
The Comparative Psychology of Avian Visual Cognition

Robert G. Cook¹

Department of Psychology, Tufts University, Medford, Massachusetts

Abstract

How do small-brained, highly mobile animals like birds so readily perceive the visual world? Despite the computational complexity of vision, recent behavioral tests have suggested that these evolutionarily distant animals may use visual mechanisms that operate in the same manner as the visual mechanisms of primates. This article reviews new evidence regarding the processes of early vision and object perception in pigeons and considers speculations about the similarities and differences between avian and primate visual cognition.

Keywords

pigeon; visual cognition; comparative psychology; texture perception; object perception

Birds are highly visual mobile animals. Vision's unmistakable importance to these creatures is reflected in both the substantial proportion of their compact brains devoted to visual processing and the huge relative size of their eyes. Birds are an important group to compare with mammals, the other major class of warm-blooded, mobile, visually dominant animals, because birds and mammals are so distant evolutionarily. When we open our eyes, we see an immediate visual world of stable, mean-

ingful, and unified objects that we are able to detect, grasp, catch, and avoid effortlessly and efficiently. Birds, too, behave as if they perceive and act upon an object-filled world. If this interpretation of their actions is correct, it creates an interesting paradox. Because of the demands of flight, birds have been under strong evolutionary pressures for the past 200 million years to keep their overall size, including their central nervous system, to a minimum. Yet if nothing else has been learned about vision, it is that vision is a demanding constructive activity requiring considerable computational prowess. Although a large portion of the avian central nervous system is devoted to visual processing, the problem is that the brains of birds are generally quite small. A pigeon's brain, for instance, is a thousandth the size of our own. It is the extraordinary mixture of visual competence and small size that makes the psychological study of birds important to our understanding of the general mechanisms of visual cognition.

The neural organization of birds is another factor that makes them of interest. Like primates, they have two major visual pathways. In birds like the pigeon, in which the eyes are placed on the sides of the head, the relative importance of these two pathways is the reverse of their importance in mammals. In these types of birds, the major visual pathway is the tectofugal pathway, which corresponds to the secondary extrastriate pathway in mammals. These birds' secondary pathway is called the thalamofugal pathway; it corresponds to the well-studied primary geniculostriate pathway in primates. Lesion studies with pigeons have found that damage to the tectofugal, but not the thalamofugal, pathway typically results in major disturbances of visual performance. This intriguing role reversal in birds suggests that neural organizations besides the one evolved and used by primates can also construct rapid internal representations of the ever-shifting pattern of object-reflected light.

One old solution to vision's complexity has been the evolution of nervous systems that respond to a limited set of features with relatively fixed responses (e.g., in amphibians and insects), but complex active animals like birds and mammals appear to possess more generalized perceptual machinery. Given their contrasting neural architectures, a natural question to ask is whether the associated psychological processes are also different in birds and mammals. One possibility is that birds and mammals have evolved different and independent solutions to the common design problems of seeing a three-dimensional world, suggesting there may be a variety of viable computational solutions to these problems. Another possibility is that mammals and birds independently evolved similar psychological solutions, but simply imple-

mented them over millions of years with different neural machinery.

Deciding between these alternatives requires that a number of interesting questions be explored. Just how similar is the visual experience of mammals and birds? Is the bird's visual world populated with distinct objects in the same way as in primates? If so, how is this type of visual experience created in birds with their limited and dissimilar neural equipment? What common and distinct rules, functions, and control mechanisms mediate visual cognition in these two classes of animals? Recently, research in my laboratory and others has tried to answer these questions by looking at the avian mechanisms of visual perception and action. The particular approach my students and I have taken has been to examine how pigeons (*Columba livia*) process visual information in laboratory tasks that allow direct comparison with the results and established principles of human perception.

MECHANISMS OF EARLY VISION AND SEARCH

We began by looking at the foundational processes of early vision and perceptual grouping in pigeons. Early vision consists of those processes responsible for taking the unrefined visual patterns from the retina and transforming them into perceptually organized groupings of edges and surfaces. Previous human research had indicated that texture stimuli were an excellent vehicle for isolating and studying these early grouping processes. Visual texture stimuli are hierarchical, multidimensional, multielement patterns in which global regions are formed from the grouping of smaller component elements (Fig. 1). These smaller elements can be distinguished by

color or shape, with combinations drawn from as many as 44 different shapes and 20 different colors in some experiments. In a typical experiment, a pigeon is trained and tested with computer-generated texture stimuli containing a small target region that has been randomly located within a larger matrix of distractor elements. The pigeon's task is to locate and peck at this target region in order to obtain food.² The dimensional arrangement of these target and distractor elements can then be manipulated to study theoretically revealing reactions to these stimuli. In now-classic studies, similar tasks demonstrated that humans can easily detect unique color or shape targets among any number of distractors (e.g., a blue *U* in a field of red *Us* and *Ts*), but have a very difficult time locating targets that are a unique conjunction of features (e.g., a blue *U* in a field of blue *Ts* and red *Us*; Treisman & Gelade, 1980). This difference between *feature* and *conjunctive* search has been a critical component to recent theoretical advances in human perception and attention. Would pigeons show this same important and fundamental perceptual effect?

We tested pigeons with different texture versions of feature and conjunctive stimuli to examine this question (Cook, Cavoto, & Cavoto, 1996). These stimuli were made from combinations of two dimensions (color and line orientation) or three dimensions (color, line length, and line orientation) and patterned directly after those tested with humans by Wolfe, Cave, and Franzel (1989). The target region of feature displays always uniquely differed along one of these dimensions. The target region of a conjunctive display was always made from an element that was a unique combination of dimensional values that were partially shared with the different types of surrounding distractors.

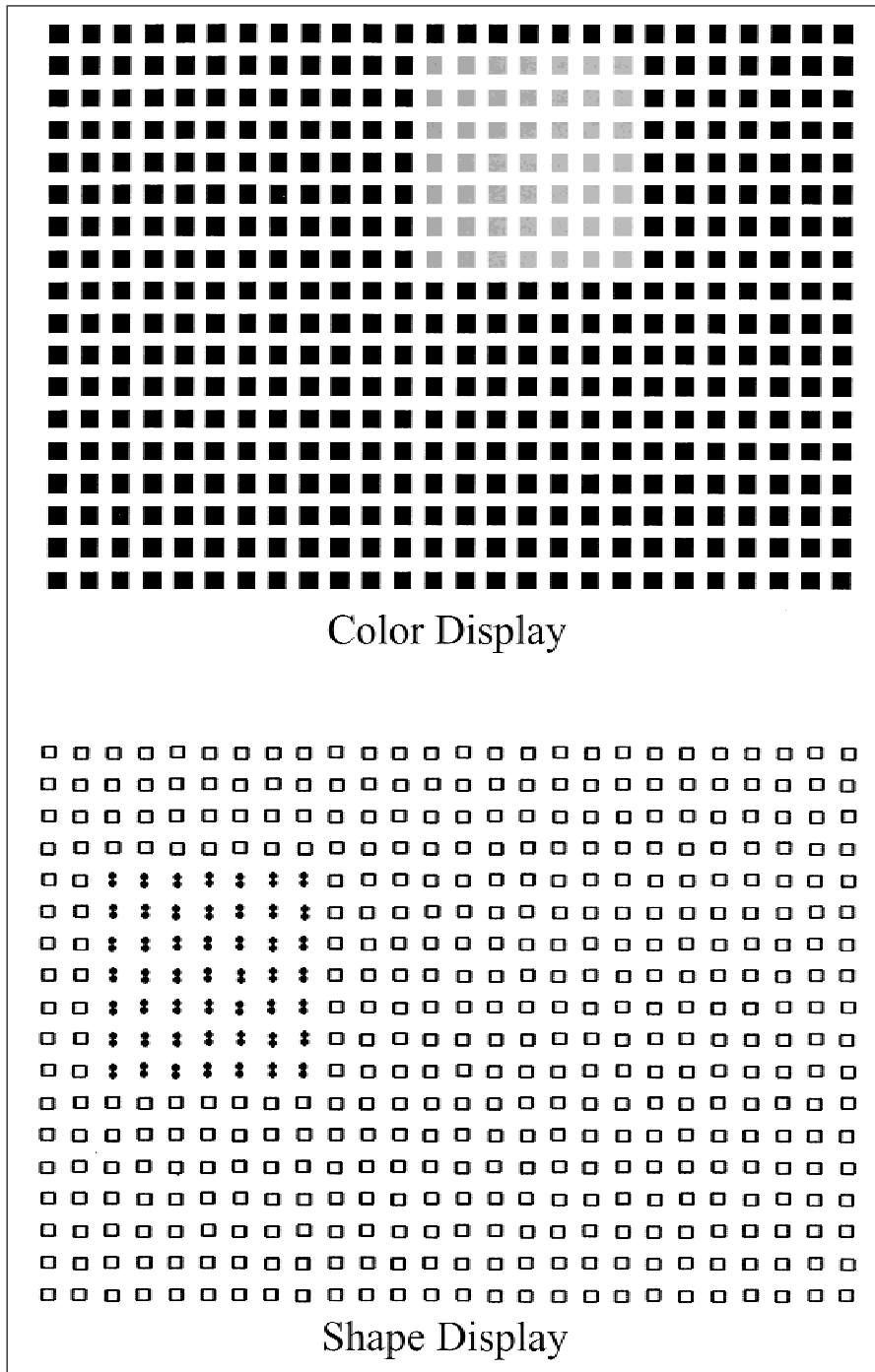


Fig. 1. Examples of color (shown here as different levels of gray) and shape texture stimuli used to train and test pigeons. The pigeons obtain a food reward if they peck at the target region (i.e., the area that is oddly colored or contains the odd shapes).

For those conjunctive targets composed from three dimensions, we also varied the number of overlapping features between the distractors and the unique element forming the target.

We found that pigeons, like hu-

mans, varied in their search efficiency depending on the display's arrangement. The pigeons were best at localizing targets in feature displays, and the pattern of search exhibited for the different conjunctive arrangements was identical to that

of humans (Fig. 2). We also found that, as in humans, increasing numbers of distractors hurt conjunctive performance, and irrelevant dimensional variation did not interfere with feature search (e.g., variations in element size or orientation within a display did not hurt searches for a color-defined target).³ To the extent that these displays and the similar behavioral reactions by pigeons and humans directly reveal underlying processing, one can conclude that the early visual registration and search processes of these distinct species are organized in a comparable fashion.

Rapidity is one of the hallmarks of perceptual grouping in humans. Using a modified rapid serial presentation procedure, in which the pigeons are tested with odd-item texture stimuli that rapidly change their colors within a trial, we have also examined the speed of these avian grouping mechanisms (Cook, Cavoto, Katz, & Cavoto, 1997). For example, for the first 100 ms, the target might have been red squares on a background of green squares, but then the squares might have changed to blue and brown, respectively, for 100 ms, and then to orange and white, to maroon and pink, to cyan and yellow, and so on until the target was located (see Fig. 3, top panel; real-time examples are available at www.pigeon.psy.tufts.edu/jep/blink/). In order to localize these constantly mutating targets, the pigeons needed visual processes sufficiently fast to partially determine the target's location within a single pair of colors.⁴ We found that the pigeons performed at above chance levels even when the entire display changed color every 100 ms (display-variable condition in Fig. 3), a time highly comparable to that established for human texture discrimination. We also included conditions in which only the target or distractor region changed colors

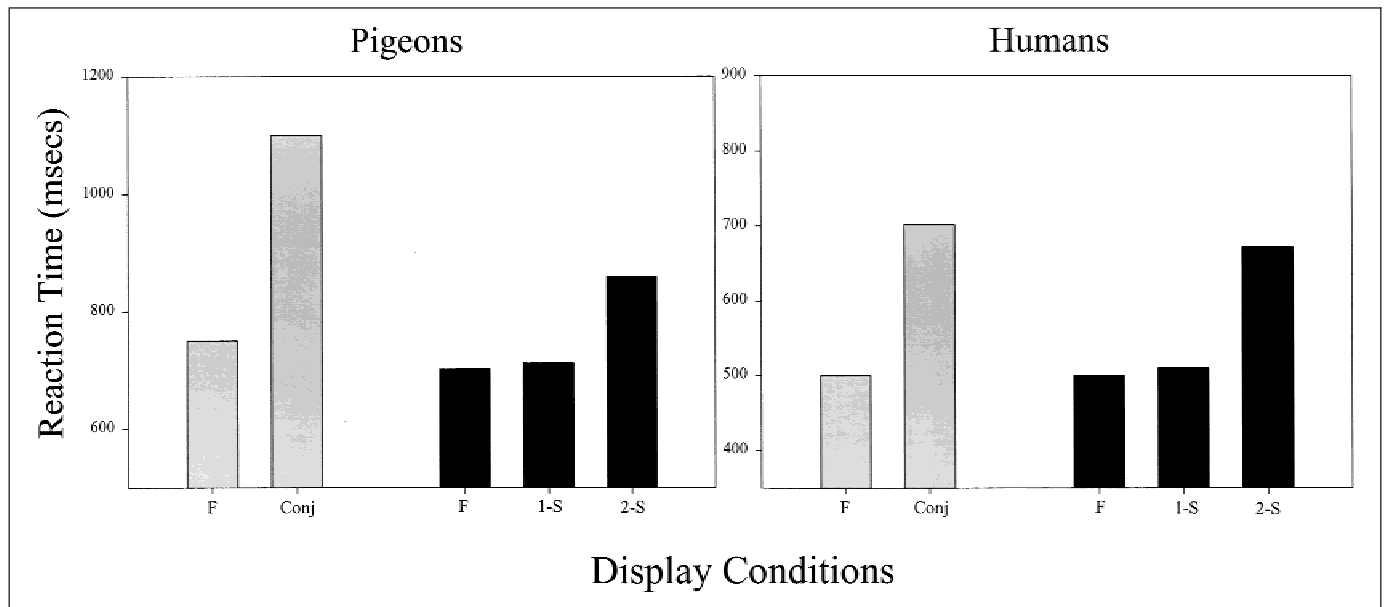


Fig. 2. Mean reaction times (RTs) in visual search tasks with pigeons (left panel) and humans (right panel). The gray bars show results for feature (F) and conjunctive (Conj) displays composed from two dimensions. The black bars show results for feature (F) and conjunctive displays composed from three dimensions (1-S = one feature of the target was shared with each distractor; 2-S = two features of the target were shared with each distractor). The left panel shows mean RTs for 6 pigeons trained and tested with texture stimuli organized to mimic the feature and conjunctive visual search displays Wolfe, Cave, and Franzel (1989) used to test humans. These data come from sessions in which one target had been repeatedly tested. The right panel shows mean RTs adapted from Experiment 9 of Wolfe et al. (1989). The data for the conjunctive displays were selected from test conditions with the maximum number of distractors (32) tested. Wolfe et al. did not test corresponding feature displays in their experiments, but a reasonable RT estimate for these feature conditions can be inferred from their conjunctive tests involving the smallest number of distractors. Such an estimate is justified based on numerous human visual search experiments demonstrating that feature conditions typically show the fastest recorded RTs in an experiment and RT does not vary as a function of the number of distractors for such conditions. Note the slight difference in RT scale between the panels. The pigeon data were adapted with permission from "Mechanisms of Multidimensional Grouping, Fusion, and Search in Avian Texture Discrimination," by R.G. Cook, K.K. Cavoto, and B.R. Cavoto, 1996, *Animal Learning and Behavior*, 24, p. 160. Copyright 1996 by the Psychonomic Society. The human data were adapted with permission from "Guided Search: An Alternative to the Feature-Integration Model for Visual Search," by J.M. Wolfe, K.R. Cave, and S.L. Franzel, 1989, *Journal of Experimental Psychology: Human Perception and Performance*, 15, p. 431. Copyright 1989 by the American Psychological Association.

within a trial. In the target-variable condition, in which color changes were spatially coincident with the target's location, a significant facilitation in localization accuracy was found in comparison to a static baseline condition (Fig. 3, bottom panel). This facilitation may be yet another similarity, the automatic attraction of the pigeons' attention to transient visual changes in a manner resembling stimulus-driven attentional capture. In humans, this latter mechanism is proposed to involuntarily direct attention to those areas of a display where attributes such as abrupt stimulus onsets, abrupt offsets, novel objects, or large changes in luminance have just occurred.

Our results to date suggest that the visual mechanisms for processing texture information in pigeons and humans are highly analogous, despite the differences in the size and organization of their visual systems. Our collective evidence suggests these early visual mechanisms in birds are fast, sensitive to edges, influenced by the similarity and proximity of the texture elements, and organized into separate channels for different types of dimension information, and that these properties are computed simultaneously over a wide area of the frontal visual field. The similarity of this list to known characteristics of human early vision is perhaps not surprising, given that

these mechanisms likely evolved to serve the same critical function of rapidly locating and identifying object boundaries and surfaces.

OBJECT PERCEPTION IN BIRDS

We have recently extended our investigations to examine how the edge and surface information presumably derived from these early visual mechanisms comes to form the more complex perception of objects, motion, and their intrinsic combination. Our conclusions regarding this issue are more ten-

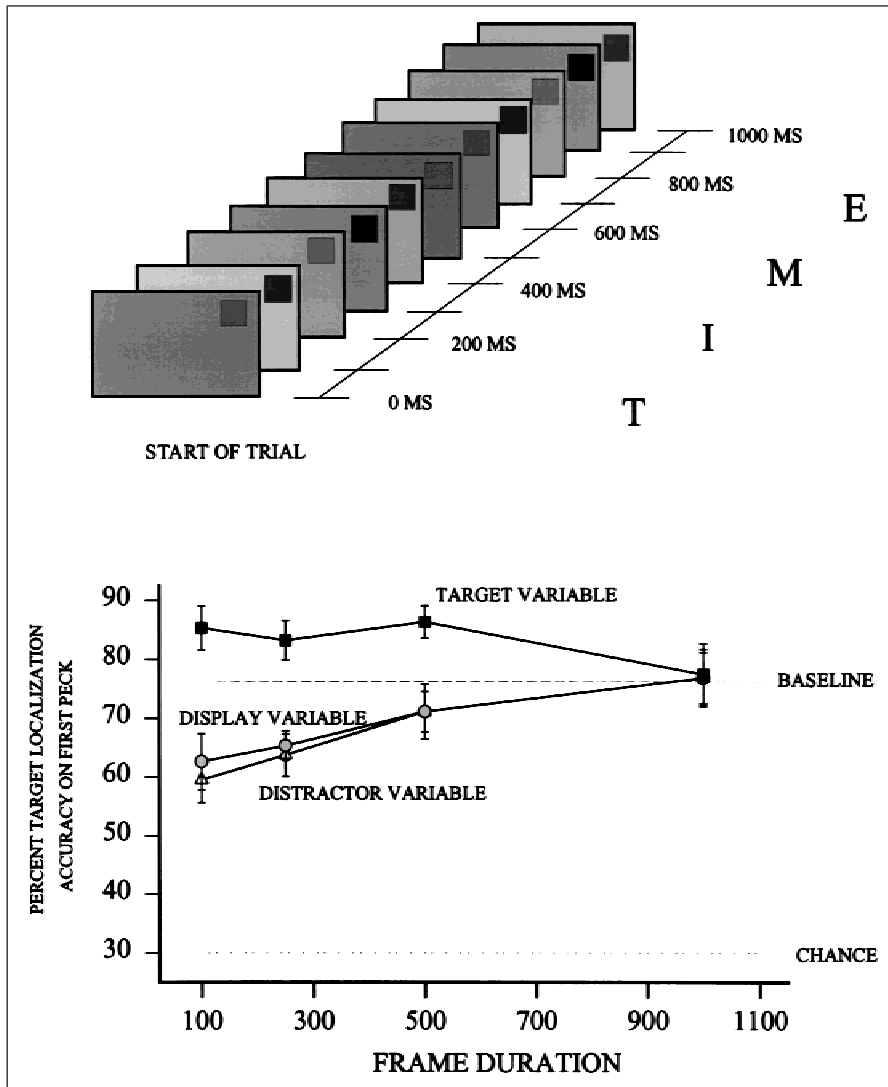


Fig. 3. Stimuli and results from experiments testing rapidly changing texture displays. The top panel illustrates a sequence of display changes over the first 1,000 ms for a condition in which the colors of the target and distractor regions changed every 100 ms (the display-variable condition). In this illustration, the target and distractor regions have been filled in with different gray levels to represent the 12 different randomly selected colors used on each trial. In addition, the actual displays were composed of smaller repeated elements, as shown in Figure 1. Each of the first six frames showed an entirely different display, and then the displays were repeated in order. In the target-variable and distractor-variable conditions (not shown), either six differently colored target regions or six differently colored distractor regions, respectively, were presented across successive frames. Four different frame rates were tested (100, 250, 500, and 1,000 ms). The lower panel shows the accuracy of locating the target on the first peck to a display for each of the three conditions at each frame rate. Adapted from "Pigeon Perception and Discrimination of Rapidly Changing Texture Stimuli," by R.G. Cook, B.R. Cavoto, J.S. Katz, and K.K. Cavoto, 1997, *Journal of Experimental Psychology: Animal Behavior Processes*, 23, pp. 395–396. Copyright 1997 by the American Psychological Association.

tative, but we have found some similarities between humans and pigeons.

In one experiment, we taught pigeons to discriminate between

computer-generated three-dimensional projections of cubes and pyramids (Cook & Katz, 1999). These object stimuli were then presented on each trial either dynami-

cally rotating around one or more of their axes or in a static position at a randomized viewing angle. Pigeons were rewarded for pecking in the presence of only one of the objects. Tests with different rotational and featural transformations of the stimuli suggested the pigeons may have been using a three-dimensional perception of these objects as the basis for their discrimination. For instance, the pigeons' performance was consistently better with the dynamic presentations than the randomly oriented static views. Further, performance was relatively unaffected by transformations in object size; the rate, direction, and combination of motions; and changes in surface color of the stimuli (at least in the dynamic condition). Lastly, 3 of the 4 pigeons tested also showed some evidence of recovering the structure or shape of these objects from just the pattern of their motion on the display. When all contour and surface information was removed in test conditions, leaving only the rigid projective geometry of the moving objects to guide performance, these birds were again better at discriminating the dynamic stimuli. That is, the birds behaved as if they saw the structure of a cube or pyramid even when really only a blob of a single color moved in a manner as if one of these objects were rotating on the screen. When these test objects were static, the birds apparently had a harder time seeing this three-dimensional shape and thus more poorly discriminated between the two objects. From this one set of experiments, it appears that pigeons may have some higher-level similarities with humans, as the experiments show some capacity for recognizing objects across different transformations and deriving structural information from the pattern of an object's motion.

CONCLUDING COMMENTS

Avian visual cognition is a rich source of information about compact visually intelligent systems. This review has emphasized the behavioral, and presumed mechanistic, similarities between pigeon and human visual cognition. It is important to keep in mind, however, that differences clearly do exist and will need to be understood before there is any final accounting of this species comparison. Pigeon color vision, for instance, involves at least four different types of cone receptors in the retina, whereas humans use three. Pigeons can also see ultraviolet and polarized light, which may play crucial roles in homing and mate selection, whereas humans cannot. Pigeons generally integrate information from a wider visual field, and often do so using two separate specialized fovea-like areas within each eye (each of these areas may be specialized for different visual functions; see Zeigler & Bischof, 1993). Humans have only one fovea (a dense region of the retina specialized for high-resolution vision) in each eye. Further, some behavioral experiments have suggested that pigeons and humans may use different sets of visual primitives, or features. Pigeons do not, for example, show differences in the speed of their visual search for certain kinds of feature reversals in the same way as humans do (Allan & Blough, 1989). Finally, pigeons may even be superior to humans in their capacity to mentally rotate visual information, as they show no increase in reaction time when judging the identity of stimuli presented at increasingly different angular orientations, whereas humans do (Hollard & Delius, 1982).

Much remains to be done to complete this comparative puzzle. Among the key issues to investi-

gate in the near future are the details and mechanisms of object, motion, and scene perception in birds, both while they are on the ground and during flight (the latter being virtually unexplored at this point); the role of attention in the control of their visual processing; and the general relation between these various behavioral processes and their specific neural substrates. Nevertheless, consider the implications of the preceding evidence suggesting that human and avian visual cognition share some operational similarities. For instance, if the essential problems of being a mobile organism in an object-filled world can be readily solved by a brain the size of a thumb (i.e., as in birds), then why do humans have such a large absolute volume of their brains devoted to visual information processing? One simple answer is that humans do something more than birds do. Perhaps it is the human capacity for mental imagery that is responsible for the difference. Mental imagery is a demanding function that birds might possess to a lesser degree, if at all. This is not to say that pigeons cannot recall visual information; their long-term reference memory is prodigious. But what they may not be able to do is actively perform mental operations (transform, compare, plan actions) on these memories like humans can.

It has also been suggested that the numerous visual areas of the primate brain add improvements to basic visual function, such as faster processing; specialized processing of object identity, human faces, or location; enhanced capacity to identify objects from different viewpoints (something pigeons are not particularly good at); or improved control of attention. Although many of these add-ons would be advantageous to birds, the evolutionary price may simply be too high. Distinguishing those visual functions or processes

shared by these two groups of animals from those that are distinct to each class will continue to be an important area for future investigation.

In conjunction with comparative research involving insects, amphibians, mammals, and computers, the study of avian visual cognition will help scientists develop a unified theory of perception and action. In addition to the important psychological and comparative implications of studies of avian cognition, such studies may yield significant practical benefits. Birds may hold the key, just as they did with the inspiration and solution for flight, to engineering self-guidance systems for small robots and compact prostheses for the visually impaired.

Recommended Reading

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Notes

1. Address correspondence to Robert Cook, Department of Psychology, Tufts University, Medford, MA 02155; e-mail: rcook1@emerald.tufts.edu. Additional information about this research can be found at www.pigeon.psy.tufts.edu and in the upcoming cyberbook *Avian Visual Cognition*, currently being edited by the author (online, fall 2000).

2. All stimuli are shown on a computer monitor located behind a clear glass panel in the front wall of the test-

ing chamber. Pecking responses are detected by means of an infrared touch screen. Mixed grain is delivered by a food hopper in the front wall and is used to reward correct responding.

3. Some researchers have speculated whether conjunction detectors might be created if an animal is given sufficient experience in such a visual search task. In unpublished observations, we have found that even following 1 year of daily testing with feature and conjunctive displays, the performance differences between these conditions never disappear, suggesting that extensive experience cannot create a conjunction detector, at least in pigeons.

4. Several additional notes about this procedure are in order. First, infor-

mation about the target's location likely did accumulate over the succession of frames. But even for this to occur, the relevant calculations for detecting the target's location had to be completed within the temporal constraint of a single frame. Second, we included test conditions to examine whether the rapidly shifting colors fused to produce new emergent colors that controlled performance. No evidence of this was found.

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