

## Birds, Brains, and Visual Behavior: The Comparative Psychology of Perception

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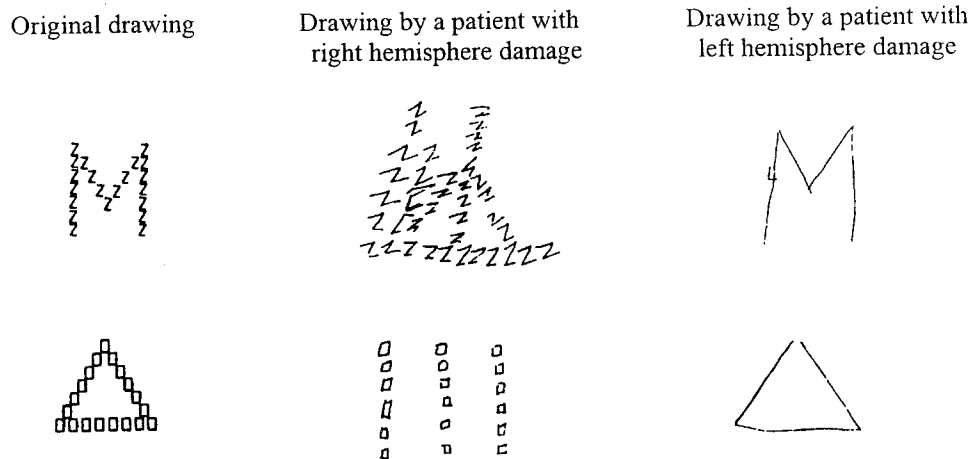
It seems so effortless to see. People open their eyes and an accurate picture of the world appears. When a person reaches out to lift a book from a table, the person knows its size, shape, and location immediately and precisely. People's ability to perceive distance, depth, and motion makes it possible for them to do things like drive a car and hit a baseball. But these visual activities are not always so easy for some.

Consider the case of a 43-year-old woman who had a stroke that damaged part of her visual cortex. After this, she reported that she no longer could see objects if they were in motion. Although visually normal in many other respects, she found it hard to follow conversations because she couldn't see other people's mouths moving; flowing liquids would look solid; and objects, like people and cars, would disturbingly appear here and then there. Engaging in any well-practiced skill involving motion, such as driving a car, was simply out of the question.

People with brain damage experience loss of visual function and perception in various ways, including the impaired sight of objects in motion in the case example above. People with another type of brain damage have difficulty seeing the global form of the things they are looking at. These people with damage to a certain visual area in the right hemisphere of the brain have trouble "seeing the forest for the trees." They cannot discern the overall form of a collection of visual elements. People with specific damage to the left hemisphere of the brain, however, have the opposite problem. They have difficulty seeing the individual elements in a collection, seeing instead only the global organization. When asked to draw the hierarchically arranged stimuli such as those shown in the left column of Figure 16.1, a person with right-hemispheric visual damage draws only the individual elements but does not reproduce the global form of the pattern, whereas a person with left-hemispheric damage draws only the global pattern but not the local elements composing it (Delis, Robertson,

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**Figure 16.1.** Drawing from two individuals with right- and left-hemisphere damage. Asked to reproduce exactly the figure on the left, each person was able to reproduce only the local elements (middle column) or the global form (right column) depending on the nature of their brain damage. From "Hemispheric Specialization of Memory for Visual Hierarchical Stimuli," by D. C. Delis, L. C. Robertson, and R. Efron, 1986, *Neuropsychologia*, 24, Figure 1. Copyright 1986 by Elsevier Science. Adapted with permission.

& Efron, 1986). Try to imagine living in a world where motion could not be perceived or where the details or overall shape of an object was perceived as a jumble or not at all. Injuries to the visual areas of the brain often result in these and other forms of visual agnosias (disorders of object perception in which certain visual functions are impaired; many of these are described in Farah, 1990) or cortical blindness (the absence of visual perception). As the above cases point out, the intricacy and importance of the brain to visual perception become evident when this neural machinery fails to operate as designed.

Can such brain damage or disorders of the perceptual system be corrected? After all, eyeglasses can easily correct for the acuity problems caused by the lens of the eye. Could a neural implant or computerized prosthetic mimic or reproduce the visual functions that have been lost as a result of damage to the brain? We know, for instance, that direct electrical stimulation of the brain causes patients to report flashes of light. Could a small computer be fashioned to simulate "seeing" for these individuals? Such cortical implants have been attempted on a very limited basis, but the resulting "vision" has been of low resolution.

The major reason for this is that from the brain's perspective, the apparently effortless act of seeing is far from a simple task. Basic research with humans, animals, and computers over the past few decades has clearly established that visual perception and its associated cognitive processes are among the most demanding activities a computational machine, be it a brain or a computer, can perform. For instance, computer scientists

working on machine vision have discovered that writing a program to accurately and rapidly perceive the world is far more difficult than programming a computer to be a world-class chess player, for instance. This is because everything people visually perceive begins with the two-dimensional and ever-shifting patterns of light falling on their eyes. This ambiguous information is then transmitted to the brain, which in a truly astounding bit of neural wizardry constructs in its entirety the detailed, organized, and dynamic three-dimensional world people experience (Hoffman, 1998). The major stumbling block to building a vision machine is that people are only just beginning to unlock how the brain actually computes this trick of the light (for a current summary, see Palmer, 1999). One potentially fruitful approach, of many, for this type of basic research is to collect information about the nature of perception in a biological system that already possesses many of the desirable features one would like in a visual prosthetic, such as small size, speedy operation, and high resolution.

Next time you walk outside, we invite you to appreciate a remarkable feat of visual cognition that flies by you everyday in the behavior of the birds above and around you. These highly mobile, warm-blooded creatures not only effortlessly fly across open spaces but can easily navigate the visual tangle of limbs in any forest. Birds are rightly renowned for their visual prowess (the inspiration for the term "eagle-eyed"). Because of their use of muscle-powered wings to get about, birds have been subjected to strong evolutionary pressure over the last 200 million years to keep their overall body and brain size small. A pigeon's brain, for example, is 1/1000th the size of a human brain and organized in a fundamentally different way. Nevertheless, a small bird like a chickadee has no problem visually navigating through the woods, avoiding collisions with small limbs, and then landing on them without mishap—and all with a brain not much larger than the tip of a human finger. It is this remarkable and paradoxical combination of small size and excellent vision that makes birds of interest to comparative psychologists.

The adept nature of avian visual behavior raises some interesting and challenging questions concerning perception and cognition. How do birds see so well with such limited neural machinery? Do they share the same perceptual world that humans do? Do they similarly encode the world as "objects?" Are the mechanisms responsible for their sight different from those of humans or are they basically organized in the same way? These and related questions constitute the foundation for the basic animal research described later in this chapter. The particular focus of our research is directed at understanding the mechanisms of visual cognition in pigeons (*Columba livia*) and their comparative relation to visual cognition in humans (Cook, 2000; Cook, Katz, & Cavoto, 1998). We hope this chapter increases your appreciation for how a comparative approach advances the study of visual cognition, how it fits into the larger framework of basic psychological science, and how it contributes in the long term to human welfare.

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### Comparative Cognitive Research

Comparative cognition research with animals is an integral constituent of modern psychological research. It adds important theoretical and empirical information about the evolution, development, and mechanisms of cognition that could not be obtained from the exclusive study of humans. Take the human use of language, for instance. It clearly did not spring fully formed at the dawn of hominid evolution. Rather, it must have been built on the cognitive precursors that were already operating in some form in our primate ancestors, who in turn built on processes inherited from their mammalian progenitors. Because neither behavior nor the soft tissues of the brain readily fossilize, the comparative examination of the genes, brains, and behavior of living animals is our best tool for reconstructing the origins and evolution of cognition (Allman, 1999; Shettleworth, 1998).

The psychological study of animals is also critical to dissecting the contributions of the environment and genetics to cognitive functioning, as researchers can control the past experience of animals and, increasingly, the structure of their DNA. Despite the recent excitement over advances in human brain imaging, the study of animals remains the best avenue for examining in detail how the brain generates behavior as well. Furthermore, particular animals or groups of animals provide researchers valuable opportunities to model specific behaviors, study them in new ways, or look at them from insightful new perspectives. It is in this latter light that we have been concentrating on studying avian visual cognition and its special contribution to understanding how small, mobile biological systems can process the visual environment around them.

The research in our lab takes the approach of examining how pigeons process visual information in tasks that permit direct comparison with the results and established principles of human perception. Our immediate objective is to better understand the mechanisms of behavior in these highly visual, but distantly related, creatures and to determine the extent to which these mechanisms are the same or different from our own. The direct outcome of this comparative research will be to inform us about the range and types of perceptual systems that are possible and how they function. For instance, one possibility is that birds and mammals have evolved independent solutions to the common design problems of seeing a three-dimensional world. This kind of answer would suggest that there are a variety of different and viable computational solutions to the general problem of vision. In addition, any such evolved solutions in birds might provide us with novel, different, or more efficient ways of processing visual information. These latter considerations might be valuable in constructing a working visual prosthetic, for instance. Another possibility is that birds and humans have independently evolved similar psychological solutions to the problems of vision but simply implemented them over millions of years with different neural machinery (see Marr, 1982, for more on the important distinction between the representation of a problem and its physical implementation). This kind of answer would suggest that there may be only a few efficient ways to successfully build a flexible perceptual

system because of the implicit constraints of the visual environment in which birds and mammals mutually evolved (Shepard, 1984). Either of these comparative outcomes is critical to developing a truly general theory of perception.

Although it is not the direct goal of our specific research program with pigeons, we believe the collective examination of these extraordinary animals, in conjunction with ongoing basic research involving humans, other animals, and computers, can provide essential clues as to the best way to build small artificial visual systems in the future. This is because basic research into avian visual cognition is a rich and immediately available source of information about the perceptual and cognitive requirements and operations of an existing, sophisticated, small visual system.

Recently, there has been a greater clamor for publicly funded research to be clearly applied in its nature. In this view, scientific research should always be seeking a specific solution to a human problem as its primary goal. This applied research approach can be contrasted with the motivations of a basic research approach, which is more theoretically oriented and not necessarily always conducted with a direct human application as its immediate or primary objective. Such basic research is increasingly viewed with suspicion and is frequently suggested to be a potential waste of tax dollars. Although the short-term benefits of supporting applied research is a highly commendable objective and has easy political appeal, doing so at the exclusion of basic research misses a crucial point about the nature of the scientific process, the development of knowledge, and its role in advancing human welfare.

It is important to remember that the solution to any problem consistently draws on a mixture of both old and new knowledge. At any moment, it is the supply of established knowledge that is the major limiting factor in developing remedies or solutions to a particular problem. Over the past century, the vast majority of this knowledge has been and continues to be developed by doing basic research in the laboratory. For instance, any effort to curb global warming will need to draw on years of prior basic research conducted in such diverse, and sometimes seemingly unrelated, fields as oceanography (e.g., the effects of El Nino), psychology (e.g., the study of environmental decision and policy making), and paleontology (e.g., the measurement of ancient temperature and oxygen conditions by the chemical composition of fossilized sea shells), as well as the obvious weather sciences. It is no different in the behavioral sciences. Building the visual image processing devices envisioned in the first part of this chapter will be an interdisciplinary effort that will likely draw on basic research from microengineering, computer science, neural computing, animal cognition, human perception and vision science, cognitive neuroscience, and genetics.

Because the scope and complexity of any major scientific problem is very large, it necessitates that it be broken down into its parts to seek a solution. This division of labor results in scientists working on only smaller, but more manageable, portions of any larger research puzzle. One outcome of this requirement is that any superficial description of a re-

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search problem can appear nonsensical at first glance, especially when the entire framework or proper background for viewing its contribution is not included. One of the goals of this book is to provide exactly this framework in understanding the benefits of using animals in biomedical and psychological settings.

The discovery of new knowledge emerges from a complex interaction of different factors, ranging from appropriate education, the rigors of the scientific method, advances in technology, competition among scientists, to simple serendipity. The majority of important scientific discoveries have been the direct product of individual scientific creativity and the free and imaginative exploration of the unknown. Thus, basic, as well as applied, animal research deserves to be supported. Together, these two research approaches can bring about fundamental and positive changes that directly benefit us and the biodiversity of the world we inhabit. But it is important to keep in mind that they do so in fundamentally distinct ways and on different time scales. Supporting basic research is much like a long-term investment in the stock market. The current fad in day trading makes for excitement and occasional immediate wealth (or poverty), but it is the patience of long-term investing that consistently returns value many times over.

In one sense, the study of avian visual cognition is one such investment. It is part of a long-term effort dedicated to understanding some of the most fundamental aspects of behavior, the nature of perception, learning, and action. In fact, the research advances described in this chapter would not have been possible without the prior basic research in animal learning and behavior supported earlier in this century. It is hoped the legacy of the current work will be to engender new ideas, experiments, and advances by future scientists that will eventually solve the mysteries of perception, whether in humans, pigeons, or machines. Our current research goals are far more humble, however, as we continue to pursue the painstaking task of understanding the pigeon's visual behavior in our various laboratory tasks. The remainder of this chapter highlights just some of our recent advances in this area to give readers a better idea of the kind of experiments we conduct.

### **The Comparative Psychology of Visual Perception**

We began our research a number of years ago by looking at the foundational processes of early vision and perceptual organization in pigeons. Early vision consists of those processes responsible for taking the unrefined visual patterns from the retina and transforming them into perceptually organized groups of edges and surfaces. These edges and surfaces in turn become the building blocks for the more complex perception and recognition of objects. Experiments with humans have shown that visual textures are an excellent vehicle for studying these types of preattentive (i.e., not requiring focused attention) and spatially parallel operations that occur early in the stream of visual processing. Texture stimuli are multi-

dimensional displays in which global regions are formed from the grouping of repeated local elements (see Figure 16.2). Studies using such texture stimuli have found that humans' visual systems are able to group similar color and shape features into regions and then quickly segregate them at their boundaries or edges.

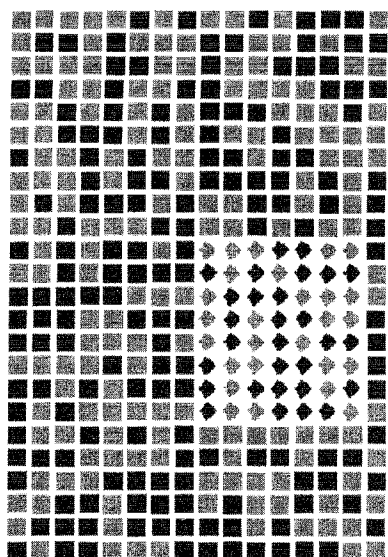
For instance, humans' visual system should have no problem segmenting the top two stimuli in Figure 16.2 into two distinct areas and then locating the smaller bounded area within each one. Research has found that people can easily segregate such *feature* stimuli whenever there are consistent groupings of either color (left stimulus) or shape (right stimulus) features used to make the different regions (Treisman & Gelade, 1980). This is because these different features are perceptually grouped in separate dimensional channels early in the recognition of surfaces. When stimuli are made that violate this dimensionally consistent organization, it becomes much harder to visually segregate the regions of such displays. Look at the texture stimulus in the lower left of Figure 16.2. Believe it or not, it has a small odd region just like the two above, but it is much harder to see (the light circles and dark triangles in the lower left part of the display), and even when it is found, the edges of this target are still not easily connected or maintained. The reason for this is that such *conjunctive* texture stimuli are made from regions formed by the unique combination of elements that require the simultaneous combining of information from both dimensions. This requirement acts to prevent them from being perceptually grouped by the dimensionally tuned channels of the human visual system. Instead, a slower more focused attentional process is required to accurately process these kinds of stimuli. This significant difference in the human ability to perceive feature and conjunctive stimuli has been a critical component to recent advances in the theoretical understanding of human perception and attention.

Would pigeons show the same pattern of discrimination for feature and conjunctive stimuli? If they did, such an outcome would suggest that their early visual system is organized in the same way as the human system. If not, it would suggest that a different set of early visual processes is at work in birds. To investigate this question, we conducted a series of experiments that used feature and conjunctive stimuli in a texture-based visual search task (Cook, 1992; Cook, Cavoto, & Cavoto, 1996). Using many different examples of computer-generated feature and conjunctive stimuli like those in Figure 16.2, we tested pigeons taught to locate and peck at any odd target region in a texture stimulus (see the bottom-right cutaway drawing of the test chamber in Figure 16.2). Whenever such an odd target was correctly "pointed out" by a pigeon, it was reinforced with a food reward. Pigeons easily learn to perform this type of "target" localization task.

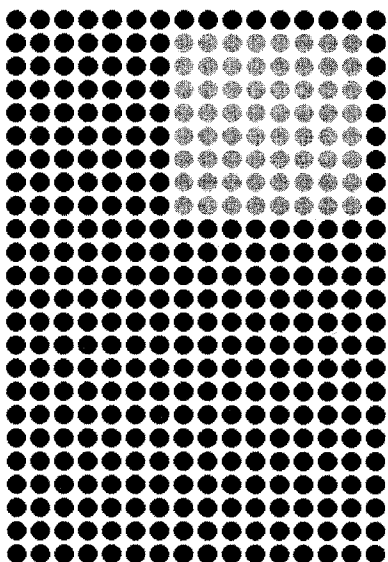
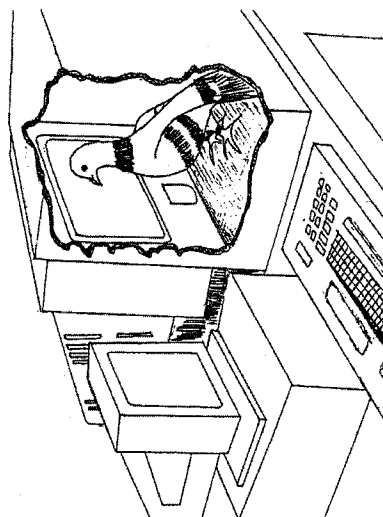
We then varied the feature and conjunctive arrangement of the elements to examine how the pigeons would respond to these manipulations. We found that the pigeons' efficiency in finding the target regions depended directly on the display's feature and conjunctive organization. Just like humans (Wolfe, Cave, & Franzel, 1989), the pigeons were best at lo-

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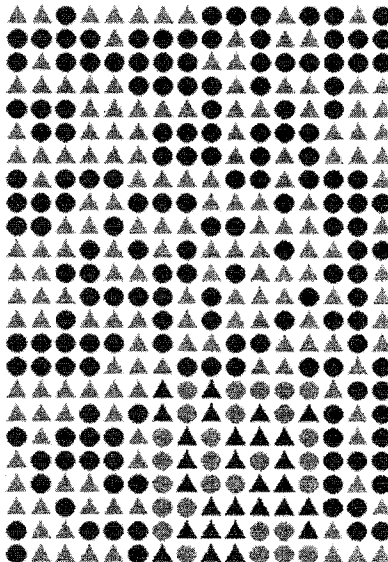
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cating targets in feature displays and poorest at finding them in conjunctive displays (Cook, 1992; Cook et al., 1996). By manipulating variables such as the number of surrounding distractors and the presence or absence of irrelevant dimensional variation, we then established a number of additional similarities in how humans and pigeons process these types of displays. In total, these outcomes and those of other allied experiments have suggested that the processes of perceptual grouping and search in humans and pigeons share many commonalities.

Once a behavioral outcome like the above is discovered and established, researchers can then proceed to study its physiological basis in the brain. Recently, we have been conducting experiments, in collaboration with Dr. Toru Shimizu of the University of South Florida, in which small controlled lesions have been made to different parts of the pigeons' visual nervous system to examine how it affects their texture perception. Pigeons and humans are similar in having two major visual pathways, but for birds like the pigeon (in which the eyes are located on the side of their heads) the relative importance of these visual pathways is reversed to what has been established for primates (for more details, see Zeigler & Bischof, 1993). We have found from this lesion research that perceptual grouping, as measured by performance with these textured stimuli, is performed in a different part of the brain in birds than in primates. This is particularly intriguing because the behavioral results suggest that the operation of the psychological mechanisms underlying texture perception are highly similar in these two groups of animals. This combination of results from behavioral and physiological studies suggests that the apparently similar mechanisms of early visual processing in humans and pigeons have independently evolved in response to the common environmental need of rapidly detecting object boundaries and surfaces.

In addition to our work on perceptual organization, we have also been looking at the more difficult topic of object perception in pigeons (Cook & Katz, 1999; Cook, Shaw, & Blaidell, in press). The results of these exper-

**Figure 16.2.** Representative examples of feature-color, feature-shape, and conjunctive texture displays used to test pigeons and humans. These displays are composed from four elements composed from combinations of two shapes and two colors. The feature-color and feature-shape labels refer to displays in which the two regions are grouped according to one of the two dimensions (color or shape). The conjunctive display is made from similar combinations of elements but is designed to make both dimensions (color and shape) relevant to finding the target. The colors and shapes used to make these displays were randomly changed each trial when testing the pigeons. The different colors in these stimuli are represented in this figure by different levels of gray. The bottom right panel shows a cutaway drawing of the operant chamber used to test the pigeons. The birds view a computer screen through a glass window in the front of the chamber. Pecks to the stimuli presented on this screen are detected with an infrared touchscreen that can tell us where and when a pigeon pecks on each trial. A food hopper, located just below the viewing window, is used to deliver mixed grain to the pigeons as a reward for correct responding.

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iments are more provisional but so far have shown some important similarities to prior human results. In one experiment, we used computer-generated three-dimensional objects that dynamically rotated in space to examine three-dimensional processing and motion processing in pigeons (Cook & Katz, 1999). The objects we used were computer-generated depictions of three-dimensional cubes and pyramids. These were presented to the birds at a random orientation and either did not move (static condition) or rotated around one of their axes (dynamic condition) on the computer screen. The birds then had to peck consistently at one of the objects (e.g., the cube) when it appeared to obtain food reward while not pecking at the other object (e.g., the pyramid). After learning this "go-no go" discrimination, the pigeons were tested with different rotational and featural transformations of the objects to study their perception and discrimination of these stimuli. We found that, like humans, birds discriminated the objects better when they were rotating dynamically than when presented standing still. Furthermore, this object discrimination was invariant across transformations in the size, rate, direction, and combinations of motion, as well as changes in the object surface color in the dynamic presentations. Such invariance is the hallmark of human object perception and tentatively suggests that pigeons might also experience an object-filled world.

The research reviewed above has emphasized the behavioral similarities between pigeon and human visual cognition. But it is important to point out that other studies have suggested that some differences may exist between these two species. For instance, pigeons can see ultraviolet light, humans cannot. Pigeons have two separate, specialized fovealike areas within each eye (each of which may also be specialized for different visual functions; see Zeigler & Bischof, 1993), whereas humans have only one in each eye. Furthermore, some behavioral experiments have hinted that pigeons may not use the same set of visual primitives or features as humans in processing some types of tasks (Allan & Blough, 1989; Van Hamme, Wasserman, & Biederman, 1992). It may even be that pigeons are superior to humans in their capacity to mentally rotate visual information (Hollard & Delius, 1982).

### Conclusion

Much remains to be done to complete this interesting and unsolved comparative puzzle. Our research has only scratched the surface of this question, and many problems and issues remain to be explored by future scientists. The comparative research looking at the processing of global and local attributes in complex figures like those described in the introduction, for instance, currently contains a number of conflicting outcomes from pigeons, nonhuman primates, and humans that still need to be resolved (Cavoto & Cook, 2001; Deruelle & Fagot, 1998, Fagot & Deruelle, 1997; Fagot & Tomonaga, 1999; Fremouw, Herbranson, & Shimp, 1998; Hopkins, 1997). Such continuing issues and problems always stand as an open in-

vation to join this or any scientific community and become part of this important human enterprise and adventure. We hope we have provided in this chapter some insights into the rationale for studying avian visual cognition and how it directly advances the effort to construct a comprehensive theory of perception and visual cognition.

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