The Analysis of Visual Cognition in Birds: Implications for Evolution, Mechanism, and Representation

Robert G. Cook[1], Muhammad A.J. Qadri and Ashlynn M. Keller
Department of Psychology, Tufts University, Medford, MA, USA
[1]Corresponding author: E-mail: Robert.Cook@tufts.edu

Contents

Abstract

How complex visual systems function to produce internal representations of the world has been one of the enduring questions in cognitive science. Because of their different evolutionary paths, birds and mammals have evolved to use dissimilar portions of their central nervous systems to mediate their visual navigation of the world. The visual excellence of each of these major groups of vertebrates, in combination with these contrasting implementations of vision, creates a special opportunity to isolate and compare the algorithms and representations mediating visual cognition in each of these groups. Here, we describe the results of experiments testing pigeons and starlings designed to investigate this question. We review the results relevant to two important topics within visual cognition. It is suggested that the early visual mechanisms of birds and primates share a strong resemblance to one another. In particular, it may be that each group of animals has evolved to initially decompose early visual

information into independent streams along comparable sets of visual features. At later stages of processing, the examination of the mechanisms underlying the processing of local and global aspects of object perception suggests that there may be important differences in regards to how birds and primates integrate such hierarchical information.

1. INTRODUCTION

One only has to step outside to see one of the remarkable marvels of nature, the rapid and controlled flight of birds. While the act and physiology of muscle-powered flight is fascinating, that birds also readily see and visually navigate the world whether on the wing or the ground has important scientific implications. Vision itself is another marvel of evolution. How the eye and brain make sense of the reflected light from the surfaces of objects has been one of the most stimulating, enduring, and difficult problems in cognitive science. This is because of the numerous computational complexities, ambiguities, and difficulties involved with the processing of visual information. Combine the demands of vision with those of flying, and the diminutive size of the avian brain, and the beauty of birds in flight turns into a compelling puzzle. How is such visual excellence implemented in the small brains of these striking animals? What exactly is the bird's eye view?

To answer these questions, my laboratory examines the mechanisms and functions of avian visual cognition using a variety of discrimination learning approaches. We compare these perceptual and cognitive investigations with those obtained from other visual systems, most frequently those of equally visual primates. We have been focused on birds and mammals because they represent the two major classes of visual, mobile, social vertebrates that have evolved on this planet. Beyond these common attributes, they each represent the zenith of visual cognition within their respective evolutionary lineages. Both of these classes of animals are typically diurnal and appear to use objects as the principal basis for visually interacting with the world. While many insects are visually sensitive, they interact with the world at a different spatial scale than that inhabited by birds and mammals (Lunau, 2014; Srinivasan, 2010; Srinivasan, Poteser, & Kral, 1999; Srinivasan, Zhang, Berry, Cheng, & Zhu, 1999). Despite the unquestioned importance of the visual modality to birds (e.g., the large relative size of their eyes), the severe weight restrictions of muscle-powered flight and its evolutionary pressure have markedly limited the overall absolute size of birds. In response, over

the last 100 million years of evolution, birds have independently evolved small visual and central nervous systems that appear to be efficient and powerful. For example, it is still beyond our capacity to build a visually directed autonomous robot or implanted prosthesis that remotely approximates a small bird's ability to navigate a forest canopy. Understanding how they have solved the inherent problems of vision, and how their solutions compare with those found in mammals, makes for a revealing and important comparison. Consequently, birds are a ready, important source of information about the psychological and neural mechanisms of cognition in a visually sophisticated, small, and contrasting biological system (Emery, 2006; Lazareva, Shimizu, & Wasserman, 2012; Marder, 2002; Smulders, 2009; Zeigler & Bischof, 1993). The capacity of birds to learn a wide variety of visual discriminations, with an established body of knowledge on their basic behavioral processes and central nervous system, makes them an excellent and tractable model system for the investigation of visual cognition (Cook, 2001; Soto & Wasserman, 2014).

There is one important difference between birds and mammals that is not as widely appreciated, but makes their psychological comparison even more interesting. Birds' similar visual behaviors are mediated by different portions of their central nervous systems. In modern birds and mammals, there are two major ascending homologous pathways from the retina that have evolved within the basic design of the vertebrate nervous system (Jarvis et al., 2005). These are called the collothalamic and the lemnothalamic pathways (for clarity these are frequently referred to as the tectofugal and thalamofugal pathways, as well). Current evidence indicates that the primary pathways mediating vision are different for birds and mammals. Birds rely on the collothalamic pathway, while mammals rely on the lemnothalamic pathway. This divergence in their neural organizations has significant implications for developing any general theory of vision and visual cognition. The origins of this difference trace back to our contrasting evolutionary histories.

The original development of image-forming vision is one of the key innovations in the success of vertebrates both before and after their emergence onto land. Of the land groups of specific interest to this paper, birds and mammals last shared a common ancestor about 300 million years ago at the end of the Paleozoic Era (Shimizu & Bowers, 1999). At this point, the lineage of tetrapod stem amniotes splits into separate major evolutionary lines that eventually become modern-day birds and mammals over millions of years (see Figure 1). These contrasting routes begin with two groups
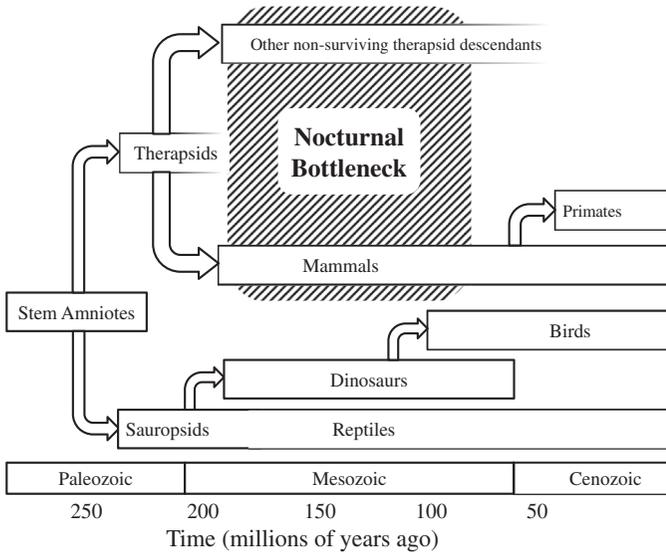
Figure 1 Evolutionary pathways and timeline of mammals and birds.

distinguished by differing characteristics such as their head anatomy. The therapsids evolved over the Triassic Period, and one group of their several descendants eventually became mammals (Rubidge & Sidor, 2001). Distinct from this lineage, the sauropsids evolved into the reptiles and dinosaurs that dominated the Mesozoic Era. Members of both of these sauropsid and therapsid groups had previously developed eye sockets, with many species well equipped for active predatory behavior, suggesting that vision was already an important and established modality in these early tetrapods. While knowledge of their brain structures and organization of these groups is limited from the fragmentary fossil record, the tectum and dorsal thalamus, which are shared in common by these groups, seem to be the most important brain structures mediating vision and controlling their interactions with the world.

Approximately 150 million years ago, during the Mesozoic, one group of dinosaurs began to evolve into the animals that we now recognize as birds. Both recent and past fossil evidence indicates that birds are the direct descendants of highly visual theropod dinosaurs (Alonso, Milner, Ketcham, Cookson, & Rowe, 2004; Corwin, 2010; Lautenschlager, Witmer, Altangerel, & Rayfield, 2013; Sereno, 1999). The major radiation of modern bird species, however, did not occur until after the Cretaceous extinction event. At this point, the avian brain reached its basic shape and size. Inferences from the

comparative anatomy of modern reptiles and birds indicate that these early birds were still using the same visual brain organization as their ancestors, relying primarily on the optic tectum and associated telencephalic structures to mediate their diurnal visual behavior. The greater demands of flight, however, represented new visual and attentional challenges for this system. Not surprisingly, there have been corresponding increases in the relative size and complexity of the avian tectum in comparison to reptilian groups.

The evolutionary story of vision within the mammalian lineage is more complex. The therapsids that survived to become mammals appear to have undergone an extended period of evolution as nocturnal animals over the time that dinosaurs were the dominant land animals. This "nocturnal bottleneck" hypothesis proposes that mammalian vision was strongly shaped by this period, which caused numerous modifications to the visual structures of mammals' diurnal therapsid ancestors (Gerkema, Davies, Foster, Menaker, & Hut, 2013; Goldsmith, 1990; Heesy & Hall, 2010; Walls, 1942). During this period there was a much greater emphasis placed on audition and olfaction as the primary means for gathering information. Because the relative importance of vision was reduced, this extended nocturnal period impacted mammalian vision in several ways. For example, it produced a greater reliance on binocularity and reduced the contribution of color vision in order to increase light sensitivity. It also caused a shift to a reliance on the lemnothalamic ascending pathway as the primary means of mediating vision, especially in primates (Aboitiz, Montiel, Morales, & Concha, 2002; Heesy & Hall, 2010). One speculative benefit of this shift is that the alternate pathway allowed for a slower, deliberate, and more detailed analysis of visual information in its cortical mechanisms as opposed to the immediate and more action-oriented functions typical of control by tectal mechanisms. This critical change in the identity of the major visual pathway in mammals resulted in a number of additional changes with the subsequent mammalian radiation. The evidence indicates a subsequent growth in the number of cortical areas associated with processing visual information (Homman-Ludiye & Bourne, 2014; Kaas, 2013). With the increase of these anatomically distinct areas, primates began to dedicate a considerable amount of cortical tissue to visual processing, presumably to aid in critical activities such as foraging. Additionally, the capacity for detailed color vision—lost in the "nocturnal bottleneck"—reemerged in some mammals, including primates.

Thus, these contrasting evolutionary stories through the Mesozoic resulted in lasting differences in the structural portions of the central nervous

systems responsible for mediating vision in these two groups of modern animals. Both groups have two ascending pathways that are involved with processing visual information and attention. Figure 2 is a highly simplified diagram of these pathways. In birds, the collothalamic pathway ascends from the retina to the optic tectum, to the nucleus rotundus, and terminates in various subdivisions of the entopallium. Evidence from lesion and physiological studies indicates that this pathway is the major avenue for processing visual information. The homologous collothalamic pathway in mammals ascends first to the superior colliculus, then to the pulvinar, and then to a variety of cortical extrastriate areas. The different names reflect a time before the modern recognition of their homology (Reiner et al., 2004). The processing of visual information in this pathway in mammals appears to be complex, but secondary. The primate superior colliculus is strongly involved with the control of eye gaze and saccadic motions, for example, while the pulvinar is critical in the computation of visual salience (Petersen, Robinson,
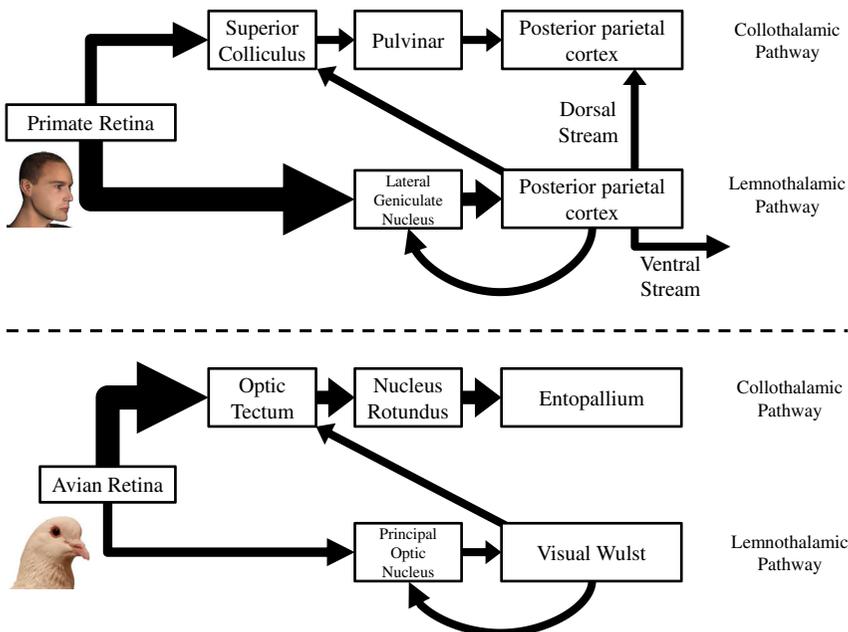

Figure 2 Comparative neuroanatomy of the two major ascending visual pathways in birds and primates. The top panel shows the major central nervous system structures found in primates. The bottom panel shows the homologous visual structures in birds. The width of the line from the retina toward each pathway depicts the relative importance to primary visual perception in each of these animal groups.

& Morris, 1987; Robinson & Petersen, 1992). This pathway jointly termi-
nates with the other pathway in cortical extrastriate areas often associated
with the hypothesized dorsal visual stream of the lemnothalamic pathway.
Nevertheless, the major pathway for vision and object recognition in mam-
mals is the well-studied lemnothalamic pathway. This major path goes from
the retina to the lateral geniculate nucleus of the thalamus before proceeding
to an extensive number of higher cortical visual structures related to object
perception and recognition. Birds have a homologous lemnothalamic
pathway that terminates in the visual Wulst, but the exact visual function
of this second pathway in birds is not well established. Lesions of the visual
Wulst, for example, typically have little or no impact on visual behavior or
performance. Given the similarities in their visually guided behavior and the
need to solve the same set of visual problems, it is interesting that birds and
mammals have evolved different portions of their central nervous systems to
mediate vision. This creates special opportunities for scientific study.

Marr (1982), in his classic book on vision, suggests a useful framework for
conceptualizing a situation where the mechanisms of visual cognition are
implemented in different systems. He suggests that understanding complex
information processing can be accomplished by looking at its nature across
three different explanatory levels: the computational, algorithmic, and
implementational levels. The computational level is concerned with the
determination of the goal or purpose of the processing. At this level, it is
clear that each of these classes of animal needs rapid and accurate information
about the nature and location of objects for navigating and organizing their
ongoing interactions with the world. Thus, the computational goal of their
respective visual systems is directly comparable: quickly determine what is in
the visual world and where it is located. The implementational level is at the
other end of Marr's explanatory spectrum, and it is concerned with the phys-
ical hardware of a system. In birds and mammals, the visual neuroanatomy
used to implement these higher level computations is clearly different.
This leaves us with an opportunity to isolate and examine Marr's middle
level of explanation related to the algorithms and representations involved
with these calculations, but as implemented in different extant biological sys-
tems. Are the algorithms and representations involved in the visual cognition
of these groups the same or different? If birds and mammals are similar, are
they similar across the different levels of visual processing from initial feature
detection to final scene perception? Where might they differ and why? Is it
because of the nature of how birds and mammals have evolved over time,
related to their contrasting natural histories, or do they differ because of

constraints in the actual neural hardware in which they are implemented? When they do differ, what costs or benefits to the veridicality of the representation of the external world do these different solutions come with?

To explore these questions, we have been actively using discrimination learning procedures to explore the bird's eye view of the world. For the majority of this research, pigeons (*Columba livia*) have proven to be an excellent and worthy research animal for us. Given the established knowledge on their basic behavioral processes and central nervous system, the pigeons' ability to learn discriminations based on a wide array of different visual properties has made them a major focus species for the study of complex perception and learning in comparative cognition (Cook, 2001; Honig & Fetterman, 1992; Spetch & Friedman, 2006; Zeigler & Bischof, 1993). The pigeon's visual system is by far the best understood of any bird species or other nonmammalian vertebrate (Cook, 2001; Lazareva et al., 2012; Zeigler & Bischof, 1993).

We have recently expanded our investigations to include a common, medium-sized, passerine species, the European starling (*Sturnus vulgaris).* They are a visual, diurnal, ground-feeding bird that forages for invertebrates by probing the upper soil surface with their long bills (Feare, 1984). The addition of a passerine bird species has been important because it ensures that our results are more representative of birds as a larger class and are not limited to any specializations specific to the dominant pigeon model. Passeriformes and columbiformes (the phylogenetic order in which pigeons belong) diverged during the Cretaceous Period between 70 and 120 million years ago according to genetic estimates (Brown, Rest, Garcia-Moreno, Sorenson, & Mindell, 2008; Chojnowski, Kimball, & Braun, 2008). A multivariate analysis of the brain composition suggests that passeriformes and columbiformes also seem to have evolved dissimilar cerebrotypes, with different relative proportions of cerebellum, brain stem, and telencephalic regions, including the relative area devoted to vision (Iwaniuk & Hurd, 2005). Since passerines are the largest order of birds, they are more frequently studied than many columbids with regards to many other aspects of bird behavior, outside of vision. Our knowledge about how passerines process complex visual information is surprisingly limited, beyond peripheral sensory mechanisms related to the eye, its anatomy, various psychophysical sensitivities, and visual field organization (Endler, Westcott, Madden, & Robson, 2005; Hart, 2001; Jones, Pierce, & Ward, 2007; Martin, 2007; Zeigler & Bischof, 1993). As a result, the testing of starlings adds an important new piece to the overall puzzle of understanding avian visual cognition.

We test the sensory and cognitive capacities of these species using operant discrimination procedures. Using stimuli that isolate different aspects of visual processing, we have examined a variety of different stimulus discriminations. The pigeons are tested in standard operant chambers in which stimulus displays are presented on a computer monitor and the pigeons' pecking responses to them are detected by touch screens located in front of the monitor. The pigeons are typically tested for 1 h each day and discriminate stimuli for food reward.

Because of their smaller size and more active nature, the starlings are tested with the same stimuli, but with a slightly different procedure. In our apparatus, attached to an otherwise normal starling cage, is a freely accessible testing chamber, which is similar to the pigeons' operant chamber. The starlings are typically tested using a choice procedure in which two stimuli are presented on the computer monitor, and the starlings indicate their choice by conditionally perching on the right or left side of the chamber depending on the location of the correct stimulus. Like the pigeons, they receive food reward for responding correctly. Unlike the pigeons, the starlings live continuously with their apparatus and engage in the discrimination to obtain all of their daily food intake. These different testing procedures required of each species appear to have little impact on their evaluation of the stimuli, however.

This chapter highlights several of our past and recent investigations of visual cognition with these two species as it compares to nonhuman primate and human visual processing. We specifically focus on two domains. The first highlights early vision. Early vision is the group of processes involved with the initial detection of visual features and their organization into useful information related to edges, surfaces, and their spatial relations to each other. The second domain examines questions related to the visual and attentional processing of emergent information at different levels of spatial organization, looking at how the global and local aspects of visual stimuli are detected, integrated, and eventually control the birds' discriminative behavior. We selected these two areas because they reveal contrasting aspects of the multifaceted puzzle that is comparative visual cognition.
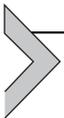
2. COMPARATIVE PSYCHOLOGY OF EARLY VISION

One of the important initial stages of visual cognition focuses on a collection of processes frequently labeled as early vision. This stage is conceptualized to consist of a set of bottom-up, spatially parallel, preattentive

processes that act to take sensory and dimensional features of different types and rapidly transform them into perceptual groups of edges, regions, and surfaces (Beck, 1982; Grossberg, Mingolla, & Ross, 1997; Marr, 1982; Palmer, 1999). The spatial and depth relations of these derived edges, regions, and surfaces eventually become the foundations for the subsequent higher order perception and recognition of both objects and organized scenes. One prominent assumption in these operations is that the visual system has a number of parallel and independent visual channels often organized in topographic representations that divide and then re-"bind" these different aspects of visual input (Barrow & Tenenbaum, 1978; Broadbent, 1977; Green, 1991; Kaas, 1997; Livingstone & Hubel, 1988; Treisman & Gelade, 1980). We started our investigation into avian visual cognition by seeking evidence of similar early visual processes in birds.

2.1 Dimensional Grouping Processes in Pigeons

One means of exploring this question in birds grew out of Treisman's research looking at the organization of visual search in humans. She and her colleagues found that unidimensional ("feature") displays in which the target and distractors differed along a single dimension supported rapid and parallel visual search, while conditionally defined multidimensional ("conjunctive") displays required slower, successive scans, and focal attention to identify targets (Treisman & Gelade, 1980). These differences in *feature* and *conjunctive* search implied that multiple processes were involved in finding these targets. Treisman suggested that feature processing involved the immediate preattentive processing of the contrasting visual features in different dimensional maps, while conjunctive displays required a second process involving the serial application of focal attention to then combine these maps and accurately detect conjunctively defined targets (Treisman & Gelade, 1980; Treisman & Gormican, 1988; Treisman & Sato, 1990). While the initial human studies used visual search paradigms, a useful extension of her theoretical ideas involved comparably organized textured fields of repeated elements that were well suited for testing with pigeons.

For this purpose, we developed an oddity-based target localization task to investigate the processing of different kinds of texture stimuli with pigeons (Cook, 1992a, 1992b; Cook, Cavoto, & Cavoto, 1996; Cook, Cavoto, Katz, & Cavoto, 1997). Texture stimuli are a type of hierarchical stimulus in which a larger global pattern is extracted from a large matrix of elements based on featural properties of the smaller elements, and they are effective at isolating the processes associated with early vision (Beck,

1982; Bergen & Adelson, 1988; Julesz, 1981). Studies of texture stimuli in humans have found that we can quickly group elements with similar color and shape features into global spatial regions and then rapidly segregate them at their boundaries or edges in order to begin establishing figure–ground relations within a scene. The key to this rapid segmentation in humans seems to depend on whether these regions and edge relations can be readily detected within separate dimensional channels. When stimuli that violate such a dimensionally consistent organization are created, the embedded targets are much harder to visually segregate. Examples of this can be seen in the texture stimuli in Figure 3, which are similar to those tested with pigeons. The top pair of stimuli shows examples of shape and color feature
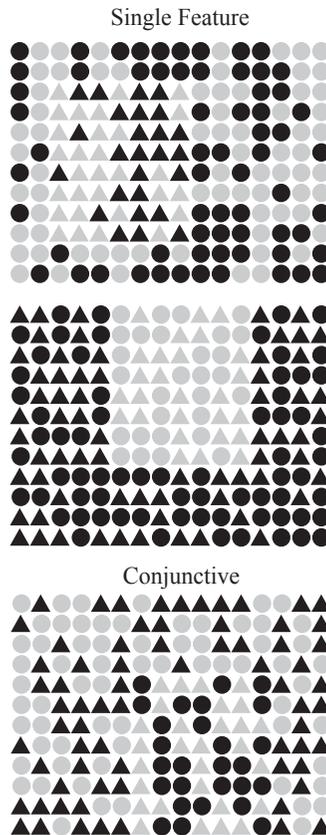

Figure 3 Representative examples of feature (shape and color) and conjunctive texture displays tested by (Cook, 1992c). The pigeon's task for each display was to find the odd target region.

displays defined by differences in a single dimension, with irrelevant and random variation in the values of the orthogonal dimension. The targets in these displays are easy to locate and the "edges" created at the boundaries of the two regions readily discernible. On the other hand, the conjunctive display has target and distractor regions created by the unique combination of features across these two dimensions. As a result, the target in this type of display is difficult to find, and even once identified, the boundary between the two regions is never visually distinct.

In a typical experiment using this approach, the pigeons were trained and tested with computer-generated texture stimuli containing an odd "target" region that was randomly located within a larger matrix of dissimilar "distractor" elements. The pigeon's task was to locate and peck ("point") at this odd target region to obtain food. We used texture stimuli dynamically generated from large collections of different colors and shapes that could be randomly combined to support this oddity-based target detection response. Testing many different stimuli of this basic design, we investigated how quickly and accurately pigeons could localize targets that were defined by featural differences in color and shape; or by their configural combination (Cook, 1992b); or with more controlled differences in color, line orientation, and size, as well as their combination (Cook et al., 1996). The results of these experiments were clear. The pigeons were both more accurate and faster at detecting feature targets than conjunctive targets across a wide variety of conditions, just like humans (e.g., Wolfe, Cave, & Franzel, 1989). Besides this feature superiority effect, we also established that pigeons and humans showed comparable benefits from the redundant combination of dimensional information, while exhibiting no interference from the additional presence of irrelevant dimensional information. This qualitative set of similarities strongly suggests that the early visual processing of information leading to dimensionally defined groups or regions, as captured by these stimuli, is likely organized in comparable ways in pigeons and humans.

Since then, newer research has shown that critical functions needed for accurate target localization in texture stimuli resides in the collothalamic pathway of the pigeons (Cook & Hagmann, 2012). In collaboration with Dr. Toru Shimizu, we lesioned the nucleus rotundus, visual Wulst, or the anterior or posterior portions of the entopallium in different groups of pigeons. These pigeons were already trained to perform the textured target localization task, so we looked for selective decreases in their accuracy following damage to these different brain structures. The pigeons with

nucleus rotundus lesions showed consistent and large post-lesion deficits in their prior capacity to accurately locate color and shape targets in textured arrays. They also showed no recovery of this capacity when extended testing was provided. After very poor performance during initial post-lesion testing, the pigeons with anterior entopallium lesions showed limited re-covery, but never achieved their pre-lesion levels of performance. These deficits were not related to any motor functions required for target locali-zation, since all of these pigeons retained their ability to start each trial by locating and pecking the ready signal on the monitor. Thus, these two important brain regions within the collothalamic pathway are critically important in the accurate processing of texture stimuli by the pigeons. The pigeons with posterior entopallium lesions revealed a slightly more complex story with no decline in color performance, but they showed a slight, yet significant, decline in shape accuracy. The latter result suggests that there may be functional differences in the entopallium (Nguyen et al., 2004). The pigeons with Wulst lesions within the lemnothalamic pathway showed no decrements, continuing to locate color and shape tar-gets at their pre-lesion levels.
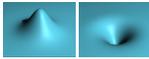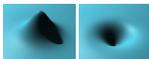
Collectively these results indicate that the collothalamic pathway is crit-ically involved in the processing of textured stimuli by pigeons and likely contains the hypothesized visual streams required to perceive the regional dimensional differences in the display. Studies have shown that the nucleus rotundus of pigeons, for example, provides input to the entopallium along several distinct anatomical streams (Benowitz & Karten, 1976; Hellmann & Güntürkün, 2001; Shimizu & Bowers, 1999). This outcome is certainly consistent with the hypothesized primacy of this pathway in dimensional processing in these birds (Hodos, 1969; Hodos & Karten, 1966; Wang, Jiang, & Frost, 1993).
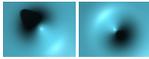
2.2 Shape-from-Shading in Birds

Beyond color and shape, another important and fundamental visual property of objects is the differential light reflected from their surfaces. This illumina-tion in the form of shading, specularity, and shadow are all thought to be evaluated early in processing as these features contain information about an object's 3D shape and physical location in the environment. Evidence that these types of lighting information contribute to the human perception of objects, depth, and scene layout is easy to find (Gibson, 1950, 1979; Mingolla & Todd, 1986; Norman, Todd, & Orban, 2004; Ramachandran, 1988).

Being highly diurnal, birds might also be sensitive to patterns associated with object illumination. Using a wide variety of approaches, several lines of earlier evidence suggested this might be the case (Cavoto & Cook, 2006; Hershberger, 1970; Hess, 1950; Reid & Spetch, 1998; Rowland, Cuthill, Harvey, Speed, & Ruxton, 2008; Young, Peissig, Wasserman, & Biederman, 2001). To more thoroughly investigate the contribution of lighting to shape perception in birds, we have recently systematically compared the contributions of shading to the discrimination of surface-mediated shapes in both pigeons and starlings (Cook, Qadri, Kieres, & Commons-Miller, 2012; Qadri, Romero, & Cook, 2014). For each species, the visual discrimination required the birds to tell us whether the smooth, curved 3D surfaces in the stimuli were either convex or concave in shape. Examples of these stimuli can be seen in Figure 4. While artificial, the stimuli were designed to have visual characteristics similar to that which might be experienced by birds in flight over a natural landscape. For instance, a convex stimulus appeared as a hill-shaped mound rising from the horizontal plane of a receding surface, while a concave stimulus appeared as a complementary depression recessed below the plane of the surface. The principal source of information in each display was the shading and shadows created from one of four lights located off-camera in the diagonal corners of the scene. By changing the directional source of the lighting among these positions across the displays, we created variability in the illumination patterns from the same surface shape, encouraging the pigeons and starlings to generally perceive the shapes of the surfaces and not just memorize specific illumination patterns.

Each bird species was tested with identical sets of shaded stimuli but, as outlined previously, with testing procedures more appropriate to the natural behaviors of each species. The pigeons were tested in a go/no-go procedure in which a single-shaded stimulus was presented on each trial. Half of the pigeons were trained to peck at images containing a convex shape (S+) for access to mixed grain, while learning to inhibit pecking toward the presentations of concave shapes (S−). The other half of the pigeons received a reversed assignment. Thus, for pigeons, we used the peck rates to the S+ shapes relative to the S− shapes to measure their discrimination. For the starlings, we used the simultaneous choice procedure with computerized perches. The starlings were presented with a side-by-side display of one concave and one convex stimulus on the monitor. The starlings then indicated the location of the designated correct shape (convex or concave depending on the starling) by landing on the perch spatially adjacent to the correct stimulus for a food reward. Thus, for the starlings, we used

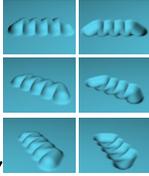| Test	Pigeons	Starlings	Stimuli
Training	< 500 go/no-go trials	< 2500 choice trials	
Baseline Perspective Variation	Small effect	Same	
Baseline Surface Color and Light Source Variation	No effect	Same	
Time to Discrimination	≈ 750 ms	≈ 500 – 600 ms	
Transfer to Novel Perspective	Good transfer until high elevations	Same	
Transfer to Novel Surface Heights	Good transfer	Same	
Transfer to Reduced Contrast	Reduced discrimination	Not tested	
Transfer to New Specularity Values	No effect	Same	
Transfer to New Shapes	Good transfer, mediated by similarity to training shape	Same	
Transfer to Untrained Lighting on Novel Shapes	Complete transfer	Good transfer	
Transfer to Dynamic Displays	Affected by changes in shape	Not tested	

Figure 4 Results from shape-from-shading experiments conducted with pigeons and starlings. The left portion outlines the results of different experiments independently tested with each species. Corresponding examples of some of the test displays used in testing the birds are provided toward the right.

choice accuracy to measure their capacity to discriminate the shapes. Both species were first trained to discriminate a sinusoidal curvature (see the top examples in Figure 4), then tested for their capacity to discriminate this and other shaded objects across a wide variety of test conditions.

Both the pigeons and starlings readily learned and used the shading information to identify the concavity or convexity of the different shapes. Both species learned the discrimination quickly and easily. The majority of the pigeons demonstrated learning within a mere handful of sessions. The starlings also exhibited no difficulty in learning, although it is difficult to judge the speed of learning because of the continuous and massed nature of their testing. Four of the five starlings reached a 75% accuracy criterion within approximately 1100 trials or the equivalent of about three days of testing. We further determined how quickly each species discriminated the information from the scenes upon their presentation. For the pigeons, this was taken to be the time it took them to first show a divergence in peck rates to the S+ and S− shapes. For the starlings we used choice reaction time to activate the correct choice perch. Both species were able to accurately respond between 500 and 1000 ms of seeing the stimulus. The ease of learning the discrimination and the rapidity of accurate responding both indicate that the critical features in these complex stimuli were readily seen by the birds, and thus, likely to be highly salient to them.

To examine their processing of these displays, we next compared the responses of the pigeons and starlings across a number of different changes in the scene. Some selected examples from these different tests are in the rightmost column of Figure 4. We observed numerous similarities across the two species, indicating that they were processing the displays in the same way. These comparisons are outlined also in Figure 4. For instance, each species was insensitive to the variation in the training set produced by changes in the direction of the lighting source or the camera's perspective. This suggests that the shape of the surface appeared invariant to the birds across these irrelevant changes. Further, both species showed a capacity to discriminate surface shapes over a range of angular perspectives of 20°−30° beyond their trained values. Both species were increasingly challenged as camera perspectives became more perpendicular to the surface of the stimuli, similar to humans (Georgieva, Todd, Peeters, & Orban, 2008). Thus, perspectives directly overhead made it much harder for the pigeons and starlings to see the convexity and concavity of the rendered shapes. Additionally, changes in the height and depth of the shapes, and their relative reflectance, or specularity, similarly affected both bird species. Finally,

both species showed transfer of this convexity discrimination to novel, untrained surface shapes. The resulting pattern indicated that this transfer performance was mediated by the resemblance of the novel shapes to the training shape. Furthermore, in a test conducted with only the pigeons because of the go/no-go nature of their responding, we found that the pigeons had the capacity to deal with continuous, dynamic changes in the scenes. Here, either the camera or the light continuously moved in a video stimulus relative to the other parts of the scene. This resulted in a display in which the patterns of illumination were continually altered. Nevertheless, the pigeons were able to recognize the shape of the surface by responding appropriately as the scene transformed.

The pattern and similarity of these outcomes suggested that the pigeons and starlings were seeing these stimuli in the same way and as intended—as receding 3D surfaces containing within them illuminated concave or convex shapes. The strong similarity in the responses of each species across these tests suggests that the shading of objects within the scene is a highly salient visual shape and depth cue that is readily processed by the avian perceptual system. Whenever this shape information was readily available from shading cues, the pigeons and starlings reacted in a way consistent with a hypothesis that they were sensitive to such illumination-based information. When such shape cues were reduced or were not available due to changes in the illumination, both species correspondingly performed poorly.

2.3 Conclusions and Implications

Overall, the results of our different analyses of early vision have suggested that these processes in birds and primates look very much alike. Color, luminance, and aspects of shape each appear to be readily processed and highly salient to pigeons. Although explored on a more limited basis, the starlings have looked similar to the pigeons. Additionally, when other details of these featural sensitivities are further explored, the responses of the birds share much in common with our own (Gibson, Lazareva, Gosselin, Schyns, & Wasserman, 2007). For birds, current evidence suggests these feature extraction processes are highly collothalamic functions (Cook & Hagmann, 2012; Nguyen et al., 2004). This suggests the algorithms and representations involved in each group are the same, despite the differing neural structures involved. Speculatively, these different aspects are likely processed in separate visual streams and portions of their visual pathways. If so, the early division of different types of visual information into independent streams or channels may be a fundamental algorithm involved with

how brains process visually complex information regardless of their structural organization.

3. COMPARATIVE PSYCHOLOGY OF EMERGENT STIMULUS PROCESSING

Whereas the previous section highlighted a domain where birds and mammals seem to have converged on algorithmically similar mechanisms, the next hints at potential complexities involving more advanced stages of processing. One area in which we and others have possibly identified a difference between these classes of animals pivots around their capacity to flexibly integrate and attend to spatial information at different levels of configural or spatial organization. One of the fundamental assumptions in vision is that higher level representations of objects are built from collections of component features, such as edges and surfaces. Objects can often be described at different levels of detail. When you see a good friend, you immediately recognize them without separately thinking about their eyes, ears, nose, or mouth. Nevertheless, if questioned we know that people differ in these features, and these features can serve to mediate recognition, as is done in caricatures. Thus, one decision that every visual cognition system needs to make concerns the level of organization or detail that will serve as the primary means of representing objects and governing our interactions with them. It is that level of detail with which we represent our world where birds and humans may vary from one another.

3.1 Hierarchical Stimulus Processing in Pigeons

To investigate the role of emergent and local features in object perception and recognition, hierarchical stimuli have been particularly useful. Hierarchical stimuli consist of smaller component shapes that are configured into a larger figure. They come in a variety of forms. One of the original instances came from Navon's work with humans testing stimuli composed of smaller letters configured to simultaneously make larger letters (Navon, 1977, 1981). The smaller letters measured the processing of information at a local or featural level of organization, while the larger letters captured the processing of the stimulus' global aspects. In humans, Navon found that processing of global information preceded the processing of local information. While this story has become more complicated, the general theme that humans have a global precedence bias in these kinds of tasks has been confirmed. Our ability to perceive, integrate, and attend to the

global organization of a wide variety of stimuli is a consistent feature of the visual behavior of humans and some, but not all, nonhuman primates in certain conditions (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997; Fagot & Tomonaga, 1999; Neiworth, Gleichman, Olinick, & Lamp, 2006; Spinozzi, De Lillo, & Truppa, 2003; Tanaka & Fujita, 2000).

Do birds exhibit this same global precedence or privileging? One of the first experiments to examine this question tested pigeons with Navon-like hierarchical stimuli (Cavoto & Cook, 2001). Here, we tested pigeons in a conditional discrimination in which they identified which of four different configurations of letters (T, N, X, H) appeared on each trial. Examples of these different stimulus configurations are in the top panel of Figure 5. We tested two types of hierarchical stimuli composed of a combination of a relevant letter at one level and an irrelevant letter (O) at the other. In the *global-relevant* condition the stimuli consisted of the local–irrelevant letter repeated in a configuration to form one of the four relevant letters in the global shape. On trials with these stimuli, only global information was available for the choice task. In the *local-relevant* condition, a relevant local letter was repeated in a configuration to form an irrelevant letter at the global level. Thus, on these trials, only the local level of these stimuli contained information relevant for the test. On any one trial, only one of the organizational levels was relevant, but both levels were tested equally often within a session. This required the pigeons to attend to both levels. We tested two other stimulus conditions consisting of the four relevant letters as solid forms, but matched to the size of the corresponding hierarchical conditions (i.e., global–equivalent and local–equivalent conditions).

The pigeons' task was to correctly peck at the choice key associated with the relevant letter that had appeared on that trial regardless of whether it had appeared at the global or local level of organization. We tested all four conditions daily with two additional important variations in their properties. First, we varied the size of the stimuli between trials. Second, we randomly varied the spatial position of the stimuli on the monitor across trials. These two manipulations ensured the pigeons were truly integrating information across the displays by disrupting strategies that might leverage consistent or fixed spatial information as a means to achieve high accuracy without perception of the entire display.

Unlike humans, the pigeons seemed to strongly prefer discriminating the local level rather than the global level of these stimuli. Two facts particularly indicated this possibility. These can be seen in the lower two portions of Figure 5. First, the pigeons acquired the local-relevant condition much faster
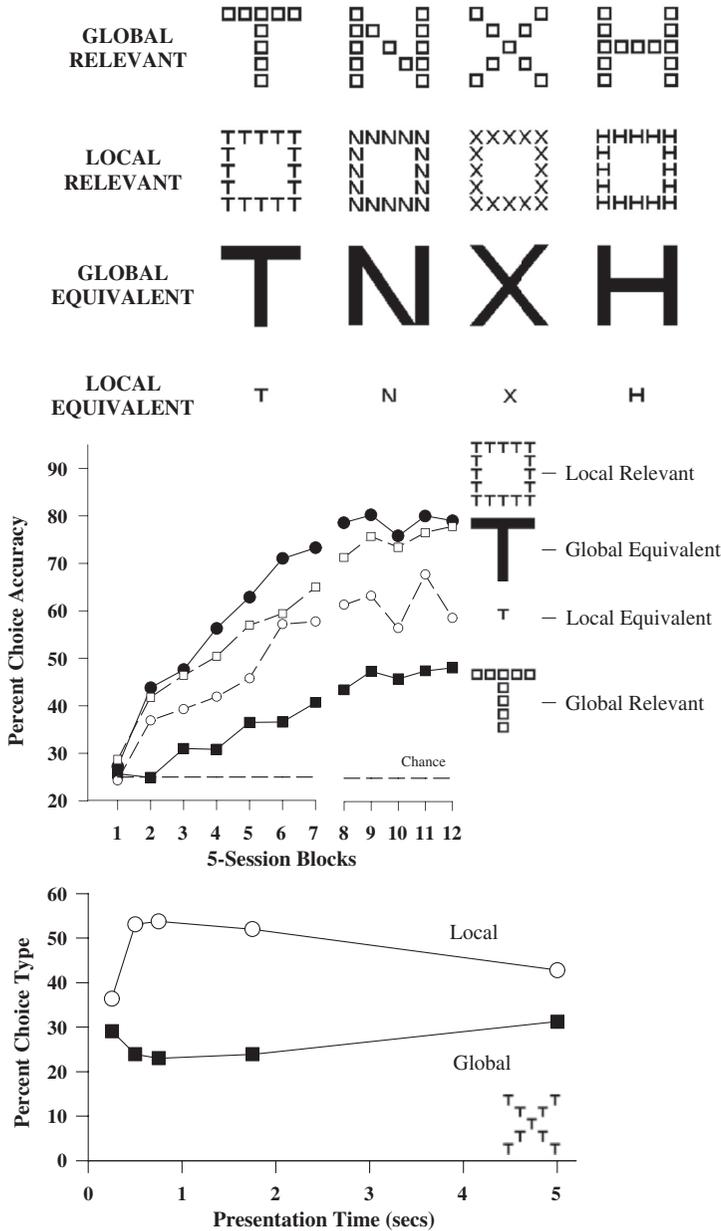
Figure 5 Hierarchical form stimuli and their processing in pigeons. The top panel shows examples of the four different stimulus conditions tested by Cavoto and Cook (2001). The middle panel shows the initial period of acquisition with the global- and local-relevant hierarchical stimuli and their correspondingly sized controls. The bottom panel depicts the results for conflict stimuli which contain relevant, but incongruous, information at the local and global levels. Because there are two potentially correct answers, these results are drawn as the percentage of correct local choice and correct global choice as a function of stimulus duration.

and to a higher level of accuracy than the corresponding global–relevant condition (middle panel). In fact, in comparison to the size controls included in the experiment, the local–relevant condition supported faster acquisition than any other condition, whereas the global–relevant condition was by far the slowest. Even after several months of training, this local advantage among the hierarchical conditions did not substantially diminish. While the pigeons were able to eventually correctly identify the letters in a global–relevant condition, this particular hierarchical organization was clearly the more difficult one for the pigeons to process.

The second important result stemmed from tests with *conflict probe stimuli*. These conflict stimuli were composed of a combination of both local– and global–relevant letters, but each assigned to a different choice key. Thus, which choice key was chosen was indicative of the level of the stimulus being processed. The lower panel of Figure 5 shows what happens as a function of the presentation duration of these conflict stimuli. Collectively, it shows that the pigeons consistently and more frequently reported the local letter than the global letter in such stimuli. Different pigeons appeared to have slightly different strategies for starting locally before eventually switching to global information. Two pigeons seemed to use the presence of an irrelevant letter as the cue to switch over to processing of the global level, while the other two pigeons used time, starting first with local information and then gradually switching to more global information as time passed.

Despite taking longer to emerge and being harder to learn, the capacity of the pigeons to identify letters in the global–relevant condition with high accuracy indicates that pigeons can group configural information at spatial scales larger than single letters. This conclusion is further strengthened by their ability to do so even when the stimuli changed in size and location between trials. That said, the local information in the stimuli was clearly easier to process and done so before information at the global level. Similar findings from a variety of studies on other topics have hinted at this same predisposition by pigeons to attend to local or featural information over more global or configural information (Aust & Huber, 2001; Cerella, 1986; Cook & Tauro, 1999; Emmerton & Renner, 2009; Goto & Lea, 2003; Lea, Goto, Osthaus, & Ryan, 2006; Spetch, Cheng, & Mondloch, 1992; Spetch & Edwards, 1988). This local precedence effect markedly contrasts with the global precedence found with humans and strongly suggests that pigeons might be predisposed to "looking at the trees before the forest" (but see Fremouw, Herbranson, & Shimp, 1998; Fremouw, Herbranson, & Shimp, 2002).

3.2 The Processing of Emergent Structure in Random Noise by Pigeons

At this juncture, we wanted to learn more about how pigeons processed globally organized information. While the Cavoto and Cook (2001) study had relevant information presented at both levels of organization, we thought there might be advantages to having to process only the global information and disregard the local information. Toward this goal, we tested pigeons with stimulus displays comprised of identical local information that could then be configured to form a variety of larger emergent or global patterns (Cook, Goto, & Brooks, 2005). Examples of some of the stimuli used in that experiment are provided in Figure 6. All the different global stimuli were made out of locally equivalent and identical black and white squares. In the first part of the experiment, the pigeons were trained to find structured areas of patterned black and white squares on a background of randomly placed black and white squares. These structured areas could be formed to create large patterns of vertical and horizontal stripes, embedded squares, or a checkerboard pattern. These structured "targets" could then be randomly placed within a larger surrounding area of randomized local elements. On a given trial, the display would contain one panel containing a structured target and one of completely randomized elements. The pigeon's task was to peck at the panel containing the target. Again, the size of the base (local) element used to build each display varied between trials as well as the target's position within the panel. This ensured that local, spatially restricted strategies would generate few correct responses and helped us to judge how element density or granularity influenced discrimination of these global organizations.

The pigeons were able to learn this target detection task fairly quickly, especially when denser elements (i.e., smaller block sizes) were used. The pigeons learned to find the striped patterns most quickly, followed by the square pattern and finally the more challenging checkerboard pattern. Element size had an important influence on target detection, as can be seen in the lower panel of Figure 6. When the elements were small, densely packed, and more repetitious (more patterns per unit measure), the pigeons were very good at detecting all of the global patterns. As the base element size increased, their ability to find the target systematically changed, with checkerboard falling off first, followed by the square pattern, and finally the stripes.

These results indicate that pigeons can recognize a broad class of emergent perceptual structures. The relative ease of global stimulus control here contrasts markedly with the difficulties seen in the Cavoto and Cook (2001)
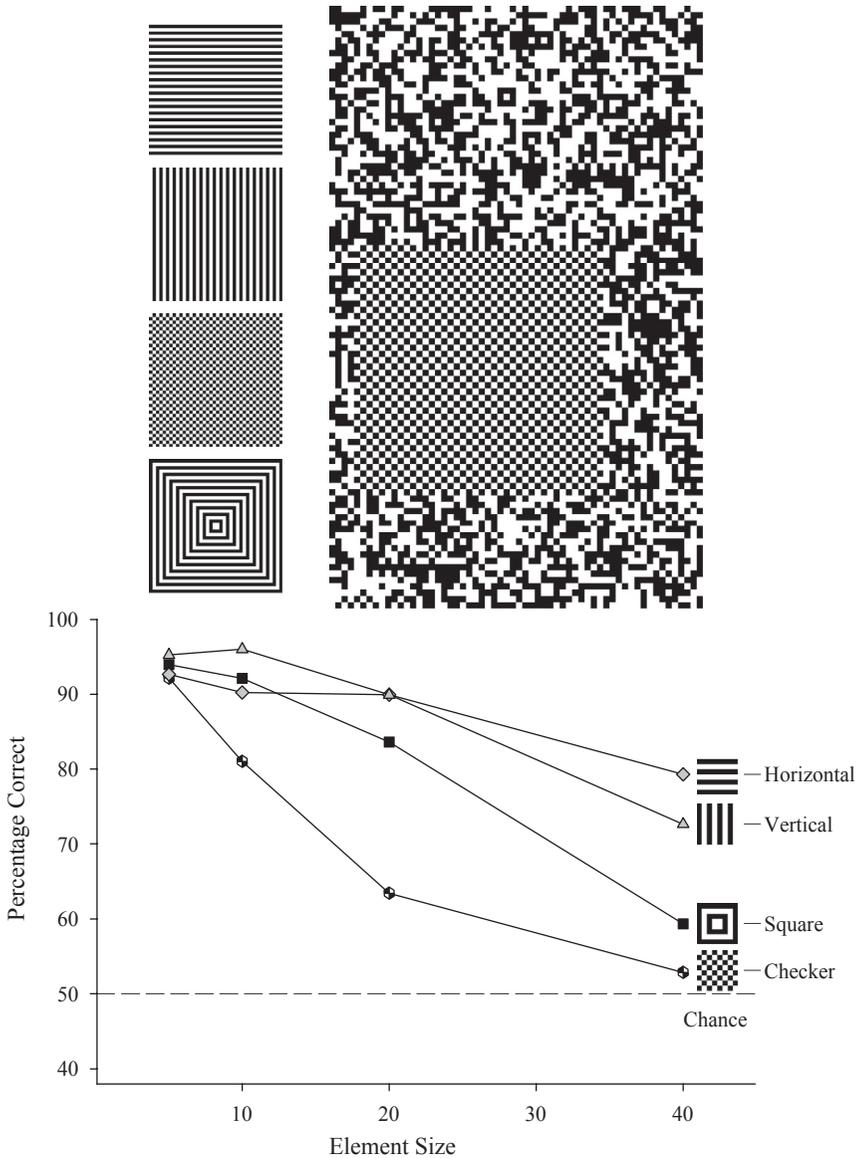
Figure 6 Pigeons' perception of patterns among noise. The left portion of the upper panel contains examples of the four different structured target types used in Cook et al. (2005). The right portion shows one of these targets embedded in an appropriately constructed random background. In the experiments, a second panel (not shown) consisting of only randomized elements was also displayed. The bottom panel depicts the pigeons' mean accuracy with each of the four target types as a function of the size of the elements used to construct the displays.

study. One possible reason for this disparity is that the global arrangements in this study were continuous and closely packed, while those of the previous study were separated by small spatial gaps. Another important factor was that the most successful displays consistently had smaller base elements. The greater repetitive structure that emerged with these smaller elements assisted in removing local ambiguities. The chances of confusing target-like blocks of randomness appearing by chance were far greater as element size increased. Finally, a third possibility is that the pigeons can only configurally integrate over a relatively small area of any display. When the base elements are small or dense, these small area grouping mechanisms can detect the structured patterns within the larger global form, but without necessarily "seeing" the entire stimulus. As these mechanisms become challenged by larger base element displays, the difficulty of seeing the larger patterns emerged. This might account for why the checkerboard and square patterns, which have more complex global features, decline before the simple linear features that are prominent in the vertical and horizontal displays.

3.3 Perception of Glass Patterns in Starlings

Recently we have been studying a different type of emergent perceptual pattern to better understand this complex issue in birds. For this investigation, we examined the perception of Glass patterns by starlings. Glass patterns are random-dot patterns, which are superimposed upon themselves with different kinds of spatial transformations. The correlated orientation patterns in the resulting numerous pairs of dots produce a strong global perception in humans (Glass, 1969). Examples of different types of Glass patterns can be seen in the top row of Figure 7. It has been found that, for humans, Glass patterns forming concentric rotations are more easily seen and resist interference from noise more than either radial or translational patterns (Kelly, Bischof, Wong-Wylie, & Spetch, 2001; Wilson & Wilkinson, 1998). It has been suggested that this concentric superiority effect may result from face-specific processing mechanisms in humans (Wilkinson et al., 2000; Wilson & Wilkinson, 1998). Evidence from monkeys suggest that Glass pattern perception is mediated by neurons in the lemnothalamic pathway, including areas known to be precursors to facial recognition regions in humans (Smith, Bair, & Movshon, 2002; Smith, Kohn, & Movshon, 2007). The capacity of such sparse local information to generate strong global percepts has made this type of stimulus of considerable interest.

Kelly et al. (2001) were the first to examine how pigeons perceive Glass patterns. They trained their pigeons to peck at any of four types of Glass
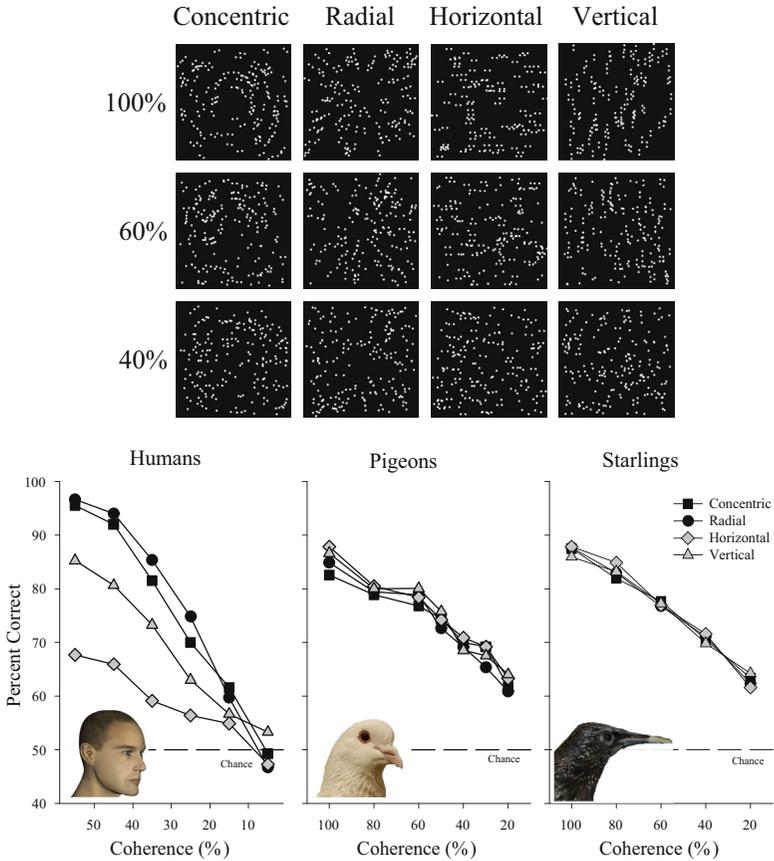
Figure 7 Comparative results of Glass pattern perception. The top panel shows selected examples of the four types of Glass patterns tested with starlings by Qadri and Cook (2014). Across the three rows, the stimuli are progressively degraded by randomly placed dots, reducing the global coherence of the displays. The left two portions of the lower panel are a depiction of the accuracy results of Kelly et al. (2001) with humans and pigeons using the same type of stimuli. For this presentation, the results have been redrawn from the original publication. The rightmost portion shows mean accuracy of starlings as a function of stimulus coherence as reported in Qadri and Cook (2014).

patterns (see Figure 7) when paired against a random–dot pattern in a simultaneous choice discrimination. Across trials, these patterns were randomly generated each time from a new set of dipole positions. They also tested humans with the same stimuli. Their results for humans can be seen in the lower left panel of Figure 7. These choice accuracy data demonstrate the superior perception by humans for detecting circularly organized Glass

patterns relative to translational ones. This superiority is maintained even as increasing amounts of random noise are added to the display (i.e., coherence level) until performance eventually declines to chance levels as coherence declines. Would pigeons show the same pattern?

Kelly et al.'s (2001) results with pigeons are displayed in Figure 7 in the same manner as the humans. Immediately noticeable is that the pigeons do not show the same effect. The pigeons exhibited no difference in their capacity to detect the overall structure of the four Glass patterns. Furthermore, this was true across all coherence levels. The simplest conclusion to draw from these results is that the two species were not seeing the Glass patterns in the same way. Because of this comparative difference and its implications for the processing of global information by birds and mammals, we thought it was an important area to target when we first started testing our starlings. By testing another bird species we could determine if Kelly and colleagues' results were representative of a true processing difference between birds and mammals or something limited to pigeons.

For these tests with the starlings, we thought it best to match Kelly et al.'s (2001) stimulus conditions (Qadri & Cook, 2014). As before, the starlings were continually tested in their live-in procedure. On each trial, the starlings were presented a Glass pattern and a random-dot stimulus side-by-side in a simultaneous choice discrimination. We trained and tested the same four types of Glass patterns as Kelly and colleagues, although we did reverse the polarity of their stimuli to white on black. We also inverted the discrimination so that the random-dot stimulus was always correct on each trial, instead of requiring the birds to learn to approach and choose all four of the Glass patterns. Because we think spatial variability is important to encourage global processing, we also varied display size across trials.

The results for the starlings are displayed in the rightmost panel at the bottom of Figure 7. The starlings behaved exactly like the pigeons and unlike humans. They showed no differentiation among the four types of Glass patterns. This was true during task acquisition, across the different display sizes, and across varying levels of coherence. What might be the origins of this comparative difference between the pigeons and starlings relative to humans?

One possibility is that birds do not have (or need) the same specialized face detectors proposed to account for the human concentric superiority effect. Given that faces appear to be important for highly social species like ourselves and have predictable components arrayed in close, compact circular-like areas on relatively flat faces, specialized processing mechanisms

might not be surprising (Kanwisher & Yovel, 2006). The natural history and lateral-eyed facial structure of birds, however, may lend no particular importance to this specific organization. Thus, the pigeons and starlings may attend to the global form of these Glass patterns just fine, but lack the specialized mechanisms responsible for our circular benefit.

Another possibility we have considered is that the pigeons and starlings attend to the local features of displays, in a manner consistent with previous examples of local control (in at least pigeons). The origin of this possibility stems from the design of the random-dot comparison stimuli used in the original pigeon experiments. While the humans may not have taken advantage of this since they can easily see the patterns, this type of random stimulus did allow the displays to be potentially discriminated using locally available inter-dot-distance statistics that differ between the Glass patterns and the random-dot displays. By attending to local areas smaller than the full Glass pattern, these stimuli could be discriminated based on the extent of these local pairings without truly "seeing" the overall global pattern. If this is the case, the use of such local cuing may be responsible for the absence of any differences among the patterns in the birds.

In unpublished experiments, we have since tested the starlings with these dipole statistical differences eliminated between the displays. In this version of the task, the starlings had to distinguish the concentric Glass pattern from all of the others patterns. The task was more difficult for the starlings, suggesting that local cues may have contributed to the earlier result. Nonetheless, they successfully discriminated among these better-matched patterns indicating that a degree of global emergent grouping controlled their behavior. Despite this, differences among the Glass patterns still did not emerge, consistent with the earlier findings. Comparable tests from pigeons are needed, but have not yet been collected. Based on our experience so far, our guess is they will look similar to the starlings' results.

Finally, there is the possibility that birds are not very good at perceptually grouping separated, disconnected elements, like dots. There are numerous instances where the connecting of information across spatial distances or gaps seems to create difficulties in the perception of the stimuli, at least as frequently tested in pigeons (Qadri, Asen, & Cook, 2014). For example, across a wide variety of conditions, pigeons have repeatedly failed to exhibit amodal completion, especially when asked to complete hidden figures located behind an occluding object (Aust & Huber, 2006; Fujita, 2001; Fujita & Ushitani, 2005; Sekuler, Lee, & Shettleworth, 1996; Ushitani & Fujita, 2005). This has caused some researchers to propose that pigeons

may experience a perceptually fragmented world (Fujita, 2006; Vallortigara, 2006). One hypothesis of this type is that the visual system of birds relies on continuous edges in its construction and recognition of objects. While they can cope with small distances between elements, perhaps, unlike humans, they cannot make good substantial global inferences from incomplete or disconnected elements, such as our Glass patterns. If this latter hypothesis has merit, it would imply that the visual world of birds diverges from our own when it comes to the edge-related building blocks underlying object perception (Rilling, De Marse, & La Claire, 1993).

3.4 Conclusions and Implications

Our research using complex, configural stimuli containing relevant information at different levels of organization indicates that pigeons, and likely starlings, can be controlled by either local or global information. In all three lines of research presented above, the birds indicated that they could see and guide their behavior using larger, emergent portions or configurations of the display. That said, pigeons have frequently shown a strong propensity to use local information when it is available. One of the hypotheses to account for this proposes that there are limits on their ability to spatially integrate separated information. One possible origin of this limitation is that most experimental procedures require the birds to use their frontal visual field to process the stimuli. While little has been made of it in this chapter, it is important to note that most birds have two functional visual fields, unlike mammals. It is believed that because the eyes of birds are laterally placed on their heads, they have evolved separate frontal and lateral visual fields that interact together to control their behavior. It has been hypothesized that the frontal visual field is specialized for viewing and foraging at close distances, while the lateral visual field offers a panoramic view of the world and may be important for the control of flight and predator detection. If the frontal field is specialized for processing information at closer distances, the capacity to integrate information over smaller areas may be of value. There have only been a few, limited studies of the psychological and cognitive contributions of the lateral visual fields and more work in this area is definitely needed.

While we have made considerable progress, exactly how perceptual and attentional mechanisms operate across different spatial scales and levels of spatial organization is still not a well understood phenomenon in birds compared to primates (Knudsen, 2011). What has emerged is a consistent and intriguing pattern of results that suggests, regardless of the source of

the difference, that this is one area where birds and mammals do not readily agree about how to process what are otherwise identical stimuli.

4. CONCLUSIONS

What is the bird's eye view? Despite appearances to the contrary based on their behavior, assuming that the avian perspective of the world mirrors our own mammalian perspective is clearly too simple. Over the millions of years of our separate evolutionary journeys, the origins, functions, and mechanisms of visual cognition in each of these highly developed classes of vertebrates has a twisted tale of similarities and differences that we are just beginning to understand. What we hope that this chapter has made clear, though, is that the answer to this question is more than simple scientific curiosity, but one that is highly revealing as to the theoretical nature of visual processing. By understanding the alien nature of the avian visual cognition, it will provide important insights into how our own system evolved into its current form and how it functions.

On one front, there is growing evidence that the early visual processing of birds and mammals share strong resemblances. The same basic visual features seem to be involved. Moreover, these features appear to be potentially divided into separate independent streams for early processing. These streams likely are built around retinotopic maps that can rapidly localize features in the visual world and potentially mediate their later recompilation in processing. The challenge for visual theorists is that these similarities are mediated by different portions of the central nervous system in these groups, and they likely represent a form of convergent cognitive evolution. For pigeons, these processes appear to happen in the collothalamic pathway, while for mammals they appear to happen in the lemnothalamic pathway. If this is the case, one implication would be that visual structure of the world may limit the number of efficient and feasible visual solutions regardless of how they are implemented in biological systems (Gibson, 1950). It may be that the neural mechanisms can only efficiently decode the visual structure of the world by having independent streams available for decomposing information.

What subsequently happens to this information as it travels upstream appears to be more complicated and variable. Our research has suggested that there may be potential differences between birds and mammals in how they process the global and local features of complex objects. At these

higher levels of processing, the pattern of results within our research and across laboratories becomes increasingly interesting, puzzling, and contradictory. For instance, there are lines of research that suggest that object perception and recognition or visual categorization share many similarities with humans. On the other hand, there are a number of other equally compelling lines of evidence that suggest that this is not the case. What is clear is that we have not yet been able to identify those key factors that can link and synthesize these results. Being able to do so represents one of the most important challenges for the area of comparative cognition.

There are a number of important areas for further exploration, especially in understanding the relationship between visual cognition and its mechanisms in birds. While we have good evidence regarding the organization of the major visual pathways of these animals, more attention is needed toward characterizing the brain-behavior relations among the different aspects of visual cognition in birds and their underlying neural mechanisms. Being able to tie more specifically the different kinds of results to their neural mediators would be valuable in advancing our insights into the function and evolution of these different aspects. Another important area for further research regards the contribution of dynamicity and object motion to object perception and recognition. While not reviewed here, my lab has been increasingly concerned with this issue in birds (Asen & Cook, 2012; Cook & Katz, 1999; Cook, Shaw, & Blaisdell, 2001; Qadri, Asen, et al., 2014; Qadri, Romero, et al., 2014). The advent of using computerized displays has made addressing this issue far more tractable to investigate with birds than at any time in the past.

Finally, investigating and testing more avian species is critical. The pigeon model for studying the nature of visual processing has been highly successful. This animal has been a worthy subject and is one of the best modeled systems currently available. However, the pigeon is just one of over 9,000 species of birds with diverse and different natural histories. The sustained attention of herons and hawks while foraging, the need of diving ducks to visually interact across the mediums of air and water, or that of chickadees navigating the tangled web of the forest canopy, all represent different kinds of visual problems than typically encountered by pigeons. Attempting to generalize from one successful ground-foraging species to this rich group of animals is fraught with peril.

Our recent use of starlings is a small step in addressing this limitation. Despite indications that starlings and pigeons represent different cerebrotypes (Iwaniuk & Hurd, 2005), our evidence has suggested that pigeons

and starlings share highly similar perceptions of the world. Our experimental tests of their abilities to recognize shape-from-shading and the perception of Glass patterns have produced strikingly equivalent results. Given that these two species are both diurnal, terrestrial foragers with strong propensities for open habitats, these commonalities may be responsible for this fact. Another important candidate to consider is that visual information processing is fundamental to individual fitness, and so basic vision may be a neural property that is highly conserved across avian species (Gutiérrez-Ibáñez et al., 2014). As a result, central visual and cognitive functions may not be able to support the same degree of plasticity needed to support ecologically driven specializations seen in more peripheral anatomy and neuroanatomy (Endler, 1993; Martin, 2007).

The study of visual perception and cognition has a long and outstanding comparative tradition of testing a wide variety of animals, the results of which have been critical to identifying many fundamental mechanisms (Fujita, Tanaka, Ito, & Cheng, 1992; Hartline & Ratliff, 1957; Hubel & Wiesel, 1962; Lettvin, Maturana, McCulloch, & Pitts, 1959; Reichardt, 1987). The investigation of visual cognition in birds stands firmly in this tradition. Its' outcomes potentially contribute to treatments or corrective solutions for humans suffering from a wide variety of visual disorders or deficits. There are proposals that the secondary collicular/tectal pathway could be highly useful in restoring different aspects of human vision when the main lemnothalamic pathway has been damaged (Chokron et al., 2008; Ro & Rafal, 2006; Wessinger & Gazzaniga, 2005). As birds represent the biological zenith of tectally mediated vision, they provide an excellent model system for investigating and developing such treatments. Combined with the avian capacity for adult neurogenesis (Chen, Bonder, & Cheng, 2006; Kerkhoff, 2000; Louissaint, Rao, Leventhal, & Goldman, 2002) and their rapid recovery of visual function following brain damage, the study of birds is also an important way to examine the possibilities of various rehabilitative treatments, including evaluating endogenous brain plasticity and the development of restorative therapies for human brain injury, particularly within visual pathways. Finally, knowledge of the mechanisms of avian vision should contribute to the understanding and engineering of small visual prostheses and other computational vision alternatives for those individuals whose blindness cannot be remedied. The potential for such scientific and translational advances from the experimental and comparative analysis of avian visual cognition offers considerable promise for the future.

ACKNOWLEDGMENTS

REFERENCES

Aboitiz, F., Montiel, J., Morales, D., & Concha, M. (2002). Evolutionary divergence of the reptilian and the mammalian brains: considerations on connectivity and development. *Brain Research Reviews, 39*, 141—153.

Alonso, P. D., Milner, A. C., Ketcham, R. A., Cookson, M. J., & Rowe, T. B. (2004). The avian nature of the brain and inner ear of Archaeopteryx. *Nature, 430*, 666—669. http://dx.doi.org/10.1038/nature02706.

Asen, Y., & Cook, R. G. (2012). Discrimination and categorization of actions by pigeons. *Psychological Science, 23*, 617—624. http://dx.doi.org/10.1177/0956797611433333.

Aust, U., & Huber, L. (2001). The role of item- and category-specific information in the discrimination of people versus nonpeople images by pigeons. *Animal Learning & Behavior, 29*, 107—119.

Aust, U., & Huber, L. (2006). Does the use of natural stimuli facilitate amodal completion in pigeons? *Perception, 35*, 333—349.

Barrow, H. G., & Tenenbaum, J. M. (1978). Recovering intrinsic scene characteristics from images. In A. Hanson, & E. Riseman (Eds.), *Computer vision systems* (pp. 3—26). New York: NY Academic Press.

Beck, J. (1982). Textural segmentation. In J. Beck (Ed.), *Organization and representation in perception* (pp. 285—318). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Benowitz, L. I., & Karten, H. J. (1976). Organization of the tectofugal visual pathway in the pigeon: a retrograde transport study. *Journal of Comparative Neurology, 167*, 503—520.

Bergen, J. R., & Adelson, E. H. (1988). Early vision and texture perception. *Nature, 333*, 363—364.

Broadbent, D. E. (1977). Levels, hierarchies, and the locus of control. *The Quarterly Journal of Experimental Psychology, 29*, 181—201.

Brown, J. W., Rest, J. S., Garcia-Moreno, J., Sorenson, M. D., & Mindell, D. P. (2008). Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. *BMC Biology, 6*, 6. http://dx.doi.org/10.1186/1741-7007-6-6.

Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 3—16. http://dx.doi.org/10.1037/0097-7403.27.1.3.

Cavoto, B. R., & Cook, R. G. (2006). The contribution of monocular depth cues to scene perception by pigeons. *Psychological Science, 17*, 628—634. http://dx.doi.org/10.1111/j.1467-9280.2006.01755.x.

Cerella, J. (1986). Pigeons and perceptrons. *Pattern Recognition, 19*, 431—438.

Chen, G., Bonder, E. M., & Cheng, M. F. (2006). Lesion-induced neurogenesis in the hypothalamus is involved in behavioral recovery in adult ring doves. *Journal of Neurobiology, 66*, 537—551.

Chojnowski, J. L., Kimball, R. T., & Braun, E. L. (2008). Introns outperform exons in analyses of basal avian phylogeny using clathrin heavy chain genes. *Gene, 410*, 89—96. http://dx.doi.org/10.1016/j.gene.2007.11.016.

Chokron, S., Perez, C., Obadia, M., Gaudry, I., Laloum, L., & Gout, O. (2008). From blindsight to sight: Cognitive rehabilitation of visual field defects. *Restorative Neurology and Neuroscience, 26*, 305—320.

Cook, R. G. (1992a). Acquisition and transfer of visual texture discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 18*, 341–353. http://dx.doi.org/10.1037/0097-7403.18.4.341.

Cook, R. G. (1992b). Dimensional organization and texture discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 18*, 351–363. http://dx.doi.org/10.1037/0097-7403.18.4.354.

Cook, R. G. (1992c). The visual perception and processing of textures by pigeons. In W. K. Honig, & J. G. Fetterman (Eds.), *Cognitive aspects of stimulus control* (pp. 279–299). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Cook, R. G. (2001). *Avian visual cognition.* Retrieved from 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. *Animal Learning & Behavior, 24*, 150–167. http://dx.doi.org/10.3758/BF03198963.

Cook, R. G., Cavoto, B. R., Katz, J. S., & Cavoto, K. K. (1997). Pigeon perception and discrimination of rapidly changing texture stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 23*, 390–400. http://dx.doi.org/10.1037/0097-7403.23.4.390.

Cook, R. G., Goto, K., & Brooks, D. I. (2005). Avian detection and identification of perceptual organization in random noise. *Behavioural Processes, 69*, 79–95. http://dx.doi.org/10.1016/j.beproc.2005.01.006.

Cook, R. G., & Hagmann, C. E. (2012). Grouping and early visual processing in avian vision. In O. F. Lazareva, T. Shimizu, & E. A. Wasserman (Eds.), *How animals see the world: Behavior, biology, and evolution of vision.* London: Oxford University Press.

Cook, R. G., & Katz, J. S. (1999). Dynamic object perception by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 25*, 194–210. http://dx.doi.org/10.1037/0098-7403.25.2.194.

Cook, R. G., Qadri, M. A. J., Kieres, A., & Commons-Miller, N. (2012). Shape from shading in pigeons. *Cognition, 124*, 284–303. http://dx.doi.org/10.1016/j.cognition.2012.05.007.

Cook, R. G., Shaw, R., & Blaisdell, A. P. (2001). Dynamic object perception by pigeons: discrimination of action in video presentations. *Animal Cognition, 4*, 137–146. http://dx.doi.org/10.1007/s100710100097.

Cook, R. G., & Tauro, T. L. (1999). Object–goal positioning influences spatial representation in rats. *Animal Cognition, 2*, 55–62. http://dx.doi.org/10.1007/s100710050024.

Corwin, S. (2010). The asymmetry of the carpal joint and the evolution of wing folding in maniraptoran theropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences, 277*, 2027–2033.

Deruelle, C., & Fagot, J. (1998). Visual search in global/local stimulus features in humans and baboons. *Psychonomic Bulletin & Review, 3*, 476–481.

Emery, N. J. (2006). Cognitive ornithology: The evolution of avian intelligence. *Philosophical Transactions of the Royal Society of London, 361*, 23–43. http://dx.doi.org/10.1098/rstb.2005.1736.

Emmerton, J., & Renner, J. C. (2009). Local rather than global processing of visual arrays in numerosity discrimination by pigeons (*Columba livia*). *Animal Cognition, 12*, 511–526.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs, 63*, 2–27.

Endler, J. A., Westcott, D. A., Madden, J. R., & Robson, T. (2005). Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution, 59*, 1795–1818.

Fagot, J., & Deruelle, C. (1997). Processing of global and local visual information and hemispherical specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). *Journal of Experimental Psychology: Human Perception and Performance, 23*, 429–442.

Fagot, J., & Tomonaga, M. (1999). Global and local processing in humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): Use of a visual search task with compound stimuli. *Journal of Comparative Psychology, 113*, 3–12.

Feare, C. (1984). *The starling*. Oxford: Oxford University Press.

Fremouw, T., Herbranson, W. T., & Shimp, C. P. (1998). Priming of attention to local and global levels of visual analysis. *Journal of Experimental Psychology: Animal Behavior Processes, 24*, 278–290.

Fremouw, T., Herbranson, W. T., & Shimp, C. P. (2002). Dynamic shifts of pigeon local/global attention. *Animal Cognition, 5*, 233–243.

Fujita, I., Tanaka, K., Ito, M., & Cheng, K. (1992). Columns for visual features of objects in monkey inferotemporal cortex. *Nature, 360*, 343–346. http://dx.doi.org/10.1038/360343a0.

Fujita, K. (2001). Perceptual completion in rhesus monkeys *(Macaca mulatta)* and pigeons (*Columba livia*). *Perception & Psychophysics, 63*, 115–125.

Fujita, K. (2006). Seeing what is not there: Illusion, completion and spatiotemporal boundary formation in comparative perspective. In E. A. Wasserman, & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 29–52). New York, NY: Oxford University Press.

Fujita, K., & Ushitani, T. (2005). Better living by not completing: A wonderful peculiarity of pigeon vision. *Behavioural Processes, 69*, 59–66.

Georgieva, S. S., Todd, J. T., Peeters, R., & Orban, G. A. (2008). The extraction of 3D shape from texture and shading in the human brain. *Cerebral Cortex, 18*, 2416–2438. http://dx.doi.org/10.1093/cercor/bhn002.

Gerkema, M. P., Davies, W. I. L., Foster, R. G., Menaker, M., & Hut, R. A. (2013). The nocturnal bottleneck and the evolution of activity patterns in mammals. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20130508. http://dx.doi.org/10.1098/rspb.2013.0508.

Gibson, J. J. (1950). *The perception of the visual world*. Boston, MA: Houghton Mifflin.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.

Gibson, B. M., Lazareva, O. F., Gosselin, F., Schyns, P. G., & Wasserman, E. A. (2007). Nonaccidental properties underlie shape recognition in mammalian and nonmammalian vision. *Current Biology, 17*(4), 336–340.

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

Goldsmith, T. (1990). Optimization, constraint, and history in the evolution of the eyes. *The Quarterly Review of Biology, 65*(3), 281–322.

Goto, K., & Lea, S. E. G. (2003). Discrimination of direction of movements in pigeons following previous experience of motion/static discrimination. *Journal of the Experimental Analysis of Behavior, 80*, 29–42.

Green, M. (1991). Visual search, visual streams, and visual architectures. *Perception & Psychophysics, 50*, 388–403.

Grossberg, S., Mingolla, E., & Ross, W. D. (1997). Visual brain and visual perception: How does the cortex do perceptual grouping? *Trends in Neuroscience, 20*, 106–111.

Gutiérrez-Ibáñez, C., Iwaniuk, A. N., Moore, B. A., Fernández-Juricic, E., Corfield, J. R., Krilow, J. M., et al. (2014). Mosaic and concerted evolution in the visual system of birds. *PLoS One, 9*, e90102.

Hart, N. S. (2001). Variations in cone photoreceptor abundance and the visual ecology of birds. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 187*, 685–697.

Hartline, H. K., & Ratliff, F. (1957). Inhibitory interaction of receptor units in the eye of Limulus. *Journal of General Physiology, 40*, 357–376.

Heesy, C. P., & Hall, M. I. (2010). The nocturnal bottleneck and the evolution of mammalian vision. *Brain, Behavior & Evolution, 75*, 195–203. http://dx.doi.org/10.1159/000314278.

Hellmann, B., & Güntürkün, O. (2001). Structural organization of parallel information processing within the tectofugal visual system of the pigeon. *Journal of Comparative Neurology, 429*, 94–112. http://dx.doi.org/10.1002/1096-9861(20000101)429:1<94:: AID-CNE8>3.0.CO;2–5.

Hershberger, W. (1970). Attached-shadow orientation perceived as depth by chickens reared in an environment illuminated from below. *Journal of Comparative and Physiological Psychology, 73*, 407–411.

Hess, E. H. (1950). Development of the chick's responses to light and shade cues of depth. *Journal of Comparative and Physiological Psychology, 43*, 112–122.

Hodos, W. (1969). Color discrimination deficits after lesions of the nucleus rotundus in pigeons. *Brain, Behavior & Evolution, 2*, 185–200.

Hodos, W., & Karten, H. J. (1966). Brightness and pattern discrimination deficits in the pigeon after lesions of nucleus rotundus. *Experimental Brain Research, 2*, 151–167.

Homman-Ludiye, J., & Bourne, J. A. (2014). Mapping arealisation of the visual cortex of non-primate species: Lessons for development and evolution. *Frontiers in Neural Circuits, 8*.

Honig, W. K., & Fetterman, J. G. (1992). *Cognitive aspects of stimulus control*. Hillsdale, N.J: L. Erlbaum Associates.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology, 160*, 106–154.

Iwaniuk, A. N., & Hurd, P. L. (2005). The evolution of cerebrotypes in birds. *Brain, Behavior and Evolution, 65*, 215–230. http://dx.doi.org/10.1159/000084313.

Jarvis, E., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience, 6*, 151–159. http://dx.doi.org/10.1038/nrn1606.

Jones, M. P., Pierce, K. E., & Ward, D. (2007). Avian vision: A review of form and function with special consideration to birds of prey. *Journal of Exotic Pet Medicine, 16*, 69–87. http://dx.doi.org/10.1053/j.jepm.2007.03.012.

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

Kaas, J. H. (1997). Topographic maps are fundamental to sensory processing. *Brain Research Bulletin, 44*, 107–112.

Kaas, J. H. (2013). The evolution of brains from early mammals to humans. *Wiley Interdisciplinary Reviews: Cognitive Science, 4*, 33–45.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*, 2109–2128. http://dx.doi.org/10.1098/rstb.2006.1934.

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. *Psychological Science, 12*, 338–342.

Kerkhoff, G. (2000). Neurovisual rehabilitation: Recent developments and future directions. *Journal of Neurology, Neurosurgery & Psychiatry, 68*, 691–706.

Knudsen, E. I. (2011). Control from below: The role of a midbrain network in spatial attention. *European Journal of Neuroscience, 33*, 1961–1972.

Lautenschlager, S., Witmer, L. M., Altangerel, P., & Rayfield, E. J. (2013). Edentulism, beaks, and biomechanical innovations in the evolution of theropod dinosaurs. *Proceedings of the National Academy of Sciences of the United States of America, 110*, 20657–20662. http://dx.doi.org/10.1073/pnas.1310711110.

Lazareva, O. F., Shimizu, T., & Wasserman, E. A. (2012). *How animals see the world: Comparative behavior, biology, and evolution of vision*. USA: Oxford University Press.

Lea, S. E. G., Goto, K., Osthaus, B., & Ryan, C. M. E. (2006). The logic of the stimulus. *Animal Cognition, 9*, 247–256. http://dx.doi.org/10.1007/s10071-006-0038-3.

Lettvin, J. Y., Maturana, H. R., McCulloch, W. S., & Pitts, W. H. (1959). What the frog's eye tells the frog's brain. *Proceedings of the IRE, 47*, 1940−1951.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science, 240*, 740−749.

Louissaint, A., Rao, S., Leventhal, C., & Goldman, S. A. (2002). Coordinated interaction of neurogenesis and angiogenesis in the adult songbird brain. *Neuron, 34*, 945−960.

Lunau, K. (2014). Visual ecology of flies with particular reference to colour vision and colour preferences. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 200*, 497−512. http://dx.doi.org/10.1007/s00359-014-0895-1.

Marder, E. (2002). Non-mammalian modes of studying neural development and function. *Nature, 417*, 318−320.

Marr, D. (1982). *Vision*. San Francisco, CA: Freeman.

Martin, G. (2007). Visual fields and their functions in birds. *Journal of Ornithology, 148*, 547−562. http://dx.doi.org/10.1007/s10336-007-0213-6.

Mingolla, E., & Todd, J. T. (1986). Perception of solid shape from shading. *Biological Cybernetics, 53*, 137−151.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9*, 353−383.

Navon, D. (1981). The forest revisited: more on global precedence. *Psychological Review, 43*, 1−32.

Neiworth, J. J., Gleichman, A. J., Olinick, A. S., & Lamp, K. E. (2006). Global and local processing in adult humans (*Homo sapiens*), 5-year-old children (*Homo sapiens*), and adult cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology, 120*, 323−330. http://dx.doi.org/10.1037/0735-7036.120.4.323.

Nguyen, A. P., Spetch, M. L., Crowder, N. A., Winship, I. R., Hurd, P. L., & Wylie, D. R. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: Implications for the evolution of "visual streams". *Journal of Neuroscience, 24*, 4962−4970.

Norman, J. F., Todd, J. T., & Orban, G. A. (2004). Perception of three-dimensional shape from specular highlights, deformations of shading, and other types of visual information. *Psychological Science, 15*, 565−570.

Palmer, S. E. (1999). *Vision science: Photons to phenomenology*. Cambridge: MIT Press.

Petersen, S. E., Robinson, D. L., & Morris, J. D. (1987). Contributions of the pulvinar to visual spatial attention. *Neuropsychologia, 25*, 97−105.

Qadri, M. A. J., Asen, Y., & Cook, R. G. (2014). Visual control of an action discrimination in pigeons. *Journal of Vision, 14*, 1−19. http://dx.doi.org/10.1167/14.5.16.

Qadri, M. A. J., & Cook, R. G. (2014). The perception of glass patterns by starlings (*Sturnus vulgaris*). *Psychonomic Bulletin & Review*, 1−7. http://dx.doi.org/10.3758/s13423-014-0709-z.

Qadri, M. A. J., Romero, L. M., & Cook, R. G. (2014). Shape-from-shading in European starlings (*Sturnus vulgaris*). *Journal of Comparative Psychology, 128*, 343−356. http://dx.doi.org/10.1037/a0036848.

Ramachandran, V. S. (1988). Perception of shape from shading. *Nature, 331*, 163−166.

Reichardt, W. (1987). Evaluation of optical motion information by movement detectors. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 161*, 533−547. http://dx.doi.org/10.1007/BF00603660.

Reid, S., & Spetch, M. L. (1998). Perception of pictorial depth cues by pigeons. *Psychonomic Bulletin and Review, 5*, 698−704.

Reiner, A., Perkel, D. J., Bruce, L. L., Butler, A. B., Csillag, A., Kuenzel, W., et al. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *Journal of Comparative Neurology, 473*, 377−414.

Rilling, M., De Marse, T., & La Claire, L. (1993). Contour deletion as a method for identifying the weights of features underlying object recognition. *Quarterly Journal of Experimental Psychology, 46*, 43–61.

Robinson, D. L., & Petersen, S. E. (1992). The pulvinar and visual salience. *Trends in Neurosciences, 15*, 127–132.

Ro, T., & Rafal, R. (2006). Visual restoration in cortical blindness: Insights from natural and TMS-induced blindsight. *Neuropsychological Rehabilitation, 16*, 377–396.

Rowland, H. M., Cuthill, I. C., Harvey, I. F., Speed, M. P., & Ruxton, G. D. (2008). Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. *Proceedings of the Royal Society B: Biological Sciences, 275*, 2539–2545.

Rubidge, B. S., & Sidor, C. A. (2001). Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics*, 449–480.

Sekuler, A. B., Lee, J. A. J., & Shettleworth, S. J. (1996). Pigeons do not complete partly occluded figures. *Perception, 25*, 1109–1120.

Sereno, P. C. (1999). The evolution of dinosaurs. (Cover story). *Science, 284*, 2137–2147.

Shimizu, T., & Bowers, A. N. (1999). Visual circuits of the avian telencephalon: Evolutionary implications. *Behavioural Brain Research, 98*, 183–191.

Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *Journal of Neuroscience, 22*, 8334–8345.

Smith, M. A., Kohn, A., & Movshon, J. A. (2007). Glass pattern responses in macaque V2 neurons. *Journal of Vision, 7*, 5.

Smulders, T. V. (2009). The relevance of brain evolution for the biomedical sciences. *Biology Letters, 5*, 138–140.

Soto, F. A., & Wasserman, E. A. (2014). Mechanisms of object recognition: What we have learned from pigeons. *Frontiers in Neural Circuits, 8*, 1–22.

Spetch, M. L., Cheng, K., & Mondloch, M. V. (1992). Landmark use by pigeons in a touch-screen spatial search task. *Animal Learning & Behavior, 20*, 281–292.

Spetch, M. L., & Edwards, C. A. (1988). Pigeons, *Columba livia*, use of global and local cues for spatial memory. *Animal Behaviour, 36*, 293–296.

Spetch, M. L., & Friedman, A. (2006). Comparative cognition of object recognition. *Comparative Cognition & Behavior Reviews, 1*, 12–35.

Spinozzi, G., De Lillo, C., & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 117*, 15–23. http://dx.doi.org/10.1037/0735-7036.117.1.15.

Srinivasan, M. V. (2010). Honey bees as a model for vision, perception, and cognition. *Annual Review of Entomology, 55*, 267–284. http://dx.doi.org/10.1146/annurev.ento.010908.164537.

Srinivasan, M. V., Poteser, M., & Kral, K. (1999). Motion detection in insect orientation and navigation. *Vision Research, 39*, 2749–2766.

Srinivasan, M. V., Zhang, S. W., Berry, J., Cheng, K., & Zhu, H. (1999). Honeybee navigation: Linear perception of short distances travelled. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 185*, 239–245.

Tanaka, H. K., & Fujita, I. (2000). Global and local processing of visual patterns in macaque monkeys. *Neuroreport, 11*, 2881–2884.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97–136.

Treisman, A., & Gormican, S. (1988). Feature analysis in early vision: Evidence from search asymmetries. *Psychological Review, 95*, 15–48.

Treisman, A., & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 459–478.

Ushitani, T., & Fujita, K. (2005). Pigeons do not perceptually complete partly occluded photos of food: an ecological approach to the "pigeon problem". *Behavioural Processes, 69*, 67–78.

Vallortigara, G. (2006). The cognitive chicken: Visual and spatial cognition in a nonmammalian brain. In E. A. Wasserman, & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 71–86). New York, NY: Oxford University Press.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation*. Bloomfield Hills: Michigan Cranbook Institute of Science.

Wang, Y. C., Jiang, S., & Frost, B. J. (1993). Visual processing in pigeon nucleus rotundus: Luminance, color, motion, and looming subdivisions. *Visual Neuroscience, 10*, 21–30.

Wessinger, C. M., & Gazzaniga, M. S. (2005). Blindsight: Hypotheses and clinical implications. *Handbook of Clinical Neurophysiology, 5*, 441–450.

Wilkinson, F., James, T. W., Wilson, H. R., Gati, J. S., Menon, R. S., & Goodale, M. A. (2000). An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings. *Current Biology, 10*, 1455–1458. http://dx.doi.org/10.1016/S0960-9822(00)00800-9.

Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in glass patterns: Implications for form vision. *Vision Research, 38*, 2933–2947.

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 419–433.

Young, M. E., Peissig, J. J., Wasserman, E. A., & Biederman, I. (2001). Discrimination of geons by pigeons: the effects of variations in surface depiction. *Animal Learning & Behavior, 29*, 97–106.

Zeigler, H. P., & Bischof, W. F. (1993). *Vision, brain, and behavior in birds*. Cambridge, MA: MIT Press.