Available online at www.sciencedirect.com

SCIENCE DIRECT®

Behavioural Processes 69 (2005) 79–95

BEHAVIOURAL PROCESSES

www.elsevier.com/locate/behavproc

Avian detection and identification of perceptual organization in random noise

Robert G. Cook [a,*], Kazuhiro Goto [b], Daniel I. Brooks [a]

[a] *Department of Psychology, Tufts University, Medford, MA 02155, USA*
[b] *Washington Singer Laboratories, School of Psychology, University of Exeter, Exeter EX4 4QG, UK*

Received 1 November 2004; received in revised form 3 January 2005; accepted 3 January 2005

Abstract

Recent research has suggested that pigeons may have difficulty globally integrating visual information in hierarchically arranged stimuli. To isolate and understand the mechanisms responsible for processing emergent perceptual structure, three pigeons were tested in a two alternative choice task that required the global integration of organized local information. They were reinforced for localizing, on randomized distractor backgrounds of black and white square elements, different types of structured targets (e.g., stripes, squares, checkerboards) arranged from these same elements. These hierarchical stimuli were tested at four different levels of spatial granularity (i.e., different element sizes). Experiment 1 found rapid acquisition for the vertical and horizontal stripes or square targets and somewhat slower learning with the checkerboard pattern. Experiment 2 demonstrated successful transfer to a novel target types (alternating bars and "diagonal" stripes). In both experiments, displays with the greatest spatial granularity (smallest elements and most repetitive structure) monotonically supported the best discrimination. These results indicate pigeons can perceive and discriminate emergent visual structure under the right circumstances and suggest they do so with a generalized rule for detecting patterns of non-random perceptual structure.

Keywords: Global perception; Pattern perception; Visual search; Pigeon; Hierarchical stimuli

A long standing question in the study of animal visual cognition centers around what mechanisms underlie how animals recognize and locate perceptual objects in their environment and use this information in meeting the daily demands of survival (Cook, 2001a,b). Donald Blough's pioneering investigations into pigeon visual perception and cognition not only provided fundamental information about the nature of these essential visual processes (e.g., Allan and Blough, 1989; Blough, 1956, 1957, 1959, 1967, 1969, 1977, 1979, 1982, 1985, 1989; Blough and Blough, 1990, 1997), but, in the process, transformed the entire methodological enterprise of animal cognition by his early adaptation of computer graphics and optical response sensing for testing animals (Blough, 1977, 1979). Although the

---

[*] Corresponding author. Tel.: +1 617 627 2456; fax: +1 617 627 4132.
E-mail address: robert.cook@tufts.edu (R.G. Cook).
URL: www.pigeon.psy.tufts.edu (R.G. Cook).

0376-6357/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.beproc.2005.01.006

important findings from his numerous studies are too abundant to review in a single article, one of his seminal papers looking at the perception and discrimination of random dot figures (Blough, 1985) provides a critical entry point for the new experiments reported in this article.

Investigations involving the visual perception of random dot patterns have a long, useful history in the study of human perception (e.g., Barlow, 1978; Burgess et al., 1981; Julesz, 1981; Uttal, 1976). One of the most significant benefits from studying the discrimination of random dot displays is that the observer is required to integrate the local geometry of the dots into an emergent perceptual structure, since the individual dots or elements are otherwise equivalent in size, shape, and luminance. As a result, random dot displays have played a critical role in isolating and studying the mechanisms of global stereopsis and perceptual grouping in humans.

Although investigated less frequently, the necessity for global integration in random dot displays makes them similarly useful in the study of visual perception and search in birds (Bischof et al., 1999; Blough, 1985; Bond and Kamil, 1998, 2002; Cook, 1993a,b, 2001; Kelly et al., 2001; Plaisted and Mackintosh, 1995; Swaddle and Pruett-Jones, 2001). This integrative requirement is of particular importance at the moment because one potential difference that has been identified between human and pigeon perceptual processing concerns how they integrate information and direct attention to the local and global features of hierarchically arranged stimuli (Cavoto and Cook, 2001; Cook, 2001a,b; Fremouw et al., 1998, 2002).

Hierarchical stimuli consist of a larger figure made out of arrangements of smaller component shapes, and in which both the information at the global and local levels are concurrently relevant. It has been demonstrated that both levels of organization are capable of controlling human and non-human behavior (Cavoto and Cook, 2001; Cook, 1992a,b, 2001; Fremouw et al., 1998, 2002; Kimchi, 1992), but that humans tend to show precedence for global information over the local information (Navon, 1977, 1981; Ward, 1982), while pigeons have been shown to give temporal precedence to the local features of such stimuli (Cavoto and Cook, 2001, but see Fremouw et al., 2002).

Other animals have also shown this local dominance by having greater difficulties in the speed or accuracy of integrating global information in hierarchical stimuli. Testing baboons and chimpanzees in a visual search task, Fagot and his colleagues (Deruelle and Fagot, 1998; Fagot and Deruelle, 1997; Fagot and Tomonaga, 1999) found a local advantage in the processing of hierarchical stimuli (i.e., faster RTs or higher accuracy with local relevant displays), especially with sparse element arrangements.

In examining of the effects of an additional configural visual context, Kelly and Cook (2003) recently reported that humans and pigeons react differently when a supplementary global context was added to a line orientation discrimination (see also Donis and Heinemann, 1993). The humans showed the classic “configural superiority effect” previously reported (Pomerantz et al., 1977), while the pigeons in contrast showed a decrement in accuracy with the addition of the global context. Congruently, Phelps and Roberts (1994) found that pigeons differed from humans and monkeys in that they do not show an inversion effect in a face discrimination, suggesting that local features were more important for the pigeons than the configural arrangement that likely guided the choice behavior of the primates. More recently, Aust and Huber (2001) found evidence of local processing of human/non-human pictures by pigeons in a categorization task.

Of more relevance to the new studies below, Kelly et al. (2001) examined the perception of Glass patterns (Glass, 1969) by pigeons and humans. Glass patterns are composed of random dot pairs positioned in different ways to produce a larger global pattern. For example, if a set of random dots is replicated and rotated by a constant amount, it will produce a perceptible concentric pattern consisting of a series of emergent “circles”. The discriminability or “visual coherence” of these global patterns can then be systematically reduced by decreasing the number of corresponding dots shifted within the display. Kelly et al. tested pigeons and humans with four different types of Glass patterns (S+) against random dot displays (S−) under varying degrees of coherence. Humans showed clear differences in their capacity to discriminate the different Glass patterns (Wilson and Wilkinson, 1998), indicating that the different emergent structures controlled their discrimination. The pigeons, on the other hand, showed no differential discrimination of the different Glass patterns, responding identically to each pattern regardless of coherence level. This latter result suggests the pigeons may have been responding only to smaller chunks of local information over a spatial scale that prevented them from seeing the overall emergent pattern. Another possibility is that they integrated over a larger spatial scale, but did not differentially respond to the patterns in the same way as humans. Bischof et al. (1999) have also found that pigeons are not as good as humans in detecting the coherent motion of multiple dots in dynamic random dot displays.

Thus, there is growing evidence that the global integration of separated visual information may be difficult for pigeons, suggesting a potential difference in its processing in humans. This is something of a paradox because perceptually grouping regions of visual space is essential to edge and surface detection and the eventual construction of object and scene representations—all processes that would be invaluable to a highly mobile animal like the pigeon. As such, we thought it would be theoretically beneficial to study in isolation the nature of the integrative processes responsible for processing emergent visual structures in these animals. Because of its necessity for global integration, we used a variation of the random dot display in which small square local elements consisting of black and white contrasts were arranged to create larger scale perceptual structures that the pigeons had to identify and localize. With a better understanding of the global and local processing systems in isolation, the more complex problem related to the interaction of these systems might better yield to empirical investigation.

1. Experiment 1

To advance this objective, we examined how pigeons discriminated displays composed from randomized and structured groups of black and white elements (see Fig. 1). On each trial, the pigeons were faced with two randomly generated displays, in one of which was a randomly located target area created by the specific structural arrangement of the black and white elements making up the randomized backgrounds (see target examples in Fig. 2). Given this arrangement, the pigeons were required to integrate across at least some area of the display in order to identify and localize the target, as limited attention to just the individual local elements would be insufficient. The primary objective of Experiment 1 was to see if and how pigeons discriminated the different types of structured patterns from a randomized and noisy background.

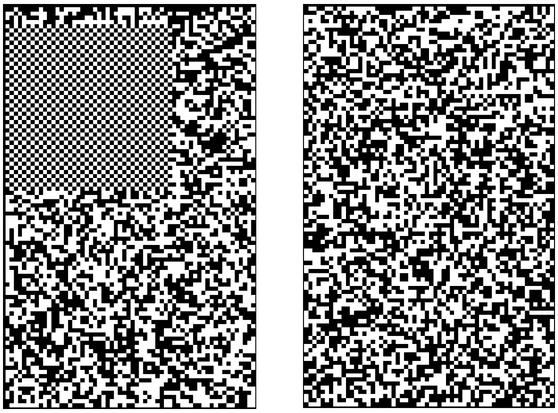

Fig. 1. An example of the display used to test the pigeons. Pecks to any portion of the panel containing the structured target were reinforced with mixed grain. Pecks to the side consisting exclusively of randomized elements received a brief timeout. Chance in the task was 50%.

Four different types of structured targets were concurrently tested. The inspiration for the design of these patterns was drawn from Garner's (1974) proposals concerning "goodness of form." He proposed that the higher degree of rotational and reflective symmetry exhibited by a pattern directly influenced its encoding and processing. Thus, "good" figures are those producing the fewest variants when transformed by reflections

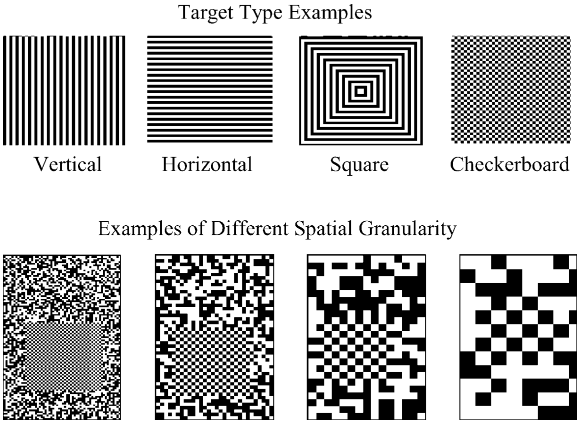

Fig. 2. Top row shows examples of four structured target types tested in Experiment 1 at the highest spatial granularity tested. The bottom row shows the checkerboard target at each of the four different spatial granularities tested.

and 90° rotations. To similarly produce "good" patterns, target structures were chosen to make the most of their rotational and reflective symmetry. The structured targets tested consisted of alternating vertical bars or stripes of different contrasts, alternating horizontal bars, concentric squares, and checkerboard patterns. Because of their higher degree of rotational symmetry, the concentric squares and checkerboard would be considered by Garner to be better forms than the horizontal and vertical stripes.

To help further examine the grouping and target search processes underlying any discrimination that formed, we also systematically manipulated the spatial granularity of the display. This was done by varying the size of the individual elements used to compose a display (see examples in the bottom panel of Fig. 2). By changing the element size, we could create highly granular displays consisting of smaller elements containing targets with a high degree of repetitive structure per unit area or sparsely granular displays made of larger elements with targets having less repetitive structure. To our human eyes, the targets in the highly granular displays were easier to detect. This element size manipulation allowed us to examine how spatial scale influenced global processing, information critical to understanding the mechanisms of any such integrative process. Soon after the pigeons learned the initial discrimination in Experiment 1, we tested a manipulation of the target's overall size. The tested target sizes were scaled to produce a series of comparisons to investigate how size and organizational repetition each affected the discrimination.

Thus, this experiment allowed us to better understand how perceptual structures emerge to control performance in a precisely controlled, but highly unpredictable context, given that the background array of elements and target location were randomly generated and different on every trial. Besides helping us understand the visual processes by which pigeons' process emergent perceptual information, the current research is also relevant to recent interests in how organisms perceive and produce structured and random patterns in general (Nickerson, 2002). Although not included in this experimentally oriented report, another important goal of this project was to generate a data set useful for developing and testing various computational models of avian grouping and visual search.

1.1. Method

1.1.1. Animals

Three naïve male White Carneaux pigeons were tested. They were maintained at 85% of their free-feeding weights in a colony room with a 12-h light:12-h dark cycle and had free access to water and grit in their home cages.

1.1.2. Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide × 36 cm deep × 38 cm high). All stimuli were presented by a computer on a color monitor (NEC, 15″ AccuSync LCD51VM; Wooddale, IL) visible through a 28.5 cm × 21.5 cm viewing window in the middle of the front panel. The viewing window's bottom edge was 13.5 cm above the chamber floor. The viewing window was bordered by 2 cm of flat-black plastic trim. Pecks to the monitor screen were detected by an infrared LED touchscreen (Carroll Touch; supplied by EloTouch Systems). A 28 V houselight was located in the ceiling and illuminated at all times, except when an incorrect choice was made. A 5 cm × 5 cm aperture was positioned 8.5 cm below the center of the bottom edge of the screen and flush with floor, giving access to a hood hopper (Coulbourn #E14-10, Lehigh Valley, PA). A computer equipped with a video card running in its 1024 pixel × 768 pixel graphics mode controlled experimental events.

1.2. Procedure

1.2.1. Display organizations

Each display consisted of two 300 pixel × 480 pixel (9 cm × 14.4 cm) randomly generated textured panels. These were separated by a 100 pixel (3.0 cm) area of black screen. Randomly located in one of the two panels was a 200 pixel × 200 pixel (6 cm × 6 cm) structured target. The four structured targets consisted of alternating vertical stripes, alternating horizontal stripes, a concentric set of square outlines, and a checkerboard pattern (Fig. 2). Each of these targets was then tested at four different spatial scales. These different spatial scales were produced by varying the size of the local elements used to create the displays. The element sizes tested were 5, 10, 20, or 40 pixels. Only one element size was used to create any particular display.

1.2.2. Discrimination testing

All the pigeons were first hopper trained, then autoshaped to peck at a white circle (2.5 cm diameter), which was subsequently used as a ready signal to begin each trial. They were then trained to peck both sides of the computer screen by randomly displaying just one of the 300 pixel × 480 pixel panels, containing a randomly selected target type, followed by food. Following this pretraining, discrimination training began with the introduction of both panels and the necessity of correctly pecking the target's panel to obtain food reinforcement.

Each trial began with a peck to the ready signal, followed by presentation of a randomly generated display. The pigeon then indicated the target's location by making five pecks to either the left or right panel. Only pecks within a panel were counted. If they pecked the panel containing the target, it was considered a correct choice and the animal received 3-s access to mixed grain from the front hopper. If they pecked the incorrect panel, they received a 5-s dark timeout. A 3-s inter-trial interval (ITI) followed either outcome. Each of the 4 target types was tested 32 times per session, with each target tested 8 times each at 4 different element sizes. Thus, each of the 5 weekly sessions consisted of 128 total trials. The first phase of the experiment consisted of 20 sessions.

1.2.3. Manipulation of target size

When all three pigeons achieved a relatively stable level of accuracy, we conducted a target size manipulation. In this second phase of the experiment, the target's overall size was set to either 25 pixel × 25 pixel, 50 pixel × 50 pixel, 100 pixel × 100 pixel, or 200 pixel × 200 pixel (baseline). In these sessions, each target was tested 28 times. Sixteen of these trials were the same as in phase 1, with each target tested four times at each element size. The remaining trials were used to test the various target sizes. Because of the fixed sized of the displays and the nature of space, certain of the new targets could not be created for some of the element sizes. Within this spatial constraint, all possible combinations were created and tested. These six target size conditions (25 pixel target size/5 pixel element, 50/5 50/10, 100/5, 100/10, 100/20) consisted of each target type being tested twice. Thus, each daily session consisted of 112 total trials (64 training trials and 48 new target size trials). Phase 2 testing lasted 40 sessions, after which testing of the target size manipulation ceased.

1.3. Results

The pigeons quickly learned the basic task. Fig. 3 separately shows accuracy for the different element sizes and the different target types across the first 60 sessions. Overall they learned to discriminate the highly granular displays constructed with the 5 pixel element size most quickly and were progressively slower as the size of the elements increased and display granularity decreased. The vertical and horizontal striped targets were the easiest to learn, followed closely by the square. The most difficult target type to learn was the checkerboard pattern, taking a number of additional sessions for all three birds to begin localizing this target. There were no significant interactions between size and target type during training, as the speed of learning was accurately reflected by the additive combination of the size and target type factors.

To better characterize the relations between element size and target type after learning, we separately examined the last 10 sessions of training. The individual and average results for these sessions are presented in Fig. 4. The pigeons were very good at finding any of the four targets in the 5 pixel element displays. As element size increased to 10, a growing spread in accuracy between the different targets appeared with the checkerboard showing the greatest decline. Further decreases in granularity caused a monotonic decline in accuracy with all targets, with the square and checkerboard supporting the poorest performance and the horizontal and vertical bars supporting the best accuracy out to the largest spatial granularity. A repeated measures analysis ANOVA (session × element size × target type) confirmed significant main effects for both target type, $F(3, 6) = 8.1$, and element size, $F(3, 6) = 12.1$ (all statistical tests of the data in this article were evaluated using an alpha level of $p < 0.05$). The omnibus interaction term, $F(9, 18) = 2.1$ reached a marginally significant level ($p = 0.09$) in this analysis, but subsequent refinements comparing specific target types showed the expected significant interactions between element size and target type present in Fig. 4.

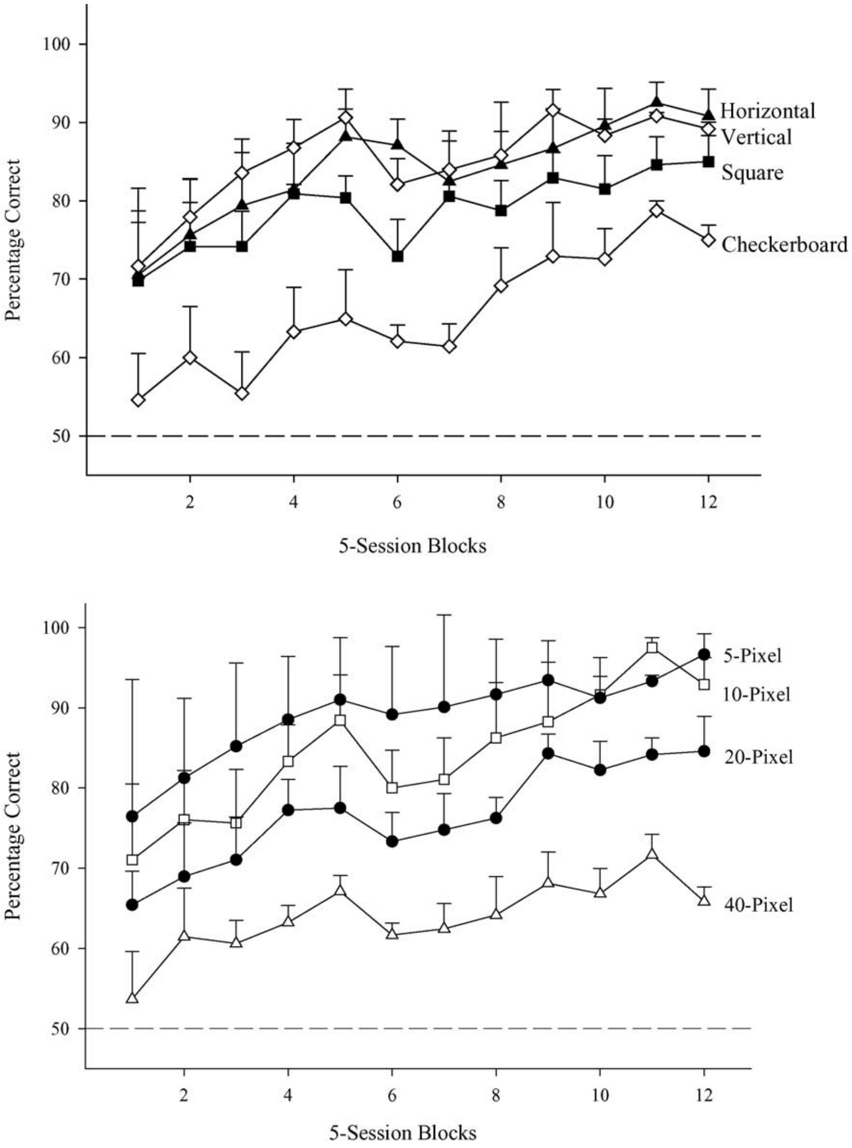

Fig. 3. The top panel displays mean choice accuracy for the four target types, collapsed across element size, as a function of five-session blocks. The bottom panel displays mean choice accuracy for the four element sizes, collapsed across target type, as function of five-session blocks. The dotted reference line in each panel depicts chance responding in the task. Error bars show the S.E.M. for each condition.

1.3.1. Effects of target size

Fig. 5 shows the results for the manipulation of target size. As expected, the main effect of reducing the target's size was to reduce accuracy. This was true regardless of element size and appeared to be a relatively constant drop across target size. The more interesting theoretical issue concerns the relation between target size and the number of structural repetitions allowed within a target area. How much did multiple repetitions of the organization within a target help to locate it? This turned out to be difficult to assess because the size of the target seemed to be the overriding factor. While the greater repetition allowed at increasingly smaller levels of granularity likely helped performance, when hold-

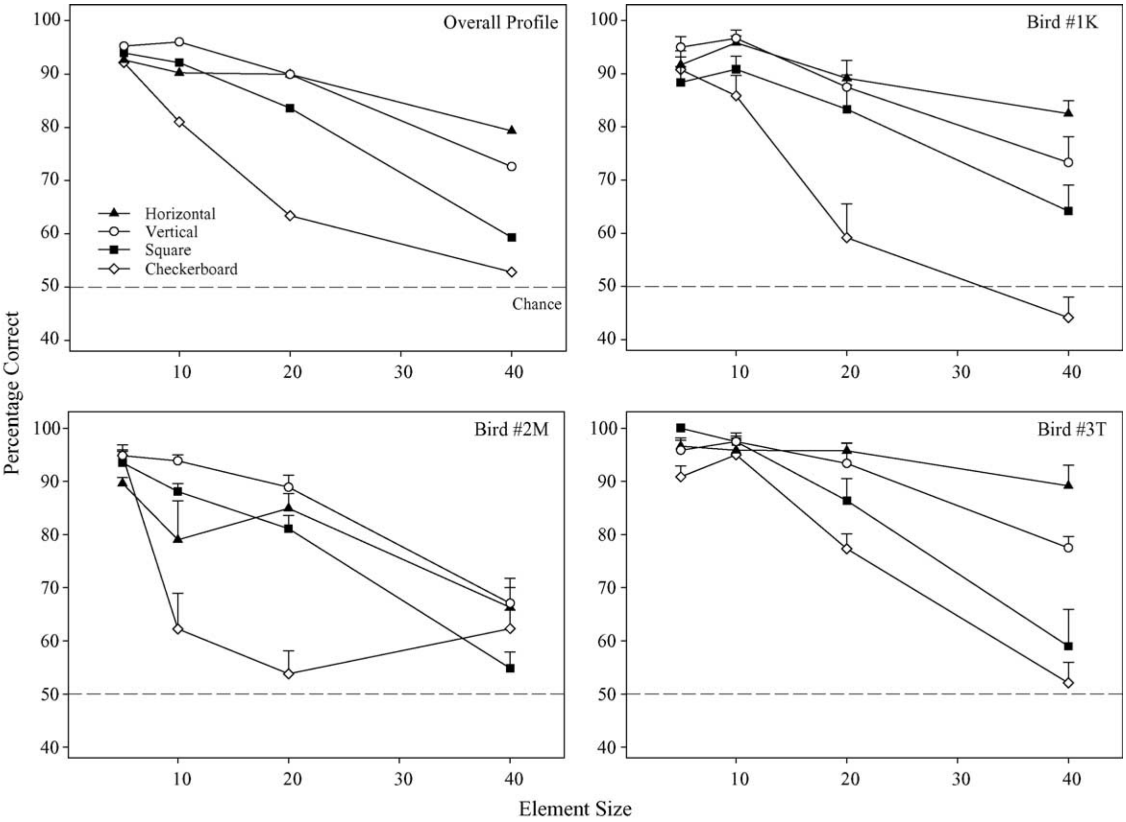

Fig. 4. The top left panel displays the mean choice accuracy profile for the four target types as function across element size at the end of Experiment 1. The remaining three panels show this for each pigeon. The dotted reference line in each panel depicts chance responding in the task. Error bars show the S.E.M. for each group.

ing the number of repetitions constant over different sized targets, the effect of target size was too great to make a strong inference about its direct contribution.

1.4. Discussion

These data indicate that pigeons can detect, integrate, and use the global structure of non-random patterns to perform a choice discrimination. This success was reflected in the integrative ability of the pigeons to perform with four different types of targets at various levels of spatial granularity in a task where local information was rendered useless. Spatial granularity was a critical factor in their capacity to perform this target localization task. When the local elements were small, densely packed, and provided a high degree of repetition in the target area, accuracy was better with all target types. As element size increased, accuracy gradually declined. Importantly, the rate of this decline varied according to target type. As granularity decreased, performance remaining highest with horizontal stripes followed by vertical stripes, with the more complex concentric square and checkerboard patterns declining the most. This suggests the global appearance of the target was an important determinant of behavior.

Two questions were of immediate concern. First, what did the pigeons perceive when they searched these displays? Second, what representations did the pigeons use to recognize or identify these targets? Taking up the latter issue first, three distinct possibilities can be considered. The first possibility is that the pigeons learned a series of independent stimulus-specific representations that were used to identify each target. This exemplar approach by necessity has to focus on the coding

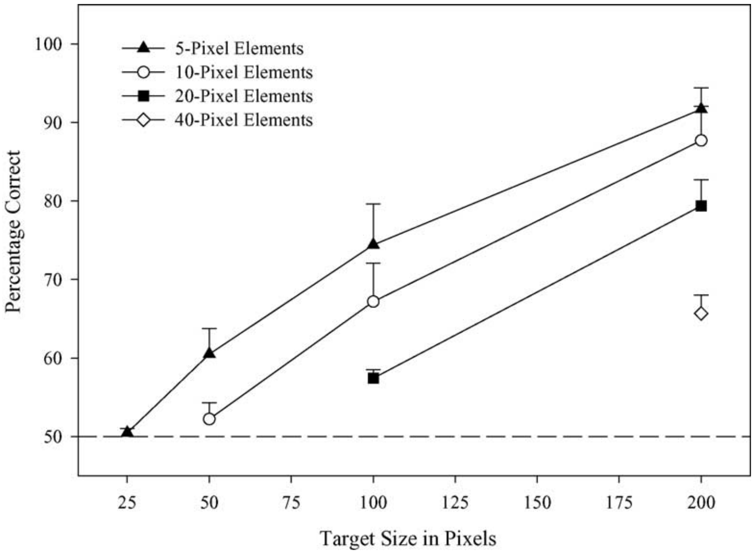

Fig. 5. Mean choice accuracy across the four target types as function of element size and target size. The dotted reference line in the figure depicts chance responding in the task. Error bars show the S.E.M. for each condition.

of the targets, as the backgrounds constantly changed throughout the experiment (cf. Katz and Cook, 2000). This approach does not easily handle the different rates at which the target types were acquired, unless perceptual factors are added that limit the ability to see some of the targets and thus interfere with their acquisition. A second possibility is that the pigeon learned something about a set of limited global features that mediated target identification. For instance, the straightforward recognition of extended straight edges could have been responsible for the rapid acquisition of the vertical, horizontal, and square targets observed in Experiment 1. It is not clear, however, how such an edge-oriented feature could have eventually mediated the learning of the intermingled elements in the checkerboard target. This edge hypothesis does not account for why the square, which had both types of line orientation (plus diagonal illusory contours) and more edges in general also did not support the best performance. It seems the pigeons would have needed to learn to search for at least two kinds of target features to account for these data, potentially consisting of alternating blocks of contrasting polarity and extended lengths of black or white edges. A third possibility is that pigeons learned to respond to a more generalized concept of target structure. In this case, target structure would be generally defined as any non-random patterning of elements. This mechanism would allow them to flexibly identify a large number of potential targets using a single generalized representation.

Regardless of the target recognition rule acting as the basis for action, these data indicate that pigeons can perceive the global relations among organized sets of local elements. Because of the strong performance supported by the line orientation stimuli, edge sensitivity over an extended area would be a very likely candidate for the perceptual grouping mechanism mediating this behavior. In other experiments conducted using closely related texture stimuli formed from separated elements (Cook, 1992a,b, 1993), we have hypothesized that the pigeon visual system is strongly disposed to spatially group highly similar information for the purposes of detecting object edges (Cook, 1993a,b, 2000). The current results are consistent with this idea.

This cannot be the whole story, however, because the pigeons also perceived patterned information, in the form of the checkerboard targets, which had no continuous edges or other singular features. As such, the pigeons must have mechanisms that can group information beyond just mere similarity (i.e., area of same color or same shape), but can operate on uniformly patterned regions of repetitive structure. A very likely candidate for such a mechanism is one designed to recognize textured surfaces on objects. While complicated by depth and lighting relations, most object surfaces have a similar appearance and texture throughout their extent. In this way, the checkerboard target may have acted like an extended surface, where its repetitive structure indicated a continuous area of common significance.

Another key question concerns how much of the display's total area is involved in constructing the structured information controlling performance. One clue comes from the target size results. As target size was reduced, performance declined. Reducing the target's size from 200 to 100 pixels, for example, reduced accuracy by about 20%. This suggests that the pigeons were using an area close to the largest target size to maximize their discriminative advantage. If so, it would suggest the pigeons were integrating over 6 cm × 6 cm area of the display when making a choice response. The advantage of using the largest area possible is that there is more structured information capable of indicating where to peck. Our informal human observations were that the reduced target sizes were much harder to see because of the limited amount of structure in a smaller area and its greater similarity to conflicting "features" created by chance in the randomized backgrounds.

Of course, the benefits of target size may also accrue from a slightly different reason. In this case, the pigeons integrate over an area smaller than the target's actual size, but the larger target area provides a greater opportunity to detect any structured area as the display is searched. These two competing hypotheses cannot be distinguished by the current results, although we slightly favor the former hypothesis. If the pigeons were only integrating over a limited area of the display, we do not think the target size effects would be as large as we observed. We suspect the target size effects are a direct reflection of the greater visibility of larger targets, due to the presence of increased repetitive structure, rather than any advantage related to or dependent on search.

2. Experiment 2

The goal of Experiment 2 was to examine the nature of the representation defining a target. To investigate this issue we introduced 20 new targets that formed 2 larger clusters of target types. These targets were again designed to have high degree of structure, but in different ways from those used in Experiment 1. If the pigeons were responding to a limited set of features to identify the targets, then these new targets should support relatively poor performance upon their introduction followed by a gradual increase in accuracy with experience. If the pigeons had learned a more generalized rule for detecting and responding to non-random patterns, then these new targets should support good performance upon their introduction.

The first set of new targets were alternating bars of different lengths of contrasting elements created by staggered set of elements, much like elongated checkerboard patterns (see Fig. 6). A total of six of these targets were created, with one set of six oriented vertically and another set oriented horizontally (as judged by the illusory contours created by this manipulation). Because extended edges seemed at least initially critical to the pigeons' success, one purpose of varying the length of the bar segments in these targets was to evaluate directly the contribution of such edges to the discrimination. We manipulated the length of the bar segments, in combination with element size, to create new targets with internal edges that were either 25, 50, or 100 pixels in length (see Fig. 6 for one, two, or three examples of these lengths depending on element size). These targets were introduced and tested for six sessions.

The second set of new targets used an alternating sequence of one and two elements of contrasting polarity to create its pattern. This sequence created an emergent staggered diagonal appearance to the targets (see Fig. 7). Because this unbalanced sequencing changed the 50/50 distribution of black and white elements used in the other targets, we adjusted the randomized backgrounds to match these targets in brightness. Thus, the "light" diagonal targets were tested on a light randomized background having more white elements (2/3) than black elements (1/3) and the "dark" diagonal targets were tested on a dark randomized background having proportionally more black elements. These targets were introduced and tested for six sessions.

Following these transfer tests, all the of the new targets from Experiment 2 and the old targets from Experiment 1 were tested for 75 sessions to collect a data on asymptotic performance with the different target types. These extended training data are quite useful for separating out experiential limitations on performance from those related to perception.

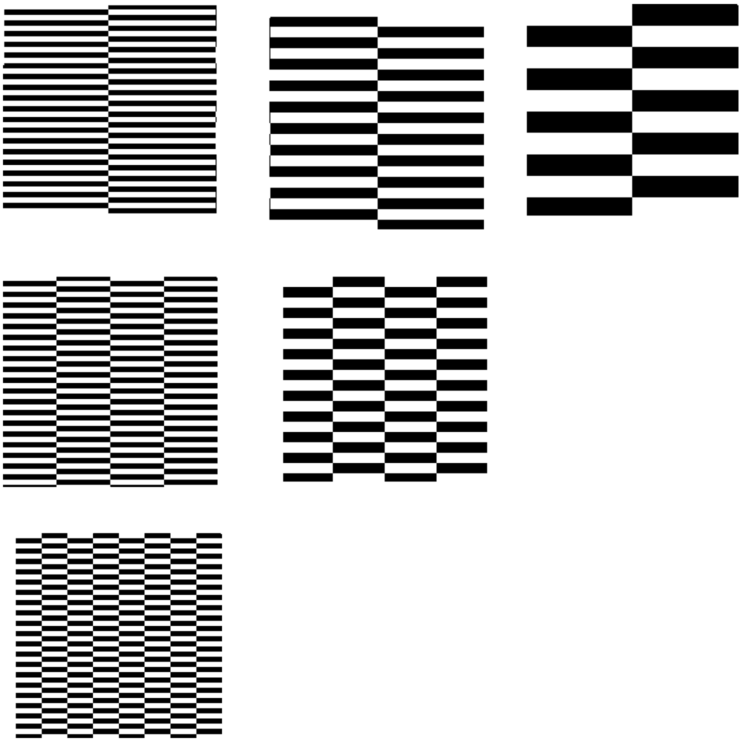

Fig. 6. The six alternating bar target types tested in Experiment 2. Only the vertical orientation is shown. A comparable horizontal set was also tested.

2.1. Method

2.1.1. Animals and apparatus

The same pigeons and apparatus were used as in Experiment 1.

2.2. Procedure

The new targets were introduced and tested in Experiment 2 in two phases. Each new target was produced by changing the relative length of black and white elements within the pattern. Phase 1 introduced new 200 pixel × 200 pixel targets consisted of alternating vertical (six new targets) and horizontal (six new targets) bar segments of varying length. The length of the bar segment tested depended on the element size used to create the display, as the software algorithm for creating these targets involved multiplying the base element a fixed number of times to create the bar segments. For the displays created from a base element size of 5 pixels, three new targets consisting of alternating black and white bar lengths of 25 pixels (5× the base element), 50 (10×), and 100 (20×) pixels were created. For the displays created from a base element size of 10 pixels, two new targets consisting of bar lengths of 50 (5×) and 100 (10×) pixels were created. For the displays created from a base element size of 20 pixels, one new target with alternating bar segments of 100 (5×) pixels was created. Each of these segmented targets was tested four times in a session (twice vertically and twice horizontally). This produced a total of 24 novel target trials. These novel trials were then randomly mixed with 134 baseline trials testing each of Experiment 1's targets at the four element sizes. Thus, each session in Phase 1 consisted of 152 trials. Again, the background displays of mixed black and white elements were randomly generated on each trial. Phase 1 consisted of six test sessions.

Phase 2 introduced two additional new targets created by an alternating sequence of two elements to one contrasting element, resulting in an emergent diagonal appearance to the target. Because these targets were not

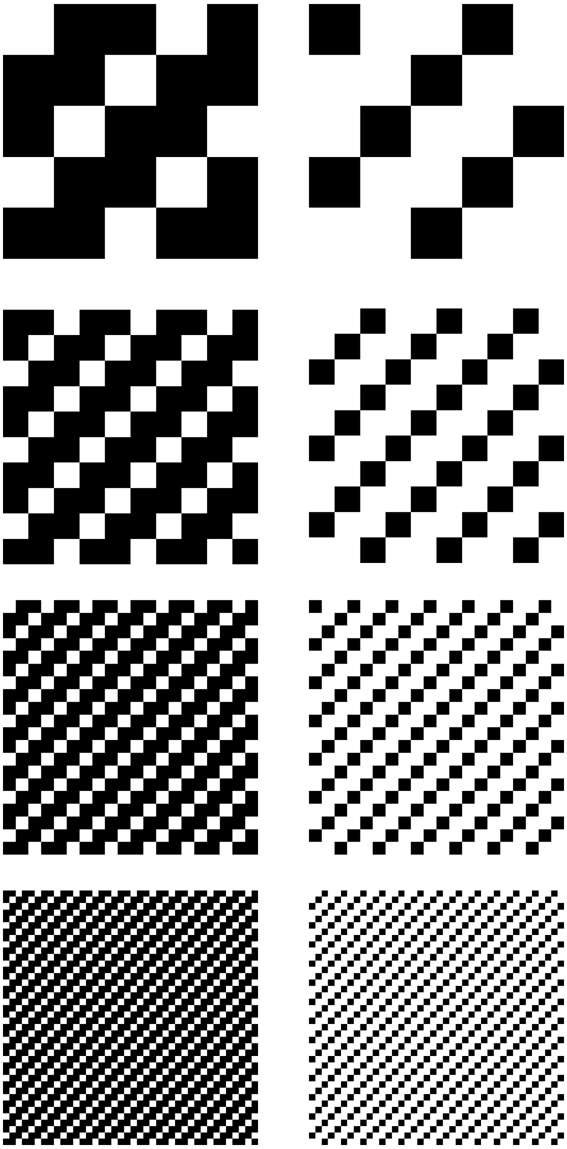

Fig. 7. Examples of the dark and light diagonal target types at the four different spatial granularities tested in Experiment 2.

made by using a 50/50 distribution of black and white elements, the relative proportion of black and white elements in the randomized background were proportionally changed to match whether the target was predominately black or white. Altogether 32 diagonal trials (16 of each type) were tested using each element size (5, 10, 20, 40 pixels, each tested four times). Testing with Experiment 1's targets and Phase 1's alternating bar targets continued in Phase 2. Testing of the four original targets was reduced from six to four times per session to make room for the novel diagonal targets in each session. Thus, each 152-trial daily session consisted of 24 alternating bar target trials, 96 original target trials, and 32 diagonal target trials. Phase 2 lasted six sessions. Following completion of this transfer testing, training was continued for an additional 75 total sessions to obtain data concerning asymptotic performance.

2.3. Results

The pigeons readily transferred to the alternating bar targets tested in Phase 1. Looking at just the results from the first test session, mean target localization accuracy for the novel vertical (100%), or horizontal orientation (97.2%) targets showed excellent transfer. Accuracy with the novel vertical (93.8%) and horizontal (91.6) targets showed no improvement over the six sessions of testing (see Fig. 8). With regards to the important issue of bar length, there was a small numerical, but statistically non-significant, effect of bar length. The shortest bar segment supported slightly lower accuracy (25 pixels = 90.2%) than the longest bar segment (100 pixels = 94.4%).

The pigeons showed a more mixed transfer response to the introduction of the diagonal targets in Phase 2. Specifically the degree of transfer was highly correlated with the spatial granularity of the display. The right panel of Fig. 8 shows accuracy for both target types combined across the first six sessions as a function of element size. When composed of elements of 5 or 10 pixel elements, the pigeons showed excellent and significant above chance transfer (binomial test), while the two larger element sizes supported very poor target localization. In fact, for the largest element size, performance was even slightly below chance upon its introduction. Part of this below chance performance was clearly tied to the proportion of black and white elements in the display. Performance was quite poor for these targets composed of large element sizes tested on the dark mixture of elements. Mean first session accuracy with the darker targets as a function of element size was 83, 67, 34, 18%, respectively, while for the lighter target these same values were 93, 67, 67, 43%. Over the first three sessions, this below chance performance moved towards chance levels of responding, but never "improved" any beyond that. A repeated mea-

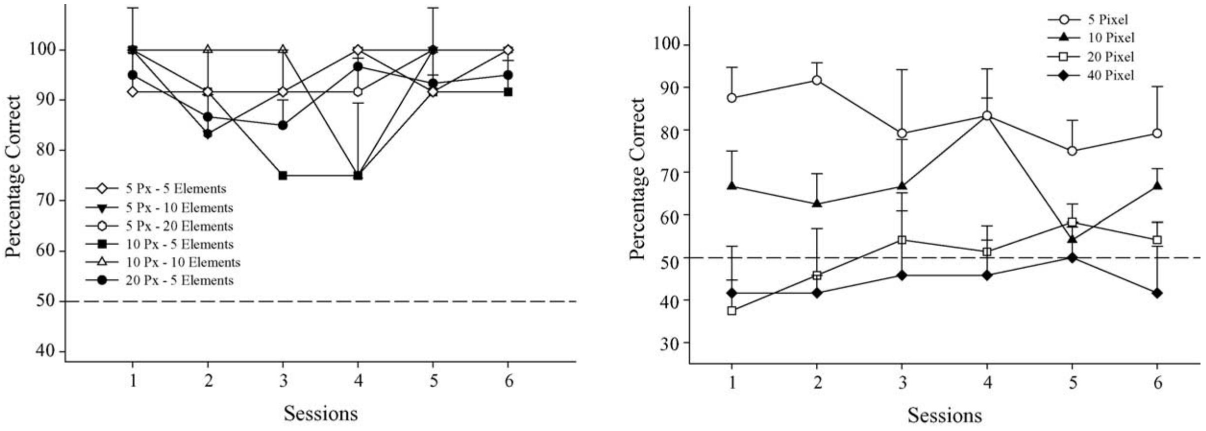

Fig. 8. The left panel displays mean choice accuracy for the alternating bar target types as function of the six sessions following their introduction. The right panel displays mean choice accuracy for the “diagonal” target types as function of the six sessions following their introduction. The dotted reference line in each panel depicts chance responding in the task.

sures ANOVA (session × target type × element size) confirmed these effects by the presence of a significant main effect of element size on accuracy, $F(3, 6) = 33.1$, and a significant triple interaction, $F(15, 30) = 2.1$, between session, target type, and element size.

2.3.1. *Steady state accuracy*

The two panels of Fig. 9 show the accuracy over the last 25 sessions of the extended training period. Accuracy with the new targets improved slightly over this period, but this effect was not large. This suggests that the performance differences between the target types are tied to the pigeons’ capacities to perceive the targets rather than to experiential factors governing the discrimination. As in Experiment 1, the pigeons were excellent at identifying the structured targets when the granularity of the display was high, with accuracy for all target types being highest in the 5 pixel condition. For all element sizes, accuracy was significantly lower with the diagonal targets than with any of the others. As the granularity of the displays decreased, accuracy gradually declined, first for the diagonal targets, then with square, checkerboard targets and alternating bar targets, followed last by the vertical and horizontal stripes.

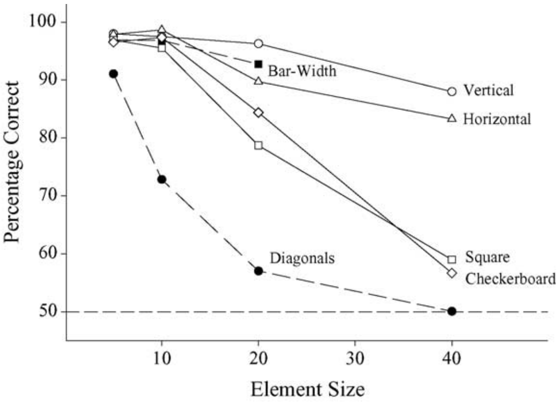

Fig. 9. Mean choice accuracy profile for the seven major target types as function across element size at the end of Experiment 2. The dotted reference line in each panel depicts chance responding in the task.

These patterns of accuracy were supported by repeated measures ANOVAs that used a combination of pairwise target type comparisons within a particular element size and target type by element size interactions to examine this issue. The results of these statistical tests can be summarized as follows: vertical striped targets supported significantly better performance over all targets out to the largest element size. This was followed closely by accuracy with the horizontal striped target. Both of these were significantly better than the alternating bar, checkerboard, and square target patterns. These latter three did not statistically differ from one another. All of the above target types were significantly better than performance with the diagonal target type. The accuracy with the lighter diagonal target type was significantly better than with darker target, but this did not significantly interact with element size.

2.4. Discussion

Both new target types supported good to excellent transfer, at least when the spatial granularity of the displays was high. Over the first six sessions, transfer accuracy was high for all targets, except in the case of the large-scale diagonal patterns. These results are most consistent with the idea that pigeons had learned some form of generalized search for non-random target structures (at least when detectable). That bar length in the alternating bar targets had little impact on accuracy suggests that recognition of extended lengths or edges of a single polarity was not the sole or critical basis for target detection in this discrimination. It also suggests that the varying number of illusory contours present in these stimuli also did not a have large impact on performance. The considerable improvement with the checkerboard target between Experiments 1 and 2 is further evidence for this conclusion.

Although perhaps not a necessary feature for target detection, the presence of extended and repeated straight edges did consistently support the best performance (i.e., the striped targets were the easiest), suggesting the salience of this feature. One possible contributor to the reduced accuracy observed with the diagonal targets in comparison to the vertically and horizontally oriented striped targets may be related to the oblique effect, in which diagonal lines tend to be harder to discriminate than vertical or horizontal ones. Like humans, pigeons have been documented to show this effect in a different setting (Donis, 1999). If this were the cause of the difference between the target types, it would be consistent with a global evaluation of target structure.

While the excellent transfer and patterns of performance between target types remain the most interesting findings of this experiment, some comment is required on the unusual below chance level of initial performance with the larger black diagonal targets. We suspect this initial bias to peck at the non-target panel had something to do with the interaction of element size and the background randomization procedure. Although brightness was an irrelevant factor in Experiment 1, the pigeons may have learned something about the average brightness of the displays. Because of chance perturbations over a limited area, background displays composed of larger element sizes (and correspondingly fewer cells) had a greater chance of a deviation from this average over a larger portion of the display than displays made from many smaller elements. As such, the birds may have been reacting to areas of the non-targets that may have had an average brightness closer to 50/50 by chance and avoiding the target area because of its fixed 66.6/33.3 brightness. Such deviations would be washed out in displays with smaller elements, allowing the global structure of these targets to emerge and control behavior. While this account applies equally well to both the darker and lighter displays, the effect seemed much greater with the darker targets for some reason. Whatever its source, it was a very transient effect lasting only two or three sessions, at which point the birds began to responding more or less at random to these large-scale displays. The pigeons struggled with diagonal targets of this size throughout testing, remaining very close to chance even after extensive training.

3. General discussion

These experiments indicate that pigeons can perceptually group and recognize a broad class of emergent perceptual structures, at least when provided with an appropriate spatial context. Against randomized backgrounds of contrasting local elements, Experiment 1 revealed very rapid localization of three of the four target types (vertical stripes, horizontal stripes, and concentric square targets) and successful, but somewhat slower acquisition with the checkerboard pattern. Experiment 2 demonstrated successful transfer to several kinds of novel target types with different arrangements (alternating bars or diagonal stripes). In both experiments, spatial granularity strongly modulated choice accuracy, with highly granular displays involving the smallest elements and most repetitive structure consistently supporting the best discrimination regardless of target organization. As granularity decreased, accuracy monotonically declined, although not to the same degree for all target types. While previous findings have shown pigeons may show a cognitive precedence or bias for local information in many discrimination settings, the present results make clear that they can also spatially integrate global information (see also Wasserman et al., 1993). This is reflected, for example, in the distinctive profiles exhibited by each target organization in response to changes in spatial scale, and contrasts with the absence of such organizational differences in Kelly et al.'s (2001) study of Glass patterns.

That spatial scale or granularity was such a critical factor in the current study has important implications for examining and comparing research that has investigated the issues of global and local perception and attention in birds. Why was this factor so important in the current experiments? The two most likely reasons are related to element size and organizational repetition. These two factors are inherently confounded in the present experiment because the smallest element sizes also allow for the greatest structural repetition per unit area. When we attempted to disassociate them in Experiment 1 by manipulating target size, the powerful effects of target size per se made it difficult to know whether size or repetition was the more important feature. Our own informal human observations hint that the number of repetitions per unit area was a key factor. Even with our greater visual angle for integrating information regardless of spatial scale, we found target detection in the low granularity displays far more difficult, especially with the complex patterns (i.e., checkerboard, square). This difficulty stemmed from the greater chance that areas of the randomized background could look more similar to these targets when fewer elements were defining it. The greater repetitive structure possible with the smaller elements eliminated this ambiguity and increased the structural signal to noise ratio of the target relative to the background. We believe that the pigeons likely suffered from the same perceptual/statistical signal detection problem of detecting degrees of visual structure against a common background of noise. For example, in the vertical and horizontal striped targets where the same size and extension of bar length defined the target in every case, the greater frequency of stripes in the smaller sized displays seems to best account for their increased detection accuracy relative to the large displays of the same type. That said, element size itself may also have been a factor. In other experiments testing random dot patterns at different distances, we have previously found that visual angle is an important factor in supporting target detection (Cook, 2001a). The smaller elements in the present displays similarly provide smaller visual angles and may have helped the birds to integrate emergent information regardless of degree of repetitive structure. While these factors still need to be disentangled, the current results clearly indicate that spatial scale is an important factor controlling how readily pigeons, and likely other animals, can integrate global information.

Because of the textured nature of these displays, it is very likely that the mechanisms responsible for the detection of these emergent target structures represent the automatic output of the early perceptual system, and not the byproduct of any higher cognitive function looking for display structure. The early visual system of the pigeon is likely specialized for edge and surface detection (Cook, 1992a,b, 1993, 2000; Cook et al., 1996). Despite being more complex than those tested in these earlier texture experiments, the discrimination of the present displays still seem best explained by the same type of grouping principles. Whereas the earlier texture experiments presented simple edges and uniform target and distractor regions, the present experiments indicate that a number of organized structures within an area can similarly support regional grouping. The performance with the checkerboard pattern is most revealing in this regard because its local and global structures are not simple—rather this target area is defined by a small-scale mosaic of element contrasts across an extended area. Despite this variation, it appears that the avian perceptual system can group these distinct elements into a single unified region. One important function of this kind of grouping in the real world would be to allow complex textured surfaces to be recognized, not just simple ones defined by extended regions of identical color or shape features.

Although contours and surfaces are an important output of the grouping system, given the organization of the present displays, another factor to consider is the potential role of spatial frequency channels. Sensitivity to spatial frequency information has been proposed to be an important factor in primate form perception and spatial vision (Campbell and Robson, 1968; DeValois and DeValois, 1988). Pigeons, too, have been shown to be physiologically and behaviorally sensitive to spatial frequency differences in oriented striped and sine wave displays (Hardy and Jassik-Gerschenfled, 1980; Hodos, 1993; Jassik-Gerschenfeld and Hardy, 1979; Nye, 1968). Consistent with the decline in accuracy with decreasing spatial granularity in the present study, most pigeon tectal cells are not as sensitive to larger spatial frequencies. Nevertheless, one way the birds may have generally detected the targets is by means of the lower spatial frequency spectra. However, outside of estimates of visual acuity in several other species (e.g., Hirsch, 1982; Reymond, 1985, 1987; Reymond and Wolfe, 1981) very little is known behaviorally about the roles of spatial frequency analyses in avian form perception. One important direction for future research will be to try and understand if and how linear and non-linear systems based on spatial frequency components may play a role in form perception in these animals and its similarity to that established in primates.

Another potentially important factor to consider is related to the potentially specialized structures and functions of the avian visual system (Husband and Shimizu, 2001; Zeigler and Bischof, 1993). Pigeons have two specialized areas or foveae in their eyes, which may serve different functions (Bloch and Martinoya, 1982, 1984; Catania, 1964; Jager and Zeigler, 1991). The frontal visual field may be specialized for binocular perception of the visual space immediately in front of the bird and has presumably evolved for myopic foraging for food on the ground. The lateral visual fields are specialized for wide field monocular perception of the visual areas to each side of the bird and have presumably evolved for predator detection and flight control (Martinoya et al., 1984). Because of the spatial proximity and central location of our stimuli, they may have been viewed with the frontal field (Goodale, 1983). While this needs to be determined empirically, if true, it would suggest that global integration, at least based on repeated fine details, is possible in the frontal field. A far better understanding of the different functions of these visual fields and their influence on the processing of information at different spatial scales is another important direction for future research.

While the detection of the emergent structures in these experiments is likely due to perceptual grouping, the subsequent identification and recognition of these targets involves elements of controlled visual search and choice behavior. On this front, the pigeons seemed relatively flexible. Upon the introduction of the new targets, and in responding to the variety of different looking targets throughout the experiments, the pigeons seemed to have learned a generalized rule that allowed them to direct behavior towards any organized area of the display, more or less regardless of its identity. Bond and Kamil (1998, 2002) have previously reported that blue jays are also able to search for structured targets against a random-noise background. Their targets were "cryptic moths" that were monochromatic and symmetrical, although each varied slightly according to a genetic algorithm. Their studies, too, showed that the jays were able to identify these variable target regions using a somewhat abstract feature such as "structure" of the "moth" target.

Nevertheless, target organization did have a role in our results. Returning briefly to Garner's (1974) rotation and reflection model which played a role in the original design of these stimuli, recall that the square and checkerboard targets are better patterns than the stripes because of their additional rotational symmetry. However, we found that the pigeons consistently discriminated the horizontal and vertical stripe targets better than the square and checkerboard. This suggests that figural symmetry was not the most important factor in recognizing these stimuli. Huber et al. (1999) have recently found that pigeons have a difficult time learning to perceive and conceptualize pattern symmetry in a somewhat similar setting. On the other hand, Swaddle and Pruett-Jones (2001) found that global symmetry could be abstracted from dot displays by starlings, although with some difficulty. Whether these symmetry results are caused by species differences in form perception remains an open question, but represents an important topic to explore further. It is a particularly important point to better understand because of the numerous findings suggesting that figural or pattern symmetry may be a critical factor in mate selection in the wild.

Acknowledgements

This research was supported by a grant from the National Science Foundation (#0316016) to R.G. Cook. K. Goto was supported by the Experimental Analysis of Behavior Fellowship from the Society for the Advancement of Behavior Analysis. The research was conducted during the K. Goto's study visit to Tufts University, supported by the Study Visit Grant by the British Psychology Society and the Experimental Psychology Society, UK. We would like to thank Taylor Johnson for her comments on an earlier draft. E-mail: Robert.Cook@tufts.edu. Reprint requests: Dr. Robert Cook, Department of Psychology, 530 Bacon Hall, Tufts University, Medford, MA 02155. Home page: www.pigeon.psy.tufts.edu.

References

Allan, S.E., Blough, D.S., 1989. Feature-based search asymmetries in pigeons and humans. Percept. Psychophys. 46, 456–464.

Aust, U., Huber, L., 2001. The role of item- and category-specific information in the discrimination of people versus non-people images by pigeons. Anim. Learn. Behav. 29, 107–119.

Barlow, H.B., 1978. The efficiency of detecting changes of density in random dot patterns. Vis. Res. 18, 637–650.

Bischof, W.F., Reid, S.L., Wylie, D.R.W., Spetch, M.L., 1999. Perception of coherent motion in random dot displays by pigeons and humans. Percept. Psychophys. 61, 1089–1101.

Bloch, S., Martinoya, C., 1982. Comparing frontal and lateral visual acuity of the pigeon. I. Tachistoscopic visual acuity as a function of distance. Behav. Brain Res. 5, 231–244.

Bloch, S., Martinoya, C., 1984. Comparing frontal and lateral visual acuity of the pigeon. III. Different patterns of eye movements for binocular and monocular fixation. Behav. Brain Res. 13, 173–182.

Blough, D.S., 1956. Dark adaptation in the pigeon. J. Comp. Physiol. Psychol. 49, 425–430.

Blough, D.S., 1957. Spectral sensitivity in the pigeon. J. Opt. Soc. Am. 47, 827–833.

Blough, D.S., 1959. Delayed matching in the pigeon. J. Exp. Anal. Behav. 2, 151–160.

Blough, D.S., 1967. Stimulus generalization as a signal detection in pigeons. Science 158, 940–941.

Blough, D.S., 1969. Attention shifts in a maintained discrimination. Science 166, 125–126.

Blough, D.S., 1977. Visual search in pigeons: hunt and peck method. Science 196, 1013–1014.

Blough, D.S., 1979. Effects of the number and form of stimuli on visual search in the pigeon. J. Exp. Psychol.: Anim. Behav. Process. 5, 211–223.

Blough, D.S., 1982. Pigeon perception of letters of the alphabet. Science 218, 397–398.

Blough, D.S., 1985. Discrimination of letters and random dot patterns by pigeons and humans. J. Exp. Psychol.: Anim. Behav. Process. 11, 261–280.

Blough, D.S., 1989. Odd-item search in pigeons: display size and transfer effects. J. Exp. Psychol.: Anim. Behav. Process. 15, 14–22.

Blough, D.S., Blough, P.M., 1990. Reaction time assessment of visual perception in pigeons. In: Stebbins, W.C., Berkley, M.A. (Eds.), Comparative Perception: Complex Signals. John Wiley and Sons, New York, pp. 245–276.

Blough, D.S., Blough, P.M., 1997. Form perception and attention in pigeons. Anim. Learn. Behav. 25, 1–20.

Bond, A.B., Kamil, A.C., 1998. Apostatic selection by blue jays produces balanced polymorphism in virtual prey. Nature 395, 594–596.

Bond, A.B., Kamil, A.C., 2002. Visual predators select for crypticity and polymorphism in virtual prey. Nature 415, 609–613.

Burgess, A.E., Wagner, R.F., Jennings, R.J., Barlow, H.B., 1981. Efficiency of human visual signal discrimination. Science 214, 93–94.

Campbell, F.W., Robson, J.G., 1968. Application of Fourier analysis to the visibility of gratings. J. Physiol. 197, 551–566.

Catania, C.A., 1964. On the visual acuity of the pigeon. J. Exp. Anal. Behav. 7, 361–366.

Cavoto, K.K., Cook, R.G., 2001. Cognitive precedence for local information in hierarchical stimulus processing by pigeons. J. Exp. Psychol.: Anim. Behav. Process. 27, 3–16.

Cook, R.G., 1992a. Acquisition and transfer of visual texture discriminations by pigeons. J. Exp. Psychol.: Anim. Behav. Process. 18, 341–353.

Cook, R.G., 1992b. Dimensional organization and texture discrimination in pigeons. J. Exp. Psychol.: Anim. Behav. Process. 18, 354–363.

Cook, R.G., 1993a. The experimental analysis of cognition in animals. Psychol. Sci. 4, 174–178.

Cook, R.G., 1993b. Gestalt contributions to visual texture discriminations by pigeons. In: Zentall, T.R. (Ed.), Animal Cognition: A Tribute to Donald A. Riley. Lawrence Erlbaum Associates, Inc., Hillsdale, NJ, USA, pp. 251–269.

Cook, R.G., 2000. The comparative psychology of avian visual cognition. Curr. Dir. Psychol. Sci. 9, 83–89.

Cook, R.G., 2001a. Hierarchical stimulus processing by pigeons. In: Cook, R.G. (Ed.), Avian Visual Cognition, available online at: www.pigeon.psy.tufts.edu/avc/cook/.

Cook, R.G. (Ed.), 2001b. Avian Visual Cognition, available online at: http://www.pigeon.psy.tufts.edu/avc/.

Cook, R.G., Cavoto, K.K., Cavoto, B.R., 1996. Mechanisms of multidimensional grouping, fusion, and search in avian texture discrimination. Anim. Learn. Behav. 24, 150–167.

Deruelle, C., Fagot, J., 1998. Visual search in global/local stimulus features in humans and baboons. Psychon. Bull. Rev. 3, 476–481.

DeValois, R., DeValois, K., 1988. Spatial Vision. Oxford, New York, NY.

Donis, F.J., 1999. The oblique effect in pigeons. J. Comp. Psychol. 113, 107–115.

Donis, F.J., Heinemann, E.G., 1993. The object-line inferiority effect in pigeons. Percept. Psychophys. 53, 117–122.

Fagot, J., Deruelle, C., 1997. Processing of global and local visual information and hemispherical specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). J. Exp. Psychol.: Human Percept. Perform. 23, 429–442.

Fagot, J., Tomonaga, M., 1999. Global and local processing in humans (*Homo sapiens*) and chimpanzees (*Pan troglodyes*): use of a visual search task with compound stimuli. J. Comp. Psychol. 113, 3–12.

Fremouw, T., Herbranson, W.T., Shimp, C.P., 1998. Priming of attention to local and global levels of visual analysis. J. Exp. Psychol.: Anim. Behav. Process. 24, 278–290.

Fremouw, T., Herbranson, W.T., Shimp, C.P., 2002. Dynamic shifts of pigeon local/global attention. Anim. Cogn. 5, 233–243.

Garner, W.R., 1974. The Processing of Information and Structure. Erlbaum, Potomac, MD.

Glass, L., 1969. Moire effect from random dots. Nature 223, 578–580.

Goodale, M.A., 1983. Visually guided pecking in the pigeon (*Columba livia*). Brain Behav. Evol. 22, 22–41.

Hardy, O., Jassik-Gerschenfled, D., 1980. Spatial organization of the excitatory regions in the receptive fields of the avian optic tectum and their spatial frequency selectivity. Brain Res. 199, 452–458.

Hirsch, J., 1982. Falcon visual sensitivity to grating contrast. Nature 300, 57–58.

Hodos, W., 1993. The visual capabilities of birds. In: Zeigler, H.P., Bischof, H. (Eds.), Vision, Brain and Behavior in Birds. MIT Press, Cambridge, MA.

Huber, L., Aust, U., Michelbach, G., Olzant, S., Lioidolt, M., Nowotny, R., 1999. Limits on symmetry conceptualization in pigeons. Q. J. Exp. Psychol. B: Comp. Physiol. Psychol. 52, 351–379.

Husband, S., Shimizu, T., 2001. Evolution of the avian visual system. In: Cook, R.G. (Ed.), Avian Visual Cognition, available online at: www.pigeon.psy.tufts.edu/avc/husband/.

Jager, R., Zeigler, H.P., 1991. Visual field organization and peck localization in the pigeon (*Columba livia*). Behav. Brain Res. 45, 65–69.

Jassik-Gerschenfeld, D., Hardy, O., 1979. Single-neuron responses to moving sine-wave gratings in the pigeon optic tectum. Vis. Res. 19, 993–999.

Julesz, B., 1981. Textons, the elements of texture perception and their interactions. Nature 290, 91–97.

Katz, J.S., Cook, R.G., 2000. Stimulus repetition effects on texture-based visual search by pigeons. J. Exp. Psychol.: Anim. Behav. Process. 26, 220–236.

Kelly, D.M., Bischof, W.F., Wong-Wylie, D.R., Spetch, M.L., 2001. Detection of glass patterns by pigeons and humans: implications for differences in higher-level processing. Psychol. Sci. 12, 338–342.

Kelly, D.M., Cook, R.G., 2003. Differential effects of visual context on pattern discrimination by pigeons (*Columba livia*) and humans (*Homo sapiens*). J. Comp. Psychol. 117, 200–208.

Kimchi, R., 1992. Primacy of wholistic processing and global/local paradigm: a critical review. Psychol. Bull. 112, 24–38.

Martinoya, C., Rivaud, S., Bloch, S., 1984. Comparing frontal and lateral viewing in pigeons. II. Velocity thresholds for movement discrimination. Behav. Brain Res. 8, 375–385.

Navon, D., 1977. Forest before trees: the precedence of global features in visual perception. Cogn. Psychol. 9, 353–383.

Navon, D., 1981. The forest revisted: more on global precedence. Psychol. Rev. 43, 1–32.

Nickerson, R.S., 2002. The production and perception of randomness. Psychol. Rev. 109, 330–357.

Nye, P., 1968. The binocular acuity of the pigeon measured in terms of the modulation transfer function. Vis. Res. 8, 1041–1053.

Phelps, M.T., Roberts, W.A., 1994. Memory for pictures of upright and inverted primate faces in humans (*Homo sapiens*), squirrel monkeys (*Saimiri sciureus*) and pigeons (*Columba livia*). J. Comp. Psychol. 108, 114–125.

Plaisted, K.C., Mackintosh, N.J., 1995. Visual search for cryptic stimuli in pigeons: implications for the search image and search rate hypotheses. Anim. Behav. 50, 1219–1232.

Pomerantz, J.R., Sager, L.C., Stover, R.J., 1977. Perception of wholes and their component parts: some configural superiority effects. J. Exp. Psychol.: Human Percept. Perform. 3, 422–435.

Reymond, L., 1985. Spatial visual acuity of the eagle, *Aquila audax*. A behavioural, optical and anatomical investigation. Vis. Res. 25, 1477–1491.

Reymond, L., 1987. Spatial visual acuity of the falcon, *Falco berigora*. A behavioural, optical and anatomical investigation. Vis. Res. 27, 1859–1874.

Reymond, L., Wolfe, J.B., 1981. Behavioural determination of the contrast sensitivity function of the eagle. *Aquila audax*. Vis. Res. 27, 263–271.

Swaddle, J.P., Pruett-Jones, S., 2001. Starlings can categorize symmetry differences in dot displays. Am. Nat. 158, 300–307.

Uttal, W.R., 1976. Visual spatial interactions between dotted line segments. Vis. Res. 16, 581–586.

Ward, L.M., 1982. Determinants of attention to local and global features of visual forms. J. Exp. Psychol.: Human Percept. Perform. 8, 562–581.

Wasserman, E.A., Kirkpatrick-Steger, K., Van Hamme, L.J., Biederman, I., 1993. Pigeons are sensitive to the spatial organization of complex visual stimuli. Psychol. Sci. 4, 226–341.

Wilson, H.R., Wilkinson, F., 1998. Detection of global structure in Glass patterns: implications for form vision. Vis. Res. 38, 2933–2947.

Zeigler, H.P., Bischof, W.F., 1993. Vision, Brain, and Behavior in Birds. MIT Press, Cambridge, MA.