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Pigeons discriminate continuous vs. discontinuous line segments

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Abstract

Three experiments examined various facets of the perception of continuous and discontinuous line segments in pigeons. Pigeons were presented with two straight lines that were interrupted by a gap. In some instances, the lines were the same angle and were positioned so that they appeared (to human observers) to form a continuous line. In other instances, the lines were different angles, or the same angle but spatially misaligned. The birds were trained to classify each stimulus as continuous or discontinuous using a go/no-go procedure. A series of tests followed in which the birds received novel discontinuous displays made up of familiar line segments; continuous and discontinuous stimuli made up of novel line segments (novel straight lines or curved lines); and familiar displays in which the gap was covered with a grey square. Results from the tests indicated that two of the three pigeons had learned a continuous/discontinuous categorization and that they appeared to use the relationship between the two line segments in discriminating the displays.

Pigeons discriminate continuous vs. discontinuous line segments

Gestalt properties such as proximity and good continuation play a prominent role in human object recognition. Good continuation is a fundamental, low level property of the visual system; it allows the observer to perceive smooth contour despite gaps or partial occlusion, permitting recognition of partially-obscured objects. In the case of a gap it allows edge relationships to become salient. This does not necessarily lead to visual completion, but is a prerequisite of the process. The human visual system is able to rapidly and automatically complete missing visual information and it has been suggested that the observer actually perceives the complete image despite partial occlusion (Kanizsa, 1979).

While the Gestalt principle of good continuation clearly contributes to human and primate vision (see Fujita, 2001; Fujita, 2006; Grossberg & Mingolla, 1985; Sekuler & Palmer, 1992; Yin, Kellman, & Shipley, 1997), the evidence relating to the operation of this principle in pigeon visual perception is unconvincing. Fujita (2001) examined perceptual completion in rhesus macaques and pigeons. They were trained to discriminate long vs. short bar lengths. Intermixed test sessions presented short bars that were touching a solid rectangle. The macaques demonstrated a continuation effect whereby the likelihood of choosing long for the short bar increased when the short bar touched the rectangle. This effect has also been observed in similar tasks with human participants (e.g., Kanizsa, 1979). Pigeons, however, did not demonstrate a choose-long effect under these circumstances, indicating that they did not experience an illusion of the bar continuing behind the rectangle.

A related means of testing for good continuation is to examine object recognition under conditions of partial occlusion. Surprisingly, pigeons do not appear to recognize familiar objects when they are partially occluded (Cerella, 1980; Ushitani & Fujita, 2005; Ushitani, Fujita, &

Yamanaka, 2001), nor do they automatically complete occluded shapes (Fujita & Ushitani, 2005; Sekuler, Lee, & Shettleworth, 1996). On the other hand, many other animals including three species of primates (Duruelle, Barbet, Dépy, & Fagot, 2000; Fujita, 2001; Sugita, 1999), chickens (Forkman, 1998; Lea, Slater, & Ryan, 1996; Regolin & Vallortigara, 1995), mice (Kanizsa, Renzi, Conte, Compostela, & Geurani, 1993), and humans (e.g., Rauschenberger & Yantis, 2001; Rensink & Enns, 1998; Sekuler & Palmer, 1992) have been shown to recognize partially occluded objects. The failure to demonstrate perceptual completion in pigeons occurs with both natural (Aust & Huber, 2006; Ushitani & Fujita, 2005; Watanabe & Furuya, 1997) and artificial (Cerella, 1980; Fujita, 2001; Fujita & Ushitani, 2005; Sekuler & Palmer, 1992; Ushitani, Fujita, & Yamanaka, 2001) stimuli, suggesting that the prior results were not a product of particular test items.

There have been two main approaches to the study of occlusion effects on shape recognition in pigeons. One is to train pigeons to discriminate intact objects, and then test with partially occluded versions. For example, Cerella (1980) trained pigeons to discriminate a triangle from other shapes using a go/no-go paradigm. He then tested the pigeons with a partially occluded or truncated version of the triangle and discovered that the pigeon’s response to the partially occluded triangle was profoundly reduced, but the response to the truncated version was much more similar to an intact triangle. Similar results have been obtained with pictures of food vs. non-food items (Ushitani & Fujita, 2005).

The second paradigm used to study occlusion effects has involved training pigeons to discriminate between normal and incomplete figures, followed by testing with occluded versions of the shapes (Fujita & Ushitani, 2005; Sekuler, Lee, & Shettleworth, 1996). For example, Fujita and Ushitani (2005) trained pigeons to discriminate between an intact square and a square with a missing notched piece along one edge. Tests were then given with versions of the notched squares in which another square was positioned so that it filled the notch (a partial occlusion condition). The pigeons showed no decrement in recognizing the notched square in the partial occlusion condition, suggesting that they did not automatically complete the square. A second experiment utilizing the same stimuli with human participants revealed that people were slower at recognizing the notched square when presented with the occluder filling the notch. Thus, the human participants appeared to automatically complete the notched square when it was partially occluded.

Despite the large body of evidence suggesting that pigeons do not experience good continuation under conditions of partial occlusion, there are three main sources indicating that they may have this ability. DiPietro, Wasserman, and Young (2002) demonstrated recognition of shapes under conditions of partial occlusion. They trained pigeons to discriminate among four different geon shapes. Later tests were conducted in which the geons were partially occluded by a brick wall, partially erased, appeared within a notch in the wall, or appeared on top of the wall. The pigeons initially performed poorly to the partially occluded geons, but they also performed poorly to geons on top of the wall. This led to the suggestion that the wall was interfering with the pigeons' perception of the geons[1]. The birds were then given additional training with geons on top of the wall, followed by tests with the wall partially occluding the geons. The remedial training allowed the birds to demonstrate strong transfer of discrimination to the partially occluded shapes. They also generalized to novel shapes and novel occluders in subsequent experiments. Thus, one issue with the previous studies may relate to a general interference in perception of shapes when presented with an occluder.

Two additional studies have demonstrated good continuation using the method of partial-contour deletion. Rilling, La Claire, and Warner (1993) examined good continuation in pigeon visual perception by training the birds to discriminate between two line drawings of simple shapes (square vs. triangle, square vs. circle, and cube vs. pyramid). Test trials presented novel versions of these shapes in which portions of their contours were deleted or in which the stimuli were broken and pulled apart to induce gaps but without loss of any contour. The pigeons transferred responding to both sets of test stimuli indicating that the principle of good continuation may have been operating. In addition, the degree of generalization decrement was systematically related to amount of contour deletion (or gap size), demonstrating the importance of proximity of contours in shape recognition. However, these results could be explained by generalization to local features alone as these features remained intact.

Van Hamme, Wasserman, and Biederman (1992) conducted a more convincing demonstration of perceptual completion in pigeons. They trained pigeons to discriminate among four line drawings of novel objects that had half of their contours deleted. Transfer tests were conducted with the complementary contours, and the pigeons demonstrated an impressive level of discrimination. Additional tests with spatially scrambled complementary contours revealed little or no evidence of transfer, ruling out the possibility that the pigeons generalized to local features alone. While this experiment did not directly test good continuation, it suggests the operation of such a process.

In examining the pattern of results in the literature, it appears that pigeons may demonstrate good continuation when line drawing stimuli are presented with gaps in the lines, but not when contours are occluded by another object (at least not in the absence of remedial training with occluders). However, there have only been two examinations with gaps and these have only indirectly demonstrated good continuation. Therefore, it seems that further study is warranted to determine the conditions under which pigeons may demonstrate good continuation/perceptual completion. The present set of experiments examined good continuation using simple line contours with gaps. The original training stimuli consisted of two lines that appeared in a continuous or discontinuous relationship. The pigeons were trained to classify the lines on the basis of continuity using a go/no-go procedure. They were then tested with various novel contours as well as the original contours but with an occluder covering the gap.

Experiment 1

The purpose of Experiment 1 was to train pigeons to classify a pair of lines on the basis of the relationship between the lines (continuous vs. discontinuous). Following initial training, the birds were tested with novel discontinuous lines to determine whether they could transfer their discrimination.

Method

Animals

Three male captive-bred pigeons (*Columba livia*) served as the experimental subjects: Orange 40 (O40), Yellow 47 (Y47), and Black 35 (B35). A fourth bird (Green 83) began the experiment, but had to be abandoned due to excessively low pecking rates. The pigeons were approximately 1 year old at the onset of the experiment, and had participated on one previous experiment involving simple color and line orientation stimuli in a standard three-key Skinner box. They were naïve to the touch screen apparatus at the onset of the experiment. The birds were housed in individual cages in a colony room on a 12:12 light-dark schedule with light onset at 8 a.m. Each bird was maintained at 85% of its free-feeding weight by the delivery of individual Noyes pigeon pellets in the experimental apparatus and supplementary access to grain in the home cage, ranging from 5-20 g per day. They were allowed free access to grit and water in the home cage.

Apparatus

The pigeons were trained and tested in two 35 x 32 x 24 cm operant chambers housed inside of a sound-attenuating shell (Med Associates). One wall of the chamber was fitted with an 18 x 25 cm touch screen (Elotouch Systems, Accutouch) that was situated in front of a 15-in TFT monitor. On the opposite wall of the chamber was a magazine pellet dispenser (Med Associates, ENV-203) and clicker (Med Associates, ENV-135M). Individual Noyes pigeon pellets were delivered through a rubber tube into a food cup (Med Associates, ENV-200-R1M) that was located 2 cm above the grid floor. A houselight (Med Associates, ENV-227M) was located on the top-right wall above the food cup; this delivered diffuse illumination to the pigeon chamber at an intensity of approximately 200 lux. A speaker, which was positioned outside of the pigeon chambers, emitted a 60-dB white noise to mask sounds outside of the room.

Responses were recorded from the touch screen via a USB touch screen controller (Elotouch Systems, 3000U). Control of the feeder and houselight was accomplished by a digital I/O card (National Instruments, PCI-6503). A video splitter (Rextron, BSA12) allowed simultaneous presentation of images to the control room and operant chamber. Two Viglen Genie P4 computers located in an adjacent room delivered the experimental procedures and recorded data in E-prime v1.1.

Procedure

Pretraining. Following some initial handshaping to train the birds to peck at the touch screen, each bird was given 12 days of pretraining to peck a 72 x 72 mm white square on a black background using a limited hold 15-s schedule. Each pretraining session consisted of 64 trials and each trial ended in reinforcement if the pigeon responded before the 15-s interval terminated. By the end of pretraining, all three birds were pecking the white square on 100% of the trials.

Training. A subset of the training stimuli is presented in Figure 1 (the displays have been reduced in size for presentation purposes). Each stimulus consisted of one long straight line measuring 2 x 57 mm that could be presented in one of four orientations (0°, 45°, 90°, and 135°), and a short straight line measuring 2 x 20 mm positioned either as a continuation of the long line or as a discontinuation. There were four categories of stimuli. In the same-continuous (Same-Con) drawings, shown in the top row of Figure 1, the two line segments were the same angle and arranged so that they appeared as a continuous line with a gap (to the human eye). The short line could appear at either end of the long line, and the gap between the lines could be either 12 or 24 mm. The spatial arrangement of the two lines was the same as if a single straight line had been drawn but then had part of its contour erased. The width of the drawings was 2 mm for all of the Same-Con stimuli. There were a total of 16 Same-Con drawings (4 angles x 2 positions x 2 gap sizes).

The same-discontinuous (Same-Dis) stimuli contained the same angle, but the line segments were spatially misaligned. The short line could appear on either side and at either end of the long line. Thus, there were 16 possible Same-Dis stimuli; eight of these were delivered in training. The short line was positioned so that there was a distance of 24 mm between the nearest ends of the two lines so that the gap size in these stimuli was the same as the larger gap in the Same-Con stimuli. The width of the Same-Dis stimuli was 28 mm on average (range = 22 to 35 mm). This was determined by drawing a rectangle around the image that was orientated in the same angle as the long line and taking the narrowest dimension of the rectangle.

In the different-discontinuous close (Diff-Dis Close) stimuli, the two line segments were a different angle, and the gap between the lines was 12 mm. The short line segment could appear at either end of the long segment and the end of the short segment nearest to the long segment appeared in the same position as the end of the short segment in the Same-Con drawings. The width of the Diff-Dis Close drawings was 21 mm on average (range = 14 to 32 mm). There were a total of 24 possible Diff-Dis Close stimuli; a subset of 12 was delivered in training with the other half reserved for testing.

The final class of training stimuli, different-discontinuous far (Diff-Dis Far) was composed of two lines that were a different angle and appeared discontinuous. The short line could appear on either side and at either end of the long line, resulting in 48 possible combinations of which 12 were delivered in training. The short line was positioned so that there was a distance of 24 mm between the nearest ends of the two lines, which was the same gap size as in the Same-Dis stimuli and the larger gap size in the Same-Con class. The mean width of the Diff-Dis Far stimuli was 37 mm (range = 33 to 43 mm).

The birds were trained to discriminate Same-Con from the other three classes using a go/no-go procedure so that they had to form their discrimination on the basis of both angle and position information. Thus, from a human point of view, the task required categorization on the basis of smooth continuity of the straight line contours vs. discontinuity. Gap size was made irrelevant because half of the Same-Con stimuli contained the same gap size as the Diff-Dis Close stimuli (12 mm), and the other half contained the same gap size as the Same-Dis and Diff-Dis Far stimuli (24 mm). Relative position alone was also irrelevant because the short segment appeared at either end of the long line in both the Same-Con and Diff-Dis Close drawings. Matching angle was also irrelevant because the Same-Con and Same-Dis stimuli both possessed this feature. Bird O40 received continuous stimuli as his S+ class and Birds Y47 and B35 received discontinuous stimuli as their S+ class.

A trial consisted of a 72 x 72 mm white square, which the pigeon had to peck once to produce a training stimulus. Following this, two line segments were presented on a 170 x 170 mm white square surrounded by a black background, with the long line centered within the white space and the short line positioned relative to the long line. Pecks anywhere within the white area were counted. On all trials, the stimulus was presented for an initial period of 15 s, during which pecks were recorded. On S+ trials, the pigeon had to peck the stimulus at least once during the 15-s period to receive a food reinforcement of 3 pellets. If the pigeon did not respond within the 15-s period, the stimulus remained on screen until the pigeon pecked it, at which point it received reward and the stimulus disappeared. Pecks during this additional time were not recorded. On S- trials, if the pigeon pecked during the initial presentation period, then the stimulus remained on the screen until the pigeon stopped responding for 5 s, at which point the stimulus disappeared and the pigeon received a 5-s blackout of the houselight. Responses during any additional exposure time were not recorded. If the pigeon successfully withheld responding during the first 15-s of an S- trial the ITI was delivered in the absence of a blackout of the houselight. Trials were separated by a 15-s intertrial interval (ITI), during which time the video monitor was dark.

There were a total of 64 trials per session, which were delivered in four randomly ordered 16-trial blocks, each consisting of a random ordering of all of the training stimuli of one of the four line orientations. There were 8 S+ and 8 S- stimuli in each block that were made up of 8 Same-Con (2 presentations of the four stimuli), 2 Same-Dis, 3 Diff-Dis Close, and 3 Diff-Dis Far drawings.

Training sessions were conducted five days a week between 1 p.m. and 4 p.m. and lasted for approximately 1 hr. The pigeons remained on training until they produced 75% of their total responses to the S+ stimuli for four consecutive days.

Testing. Following training, the pigeons were tested on two types of novel stimuli, a sample of which are shown in Figure 2. The novel different test involved presentations of novel Diff-Dis Close and Diff-Dis Far stimuli. There was one novel Diff-Dis Close and one Diff-Dis Far for each long line angle, yielding a total of 8 test stimuli. These were generated using the same principles as the training stimuli, but with novel pairings of the lines. The test stimuli were 28 mm in width on average (range = 17 to 35 mm).

The novel discontinuous test involved presenting novel discontinuous stimuli in which the short line was displaced from its usual position. The short line was centered relative to the long line and appeared at a distance of 48 mm from the long line. There were two Same-Dis and two Diff-Dis Far test drawings for each angle, yielding a total of 16 test stimuli. The width of the test stimuli increased dramatically due to the spatial separation of the lines, resulting in a mean width of 53 mm (range = 45 to 64 mm).

The test stimuli were presented once in each session randomly intermixed with training trials, with an equal number of test stimuli in each block. Test trials were conducted in the same fashion as training trials, except that there was no response contingency (i.e., no reinforcements or blackouts). Test stimuli were presented for 15 s, after which the intertrial interval was delivered. Each type of test was delivered in a separate session, and a total of 8 sessions of each test type were delivered. The test sessions were delivered in blocks of four sessions, with at least one retraining session between blocks of testing. Analyses of test performance were only conducted for sessions in which discrimination accuracy on training trials met the 75%

performance criterion, so that test performance would not be marred by temporary lapses in discrimination accuracy; only occasionally did test sessions need to be excluded.

Results

Training

Figure 3 displays the acquisition of discriminative responding by each bird. A discrimination ratio (DR) was calculated on the basis of same angle, relative position, or combined information (both). The discrimination ratios are collapsed across long line angle, as this did not affect the level of discrimination, F(3,6) = 1.2. For the angle discrimination, the DR was calculated from the response rates to the Same-Con and Diff-Dis Close stimuli. The DR was the mean response rate to the S+ stimuli (O40 = Same-Con, Y47 and B35 = Diff-Dis Close) divided by the sum of the response rates to the two sets of stimuli. It was therefore possible to track discriminative responding to stimuli that differed on the basis whether the short line angle matched the long line angle, but in which the position of the nearest ends of the lines was the same. Similar DRs were determined for stimuli that differed according to relative position (Same-Con vs. Same-Dis) or both angle and relative position (Same-Con vs. Diff-Dis Far).

As seen in the figure, all three birds learned to discriminate on the basis of angle, relative position, and combined cues, but there were some differences in speed of learning. Bird O40 displayed faster learning when both cues were available and Y47 more readily learned to discriminate same vs. different angle stimuli. Bird B35 learned all cues equally quickly. The DRs were assessed during the last block of training with an ANOVA, which revealed no difference in discrimination accuracy across the three stimulus variations, F(2,4) = 1.2. In addition, the DRs were all above the chance level of 0.5, as assessed by one-sample t-tests, smallest t(2) = 6.2, p < .05.

One feature that varied systematically between the continuous and discontinuous lines was the width of the display (see *Method* for details) in that the continuous drawings were narrower than the discontinuous drawings. To determine whether the pigeons were categorizing the stimuli on the basis of their width, a regression analysis was conducted with the variable of width as a predictor of response rate for the discontinuous stimuli. The analysis was conducted in this way because the widths varied considerably across discontinuous drawings, but the response contingency was the same. If the birds had learned to categorize the drawings on the basis of width, then they should be more likely to make errors to stimuli with narrower widths (which would be closer to the width of the continuous class). This analysis disclosed a modest relationship between width and response rate, but it did not approach statistical significance, $\underline{t}(11) = -1.0$.

Testing

The novel different and novel discontinuous tests examined transfer of discriminative performance to novel versions of the discontinuous stimuli. The results of these two tests are presented in Figure 4, which displays the mean pecking rate (in pecks per minute) to the training and test stimuli during the test sessions. The discontinuous test stimuli were similar to stimuli from the S- class administered to Bird O40 and were similar to the S+ training stimuli for the other two birds. Data from individual test sessions for each bird appear in the Appendix, Table 1. The response rate to the discontinuous training stimuli (Train S- for Bird 040; Train S+ for Birds Y47 and B35) was taken from the training trials delivered during the test sessions and included only those training stimuli from the same sets as the test stimuli. Bird O40, who received discontinuous stimuli as his S- category, produced a similarly low rate of response to the training and test S-s in both tests; in contrast, he responded at a high rate to the Same-Con training stimuli (Train S+). On the other hand, Birds Y47 and B35 responded at a similarly high rate to the discontinuous training and test S+s, but responded at a low rate to the Same-Con training stimuli (Train S-).

Wilcoxon signed ranks tests were conducted separately for each bird to examine whether the pecking rates during each test differed between the test stimuli and comparable training stimuli. In both tests, Birds Y47 and B35 both displayed no difference between their training and test stimuli of the same class, largest $z = 1.2$. Bird Y47 displayed somewhat lower pecking rates to the novel different test stimuli, $z = 2.1$, $p < .05$, but did not show a significant difference in pecking to the novel discontinuous test stimuli compared to the training stimuli, $z = 1.7$. Response rates to the test stimuli were compared against the opposing Same-Con class, revealing that the novel discontinuous test stimuli were discriminated significantly from the Same-Con stimuli, smallest $z = 2.2$, $p < .05$.

Discussion

All three birds learned the original continuous vs. discontinuous discrimination, requiring 40 to 50 sessions to reach criterion. There were some individual differences in the speed of learning to discriminate on the basis of angle (Same-Con vs. Diff-Dis Close), position (Same-Con vs. Same-Dis) or both (Same-Con vs. Diff-Dis Far) cues. However, by the end of training, all three birds exhibited a reasonably high level of discrimination to all of the categories of stimuli. Discrimination accuracy was maintained throughout testing as well, with over 85% of responses to the S+ class during the vast majority of test sessions. Thus, it appears that the birds learned to categorize the line stimuli accurately.

One cue that the birds might have used in place of continuity is the width of the drawings. The continuous lines were narrower than the discontinuous lines. However, an analysis of the effect of width on responding revealed only a modest non-significant trend, suggesting that width was not playing a pivotal role in forming the discrimination. This issue will, however, be examined further in the subsequent experiments.

The tests with novel different and novel discontinuous stimuli revealed excellent transfer to the novel versions of the discontinuous stimuli. The novel different test examined novel Diff-Dis Close and Diff-Dis Far stimuli that were constructed with the same constraints and same parts as the training stimuli and thus indicate that the birds did not merely memorize the discontinuous training stimuli. For example, the birds received Diff-Dis Close training stimuli where the 0° long line was paired with a 45° short line on the right side, 135° left, and 90° right. The Diff-Dis Close test was with 90° left. Thus, the results suggest that the birds did not merely memorize the particular discontinuous training stimuli.

The novel discontinuous test examined the role of gap size in mediating the discrimination. When the birds experienced the tests with the two lines that were farther apart than normal (48 mm vs. the usual 24 mm) and were spatially displaced, they nonetheless were able to respond appropriately. Thus, the gap size between the two lines was not a significant factor in their discrimination, which is not entirely surprising because the training contingencies were designed to discourage learning on the basis of gap size alone.

The results of Experiment 1 suggested that the birds learned a continuous vs. discontinuous categorization. However, the flexibility of their categorical learning remains to be determined. In other words, would the discrimination transfer to different types of lines that the birds had not been explicitly trained to discriminate?

Experiment 2

Experiment 2 assessed whether the birds would transfer their original discrimination to two novel line types. One was a straight line that was displayed at a novel angle of 112.5° and was paired with a short straight line that was either continuous or discontinuous. The other was a long curved line that appeared along with a short curved line in a continuous or discontinuous relationship.

Method

Animals

The birds from Experiment 1 participated in Experiment 2.

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

The general training and testing procedures were the same as in Experiment 1. Prior to each of the tests, the birds received retraining with the original training task until they had met a criterion of four consecutive sessions with at least 75% responses to the S+ category.

Following retraining the birds received two types of tests: novel angle and curved lines. A sample of these test stimuli is shown in Figure 2. The novel angle test delivered stimuli from each of the four categories, with the long line positioned at an angle of 112.5°. A full set of 16 test stimuli was developed with the novel angle, using the same principles as the training stimuli (see Experiment 1 *Method*). The mean widths of the novel angle Same-Con, Same-Dis, Diff-Dis Close, and Diff-Dis Far drawings were 2 mm, 19 mm (range = 16 to 22 mm), 28 mm (range = 23 to 32 mm), and 32 mm (range = 27 to 36 mm), respectively.

The curved line test involved presenting a curved long line that was positioned at an angle of 90° coupled with curved short lines at each of the four possible angles (0°, 45°, 90°, and

135º). A full set of 16 curved lines was developed in the same manner as the training stimuli. The mean widths of the curved Same-Con, Same-Dis, Diff-Dis Close, and Diff-Dis Far drawings were 24 mm (range = 23 to 25 mm), 28 mm (range = 25 to 31 mm), 19 mm (range = 18 to 20 mm), and 35 mm (range = 31 to 39 mm), respectively.

Two four-session blocks of testing were conducted with the novel angle test stimuli, followed by two further blocks of testing with the curved line test stimuli. A single retraining session was administered between each four-session block in each test.

Results

Figure 5 presents the pecking rates to the S+ and S- training and testing stimuli for each of the two test types; the training results were taken from training trials during the test sessions. The corresponding data collected from each individual bird in each individual test session appears in the appendix (Tables 2 and 3). As seen in the figure, all three birds displayed a robust discrimination to the training stimuli. All of the birds produced mean DRs to the training stimuli in excess of 0.85 on both tests (see Tables 2 and 3 for DRs on individual test sessions). Those DRs were all significantly above chance, as assessed by one-sample t-tests, smallest $\underline{t}(2) = 36.0$, $\underline{p} < .001$.

There was evidence of a generalization decrement to the test stimuli. Bird O40 demonstrated an initial response to the novel angle tests that was followed by a period of disruption of discrimination followed by a cessation of responding to the test stimuli altogether (see Table 2). This bird did not respond during the curved line test (see Table 3). Birds Y47 and B35 demonstrated better transfer of performance on both tests, with largely intact responding during the novel angle test, but lower rates of response to the curved lines.

Novel Angle Test. Bird O40 demonstrated a disruption in performance after the first three sessions of testing (see Table 2). Overall, there was a trend towards higher rates of responding to the S+ stimuli (8.2 responses/min) than the S- stimuli (5.5 responses/min), but a Wilcoxon signed ranks test failed to reveal any difference, $z = 0.7$. The DRs to the test stimuli (0.60) were lower than the DRs to the training stimuli (0.88), and test DRs were not significantly different from chance, as assessed by a one-sample t-test, $t(6) = 0.7$. The test DRs were not formally compared with the training DRs because the response rates to test stimuli were noticeably lower than the response rates to training stimuli and DRs values can be affected by absolute response rates.

Bird Y47 pecked the S+ test stimuli at a rate of 43.4 responses per minute compared to a rate of 4.6 responses/min to the S- test stimuli; he pecked the S+ test stimuli at a higher rate than the S- test stimuli on 100% of the test sessions. The difference in pecking to the S+ vs. S- test stimuli was statistically confirmed by a Wilcoxon signed ranks test, $z = 2.5$, $p < .05$. The test DRs were similar to the training DRs on all but one session (mean test DR = 0.93) and these were significantly above chance, $t(7) = 10.9$, $p < .001$.

Bird B35 showed a similar pattern with a rate of 28.3 responses/min to the S+ test stimuli compared to a rate of 1.1 responses/min to the S- test stimuli; he pecked the S+ test stimuli at a higher rate than the S- test stimuli on 100% of the test sessions. The higher response rate to S+ test stimuli was confirmed statistically, $z = 2.4$, $p < .05$. The test DRs were similar to the training DRs throughout testing (mean test DR = 0.97) and these were significantly above chance, $t(6) = 28.6$, $p < .001$.

Curved Line Test. Because Bird O40 only produce one peck over the course of the curved line test, he was omitted from statistical analyses.

Bird Y47 pecked the S+ test stimuli at a higher rate than the S- test stimuli on 86% of the test sessions, with a mean pecking rate of 17.9 pecks/min to the S+s versus 8.6 pecks/min to the S- test stimuli. Statistical analyses indicated a significant discrimination of the S+ and S- test stimuli, z = 2.2, $\underline{p} < .05$. There was an indication of weaker DRs to the test stimuli (mean = 0.71), but the test DRs were significantly above chance, as assessed by a one-sample t-test, $\underline{t}(6) = 2.7$, $\underline{p} < .05$.

Bird B35 pecked the S+ test stimuli at a higher rate than the S- test stimuli on 100% of the sessions, with a mean pecking rate of 14.5 pecks/min to the S+ test stimuli versus 3.6 pecks/min to the S- test stimuli. This bird showed significantly higher rates of pecking to the S+ vs. S- test stimuli, z = 2.5, $\underline{p} < .05$. The test DRs were similar to the training DRs on 5/8 of the test sessions, and the test DRs were significantly above chance, $\underline{t}(7) = 8.4$, $p < .001$.

Discussion

The tests with novel angle and curved line stimuli revealed evidence of significant transfer of discrimination in Birds Y47 and B35. The transfer of discrimination indicates that the birds may have learned a general category of continuous vs. discontinuous that could be applied to new types of lines.

In Experiment 1, a modest (non-significant) effect of stimulus width was disclosed suggesting that this cue may have contributed to performance. In Experiment 2, the curved lines possessed widths that were highly similar in the continuous vs. discontinuous categories. Thus, the observation of discriminative performance indicates that stimulus width did not play a critical role in categorization.

However, all of the birds demonstrated a reduction in pecking rates to the test stimuli, particularly in the curved line test, with the extreme case of Bird O40 who did not peck these stimuli. The pattern of results indicates that the birds recognized the test stimuli as different from the training stimuli, but they were still able to categorize them. This underlines the fact that the test stimuli were clearly discriminable from the training stimuli on the basis of angle and curvature of the lines.

The transfer of discrimination to the novel tests indicates that the birds may have learned to discriminate the stimuli on the basis of a combination of features (e.g., matching angle + correct relative position). However, it is possible that the birds attended to local cues surrounding the gap in forming and transferring their discrimination. This issue will be examined in a final experiment.

Experiment 3

The formation of a continuous vs. discontinuous category that is flexible enough to transfer to novel line types requires attention to both the angle and spatial relationship of the two lines in the set. The pigeons were able to learn this discrimination and transfer to novel line types. This suggests that they may have been attending to combined local (matching line angle) and global (relative position) cues in the line sets. However, the possibility remains that the birds were able to solve the task on the basis of more localized cues. In particular, one feature that is possessed by all of the Same-Con stimuli is that the line edges directly on either side of the gap match exactly in their size and orientation. It is possible that the pigeons learned to discriminate the classes of stimuli on the basis of whether: (a) the line ends matched in both size and orientation and (b) the line ends were spatially aligned. Although this explanation relies on both a shape cue and a spatial cue, it is presumably a simpler form of learning than attending to both the angle of the line segments and their relative spatial position. Learning of the local cues surrounding the gap could result in transfer to novel different and novel discontinuous stimuli

(Experiment 1) because these would lack the appropriate local cues that define the Same-Con class. Likewise, the novel angle and curved lines would possess the appropriate features surrounding the gap to allow for a transfer of discrimination. Experiment 3 tested for discrimination based on edges surrounding the gap by covering the gap with an occluder.

Method

Animals

The birds from Experiments 1 and 2 participated in Experiment 3.

Apparatus

The apparatus was the same as in previous experiments.

Procedure

The general training and testing procedures were the same as in Experiments 1 and 2. Prior to each of the tests, the birds received retraining with the original training task until they had met a criterion of four consecutive sessions with at least 75% responses to the S+ category.

Following retraining, the birds received an occlusion test whereby a subset of the training stimuli was presented with a gray square (17 x 17 mm) that was superimposed over the gap between the lines. A sample of the testing stimuli is shown in the rightmost column of Figure 2. The test stimuli comprised a randomly selected training drawing from each of the four categories for each of the four angles, yielding a total of 16 stimuli. As seen in the figure, the ends of the lines surrounding the gap differed from the training drawings for the majority of the test stimuli (9 of 16). For example, in the Same-Con test drawing, the gap area in the original stimulus was bounded by two parallel segments oriented at 0, but the occluder created a notch in the lines. In 5/16 of the test stimuli, one or both of the segments on either side of the gap changed in angle and in 4/16 of the stimuli one or both of the segments changed in shape. Thus, the line segments near the gap changed in many of the drawings, and the gap was widened and shaded in all drawings. The overall width of the drawings also changed. The width of the Same-Con, Same-Dis, Diff-Dis Close, and Diff-Dis Far were: 35 mm (range = 28 to 41 mm), 38 mm (range = 30 to 43 mm), 35 mm (range = 28 to 41 mm), and 44 mm (range = 36 to 54 mm). The occlusion test sessions were delivered in two four-session blocks with a retraining session in between the two blocks.

Results

Discrimination of the training stimuli during the occlusion test, measured by a DR, was maintained at a high level (see Appendix, Table 4). The training DRs were significantly above chance, as assessed by a one-sample t-test, $\underline{t}(2) = 53.3$, $\underline{p} < .001$. Thus, the addition of an occluder to some of the training stimuli did not appear to disrupt discrimination accuracy on normal training trials.

The occlusion test stimuli elicited low pecking rates, but all three birds did peck the test stimuli. The DRs produced by Birds O40, Y47 and B35 were 0.74, 0.95, and 0.97, respectively. The DRs produced by Birds Y47 and B35 were as high as their DRs on normal training trials during the same sessions, but bird O40 produced a lower DR on test trials.

Each bird was analyzed separately for evidence of discrimination of the training and test stimuli. Bird O40 displayed the weakest discrimination on test trials, pecking the S+ stimuli at a higher rate on only 63% of test sessions. His mean pecking rates to the S+ and S- test stimuli were 5.0 and 1.0 pecks/min, respectively. The difference in pecking rates between test S+ and S- stimuli was not quite significant, $z = 1.9$, $\underline{p} = .06$. The test DRs were similar to training on 5/8 of the sessions, but were at chance during the other three sessions. Despite the variation in test DRs, they were significantly above chance, $t(7) = 2.8$, $p < .05$, indicating significant (albeit variable) discrimination.

Bird Y47 pecked the S+ stimuli at a higher rate on 100% of the sessions and produced a mean pecking rate of 7.5 pecks/min to the S+ tests versus 0.4 pecks/min to the S- tests. He demonstrated significantly higher rates to S+ test stimuli compared to S- test stimuli, $z = 2.4$, $p < .05$. The test DRs were perfect on all but one test session, and these were significantly above chance, $t(6) = 8.3$, $p < .001$.

Finally, Bird B35 pecked the S+ test stimuli at a higher rate on 88% of the sessions, with a mean pecking rate of 3.1 pecks/min to the S+ stimuli versus 0.1 pecks/min to the S- stimuli. The statistical analysis of performance by this bird was similar to Bird Y47, with significant discrimination of S+ and S- test stimuli, $z = 2.4$, $p < .05$. The test DRs were similar to training DRs on 6/8 of the test sessions, and the test DRs significantly exceeded chance levels, $t(6) = 14.2$, $p < .001$.

Discussion

The occlusion test yielded evidence of significant transfer of discrimination despite considerable loss of visual information. All three birds displayed substantial reductions in their pecking rates to the test stimuli, but their discrimination accuracy was maintained above chance.

The maintenance of discrimination provides further evidence for evaluating the possible role of the width of the stimuli. The addition of the occluder resulted in the four types of stimuli having highly stimuli widths and almost complete overlap in width across the continuous and discontinuous categories. The results indicate that differential width was not a necessary condition for discrimination.

The decrease in pecking rates indicates that the birds recognized the test stimuli as different from the training stimuli. An additional source of decrease in pecking rates may have been due to the prolonged testing that had occurred prior to the present experiment. The birds had been repeatedly tested with novel stimuli over the course of many prior sessions. They may have learned that novel stimuli were associated with nonreinforcement and hence reduced their pecking rates to them. There was some indication of progressively lower rates to each successive test (see prior experiments). However, it is also the case that the later tests involved larger changes in the visual features of the test stimuli, so it is difficult to discern the cause of the lower pecking rates.

The fact that all three birds demonstrated significant discrimination to the occluded training stimuli indicates that they did not simply attend to local features immediately surrounding the gap in making their discrimination as these features were now covered. It is possible that, because the occluder was not black (and therefore did not remove all the features surrounding the gap) the birds could have attended to some features near the occluder that were preserved. This seems unlikely, however, because the contrast differed (grey instead of white) and the line ends surrounding the occluder were different from the line ends surrounding the normal gap in most of the occluded stimuli. It seems more likely that the birds based their discrimination on the visible portion of the lines.

An additional noteworthy observation in the present experiment is that the birds were able to recognize the line drawings despite partial occlusion. This result is inconsistent with previous studies examining the effect of partial occlusion on shape/object recognition in pigeons (Cerella, 1980; Ushitani & Fujita, 2005). The present results are more consistent with those of DiPietro et al. (2002), who showed that pigeons were able to recognize partially occluded geons, but that recognition was reduced when the pigeons were unaccustomed to geons that were proximal to an occluder. Our pigeons had no prior experience with the occluder so this may have caused a general disruption in performance, resulting in reduced pecking rates to the test stimuli.

There are at least two reasons for the discrepancy between our results and the prior failures to demonstrate recognition of partially occluded stimuli in pigeons. Firstly, the previous studies involved training with S+ and S- classes in a go/no-go paradigm, but the focus of analysis was based on responding to the S+ class. The pecking rate to the S+ training vs. test stimuli is likely to assess a similarity judgment, whereas the rate to the S+ vs. S- test stimuli assesses transfer of discrimination. Although our birds judged the partially-occluded stimuli as dissimilar to the originals, they were nonetheless able to extract the critical features for discrimination. The pigeons in the DiPietro et al. (2002) study were also tested for discrimination performance under conditions of partial occlusion, and they too demonstrated substantial transfer of discrimination. While significant discrimination of the test stimuli is indicative of classification, it does not necessitate perceptual completion because discrimination could take place based on visible parts of the stimuli. This certainly appeared to be the case in the present study where the visible portion of the lines contained sufficient information to allow for classification.

Another possible difference may be the nature of the training given to the birds. The pigeons in the present study were explicitly trained to categorize the stimuli on the basis of both local and global features, and to attend to features that related to whether or not the two lines were in a continuous relationship. Previous experiments have involved training with simple shapes that differed on many local features. Attention to local features would presumably lead to greater disruption under partial occlusion where some of the local features are covered. Thus, it is possible that the differences in the effect of occlusion may be due, at least in part, to an attentional bias towards local vs. global features.

General Discussion

Experiment 1 revealed that the pigeons learned to categorize pairs of lines as continuous or discontinuous. The size of the gap between the two lines, the relative position of the lines, the angle of the long line, and whether or not the two angles matched were all irrelevant to the task. The high degree of discrimination on the task, with asymptotic performance exceeding 85% on most sessions, indicates that the birds must have largely ignored these irrelevant features. One possible confounding cue that the birds may have used to learn the original discrimination is the width of the displays. However, an analysis of the contribution of display width did not reveal any noticeable effects, and in many of the subsequent tests the width of the displays was altered dramatically but did not disrupt discrimination accuracy.

A series of five different types of transfer tests were administered across the three experiments (see Figure 2) and these revealed evidence of transfer of discrimination to varying degrees. Bird O40 demonstrated full transfer to the novel different and novel discontinuous stimuli in Experiment 1, but poor transfer to the novel angle and curved line tests in Experiment 2, and only partial transfer to the occlusion stimuli in Experiment 3. On the other hand, Birds Y47 and B35 displayed much better performance on the tests, with near complete transfer to the novel different, novel discontinuous, and novel angle stimuli. On the curved line and occlusion tests, response rates were lower to the test stimuli, but discrimination accuracy was maintained above chance (albeit weaker on the curved line test).

There are three most probable mechanisms that could have allowed for successful learning and transfer of the present task. One possibility is that the birds engaged in perceptual completion of the items, thereby automatically seeing the continuous lines as continuous and the others as discontinuous. While amodal completion appears to be an effortless and automatic task for many species (Duruelle, Barbet, Dépy, & Fagot, 2000; Forkman, 1998; Fujita, 2001; Kanizsa, 1979; Kanizsa, Renzi, Conte, Compostela, & Geurani, 1993; Lea, Slater, & Ryan, 1996; Rauschenberger & Yantis, 2001; Regolin & Vallortigara, 1995; Rensink & Enns, 1998; Sugita, 1999), prior research has indicated that pigeons do not appear to possess this ability (Aust & Huber, 2006; Cerella, 1980; Fujita, 2001; Fujita & Giersch, 2005; Sekuler, Lee, & Shettleworth, 1996; Ushitani & Fujita, 2005; Ushitani, Fujita, & Yamanaka, 2001; Watanabe & Furuya, 1997). It is unlikely that the birds in the present study engaged in amodal completion as this process would have yielded preservation of response rates in the curved line and occlusion tests. Instead, all of the birds displayed a substantial generalization decrement to these stimuli.

A second plausible interpretation of the present results is that the birds simply memorized the individual training stimuli and then generalized from these stimuli to the test drawings. It is well known that birds can memorize large numbers of individual stimuli (Cook, Levinson, Gillett, & Blaisdell, 2005; Vaughan & Greene, 1984), but in categorization experiments, memorization is more often observed in tasks where the stimulus set is limited in size (e.g., Wasserman, 1995). The pattern of results obtained from Bird O40 is consistent with memorization of the Same-Con stimuli, which were S+s for this bird; the other two birds received discontinuous S+ stimuli. The Same-Con stimuli comprised fewer variations and would have been easier to memorize. If Bird O40 learned the specific S+s and then withheld pecking to all non-S+ stimuli, then this would lead to good transfer in the novel discontinuation and novel different tests in Experiment 1 as these were S- stimuli. This would also lead the bird to withhold pecking to the novel angle, curved lines, and occlusion stimuli from both classes. Although this bird did peck the S+ stimuli in the novel angle and occlusion tests to some degree, his discrimination performance was weaker on these tests than on the training stimuli. Thus, the poor performance on these three tests could be explained memorization of the S+ stimuli. Unfortunately, this bird was the only one to receive continuous S+ stimuli, so one cannot determine whether the results were due to an idiosyncrasy of this bird or due to the assignment of contingencies.

This pattern of results was not evident in the other two birds indicating that they did not simply memorize one of the classes of stimuli. They could conceivably have memorized all of the training stimuli, but this would have led to a generalization decrement in Experiment 1 tests because the novel different and novel discontinuous stimuli were generated with novel pairings of the short and long segments. Thus, memorization seems unlikely as the sole explanation of their results.

The final possibility is that Birds Y47 and B35 learned to classify the lines on the basis of whether the two lines were the same angle combined with whether the two lines were spatially aligned. Previous research has shown that pigeons conjointly attend to the local features (components) and their spatial relationship when learning to discriminate line drawings of objects (Kirkpatrick-Steger, Wasserman, & Biederman, 1996a, 1996b, 1998, 2000; Kirkpatrick, 2001; Wasserman, Kirkpatrick-Steger, Van Hamme, & Biederman, 1993). Thus, the combined use of both local and global cues is well within the capabilities of the pigeon. Learning of the combined angle and feature information would lead to successful discrimination and good transfer, but could result in a generalization decrement if one presumed that the pigeons learned aspects of the stimuli such as the particular angles or that the lines were straight (not curved).

The transfer tests indicated that there were two processes that guided test performance. One appeared to be a similarity judgment whereby the pigeons gauged the similarity of the test items against the training items. Similarity appeared to be affected by the specific features of the lines (e.g., angle and curvature). The other process seemed to involve a category (or discrimination) judgment whereby the test stimuli were assessed in terms of likely category membership. The category judgment was largely unaffected by the particular features of the test stimuli and rather seemed to reflect the continuity of the line segments (combined angle and relative position) regardless of their particular properties.

Previous research in this area has focused on whether pigeons automatically complete missing visual information under conditions of partial occlusion or erasure of contour. The present investigation addressed a different issue of whether pigeons could be explicitly trained with stimuli in which attending to cues related to continuation vs. discontinuation of lines was essential for discrimination. Recognition of continuity is a prerequisite of completion, and two of the pigeons in the present study demonstrated this ability. This does not necessitate the implication that the pigeons saw the lines as continuous. However, the present experiments do demonstrate that pigeons can be trained to attend to features relevant to making continuity/discontinuity judgments. It would be interesting to investigate amodal completion with stimuli more akin to the present ones, particularly using contour erasure as opposed to partial occlusion. In any event, the present results encourage further research examining the role of Gestalt processes in pigeon visual perception.

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Footnotes

[1] This argument does not necessarily conflict with the findings of Fujita (2001) that the pigeons' judgments of the length of the bar were unaffected by occlusion. This judgment would likely tap into the metric properties of the image rather than shape properties, which may reside in different parts of the pigeon visual system (Kirkpatrick, 2001; Peissig, Kirkpatrick, Young, Wasserman, & Biederman, 2006).

Figure Captions

Figure 1. The 16 training displays presented during original training and throughout testing in all three experiments. There were four different line angles (0º, 45º, 90º and 135º) and four relationships that the two lines could take (Same-Continuous, Same-Discontinuous, Different-Discontinuous Close, and Different-Discontinuous Far), depending on whether the angles were the same or different and whether they appeared in a continuous or discontinuous spatial arrangement. The stimuli have been reduced in size for presentation purposes.

Figure 2. A subset of the test stimuli delivered during the novel different and novel discontinuous tests in Experiment 1, during the novel angle and curved line tests in Experiment 2, and during the occlusion test in Experiment 3. The stimuli have been reduced in size for presentation purposes.

Figure 3. Acquisition of discrimination by each of the three birds for stimuli that differed according to angle (Same-Con vs. Diff-Dis Close), relative position (Same-Con vs. Same-Dis) or both (Same-Con vs. Diff-Dis Far) over the course of original training in Experiment 1.

Figure 4. Mean pecking rates (in pecks/min) to the test displays during novel different and novel discontinuous tests in Experiment 1 for each bird (Bird O40, Test S-; Birds Y47 and B35, Test S+). Pecking rates to the training stimuli are included for comparison purposes. Hatched bars represent results from the novel different test and stippled bars represent the novel discontinuous test.

Figure 5. Mean pecking rates (in pecks/min) to the S+ and S- training and test stimuli presented during the novel angle and curved line tests in Experiment 2 for each bird. Bird O40 received the Same-Con stimuli as its S+ class and the other three categories as its S- class; the reverse was

true for Birds Y47 and B35. Hatched bars represent results from the novel angle test and stippled bars represent the curved line test.

Figure 6. Mean pecking rates (in pecks/min) to the S+ and S- training and test stimuli presented during the occlusion test in Experiment 3 for each bird. Bird O40 received the Same-Con stimuli as its S+ class and the other three categories as its S- class; the reverse was true for Birds Y47 and B35.

Figure 1

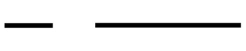
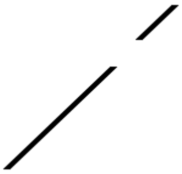
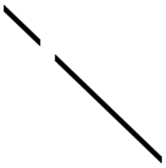
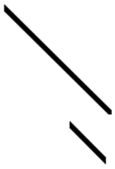
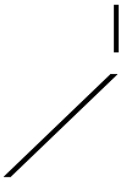
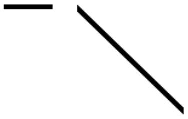
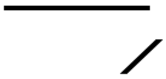
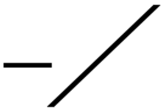
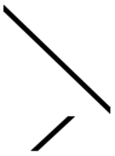
Stimulus Type	**Training Angle**			
	0º	45º	90º	135º
Same-Con				
Same-Dis				
Diff-Dis Close				
Diff-Dis Far				

Figure 2

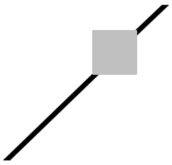
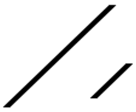
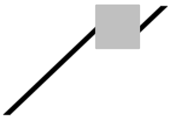
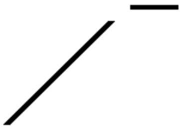
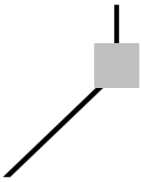
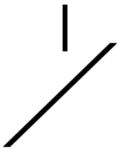
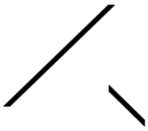
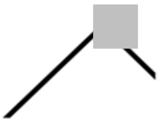
Stimulus Type	**Test Type**				
	Novel Diff	Novel Dis	Novel Angle	Curved Line	Occlusion
Same-Con					
Same-Dis					
Diff-Dis Close					
Diff-Dis Far					

Figure 3

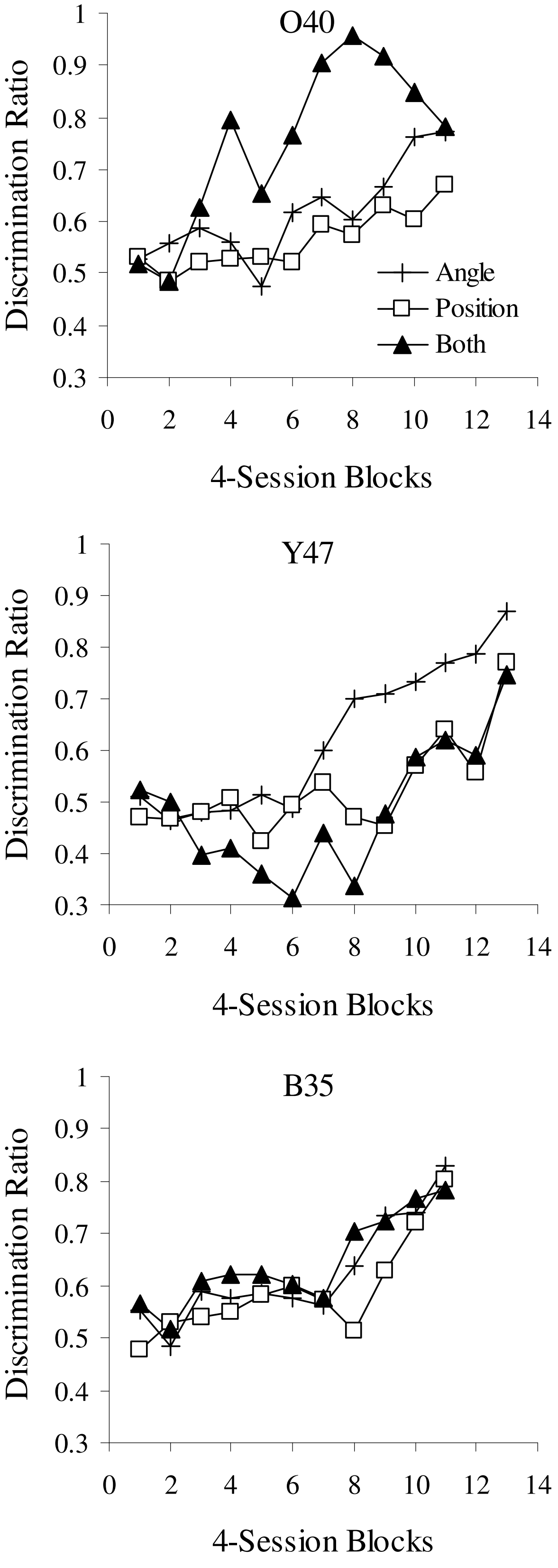

O40
Y47
B35
Discrimination Ratio
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
2
4
6
8
10
12
14
4-Session Blocks
Angle
Position
Both

Figure 4

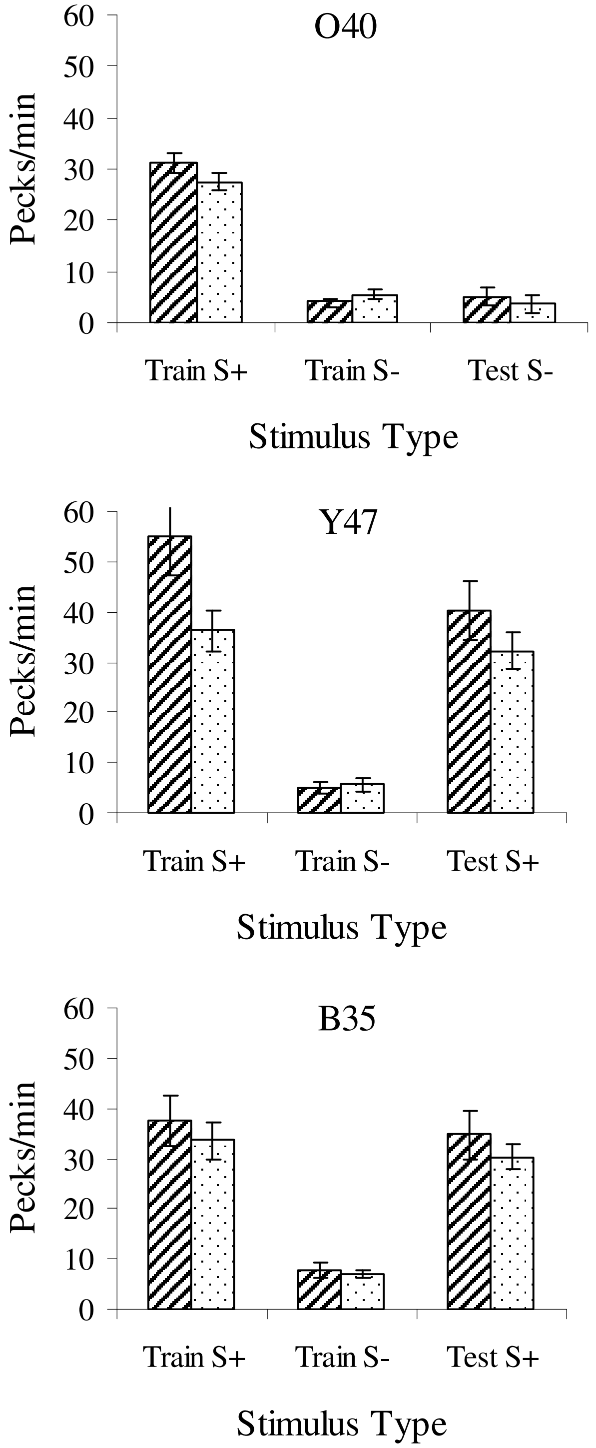

O40
Pecks/min
60
50
40
30
20
10
0
Train S+
Train S-
Test S-
Stimulus Type
Y47
Pecks/min
60
50
40
30
20
10
0
Train S+
Train S-
Test S+
Stimulus Type
B35
Pecks/min
60
50
40
30
20
10
0
Train S+
Train S-
Test S+
Stimulus Type

Figure 5

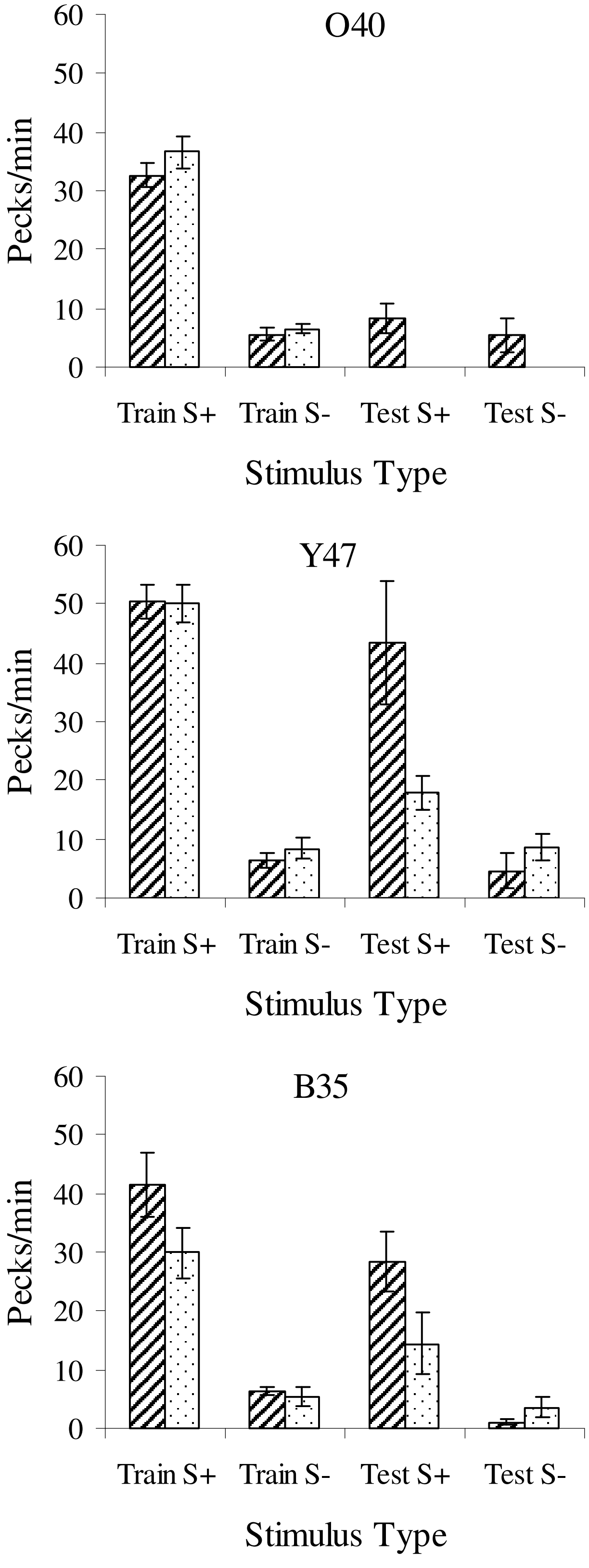
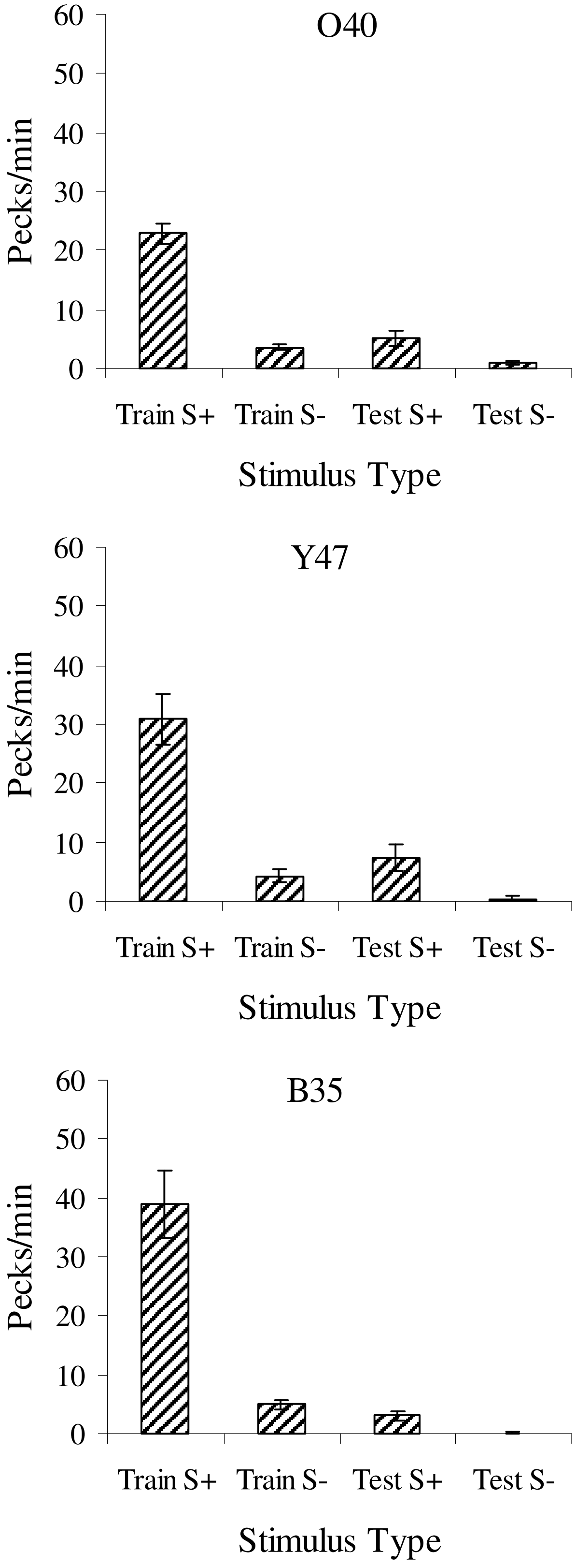

O40
Y47
B35
Pecks/min
0
10
20
30
40
50
60
Train S+
Train S-
Test S+
Test S-
Stimulus Type

Figure 6


O40
Pecks/min
60
50
40
30
20
10
0
Train S+
Train S-
Test S+
Test S-
Stimulus Type
Y47
Pecks/min
60
50
40
30
20
10
0
Train S+
Train S-
Test S+
Test S-
Stimulus Type
B35
Pecks/min
60
50
40
30
20
10
0
Train S+
Train S-
Test S+
Test S-
Stimulus Type

Appendix

Response rates and discrimination rations to positive and negative test stimuli produced by each bird during individual test sessions

Table 1. Response rates (in responses/min) to training and testing discontinuous (Dis) and continuous (Con) stimuli in Experiment 1. Each row presents data from a different individual test sessions delivered to a particular bird.

	Novel Diff Test			Novel Dis Test		
	Train Dis	Test Dis	Test Con	Train Dis	Test Dis	Test Con
O40	4.0	6.0	36.3	9.2	0.5	33.3
	6.0	4.0	26.5	5.2	10.5	30.6
	2.8	1.5	28.1	4.3	0.5	21.9
	4.2	4.5	30.6	5.3	4.0	24.3
	5.2	0.5	36.0	5.8	5.8	27.3
	4.0	14.5	35.4	2.8	0.8	27.4
	2.2	4.0	24.3			
Mean	4.0	5.0	31.0	5.4	3.7	27.4
SEM	0.5	1.7	1.9	0.9	1.6	1.7
Y47	23.8	14.5	0.9	22.9	20.5	4.4
	23.7	25.0	2.4	39.8	23.3	9.4
	50.3	29.5	4.5	38.4	43.8	11.8
	73.0	47.0	10.5	39.3	33.8	1.4
	56.2	64.0	4.0	34.9	28.3	5.5
	65.8	50.5	6.8	31.2	32.8	0.6
	75.7	47.0	9.4	57.4	51.5	8.3
	70.0	44.5	1.5			
Mean	52.6	39.6	5.5	37.7	33.4	5.9
SEM	7.6	6.1	1.3	4.0	4.2	1.6
B35	24.5	49.0	38.2	16.3	14.0	4.0
	43.0	86.0	41.5	30.3	33.5	8.6
	50.0	100.0	53.2	29.3	33.3	10.5
	39.0	78.0	39.3	38.2	31.8	8.3
	34.0	68.0	37.7	28.4	38.3	5.6
	17.5	35.0	16.5	43.6	33.3	5.1
				36.2	29.0	5.1
				45.9	32.3	7.5
Mean	34.7	69.3	37.7	33.5	30.7	6.8
SEM	4.9	9.8	4.9	3.4	2.5	0.8

Table 2. Response rates (in responses/min) to training and testing S+ and S- stimuli, and discrimination ratios based on those rates during the novel angle test in Experiment 2. Each row presents data from a different individual test session delivered to a particular bird.

	Train S+	Train S-	Train DR	Test S+	Test S-	Test DR
O40	39.0	10.4	0.80	20.0	1.5	0.93
	36.0	5.3	0.89	17.5	4.0	0.81
	34.1	9.5	0.82	6.0	1.0	0.86
	40.8	5.9	0.88	7.5	24.0	0.24
	28.6	1.9	0.94	9.5	0.5	0.95
	27.5	4.0	0.90	5.0	7.5	0.40
	30.5	2.7	0.94	0.0	5.5	0.00
	24.3	4.0	0.87	0.0	0.0	---
Mean	32.6	5.5	0.88	8.2	5.5	0.60
SEM	2.1	1.1	0.02	2.6	2.8	0.14
Y47	50.7	6.3	0.89	54.5	26.0	0.69
	34.6	3.9	0.90	6.0	0.0	1.00
	48.9	4.1	0.92	35.0	0.5	0.99
	49.0	9.9	0.83	19.0	0.0	1.00
	58.9	3.3	0.95	98.5	3.5	0.97
	61.7	13.8	0.82	21.0	3.5	0.86
	49.6	4.4	0.92	61.5	1.0	0.98
	49.1	5.1	0.91	52.0	2.5	0.95
Mean	50.3	6.3	0.89	43.4	4.6	0.93
SEM	2.9	1.3	0.02	10.5	3.1	0.04
B35	35.2	7.4	0.83	33.5	4.0	0.89
	26.3	3.5	0.89	36.0	3.0	0.92
	20.5	4.3	0.83	14.0	0.0	1.00
	48.6	8.1	0.86	30.0	0.5	0.98
	48.1	6.3	0.88	45.0	0.5	0.99
	52.7	7.0	0.88	33.5	0.0	1.00
	58.9	8.4	0.88	6.0	0.0	1.00
Mean	41.5	6.4	0.86	28.3	1.1	0.97
SEM	5.4	0.7	0.01	5.1	0.6	0.02

Table 3. Response rates (in responses/min) to training and testing S+ and S- stimuli, and discrimination ratios based on those rates during the curved line test in Experiment 2. Each row presents data from a different individual test session delivered to a particular bird.

	Train S+	Train S-	Train DR	Test S+	Test S-	Test DR
O40	48.4	10.8	0.84	0.0	0.0	---
	42.1	5.5	0.90	0.0	0.0	---
	33.5	3.9	0.91	0.0	0.0	---
	25.1	4.4	0.88	0.0	0.0	---
	34.6	7.0	0.85	0.0	0.0	---
	42.4	9.1	0.86	0.0	0.0	---
	38.5	6.8	0.87	0.0	0.0	---
	28.1	4.2	0.88	0.0	0.5	---
Mean	36.6	6.5	0.87	0.0	0.1	---
SEM	2.7	0.9	0.01			
Y47	38.2	3.9	0.90	15.3	8.0	0.66
	56.1	5.1	0.91	8.0	15.0	0.35
	41.9	4.6	0.90	23.3	11.0	0.68
	44.2	12.4	0.80	22.0	9.0	0.71
	59.2	5.4	0.91	30.0	15.0	0.67
	57.0	11.1	0.84	17.3	2.0	0.90
	53.3	16.3	0.78	9.3	0.0	1.00
Mean	50.0	8.4	0.86	17.9	8.6	0.71
SEM	3.2	1.8	0.02	3.0	2.2	0.08
B35	52.0	5.5	0.93	42.0	15.0	0.74
	31.6	5.0	0.89	33.3	6.0	0.85
	11.6	1.5	0.84	10.7	2.0	0.84
	24.0	5.0	0.89	2.0	0.0	1.00
	41.3	5.0	0.87	10.7	4.0	0.73
	30.9	0.0	0.86	6.0	2.0	0.75
	27.1	14.0	0.82	9.3	0.0	1.00
	20.7	7.0	0.84	2.0	0.0	1.00
Mean	29.9	5.4	0.87	14.5	3.6	0.86
SEM	4.4	1.5	0.01	5.3	1.8	0.04

Table 4. Response rates (in responses/min) to training and testing S+ and S- stimuli, and discrimination ratios based on those rates during the occlusion test in Experiment 3. Each row presents data from a different individual test session delivered to a particular bird.

	Train S+	Train S-	Train DR	Test S+	Test S-	Test DR
O40	32.5	4.8	0.90	8.0	0.3	0.96
	21.4	3.7	0.87	10.0	0.5	0.95
	13.8	1.7	0.90	5.0	1.0	0.83
	19.8	3.1	0.87	2.0	2.5	0.44
	22.9	3.7	0.88	1.0	1.0	0.50
	23.4	2.8	0.91	2.0	0.5	0.80
	26.0	5.9	0.84	10.0	0.0	1.00
	23.1	3.6	0.89	2.0	2.5	0.44
Mean	22.8	3.6	0.88	5.0	1.0	0.74
SEM	1.9	0.5	0.01	1.3	0.3	0.09
Y47	43.6	10.0	0.90	18.3	0.0	1.00
	48.7	2.8	0.95	5.0	3.0	0.63
	32.6	1.6	0.95	12.0	0.0	1.00
	20.1	4.6	0.82	1.7	0.0	1.00
	25.9	3.8	0.88	8.3	0.0	1.00
	18.1	3.4	0.85	4.3	0.0	1.00
	26.9	3.9	0.88	2.7	0.0	1.00
Mean	30.8	4.3	0.89	7.5	0.4	0.95
SEM	4.4	1.0	0.02	2.2	0.4	0.05
B35	12.9	1.9	0.87	7.0	0.0	1.00
	32.6	2.5	0.92	4.7	0.0	1.00
	55.6	6.3	0.92	1.3	0.0	1.00
	56.6	7.1	0.88	4.7	0.0	1.00
	53.9	5.8	0.90	3.3	0.0	1.00
	45.9	8.0	0.85	3.3	1.0	0.77
	26.2	4.0	0.87	0.0	0.0	---
	27.2	4.9	0.85	0.3	0.0	1.00
Mean	38.9	5.0	0.88	3.1	0.1	0.97
SEM	5.8	0.8	0.01	0.9	0.1	0.03