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Object discrimination in pigeons: Effects of local and global cues ☆

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Abstract

We trained two pigeons to report whether a pair of differently colored 2-D objects had two target dots on either one or both of the objects. Follow-up tests disclosed that the colored regions surrounding the task-relevant targets were necessary, but not sufficient to support the birds' discrimination. Moreover, when local and global color cues provided contradictory information, pigeons failed to discriminate the stimuli, suggesting that the birds attended to both local and global information. Finally, one bird learned the object discrimination in the absence of differential color cues suggesting that, with suitable training, pigeon can attend to entire objects.

Keywords: Pigeons; Visual discrimination; Attention

1. Introduction

Every time we open our eyes, our visual system must process an enormous amount of information from the current visual scene. To help us cope with this daunting task, we selectively attend to different aspects of the scene depending on the situation and the prevailing behavioral demands. Indeed, humans can flexibly attend to a specific *location*, to a specific *object*, or to a specific *part* of an object (Duncan, 1984; Egly, Driver, & Rafal, 1994; Vecera, 2000; Vecera, Behrmann, & McGoldrick, 2000; Zemel, Behrman, Mozer, & Bavelier, 2002).

1.1. Space-based attention

Out of the many kinds of attention that may exist, two are particularly salient: spatial (or location-based) attention and object-based attention (see Egeth and Yantis, 1997; for an overview). Spatial attention has a long history in the research literature, with abundant supporting evidence coming from a variety of experimental paradigms. Perhaps the most widely used task to assess location-based attention in humans is Posner's (1980) cuing paradigm, in which observers must detect the onset of a visual target that is preceded by a spatial cue. The cue may be either *valid*, in which case it predicts the upcoming target's location (i.e., the cue and the target appear in the *same* spatial position), or *invalid*, in which case the cue does not predict the upcoming target's location (i.e., the cue and the target appear in *different* locations). People detect the target faster when it is validly cued than when it is invalidly cued, suggesting that the preceding cue draws attention to a specific location in the visual field.

Location-based theories of attention typically assume that attention is directed toward *ungrouped* locations in the visual field; therefore attention is not shaped by the particular stimuli falling within those regions (e.g., Downing & Pinker, 1985; Eriksen & Eriksen, 1974; LaBerge & Brown, 1989; Posner, 1980). Instead, the spatial focus of attention has some assumed structure, for example, a circle, with the organism being able to focus on larger or smaller scales in the case of the "zoom lens" (Eriksen & Eriksen, 1974; Eriksen & St. James, 1986).

Several behavioral and neurobiological reports suggest that nonhuman animals, including pigeons, are also able to

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focus on a specific region of the visual field (e.g., Moran & Desimone, 1985; Sharma, Dragoi, Tenenbaum, Miller, & Sur, 2003; Shimp & Friedrich, 1993). The most direct behavioral evidence for spatial attention in animals was reported by Shimp and Friedrich (1993), who used a modification of Posner's task, in which pigeons were required to detect the onset of a target (red light appearing on either the right or left key) within 5 s of its appearance. The preceding spatial cue (white light) could appear on either the same key as the target (*valid* trial) or on the different key (*invalid* trial). Pigeons exhibited the same pattern as did humans: Validly cued targets were detected faster than invalidly cued targets, demonstrating pigeons' ability to attend to the specific location that had been cued prior to the target's appearance.

1.2. Object-based attention

In contrast to location-based accounts, object-based accounts suggest that attention is directed to grouped "chunks" in the visual field that correspond to objects or shapes, irrespective of their location. One of the earliest demonstrations of this *same-object* benefit was provided by Duncan (1984), who presented participants with two overlapping objects, a box and a line, each of which varied in two dimensions. The box could be either short or tall and have a gap on either the left or the right; the line could either be dotted or dashed and tilted either clockwise or counterclockwise. The participants were more accurate at reporting two dimensions from the same object (i.e., box height and gap location) than two dimensions from different objects (i.e., box height and line tilt), suggesting that participants were attending to the entire object. Similar results were reported by many subsequent researchers (Baylis & Driver, 1993; Egly et al., 1994; Vecera & Farah, 1994; Watson & Kramer, 1999). Cueing tasks have also demonstrated an object-based effect. In this task, targets can appear at the cued location (valid cue) or at one of two uncued locations (invalid cues). One invalidly cued target appears in the cued object, but not at the cued location; the other invalidly cued target appears in the uncued object. Participants were faster to detect invalidly cued targets when they appeared in the cued object than when they appeared in the uncued object, even though the distance between the targets was the same for both trial types (Egly et al., 1994; Vecera, 1994).

A straightforward account of object-based attention focuses on selection from a spatiotopic, array-format representation, in which an object's edges and features are grouped according to Gestalt principles. This "grouped array" representation hypothesis (Vecera, 1994, 2000; Vecera & Farah, 1994) proposes that object-based attention effects arise because spatial attention is influenced by grouping cues, including surface similarity, connectedness, closure, and good continuation. Spatial attention is thus directed to groups of locations that have been organized or chunked based on those cues. The term "object" in the present paper is used in this latter sense and does not require the presence of "late" object-centered representations.

Given the substantial human literature on object-based visual attention, we were interested in answering the question: Can nonhuman animals also attend to visual stimuli as whole, coherent objects? Very little research has explicitly explored this question.

Recent neurobiological evidence suggests that nonhuman animals may have neuronal mechanisms which operate on objects as entities rather than as mere "lists" of abstract features. In one representative study (Roelfsema, Lamme, & Spekreijse, 1998), monkeys performed a task requiring them to attend to one irregular curve and to ignore another overlapping curve. Multi-unit recording in area V1 of primary visual cortex disclosed that neurons with receptive fields containing segments of the attended curve simultaneously enhanced their responsiveness, whereas neurons with receptive fields containing segments of the distractor curve did not. Neurons which detect different segments of the same, attended curve fire in unison, even when the attended curve overlapped with the distractor curve, documenting the existence of a very early visual mechanism which seems to operate in accord with such Gestalt principles as connectivity and proximity.

Additional behavioral evidence suggests that other animals, particularly pigeons, might also be able to attend to organizational properties of the object rather than to its local features. Research in our laboratory has found that pigeons trained to recognize line drawings of objects show a significant decrement in recognizing modified drawings which do not preserve the correct spatial arrangement of the object's parts (Kirkpatrick-Steger, Wasserman, & Biederman, 1996, 1998); hence, pigeons are sensitive to organizational properties of complex objects (see also Kirkpatrick-Steger & Wasserman, 1996).

A later experiment by Matsukawa, Inoue, and Jitsumori (2004) found that pigeons may attend to either local or global (organizational) properties of an image depending on the behavioral task. When pigeons were taught to discriminate simple line drawings of cartoon faces on a white background, they were relatively insensitive to spatial scrambling and appeared to attend primarily to the eyes and eyebrows. But, when the pigeons were trained to discriminate line drawings of cartoon faces on a variety of backgrounds scenes, their performance with scrambled images reliably deteriorated, suggesting that the birds were now attending to configural properties of the image. These data suggest that, at least under some circumstances, pigeons may attend to global rather than to local properties of objects.

1.3. Our studies of object discrimination in pigeons

Recently, we have adapted for use with pigeons a task that requires reporting whether two target dots are located on a single object or on two different objects, what we here term an "object discrimination" task. For example, in Vecera and Farah (1997), human participants saw two transparent, overlapping shapes that had two small Xs either on one shape or on both shapes. Critically, the spatial distance between the Xs was equivalent on *same-object* trials and on *different-object* trials; thus, differential performance on these two types of trials cannot be explained by people's attending to different spatial areas of the display. Yet, participants responded faster and more accurately when the two Xs were on the same object than when they were on two different objects—a common result in many object-based attention studies (Behrman, Zemel, & Mozer, 1998; Duncan, 1984; Egly et al., 1994; Watson & Kramer, 1999).

To adapt this task for pigeons, we used a go/no-go discrimination method involving Differential Reinforcement of High (DRH) and Differential Reinforcement of Low (DRL) rate schedules of food reinforcement. With this method, one class of stimuli, for example, *same-object* displays, is associated with a DRH schedule that encourages responding at a high rate. According to the DRH schedule, reinforcement is delivered only if a response is made *within* a certain amount of time following the preceding response. The second class of stimuli, *different-object* displays, is associated with a DRL schedule that encourages responding at a low rate. According to the DRL schedule, reinforcement is delivered only *after* a certain amount of time has elapsed since the preceding response.

We chose the DRH/DRL procedure because it is supports generally faster discrimination learning by pigeons than two-alternative forced-choice procedures. The DRH–DRL technique associates *same-object* and *different-object* stimuli with distinctively different schedules of reinforcement, whereas two alternative forced-choice procedures involve the same schedule of reinforcement to *same-object* and *different-object* stimuli. Rapid pecking is natural for pigeons and is encouraged under the DRH schedule; under the DRL schedule, rapid pecking postpones the delivery of reinforcement. So, pigeons more quickly come to respond in accord with the DRH schedule than with the DRL schedule. Hence, with this procedure, we cannot directly compare the speed of acquisition on *same-object* and *different-object* trials. Likewise, the DRH–DRL technique does not permit direct comparisons of accuracy or reaction time on *same-object* and *different-object* trials—comparisons that can be achieved with forced-choice procedures.

Importantly, the DRH–DRL technique avoids a key problem with the most common go/no-go discrimination learning procedure, which associates one class of stimuli with a Variable-Interval (VI) schedule (in which reinforcement is delivered after a variable amount of time has elapsed since the last response) and another class of stimuli with experimental extinction (EXT). This VI–EXT procedure encourages pigeons to cease responding (and, perhaps, attending) to the class of stimuli associated with EXT, whereas the DRH–DRL procedure maintains responding (and probably attending) to both classes of stimuli because each is associated with the same reinforcer.

In an earlier report (Lazareva, Levin, Vecera, & Wasserman, 2005), we trained pigeons with this DRH–DRL procedure to discriminate a pair of differently colored two-dimensional objects, an oval and a rectangle, that had two targets either on a single object or on two different objects (Fig. 1). The distance between the targets was equivalent on *same-object* and *different-object* images. Moreover, each target equally often appeared on the *same-object* and *different-object* stimuli; so, a specific target location could not serve as a discriminative cue. We found that pigeons could accurately discriminate whether the two target dots were located on a single object or on two different objects, and that this ability was not entirely based on memorization of the dot patterns and locations. Follow-up tests disclosed that our pigeons' ability to perform the object discrimination depended critically on the colors of the

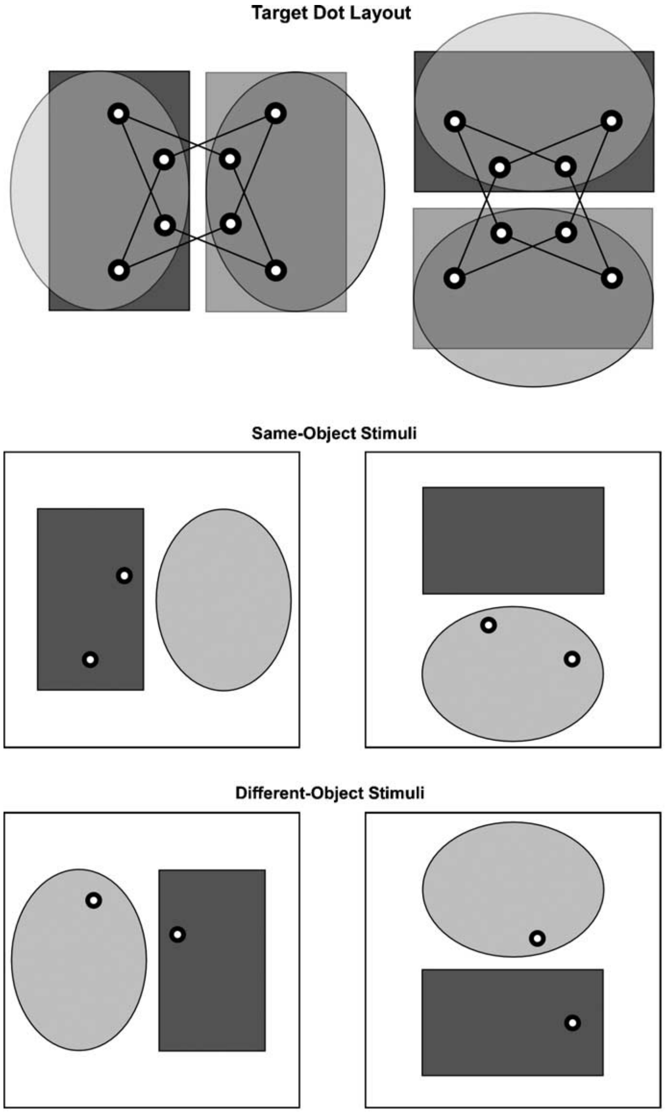

Fig. 1. Construction of the experimental stimuli. The upper row illustrates the geometric constraints that held in creating the 32 training stimuli. Note that the connecting lines are shown for illustrative purposes only. The lower two rows show examples of the *same-object* and *different-object* stimuli.

objects. If the two objects were of the same color, then the pigeons could not discriminate *same-object* from *different-object* displays, even though the shapes of the objects were different. If, however, the objects were of different colors, then excellent discrimination was supported, even though the objects were of the same shape. It is possible therefore, that the birds might simply have been comparing the colors in the immediate vicinity of two target dots, instead of attending to the two objects—a strategy that would reduce object discrimination task to color matching-to-sample.

In the present report, we explored whether pigeons performing the object-discrimination task attended exclusively to features available in the immediate vicinity of the task-relevant targets or used more distant spatial information. We term the first kind of cue "local" and the second kind of cue "global." Our use of the term "global" does not imply that pigeons form integral representations of an object in which all features of the object are bound together (Feldman, 2003); rather, we use the term "global" to indicate that pigeons are attending to information that is spatially removed from the task-relevant targets.

2. Experiment 1

The simplest hypothesis as to the cues controlling the pigeons' object discrimination performance is that the birds may merely have compared the colors in the immediate vicinity of the target dots. If the two colors were the same, then the pigeons may have responded quickly (or slowly); if the two colors were different, then the pigeons may have responded slowly (or quickly). To explore this possibility, we conducted a series of Proximal-Distal tests.

2.1. Method

2.1.1. Subjects

The subjects were 2 feral pigeons (*Columba livia*) maintained at 85% of their free-feeding weights. Prior to this study, the pigeons had participated in studies reported elsewhere (Lazareva et al., 2005; Lazareva, Levin, Vecera, & Wasserman, 2006).

2.1.2. Apparatus

The experiment used two operant conditioning chambers and two Macintosh computers. One wall of each chamber contained a large opening with a frame attached to the outside that held a clear touch screen. An aluminum panel in front of the touch screen allowed the pigeons to access to circumscribed portions of a video monitor behind the touch screen. There were five openings or buttons in the panel: a 7 × 7-cm square central display area in which the stimuli appeared and four round areas (1.9-cm diameter) located 2.3 cm from each of the four corners of the central opening. Only the central opening was used in this experiment. 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 house light mounted on the rear wall of the chamber provided illumination during the session. The experimental procedure was programmed in HyperCard, Version 2.4 (Apple Computer, Inc., Cupertino, CA).

2.1.3. Training stimuli

Fig. 1 (top) illustrates the constraints that were placed on constructing the training stimuli. Each display comprised either a red oval and a green rectangle (Bird 25Y) or a green oval and a red rectangle (Bird 12Y). The rectangle was 5.27 cm high and 3.09 cm wide and the oval was 5.28 cm high and 3.93 cm wide; both the rectangle and the oval had equal areas of 16.28 cm^2. The oval and the rectangle were either left-right or top-bottom oriented.

Four isosceles triangles with two long sides of 2.68 cm were positioned so that the apexes of all four triangles were evenly spaced on top of the oval and the rectangle. The eight possible targets (black dots, 0.49 cm in diameter, with a white center 0.21 cm in diameter) could be placed at the corners of all four triangles. Only those pairs of targets that were connected by the lines drawn in the top of Fig. 1 were allowed, ensuring an equal distance (2.68 cm) between all target pairs; therefore, eight displays with the targets on the same object and eight displays with the targets on different objects were possible.

Randomizing the left-right and top-bottom positions of the objects yielded 32 training stimuli: 16 with dots on one of the objects (*same-object* stimuli) and 16 with dots on both of the objects (*different-object* stimuli). Four examples of these stimuli are shown in the bottom of Fig. 1. We earlier found that pigeons could memorize and use the exact spatial locations of a target dot for discriminating *same-object* and *different-object* stimuli (Lazareva et al., in 2006). So, in this experiment, we ensured that each target was equally often presented in the *same-object* and *different-object* stimuli and that a specific target location could not serve as a discriminative cue. The stimuli were placed on a white square (3.4 × 3.4 cm) background, so that the gap between the objects was always positioned in the middle of the square. The minimal distance between the objects was 0.37 cm.

Testing stimuli involved various modifications of the training stimuli; the details of each modification are described below. All of the stimuli were created in Canvas Standard Edition, Version 7.0 (Deneba Software, Inc.) and were saved as PICT files with 144 dpi resolution.

2.1.4. Testing stimuli

The training images were modified by drawing a circle of a specified diameter around each target and replacing the color with 40% gray shading either outside the circles leaving only *proximal* color cues (Proximal Tests) or inside the circles leaving only *distal* color cues (Distal Tests). Fig. 2 shows examples of these testing images. By convention, a stimulus that did not contain a target dot remained unmodified. Therefore, only one of the two objects in the *same-object* stimulus displays underwent color erasure. In

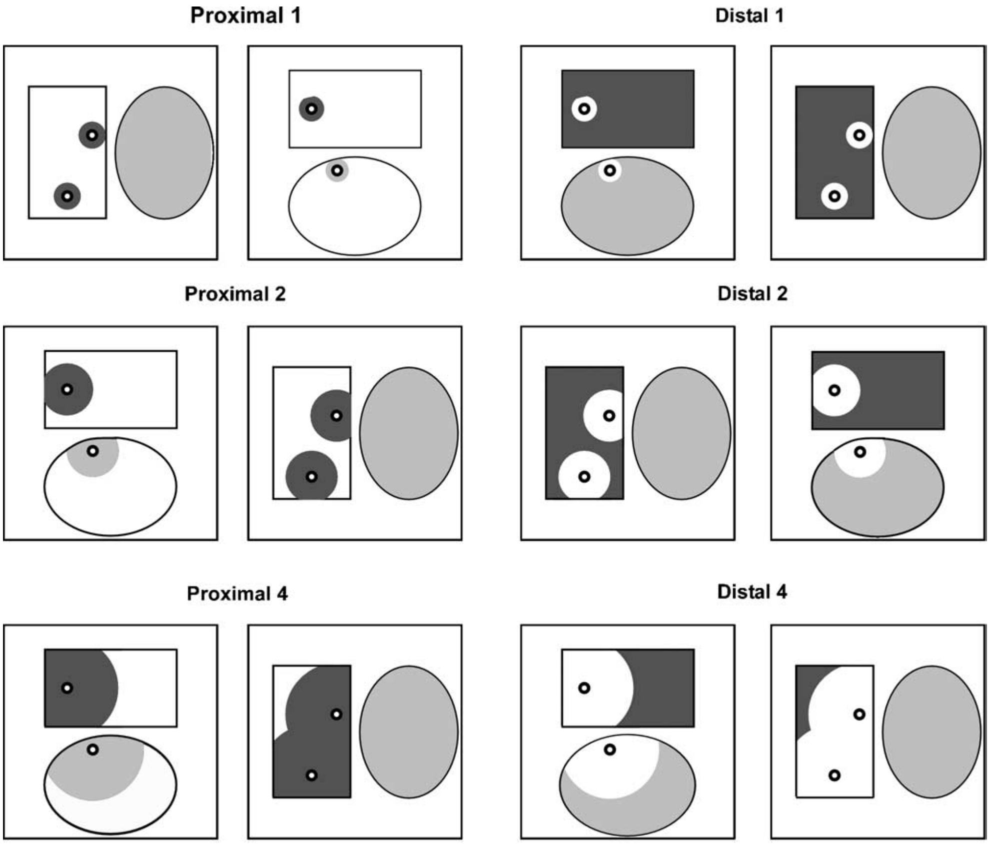

Fig. 2. Examples of the testing stimuli in the Proximal-Distal Tests.

addition, the modified area of each stimulus was defined exclusively by the circle drawn around the target dot placed on top of that stimulus; so, when the circle overlapped with the second object, that second object remained unmodified. The luminance of gray shading was 1.5 times higher than the luminance of either red or green colors (measured by IL-1700 radiometer, UV Process Supply, Inc., Illinois).

2.1.4.1. Proximal 1 and Distal 1 Tests. The diameter of the circle in this test was equal to 1 cm. Recall that the colored area of both objects in the training displays (minus the target area) was equal to 31.05 cm^2. Thus, the colored area that remained in the testing objects in the Proximal 1 Test constituted 14.41% (4.78 cm^2) of the total colored area in the training images. Likewise, the colored area that remained in the testing objects in the Distal 1 Test constituted 84.62% (26.28 cm^2) of the total colored area in the training images.

2.1.4.2. Proximal 2 and Distal 2 Tests. Here, the diameter of the circle was equal to 2 cm. The colored area that remained was 17.97% (5.58 cm^2) in the Proximal 2 Test and 82.03% (25.47 cm^2) in the Distal 2 Test.

2.1.4.3. Proximal 4 and Distal 4 Tests. Here, the diameter of the circle was equal to 4 cm. The colored area that remained was 52.84% (16.41 cm^2) in the Proximal 4 Test and 47.16% (14.64 cm^2) in the Distal 4 Test.

2.1.5. Procedure

2.1.5.1. Pretraining. Following weight reduction, the pigeons began pretraining, in which they were required to peck at the center button for food reinforcement.

2.1.5.2. Training. The sequence of events in the course of a training trial is shown in Fig. 3 (first and second rows). At the start of a training trial, the pigeons were shown a black cross in the center of a white display screen. Following one peck anywhere on the white display, the training stimulus appeared for a fixed interval of 10 s. Pecks during this 10-s interval were recorded and were used as the dependent measure. After the 10 s elapsed, the birds had to complete either the DRH or the DRL schedule requirement. On a DRH trial (first row of Fig. 3), the birds had to peck twice within a fixed interval (7 or 11 s); on a DRL trial (second row of Fig. 3), the birds had to peck 7 or 11 s apart. The duration of the second interval was varied from 5 to 11 s during training to make indiscriminate responding more punishing. Bird 25R was always tested under the 7-s DRH–DRL schedule and Bird 12Y was always tested under the 11-s DRH–DRL schedule. For Bird 25R, *same-object* stimuli were associated with the DRL schedule and *different-object* stimuli were associated with the DRH schedule; Bird 12Y was exposed to the reverse contingencies. After the pigeons completed the DRH–DRL schedule requirement, food was delivered and the intertrial interval ensued,

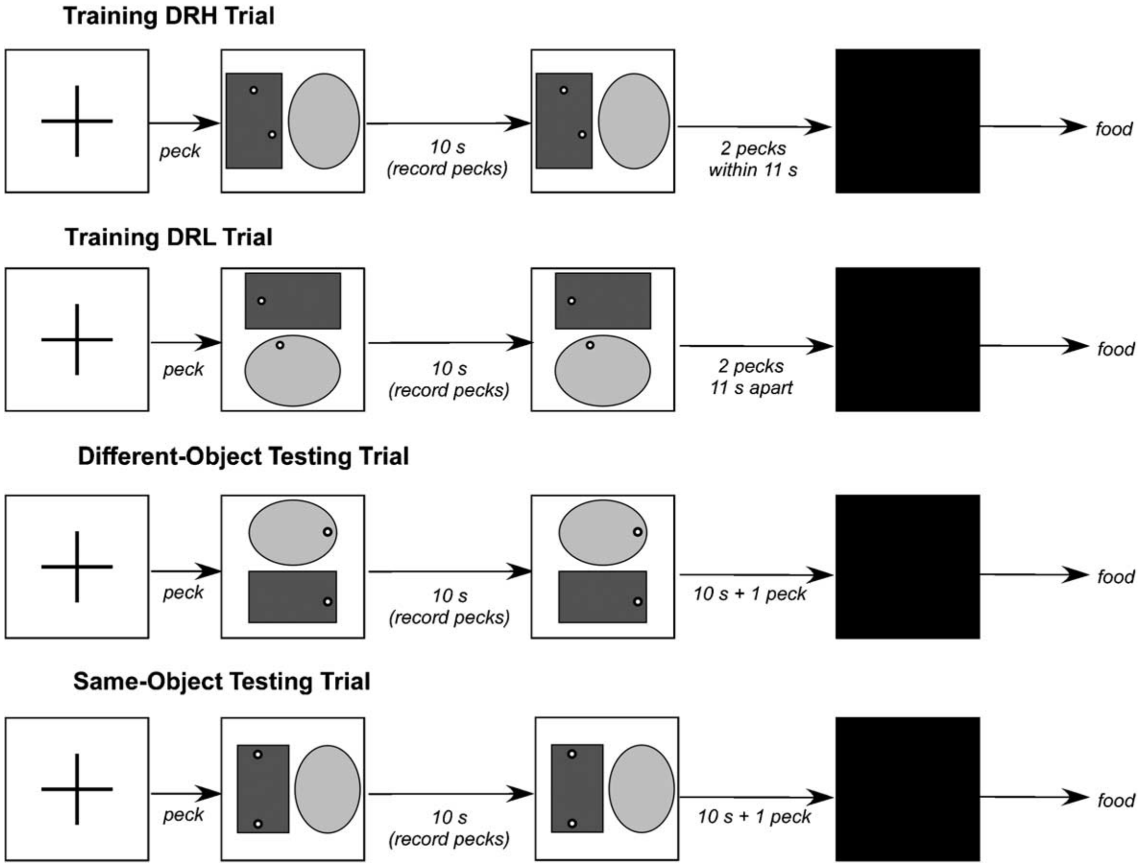

Fig. 3. Sequence of events in the course of a DRH training trial, a DRL training trial, a *different-object* testing trial, and a *same-object* testing trial for Bird 12Y. For Bird 25R, *same-object* stimuli were associated with a 7-s DRL schedule and *different-object* stimuli were associated with a 7-s DRL schedule.

randomly ranging from 5 to 10 s. During training, each session comprised 128 trials composed of 4 blocks of 32 trials.

Pigeons tend to peck at a high rate if they expect the DRH schedule to follow, whereas they tend to peck at a low rate if they expect the DRL schedule to follow. A large difference in peck rate to DRH-paired and DRL-paired stimuli would thus indicate a bird's successful discrimination of *same-object* from *different-object* training stimuli.

2.1.5.3. Testing. Both pigeons were required to meet a criterion of no overlap between response rates to the individual *same-object* and *different-object* stimuli. So, if the *same-object* stimuli were associated with the DRH schedule and the *different-object* stimuli were associated with the DRL schedule, then, to achieve criterion, the highest peck rate to any of the *same-object* stimuli had to be lower than the lowest peck rate to any of the *different-object* stimuli. At least one training session was conducted after each testing session, and the birds were again required to meet the discrimination criterion before the next testing session could be given.

We planned to train both pigeons until they reached the above criterion in two consecutive sessions. But, only one bird reached this criterion in a timely fashion (Bird 25R, 25 sessions); the other bird (12Y) failed to reach this criterion after 70 training sessions. So, Bird 12Y was required to reach criterion during only one training session; it reached this criterion in three additional sessions (total of 73 sessions).

The sequence of events in the course of a testing trial is shown in third and fourth rows of Fig. 3. Both *same-object* and *different-object* trials used the same testing procedure. First, the pigeons had to start the trial by pecking at the white display screen with the black cross in the middle. Then, the testing stimulus appeared for a fixed interval of 10 s. Pecks during this 10-s interval were recorded and used as the dependent measure. After this recording period elapsed, an additional 10-s interval was implemented. Pecks during this interval were not recorded and could not advance the trial. We conducted testing trials in this manner to make them as close to training trials as possible without arranging differential contingencies of reinforcement on *same-object* and *different-object* trials. Following the second 10-s interval, the pigeons had to peck the testing stimulus once. Food was delivered then and the intertrial interval ensued.

Each testing session contained 4 blocks of 32 training trials and 8 testing trials (160 trials total), so that the pigeons received 4 presentations of each training stimulus and 1 presentation of each testing stimulus. All tests included 2 testing sessions separated by at least 1 training session unless noted otherwise. Thus, the pigeons were twice exposed to each testing stimulus.

2.1.6. Behavioral measures

To simplify our comparisons of training and testing performance, we used the following procedure. In each session, the first DRH training stimulus was paired with the first DRL training stimulus. Then, the number of pecks to the DRH stimulus divided by the sum of pecks to both the DRH and DRL stimuli was calculated and multiplied by 100, yielding a discrimination ratio which could range from 0.0% to 100.0%. (Because pigeons always respond on DRH trials, the pairs of empty trials with 0 pecks in the denominator never occur in practice.) The procedure thus was repeated until each of the succeeding DRH training stimuli were paired with each of the succeeding DRL training stimuli, resulting in 64 discrimination ratios per session. Similarly, the first DRH testing stimulus was paired with the first DRL testing stimulus and so forth, resulting in 16 discrimination ratios per session. Because discrimination ratios are bounded between 0 and 100, their distribution deviates from the normal distribution required for analyses of variance (ANOVA). We thus subjected the discrimination ratios to arcsine transformation (Cohen, Cohen, West, & Aiken, 2003) and then used these transformed scores in all later statistical analyses. For all statistical tests, α was set to 0.05.

Recall that successful discrimination is indicated by a high rate of response to the DRH stimuli and by a low rate of response to the DRL stimuli. Thus, discrimination ratios higher than 50% indicate that the birds pecked more often on DRH than on DRL trials (successful discrimination); 50% ratios indicate that the birds pecked equally often on both DRH and DRL trials (no discrimination); and, discrimination ratios lower than 50% indicate that the birds pecked more often on DRL than on DRH trials (discrimination reversal).

2.2. Results and discussion

Table 1 shows the means and standard deviations of pigeons' pecking on the DRH and DRL training and testing trials in the Proximal Tests, in which the immediate areas around the targets retained their colors and the distal area was replaced with gray shading. Fig. 4 shows these data transformed to discrimination ratios, which were used in all inferential statistical tests. Both birds discriminated *same-object* from *different-object* testing images at levels significantly higher than chance [two-tailed t test, $t \geqslant 2.13$]. However, both birds' performance to the testing stimuli was much less discriminative than was their performance to the training stimuli, especially in the Proximal 1 and Proximal 2 Tests, suggesting that the distal area also contributed to the pigeons' discrimination performance.

Table 1
Pigeons' pecking (number of pecks per 10-s interval) on the DRH and DRL training and testing trials in the Proximal tests of Experiment 1

	DRH Training		DRH Testing		DRL Training		DRL Testing	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Proximal 1								
12Y	21.91	7.11	19.53	3.67	4.27	6.75	16.56	4.79
25R	8.04	3.02	4.00	1.69	1.59	2.95	2.76	0.93
Proximal 2								
12Y	23.07	6.09	20.50	5.74	2.30	4.75	16.66	5.97
25R	5.43	2.96	5.66	2.39	1.09	2.17	3.09	2.10
Proximal 4								
12Y	24.26	5.13	24.00	4.12	4.00	7.22	7.31	8.56
25R	6.65	3.03	7.38	2.66	1.43	2.36	3.81	2.46

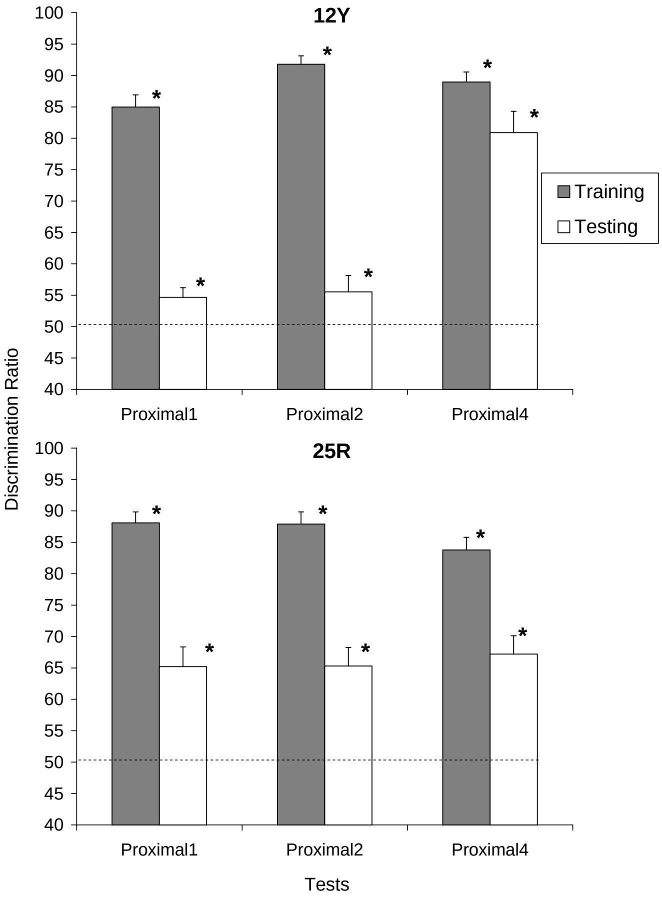

Fig. 4. Percentage of correct responses to the training and testing stimuli in the Proximal Tests. Asterisks indicate a significant difference from chance.

ANOVA revealed a significant main effects of Trial Type [$F_{1,1} = 241.91$] and Test [$F_{2,2} = 3.97$] plus a Trial Type × Test interaction [$F_{1,2} = 8.67$], suggesting that responding to the training and testing stimuli differed from test to test. ANOVA also found a significant Bird × Test interaction [$F_{1,2} = 8.55$], but no significant main effect of Bird nor Bird × Trial Type interaction [Fs < 1]. Planned comparisons indicated that, for Bird 12Y, discrimination of the training stimuli was significantly higher than to the testing stimuli in the Proximal 1 and Proximal 2 Tests, but not in the Proximal 4 Test; Bird 12Y exhibited reliably higher training than testing performance in all three tests. Lower testing discrimination ratios were the result of lower rates of response on DRH trials (in 4 out of 6 cases) and higher rates of response on DRL trials (in 6 out of 6 cases).

Table 2 shows the means and standard deviations of pigeons' pecking on the DRH and DRL training and testing trials in the Distal Tests, in which only distal color cues could be used to support discrimination behavior. Fig. 5 shows the same data transformed to discrimination ratios. Neither bird exhibited significant discrimination of the testing images even in the Distal 1 Test, in which very small areas in the immediate vicinity of the target dots had been replaced by gray shading. ANOVA found a significant main effect of Trial Type [$F_{1,1} = 786.28$], but no significant effect of Test nor Test × Trial Type interaction [$Fs \leqslant 2.59, p \geqslant 0.08$], suggesting that discrimination of the testing stimuli was always lower than discrimination of the training stimuli and did not significantly depend on the type of Distal Test. Lower testing discrimination ratios were the consequence of lower rates of response on DRH trials (in 6 out of 6 cases) and higher rates of response on DRL trials (in 6 out of 6 cases).

Table 2
Pigeons' pecking (number of pecks per 10-s interval) on the DRH and DRL training and testing trials in the Distal tests of Experiment 1

	DRH Training		DRH Testing		DRL Training		DRL Testing	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Distal 1								
12Y	24.15	4.37	21.13	4.61	5.44	7.12	18.66	4.98
25R	7.12	3.63	5.75	3.36	0.87	2.20	5.06	2.86
Distal 2								
12Y	24.62	5.80	20.25	5.51	5.57	7.83	18.66	5.27
25R	6.55	2.85	5.91	2.83	0.95	1.90	5.59	2.64
Distal 4								
12Y	26.05	3.72	15.44	4.70	4.29	6.99	18.19	4.18
25R	6.01	2.26	3.94	2.99	0.53	1.42	3.53	2.84

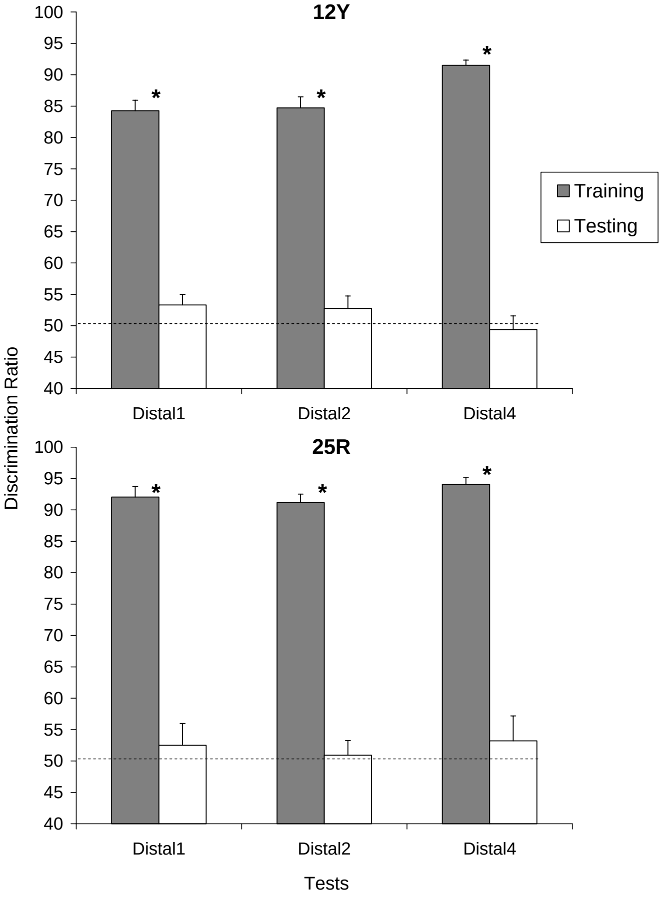

Fig. 5. Percentage of correct responses to the training and testing stimuli in the Distal Tests. Asterisks indicate a significant difference from chance.

In summary, the results of both the Proximal and Distal Tests suggest that the colors surrounding the target dots were critical for the pigeons' discriminating *same-object* from *different-object* images. Proximal Tests retained those colors and afforded reliable discrimination behavior, whereas Distal Tests eliminated those colors and did not afford reliable discrimination behavior. Nevertheless, even with the neighboring colors preserved in the Proximal Tests, the birds' discrimination behavior was decidedly lower than it was to the fully-colored training stimuli. This result suggests that the colored area immediately surrounding the target dots did not solely support the pigeons' discrimination performance.

3. Experiment 2

One might suggest that, instead of comparing the colors surrounding the two target dots, the pigeons might have simultaneously attended to both target dots. In this case, the pigeons' attentional field ought to entail the elliptical area that encompasses both dots (see Fig. 6, top section). Note that in the *same-object* images such an attentional field would always be of one continuous color (either red or green), whereas in the *different-object* images such an attentional field would encompass subfields of green, white, and red. These color combinations may therefore serve as discriminative cues.

To test this possibility, we modified the training images so that the oval and the rectangular training objects slightly overlapped one another (Occlusion Test; Fig. 6, bottom left section). Therefore, the hypothetical field of attention on *different-object* trials would now include only red and green, but not white. Consequently, we might expect a decrease in discrimination performance on *different-object* trials, but not on *same-object* trials, which were not functionally changed by one object occluding the other. In a complementary fashion, we also inserted a thin white strip, either vertically or horizontally, in the middle of the image (Split Object Test; Fig. 6, bottom right section). Now, the hypothetical field of attention on *same-object* trials would include white plus either red or green. We might therefore expect to see impaired discrimination performance on *same-object* trials (which never before involved a white strip of color), but no change on *different-object* trials (which involved no functional change in the area between the target dots).

3.1. Method

3.1.1. Subjects

The same two birds as in Experiment 1 were used, housed and maintained as described earlier.

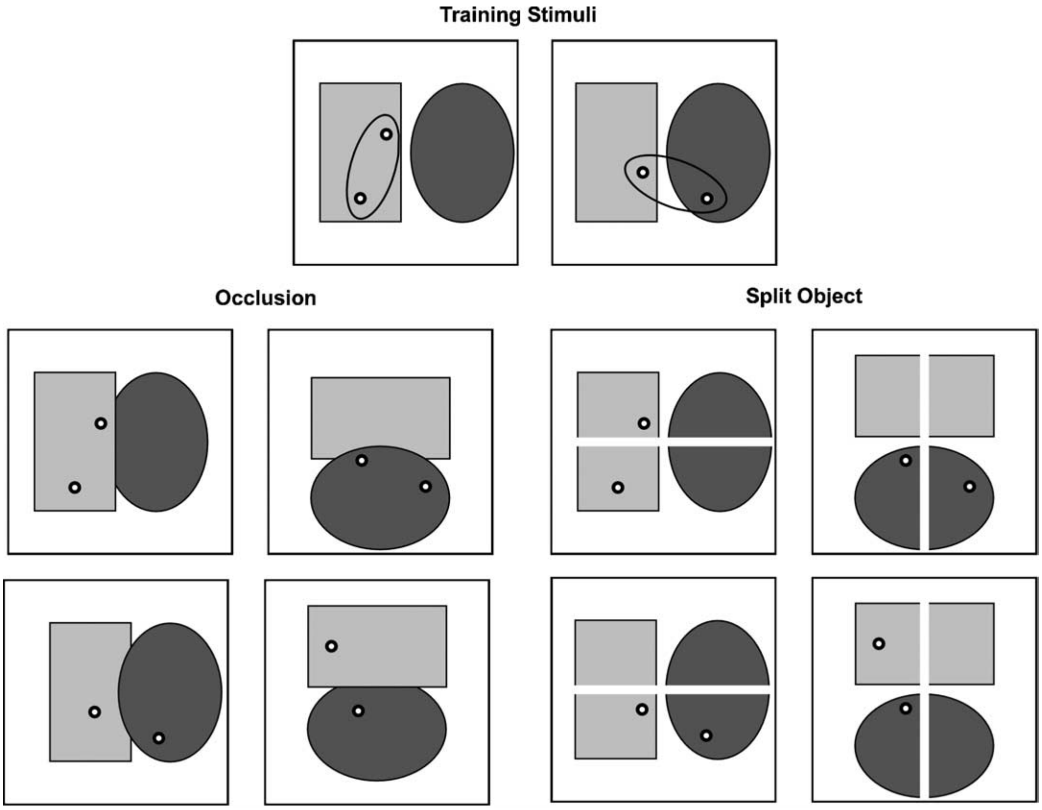

Fig. 6. Examples of the testing stimuli in the Occlusion Test and in the Split Object Test.

3.1.2. Apparatus and stimuli

The same apparatus and training stimuli as in Experiment 1 were used. To construct the testing stimuli, we modified the training stimuli as shown in Fig. 6. In the *Occlusion Test*, one of the two objects in the display was slid behind the other by 0.93 cm. After counterbalancing, each training display produced 2 testing displays (for a total of 64 displays). The target dots remained surrounded by the same color as in the original display, although the distance to the nearest colored edge might have decreased or increased. In the *Split Object Test*, a white vertical or horizontal strip was inserted in the middle of each training image (yielding a total of 32 images). The width of the strip was equal to the minimal distance between objects—0.37 cm.

3.1.3. Procedure

We used the same training procedure as in Experiment 1. Before testing, the pigeons had to meet criteria of no overlap between response rates to the individual *same-object* and *different-object* stimuli in 2 training sessions (Bird 25R) or in 1 training session (Bird 12Y).

Each testing session contained 4 blocks of 32 training trials and 8 testing trials (160 trials total), so that the pigeons received 4 presentations of each training stimulus and 1 presentation of each testing stimulus. The Occlusion Test included 4 testing sessions separated by at least 1 training session, whereas the Split Object Test included 2 testing sessions separated by at least 1 training session. Thus, in each test, the pigeons were exposed to each testing stimulus twice.

3.2. Results and discussion

Table 3 shows the means and standard deviations of pigeons' pecking on the DRH and DRL training and testing trials in the Occlusion and Split Object tests. We earlier proposed that the pigeons might have attended to the local, elliptical area that encompassed both target dots (Fig. 6, top section). If this proposal were true, then we would expect a loss of discrimination performance on *different-object* trials, but no change in discrimination performance on *same-object* trials in the Occlusion Test; likewise, we would expect a loss of discrimination performance on *same-object* trials, but no change in discrimination performance on *different-object* trials in the Split Object Test.

Table 3
Pigeons' pecking (number of pecks per 10-s interval) on the DRH and DRL training and testing trials in the Occlusion and Split Object tests of Experiment 2

	DRH Training		DRH Testing		DRL Training		DRL Testing	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Occlusion								
12Y	24.93	6.01	22.67	4.97	3.60	6.39	**18.36**	**6.09**
25R	5.99	2.62	**6.38**	**2.54**	1.40	1.75	4.30	2.27
Split Object								
12Y	25.35	5.58	**23.38**	**3.87**	9.27	9.79	20.41	5.98
25R	5.41	2.79	5.75	3.22	1.02	1.79	**3.00**	**2.87**

Bold font indicates cases in which we expected a loss of discrimination (see text for details).

Recall that *same-object* trials were associated with the DRH schedule for Bird 12Y and with the DRL schedule for Bird 25R; likewise, *different-object* trials were associated with the DRL schedule for Bird 12Y and with the DRH schedule for Bird 25R. Hence, in the Occlusion test, we expected a loss of discrimination performance on DRL testing trials for Bird 12Y and on DRH testing trials for Bird 25R and we expected no change in discrimination performance on the other trials. Instead, *both* birds showed an increase in the rate of responding on DRL testing trials and little change in the rate of responding on DRH testing trials (Table 3). Similarly, in the Split Object Test, we expected a loss of discrimination performance on DRH testing trials for Bird 12Y and on DRL testing trials for Bird 25R. Again, *both* birds increased their rate of responding to the DRL testing stimuli, but they showed little change in their rate of responding to the DRH testing stimuli.

In all of the tests, the rates of responding to the DRH testing stimuli was higher than the rates of responding to the DRL testing stimuli by at least half a standard deviation, suggesting that the birds' discrimination performance did not entirely disappear. Our analysis of the discrimination ratios shown in Fig. 7 supports this conclusion. Both birds exhibited significant discrimination performance in both tests [two-tailed t test, $t \geqslant 2.08$]. An ANOVA found a significant main effect of Trial Type [$F_{1,1} = 233.78$], but no significant main effect of Test [$F_{1,1} = 0.23$], suggesting that testing performance similarly decreased compared to training performance in the Occlusion and Split Object Tests. The ANOVA also revealed a significant Bird effect [$F_{1,1} = 5.43$], indicating that Bird 25R generally discriminated the training and testing stimuli more accurately than Bird 12Y.

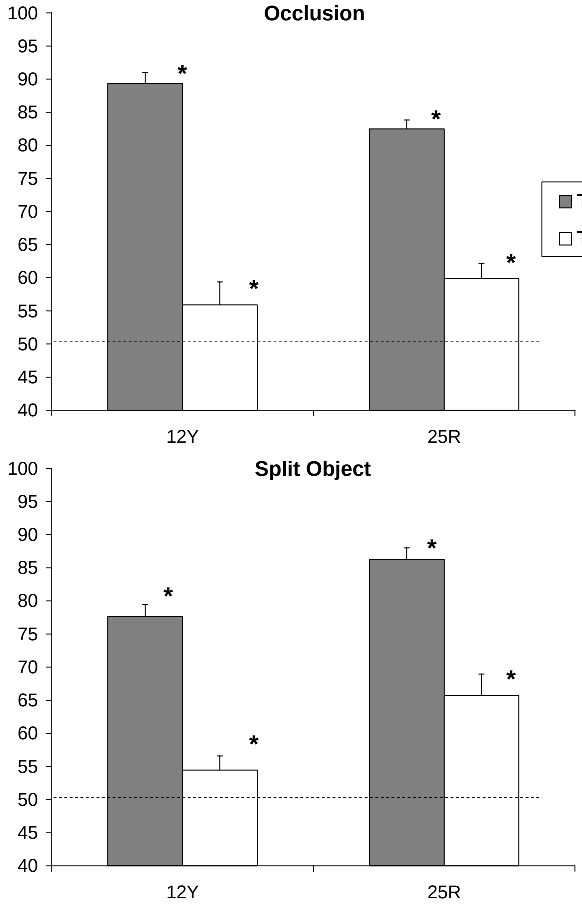

Fig. 7. Percentage of correct responses to the training and testing stimuli in the Occlusion and Split Object Tests. Asterisks indicate a significant difference from chance.

In summary, instead of the expected selective changes in testing performance in the Occlusion and Split Object Tests, we observed increases in the rates of responding to the DRL stimuli and little change in the rates of responding to the DRH stimuli for both birds, regardless of their stimulus-schedule assignments. This pattern of results suggests that the birds may have noticed the novelty of all of the testing stimuli, but only changed their rate of responding on DRL trials. This asymmetry is often observed in go/no-go experiments: nonselective changes are more likely to affect responses that are withheld (DRL) than responses that are performed (DRH). This pattern of results also suggests that the pigeons may have attended to more of the training stimuli than the two target dots and the area between them.

4. Experiment 3

If the colored areas surrounding the target dots primarily controlled the pigeons' discrimination performance, then one might expect that, in the case of *conflicting* local and global information, the pigeons' behavior would be predominately governed by the local information. In the *Half Reversal Test* (shown in Fig. 8), we filled in one half of an object with green and the other half of an object with red. As a result, the two targets in a *same-object* testing trial were surrounded by *different* colors; conversely, the two targets in a *different-object* testing trial were surrounded by the *same* color. So, if the birds simply compared the colors around the two targets, then they

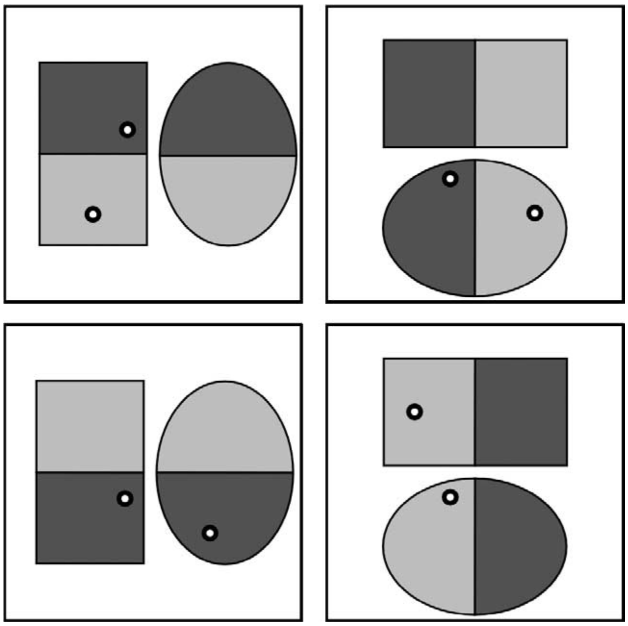

Fig. 8. Examples of the testing stimuli in the Half Reversal Test.

should have responded to *same-object* trials as if they were *different-object* trials, and they should have responded to *different-object* trials as if they were *same-object* trials.

4.1. Method

4.1.1. Subjects

The same two birds as in Experiments 1 and 2 were used.

4.1.2. Apparatus and stimuli

The same apparatus and training stimuli were used as in Experiments 1 and 2. To construct the *Half Reversal* testing stimuli, we modified the training stimuli as shown in Fig. 8. Half of each object was red and the other half was green (for a total of 32 images; see Fig. 8 for four examples). The minimal distance from the target dot to the middle colored edge was either 0.68 or 1.73 cm.

4.1.3. Procedure

We used the same training and testing procedure as described in Experiments 1 and 2. Before testing, the pigeons were required to meet criteria of no overlap between response rates to the individual *same-object* and *different-object* stimuli in 2 training sessions (Bird 25R) or in 1 training session (Bird 12Y).

Each testing session contained 4 blocks of 32 training trials and 8 testing trials (160 trials total), so that the pigeons received 4 presentations of each training stimulus and 1 presentation of each testing stimulus. The test involved 2 testing sessions separated by at least 1 training session; thus, the pigeons were exposed to each testing stimulus twice.

4.2. Results and discussion

Table 4 shows the means and standard deviations of pigeons' pecking on the DRH and DRL training and testing trials in the Half Reversal Test of Experiment 3. Fig. 9 shows the same data as discrimination ratios. Here, comparison of the colored areas in the immediate vicinity of the target dots should lead to complete discrimination reversal: the birds should respond to *same-object* trials as if they were *different-object* trials and vice versa. So, the birds ought to respond as much *below* chance on testing trials as they respond *above* chance on training trials. Both birds did respond at below chance levels; but, only the testing performance of Bird 25R fell significantly below chance [two-tailed t test, $t = -4.55$]. Moreover, even for Bird 25R, the discrimination reversal was incomplete and equaled 40.75%, when complete discrimination reversal ought to have equaled 15%. As in Experiments 1 and 2, the loss of discriminative control was more strongly determined by the increase in responding on DRL testing trials than by the decrease in responding on DRH testing trials (Table 4).

Table 4
Pigeons' pecking (number of pecks per 10-s interval) on the DRH and DRL training and testing trials in the Half Reversal Tests of Experiment 3

	DRH Training		DRH Testing		DRL Training		DRL Testing	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
12Y	24.80	4.17	20.19	6.11	7.14	9.28	21.58	6.39
25R	6.97	2.86	5.25	3.27	2.30	2.92	7.30	3.33

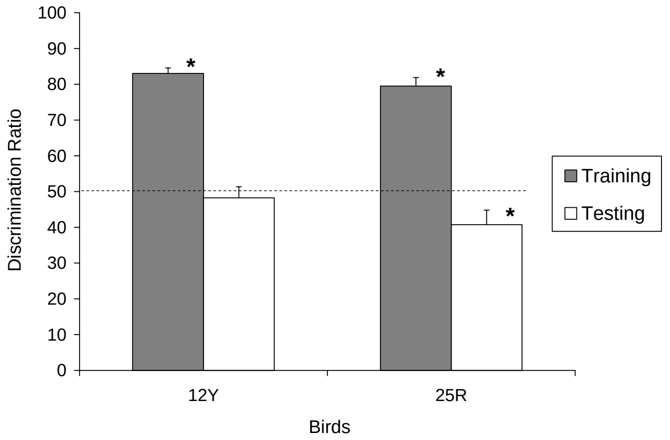

Fig. 9. Percentage of correct responses to the training and testing stimuli in the Half Reversal Test. Asterisks indicate a significant difference from chance.

ANOVA revealed a significant main effect of Trial Type [$F_{1,1} = 302.61$], a significant main effect of Bird [$F_{1,1} = 6.27$], but no significant Bird × Trial Type interaction [$F_{1,1} = 0.15$], suggesting that both birds performed more accurately on training trials than on testing trials. Hence, when local and global information ought to have controlled conflicting patterns of performance, the birds' discrimination behavior suggested control by both local and global cues, attesting to the birds' attending to more than the small areas of the training objects that contained the target dots.

5. Experiment 4

In the three previous experiments, we found that the colors immediately surrounding the target dots strongly controlled pigeons' discrimination performance. Early reports on attention in pigeons found the color of a color-shape compound stimulus to be dominant in gaining stimulus control, although birds could attend to the shape of the stimulus as well (Farthing & Hearst, 1970; Kendall & Mills, 1979; Wilkie & Masson, 1976). Perhaps unsurprisingly, the pigeons in our study attended primarily to the colors of the objects when this cue was available. In our final experiment, we explored whether pigeons can learn to discriminate the displays in the absence of the color cue—i.e., when two objects have the *same color* and *different shapes.*

5.1. Method

5.1.1. Subject

We studied Bird 12Y, housed and maintained as described above (Bird 25R was unavailable for inclusion in this investigation).

5.1.2. Apparatus and stimuli

The same apparatus as in Experiments 1, 2, and 3 was used. Fig. 10 shows a subset of the training and testing stimuli that we presented in this experiment. For the training stimuli, the images comprised an oval and a rectangle of the same color (both red or both green; for a total of 64 images), so that the objects on the display differed in shape, but not in color. For the testing stimuli (Same Color, Same Object Test), each image comprised either two ovals or two rectangles of the same color (both red or both green; for a total of 32 testing stimuli), so that the testing objects differed in neither color nor shape. The bird had earlier been exposed to each of those sets of stimuli under nondifferential reinforcement (see Lazareva et al., 2005).

5.1.3. Procedure

We used the same training and testing procedures described in Experiment 1. Before testing, the bird was required to meet the criterion of no overlap between response rates to the individual *same*-*object* and *different*-*object* stimuli in a single training session.

Each testing session contained 4 blocks of 32 training trials and 8 testing trials (160 trials total), so that the pigeon received 4 presentations of each training stimulus and 1 presentation of each testing stimulus. The test involved 2 testing sessions separated by at least 1 training session; thus, the pigeon was exposed to each testing stimulus twice.

5.2. Results and discussion

Fig. 11 depicts changes in the rates of pecking on DRH (white triangles) and DRL (black triangles) trials, and the corresponding changes in discrimination ratios (black circles) throughout discrimination training. The pigeon showed signs of separation in its rates of pecking to the DRH and DRL stimuli early in training. By the end of training, the mean rate of pecking the DRH stimuli was clearly much higher than to the DRL stimuli, disclosing that the pigeon could discriminate *same*-*object* from *different*-*object* stimuli even though the colors of the objects could no longer serve as discriminative stimuli.

Recall that this pigeon was originally trained to discriminate displays that comprised two objects that differed in both shape *and* color (cf. Fig. 1). In our earlier report, we investigated which property of the objects, color or shape, was essential for pigeons' discrimination behavior (Lazareva et al., 2005). We found that pigeon' performance of this object discrimination depended critically on the colors of the two objects; pigeons failed to discriminate *same*-*object* displays from *different*-*object* displays in the Same Color, Different Shape Test. Predictably, pigeons also failed to discriminate *same*-*object* displays from *different*-*object* displays in the Same Color, Same Shape Test, in which the testing displays comprised either two ovals or two rectan-

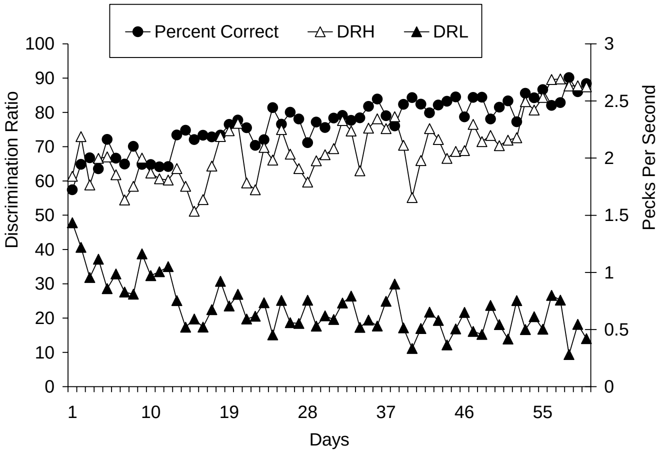

Fig. 11. Rate of pecking to the DRH and DRL stimuli, and the corresponding percentage of correct responses during training in Experiment 4.

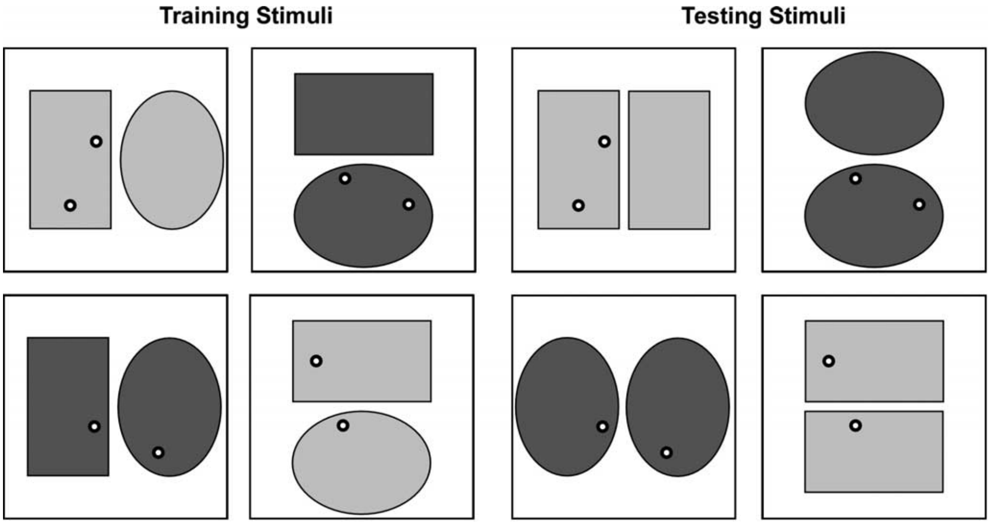

Fig. 10. Examples of the training and testing stimuli in Experiment 4.

gles of the same color (Fig. 10, right panel). It was conceivable that training to discriminate displays containing objects of the same color (Fig. 10, left panel) might shift pigeons' attention from color to other properties of the object. Thus, after Bird 12Y completed Same Color, Different Shape Training, it was again given the Same Color, Same Shape Test.

Table 5 depicts the means and standard deviations of the pigeon's pecking on DRH and DRL training and testing trials in the Same Color, Same Shape Test conducted after training with objects that differed in both color and shape (Lazareva et al., 2005) and after additional training with objects that differed in shape, but not color (Experiment 4). Fig. 12 illustrates the same data as discrimination ratios. When the original training stimuli comprised two objects that differed in both color and shape, the bird failed to discriminate the testing displays (Fig. 12, left section). But, when the bird was subsequently trained with displays containing two identically colored objects of different shapes, it showed significant discrimination of the testing displays in which the objects differed in neither color nor shape [two-tailed t test, $t = 22.34$]. Planned comparisons indicated that the bird's testing performance in Experiment 4 did not differ significantly from its training performance [$t = 1.65, p = 0.10$].

In summary, we found that a pigeon can discriminate *same-object* displays from *different-object* displays when both objects are the same color. Indeed, it is even possible for a pigeon to discriminate *same-object* displays from *different-object* displays in the Same Object, Same Color Test, in which the objects differed in neither color nor shape.

Table 5
Bird 12Y's pecking (number of pecks per 10-s interval) on DRH and DRL training and testing trials in the Same Object, Same Color tests both before and after training to discriminate two objects of the same color, but different shapes

	DRH Training		DRH Testing		DRL Training		DRL Testing	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Before	24.69	5.06	15.31	10.28	10.77	9.95	14.00	9.86
After	23.30	5.42	24.23	4.19	3.22	5.27	5.47	7.23

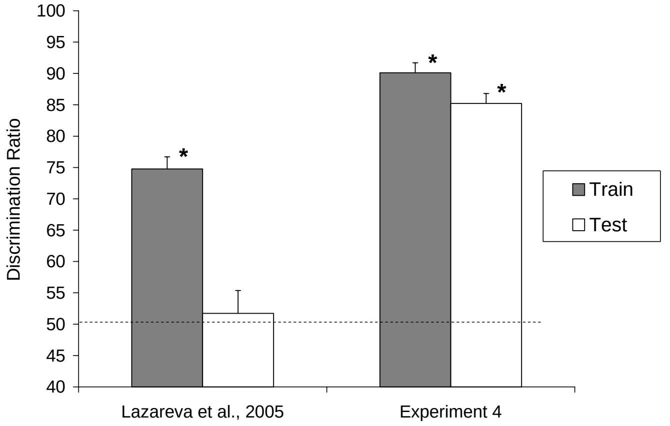

Fig. 12. Percentage of correct responses to the training and testing stimuli in the Same Color, Same Shape Test conducted after training with objects that differed in both color and shape (Lazareva et al., 2005) and after training with objects that differed in shape, but not color (Experiment 4). Asterisks indicate a significant difference from chance.

6. General discussion

In earlier experiments (Lazareva et al., 2005), we found that pigeons can discriminate whether two targets are located on a single object or on two different objects. We also found that the color of the objects, but not their shape, is critical for this discrimination. But, just how much of the shapes' colors do pigeons need in order to perform this discrimination? It is entirely possible that the pigeons' discrimination strategy was merely to attend to the small areas immediately encircling the target dots and to compare their colors. This strategy would convert an object-based discrimination into a color matching-to-sample task. The experiments reported here explored this possibility.

Experiment 1 found that the colors in the immediate vicinity of the target dots did exert strong control over pigeons' discrimination performance: The birds failed to discriminate *same-object* from *different-object* displays when the areas around the target dots were replaced by gray shading (Distal Tests). However, when local color cues were available but the rest of the object was replaced with gray shading (Proximal Tests), the birds' discrimination performance deteriorated significantly, suggesting that more global cues also contributed to pigeons' discrimination performance.

It is important to note that object-based attention in humans is also affected by cues such as object color. Watson and Kramer (1999) presented participants with a picture of two wrenches and asked the participants to report whether two target properties, a bent end and an open end, appeared on the same object or on two different objects. People were faster to produce *same-object* reports than *different-object* reports—a classic object-based attention result. But, when the handle of the wrench had its surface pattern differ from the pattern on the ends, people produced both reports at a similar speed and the *same-object* benefit disappeared. This latter pattern of results suggests that, when the surface of the wrench handle differed from the wrench ends, people did not perceive the wrench as a single object. More generally, people tend to group connected regions of uniform visual properties—including surface properties such as color, lightness, or texture—as a single perceptual unit (Palmer & Rock, 1994).

In Experiment 2, we investigated the possibility that the birds attended to a single small area that encompassed both target dots. Such an area would always entail one color on *same-object* displays and it would always encompass subfields of red, white, and green on *different-object* displays. Hence, these color combinations might be serving as the discriminative stimuli. We found that pigeons still discriminated *same-object* from *different-object* displays in the

Occlusion Test (where the focal area on *different*-*object* displays involved red and green, but not white) and in the Split Object Test (where the focal area on *same*-*object* displays involved white, in addition to either red or green). These results again suggest that the birds were attending to more of the training stimuli than just the two target dots and the area between them.

In Experiment 3, we compared the strength of behavioral control exerted by local and global cues by filling in one half of the objects with green and the other half of the objects with red. If the pigeons' behavior was primarily controlled by the color of the area near the targets, then the birds should have responded to *same*-*object* displays as if they were *different*-*object* displays and vice versa. We found little (Bird 25R) or no (Bird 12Y) indication of such discrimination reversal, further suggesting that the birds were using both global and local visual information.

Finally, in Experiment 4, we trained a pigeon to discriminate *same*-*object* from *different*-*object* displays when the objects had the same color and different shapes (Fig. 10). Notably, after such training, the same bird that had earlier failed to discriminate *same*-*object* from *different*-*object* displays in the absence of color cues (see Lazareva et al., 2005) now exhibited strong discrimination performance when the objects differed by neither color nor shape. This result suggests that the relative salience of object features, like color and shape, can be modified by experience. It also implies that training to discriminate *same*-*object* from *different*-*object* displays in the absence of local color differences teaches the organism to rely on more general segregation cues that may include contours or the spatial separation of homogenous object surfaces. Our future research will explore how the pigeon's visual system uses those image properties to guide selective attention.

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