq .02$), indicating that the birds made more "background" than "figure" responses when the testing displays were presented. Contrary to our expectations, the lower region displays did not prompt "figure" reports; instead, the birds were more inclined to report "background" in presence of those images. Note that this result again supports our previous conclusion that the pigeons did not rely on the distance to the nearest colored edge for figure–ground discrimination: For all of the testing displays, the distance to the nearest colored edge matched the distance on figure training trials, rather than on background trials.

A repeated measures ANOVA with test and trial type (lower region, upper region, left region, and right region displays) as factors found no significant effect of trial type [$F(5,19) = 1.00, p = .44$]. We expected to find no difference in responding to left region trials and right region trials; planned comparisons supported our expectations [$t(3) = 1.65, p = .13$]. We also expected to find more "figure" responses on lower region trials than on upper, left, or right region trials; however, planned contrasts found no difference between lower region and upper region trials [$t(3) = 0.50$, $p = .63$], suggesting that the lower region did not reliably affect figure–ground assignment in pigeons. Although the pigeons tended to produce more "background" responses in Test 2, the main effect of test failed to reach significance [$F(1,3) = 6.14, p = .09$]. As well, the trial type × test interaction was not significant

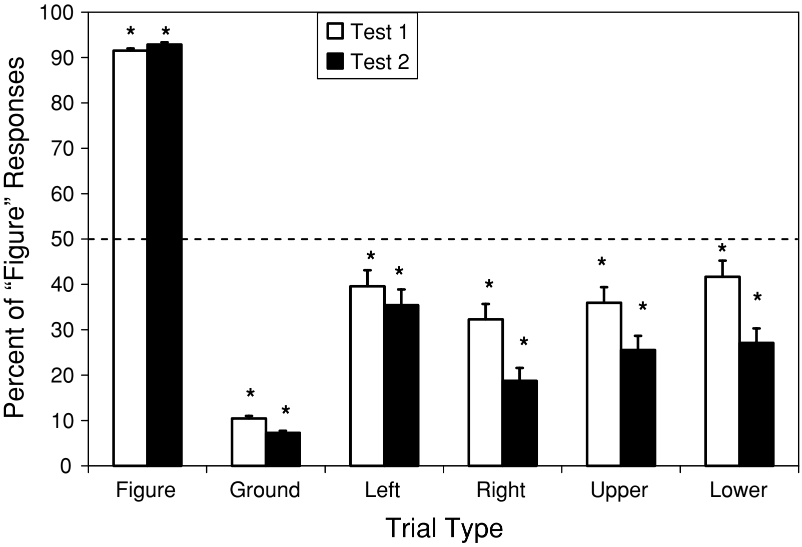

Figure 7. Mean discrimination performance in the lower region test (Experiment 3). Asterisks indicate the trial types that differed significantly from chance.

($F < 1$), indicating that the pattern of "figure" responses did not differ from test to test.

Discussion

Vecera et al. (2002) found that, all other things being equal, people are more likely to perceive the lower region of a display as figure and the upper region of a display as background. Moreover, the lower region bias in humans is relative to the stimulus configuration, specifically to the horizon line, rather than to the fixation point: The region below the horizon is perceived as a figure.

Why did we not find a lower region effect in pigeons? Several explanations may be offered. First, the absence of a lower region effect might have been a consequence of extensive earlier training, which might have effectively taught the pigeons to ignore the orientation of the figural region and to rely only on surroundedness and smaller area for figure–ground assignment. Nevertheless, we had earlier found (see the Results section of Experiment 1) that our pigeons did not exhibit a reliable lower region bias during initial training.

Second, if the lower region bias reflects the influence of relative position (a pictorial depth cue) on figure–ground assignment (Vecera et al., 2002), then the absence of a lower region bias might have been due to the pigeons' inability to use relative position for depth perception. Pigeons have recently been shown to use a number of monocular cues, including texture gradient, occlusion, and relative size, to judge depth in pictorial stimuli (Cavoto & Cook, 2006). Still, it is possible that pigeons' perception of some pictorial depth cues—namely, relative position—is fundamentally different from that of humans.

Finally, an ecological consideration of figure–ground assignment may help us understand the absence of a lower region bias in pigeons. The process of figure–ground assignment establishes which visual regions correspond to figural regions, or objects, that possess stable, nonaccidental properties, and which regions are accidentally shaped backgrounds or spaces between objects (Lowe, 1985; Palmer, 1999). Figure–ground cues might therefore reflect regularities in the environment that help organisms to determine the most likely objects in a complex scene. For example, surrounded regions are more likely to be perceived as figures because the most probable interpretation of the scene is that an object is surrounded by a background. Although the surrounding region may be a background (e.g., holes; see Nelson & Palmer, 2001), this situation is less likely. Following the same logic, Vecera et al. (2002) suggested that lower regions are more likely to be perceived as figures because, for humans, regions below the horizon are physically closer to the observer and, therefore, are more likely to be objects that require attention and action. But, for a flying bird, objects requiring attention (e.g., a hawk or a tree branch) may often appear above the horizon line, thereby rendering this cue less significant. Other Gestalt cues, such as surroundedness, do reflect the regularities that hold in the worlds of both humans and pigeons; our future research will explore whether surroundedness affects pigeons' figure–ground assignment.

EXPERIMENT 4

In Experiments 1–3, we found a figural advantage in choice accuracy, TDT, and CRT. We also found that the pigeons were not using local cues such as the distance to the nearest colored edge for figure–ground discrimination; instead, they seemed to rely on area and surroundedness. Why might the pigeons preferentially attend to the figural region? On the one hand, attention might be automatically summoned to figural regions defined by Gestalt cues to which the pigeon's visual system is particularly sensitive. If this were true, then we should expect to find the same figural advantage even when the pigeon's task does not require an explicit figure–background response. On the other hand, pigeons might attend to the figural region because they are required to perform the figure–background discrimination at the end of the trial. In this case, we would not expect to find a reliable figural advantage in the absence of the figure–background discrimination. Testing these two alternatives was the aim of Experiment 4.

Method

Subjects

The subjects were 4 different, feral pigeons housed and maintained as described in Experiment 1.

Apparatus and Stimuli

The apparatus and stimuli were the same as those used in Experiment 1.

Procedure

Pretraining. The pretraining procedure was the same as that used in Experiment 1.

Acquisition. Following pretraining, the birds entered the training phase, in which they were taught to detect the target on either the figure or the background (cf. Figure 1). At the beginning of a trial, the pigeons were shown a black cross in the center of the white display screen. Following one peck anywhere on the white display, the training stimulus display and the target simultaneously appeared. The pigeons had to complete an observing response requirement to the target button that was increased from 3 to 10 pecks. This requirement was increased up to 10 pecks because, in other experiments in our laboratory, we have found the greatest figural advantage under this response schedule. The time from the onset of the stimulus display to the first peck at the target button (TDT) was recorded, as well as the time to complete the observing response requirement.

When the pigeons completed the observing requirement, food reinforcement was delivered and the ITI ensued; the ITI randomly ranged from 5 to 15 sec. As in Experiment 1, each session comprised one block of 128 trials, so that each combination of stimulus display and target location was shown once per session. The pigeons were trained for a total of 35 sessions. In Experiment 1, we found that the combined data from 35 maintenance sessions were sufficient to reveal a highly significant figure advantage for all three dependent measures; therefore, we assumed that 35 training sessions here would provide enough data for detecting any differences in TDT, since no figure–background discrimination was required.

Behavioral measures. In this experiment, the pigeons were not required to report whether the target was located on the figure or the background. Therefore, instead of three dependent measures, as in Experiment 1, there was only a single dependent measure—TDT.

Results and Discussion

When the pigeons were not required to report the location of the target (on the figure vs. on the background), their TDT on figure trials was 4,203.1 ± 365.2 msec, and their TDT on background trials was 4,266.9 ± 524.4 msec. Apparently, in the absence of a required choice response, the mean figural advantage in TDT was greatly diminished, relative to that in Experiment 1, when a choice response was required (63.8 and 685.0 msec, respectively). An ANOVA with subject and trial type as independent variables and log-transformed TDT scores as the dependent variable yielded no significant effect of trial type [$F(1,3) = 1.83, p = .18$] or subject × trial type interaction [$F(1,3) = 1.71, p = .16$], indicating that no reliable figural advantage was obtained in the absence of a figure–background choice response.

It is, of course, possible that the pigeons' attention is automatically deployed to figural regions regardless of task demands; but, the resulting figural advantage may be very small and difficult to detect in the present task due to inherent variability in the pigeons' RTs. Nelson (2003) reported that, in the absence of an explicit figure–ground discrimination, humans are faster to detect the target on the figural region rather than on background by about 45 msec on average. Looking at the size of the standard errors for TDT in this experiment (365.2 msec on figure trials and 524.4 msec on background trials), it is understandable that a difference of this size could not be detected with the present procedure. Still, it is clear that a large and reliable figural advantage was found in Experiment 1 when the pigeons were required to discriminate the figure from the background.

GENERAL DISCUSSION

In the present series of four experiments, we explored pigeons' ability to discriminate whether a target figure was located on a figural region (defined by smaller area and surroundedness) or on a background. Although the figure and the background in each display were of two different colors, these colors were changed randomly from one display to the next; thus, the pigeons could not use the color of the region around the target to perform this discrimination.

We found that pigeons can readily master this figure–background discrimination. Furthermore, all of our dependent measures suggested privileged status for the figural region relative to the background. The pigeons were faster to learn the correct report response on figure trials; they were faster to detect the target when it appeared within a figural region; and, they were faster to make a correct choice response on figure trials. Although the difference in accuracy diminished with prolonged training, the reliable difference in both TDT and CRT was maintained for many weeks after original training was completed. Follow-up tests revealed that the pigeons did not use local cues, such as the distance to the nearest colored edge, to perform the figure–ground discrimination. Rather, the overall pattern of results implied that the pigeons might have been relying on smaller area and surroundedness to perform the figure–ground discrimination.

Note that, in interpreting these results, we have been cautious not to imply that the pigeons perceived the differently colored regions as close, foreground "figures" or more distant "grounds" (backgrounds); rather, we have treated the results in terms of a figural superiority, where "figure" is objectively defined as the smaller, surrounded region. At the moment, we do not know whether pigeons' perception of these figural regions is similar to humans' in other respects. For example, we cannot say whether the figural regions are perceived as being closer to the observer than the background or whether pigeons perceived the background regions to continue behind the objects. Similar difficulties arise when one studies figure–ground phenomena in nonverbal human infants (e.g., Ross-Sheehy, Oakes, & Vecera, 2003).

Furthermore, if we set aside verbal reports as possibly colored by response biases or demand characteristics, then studying figure–ground phenomena in adult humans must also rely on indirect response measures, such as memory matching performance (Driver & Baylis, 1996; Vecera et al., 2004; Vecera et al., 2002), perceptual matching performance (Peterson & Kim, 2001; Treisman & DeSchepper, 1996; Vecera, Brodson, & Flevaris, 2003), and detection RTs (Nelson, 2003). We have clearly demonstrated, using similar indirect measures of figure–ground discrimination, that pigeons behave as do humans when the figural region is defined by smaller area and surroundedness.

We did find a disparity in at least one factor affecting figure–ground assignment in pigeons and people. Unlike people (Vecera et al., 2002), pigeons showed no evidence of a lower region bias: That is, a figural region located in the lower part of the display did not prompt more "figure" responses than a figural region located in the upper part of the display. This disparity may be related either to fundamental differences in the perception of pictorial depth cues or to the different ecologies of the two species. In human vision, regions below the horizon are usually physically closer to the observer and, therefore, are more likely to be granted figural status. For flying birds, objects requiring attention appear both above the horizon (when flying) and below the horizon (when walking), thereby diminishing the significance of the lower region as a cue for figure–ground assignment. Other Gestalt cues may have high predictive value for both pigeons and people, such as surroundedness and symmetry. Our future research will explore the effects of these and other cues on figure–ground assignment.

In Experiment 4, when the pigeons were not required to discriminate whether the target was located on the figure or on the background, we did not find a significant figural benefit in TDT, although we did detect a small numerical advantage for targets on the figure relative to those on the ground. In related experiments reported by Nelson (2003)—which did yield a reliable figural advantage—human participants were simply instructed to detect the target or to report the identity of the target; they were not required to discriminate between the figure and the background as were our pigeons. However, it is possible that our experimental method might not have been sufficiently sensitive to detect the small figural benefit that pigeons may exhibit in the absence of an explicit figure–background discrimination. It would be interesting to see whether the figural advantage in people can be enhanced by requiring them to make an analogous figure–background discrimination response.

CONCLUDING COMMENTS

The idea of a foreground (figural) object plays a central role in vision science. Feldman (2003) calls such objects "the units of our perceived world—spatially coherent bundles of visual stuff" (p. 256). Numerous studies have documented the importance of objects to human vision: Objects command visual attention, they influence both short-term and long-term memory, and they direct both perception and action (Driver & Baylis, 1996; Rubin, 1915/1958; Vecera, 2000; Vecera & Farah, 1994). We believe that it is plausible to expect that the visual systems of nonhuman animals will exhibit many of the same basic features and operating principles as does the human visual system. After all, nonhumans also evolved in a figure-filled world, where they must continually determine the most relevant objects for their current activities. Our data encourage the idea that foreground figures may be as important for other animals as they are for human beings.

Nevertheless, we must remain vigilant to possible between-species differences in object discrimination behavior. The results of several studies suggest profound differences in object recognition processes in pigeons and humans. Unlike people, pigeons have exhibited no difference in latency to match two objects when one of them was rotated in the picture plane, thereby appearing not to engage in mental rotation (Hollard & Delius, 1982). As well, people have been found to be equally good at recognizing objects photographed in full color or presented as simplified line drawings, suggesting that surface cues may be less important for object recognition in humans than the edges of objects (Biederman & Ju, 1988). In contrast, surface features play an important role in object recognition in pigeons; indeed, pigeons appear to see no correspondence between shaded images and line drawings of the same objects (Peissig, Young, Wasserman, & Biederman, 2005; Young, Peissig, Wasserman, & Biederman, 2001; see also Friedman, Spetch, & Ferrey, 2005).

One might imagine that these disparities are traceable to the divergence of human and avian visual systems. It is quite possible, however, that the type of the task and the organism's prior visual experience account for much of these behavioral disparities.

As to mental rotation, later research has suggested that pigeons' failure to exhibit mental rotation effects may be attributable to the experimental stimuli and the behavioral tasks that were used (Delius & Hollard, 1995). With new visual stimuli and a different experimental procedure, pigeons exhibited linear effects of angular rotation in both RT and discrimination ratio (Hamm, Matheson, & Honig, 1997).

As to attention to surface features, it is instructive to note that pigeons do not have as much experience with 2-D representations of real-world objects as do humans. Studies of infants' perception suggest that even humans may not immediately recognize 2-D representations of 3-D objects, especially in the form of stylized drawings (Smith, 2003). Similarly, pigeons presented with line drawings on a computer screen may require additional experience before they can recognize them as representations of real-world objects. Further research is needed to disclose whether the behavioral disparities in object recognition by pigeons and humans are grounded in the anatomy and physiology of their visual systems or are traceable to their earlier experiences. The results of such studies will enable us to learn much more about the ontogeny and phylogeny of perception and adaptive action.

REFERENCES

Bahnsen, P. (1928). Eine Untersuchung über Symmetrie und Asymmetrie bei visuellen Wahrnehmungen [A study of symmetry and asymmetry in visual perception]. *Zeitschrift für Psychologie*, **108**, 129-154.

Biederman, I., & Ju, G. (1988). Surface versus edge-based determinants of visual recognition. *Cognitive Psychology*, **20**, 38-64.

Blough, D. (1989). Odd-item search in pigeons: Display size and transfer effects. *Journal of Experimental Psychology: Animal Behavior Processes*, **15**, 14-22.

Cavoto, B. R., & Cook, R. G. (2006). The contribution of monocular depth cues to scene perception by pigeons. *Psychological Science*, **17**, 628-634.

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

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

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

DiPietro, N. T., Wasserman, E. A., & Young, M. E. (2002). Effects of occlusion on pigeons' visual object recognition. *Perception*, **31**, 1299-1312.

Driver, J., & Baylis, G. (1996). Edge-assignment and figure–ground segmentation in short-term visual matching. *Cognitive Psychology*, **31**, 248-306.

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

Feldman, J. (2003). What is a visual object? *Trends in Cognitive Sciences*, **7**, 252-256.

Friedman, A., Spetch, M. L., & Ferrey, A. (2005). Recognition by humans and pigeons of novel views of 3-D objects and their photographs. *Journal of Experimental Psychology: General*, **134**, 149-162.

Fujita, K. (2001). Perceptual completion in rhesus monkeys (*Macaca mulatta*) and pigeons (*Columba livia*). *Perception & Psychophysics*, **63**, 115-125.

Gibson, B. M., Wasserman, E. A., Frei, L., & Miller, K. (2004). Recent advances in operant conditioning technology: A versatile and affordable computerized touchscreen system. *Behavior Research Methods, Instruments, & Computers*, **36**, 355-362.

Goto, K., & Lea, S. E. G. (2003). Discrimination of direction of movements in pigeons following previous experience of motion/static discrimination. *Journal of the Experimental Analysis of Behavior*, **80**, 29-42.

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

Herrnstein, R. J., Vaughan, W., Jr., Mumford, D. B., & Kosslyn, S. M. (1989). Teaching pigeons an abstract relational rule: Insideness. *Perception & Psychophysics*, **46**, 56-64.

Hollard, V., & Delius, J. D. (1982). Rotational invariance in visual pattern recognition by pigeons and humans. *Science*, **218**, 804-806.

Hulleman, J., & Humphreys, G. W. (2004). A new cue to figure–ground coding: Top-bottom polarity. *Vision Research*, **44**, 2779-2791.

Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience*, **6**, 151-159.

Kling, J. W., Riggs, L. A., et al. (1971). *Woodworth and Schlosberg's experimental psychology* (3rd ed.). New York: Holt, Rinehart & Winston.

Klymenko, V., & Weisstein, N. (1986). Spatial frequency differences can determine figure–ground organization. *Journal of Experimental Psychology: Human Perception & Performance*, **12**, 324-330.

Klymenko, V., Weisstein, N., Topolski, R., & Hsieh, C.-H. (1989). Spatial and temporal frequency in figure–ground organization. *Perception & Psychophysics*, **45**, 395-403.

Lamme, V. A. F. (1995). The neurophysiology of figure–ground segregation in primary visual cortex. *Journal of Neuroscience*, **15**, 1605-1615.

Lamme, V. A. F., Zipser, K., & Spekreijse, H. (1998). Figure–ground activity in primary visual cortex is suppressed by anesthesia. *Proceedings of the National Academy of Sciences*, **95**, 3263-3268.

Lee, S.-H., & Blake, R. (1999). Visual form created solely from temporal structure. *Science*, **284**, 1165-1168.

Lowe, D. G. (1985). *Perceptual organization and visual recognition*. Boston: Kluwer.

Medina, L., & Reiner, A. (2000). Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends in Neurosciences*, **23**, 1-12.

Nelson, R. A. (2003). *Attention and figure–ground perception*. Unpublished doctoral dissertation, University of California, Berkeley.

Nelson, R. [A.], & Palmer, S. E. (2001). Of holes and wholes: The perception of surrounded regions. *Perception*, **30**, 1213-1226.

Palmer, S. E. (1999). *Vision science: From photons to phenomenology*. Cambridge, MA: MIT Press.

Palmer, S. E. (2002). Perceptual organization in vision. In H. Pashler & S. Yantis (Eds.), *Stevens' handbook of experimental psychology: Vol. 1. Sensation and perception* (3rd ed., pp. 177-234). New York: Wiley.

Palmer, S. E., Nelson, R. [A.], & Brooks, J. L. (2001). Rethinking figure–ground organization: Relative depth and attention. *Abstracts of the Psychonomic Society*, **6**, 63.

Peissig, J. J., Young, M. E., Wasserman, E. A., & Biederman, I. (2005). The role of edges in object recognition by pigeons. *Perception*, **34**, 1353-1374.

Peterson, M. A. (1994). Object recognition processes can and do operate before figure–ground organization. *Current Directions in Psychological Science*, **3**, 105-111.

Peterson, M. A. (1999). What's in a stage name? Comment on Vecera and O'Reilly (1998). *Journal of Experimental Psychology: Human Perception & Performance*, **25**, 276-286.

Peterson, M. A., & Gibson, B. S. (1991). The initial identification of figure–ground relationships: Contributions from shape recognition processes. *Bulletin of the Psychonomic Society*, **29**, 199-202.

Peterson, M. A., & Gibson, B. S. (1993). Shape recognition inputs to figure–ground organization in three-dimensional grounds. *Cognitive Psychology*, **25**, 383-429.

Peterson, M. A., Harvey, E. M., & Weidenbacher, H. J. (1991). Shape recognition contributions to figure–ground reversal: Which route counts? *Journal of Experimental Psychology: Human Perception & Performance*, **17**, 1075-1089.

Peterson, M. A., & Kim, J. H. (2001). On what is bound in figures and grounds. *Visual Cognition*, **8**, 329-348.

Rock, I. (1975). *An introduction to perception*. New York: Macmillan.

Rossi, A. F., Desimone, R., & Ungerleider, L. G. (2001). Contextual modulation in primary visual cortex of macaques. *Journal of Neuroscience*, **21**, 1698-1709.

Ross-Sheehy, S. M., Oakes, L. M., & Vecera, S. P. (2003, April). *Figure–ground segregation in human infants*. Poster presented at the 2003 Biennial Meeting of the Society for Research in Child Development, Tampa, FL.

Rubin, E. (1958). Figure and ground. In D. C. Beardslee & M. Wertheimer (Eds.), *Readings in perception* (pp. 194-203). Princeton, NJ: Van Nostrand. (Original work published in 1915)

Sekuler, A. B., Lee, J. A., & Shettleworth, S. J. (1996). Pigeons do not complete partially occluded figures. *Perception*, **25**, 1109-1120.

Smith, L. B. (2003). Learning to recognize objects. *Psychological Science*, **14**, 244-250.

Supèr, H., Spekreijse, H., & Lamme, V. A. F. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, **4**, 304-310.

Treisman, A., & DeSchepper, B. (1996). Object tokens, attention, and visual memory. In T. Inui & J. L. McClelland (Eds.), *Attention and performance XVI: Information integration in perception and communication* (pp. 15-46). Cambridge, MA: MIT Press, Bradford Books.

Vecera, S. P. (2000). Toward a biased competition account of object-based segregation and attention. *Brain & Mind*, **1**, 353-384.

Vecera, S. P., Brodson, N. S., & Flevaris, A. V. (2003, November). *The fate of the ground in figure–ground assignment*. Poster presented at 44th Annual Meeting of the Psychonomic Society, Vancouver, BC.

Vecera, S. P., & Farah, M. J. (1994). Does visual attention select objects or locations? *Journal of Experimental Psychology: General*, **123**, 146-160.

Vecera, S. P., Flevaris, A. V., & Filapek, J. C. (2004). Exogenous spatial attention influences figure–ground assignment. *Psychological Science*, **15**, 20-26.

Vecera, S. P., & O'Reilly, R. C. (1998). Figure–ground organization and object recognition processes: An interactive account. *Journal of Experimental Psychology: Human Perception & Performance*, **24**, 441-462.

Vecera, S. P., & O'Reilly, R. C. (2000). Graded effects in hierarchical figure–ground organization: Reply to Peterson (1999). *Journal of Experimental Psychology: Human Perception & Performance*, **26**, 1221-1231.

Vecera, S. P., Vogel, E. K., & Woodman, G. F. (2002). Lower region: A new cue for figure–ground assignment. *Journal of Experimental Psychology: General*, **131**, 194-205.

Young, M. E., Peissig, J. J., Wasserman, E. A., & Biederman, I. (2001). Discrimination of geons by pigeons: The effects of variations in surface depiction. *Animal Learning & Behavior*, **29**, 97-106.

Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience*, **20**, 6594-6611.

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