

The perception of Glass patterns by starlings (*Sturnus vulgaris*)

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Published online: 13 August 2014
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Abstract Glass patterns are structured dot stimuli used to investigate the visual perception of global form. Studies have demonstrated that humans and pigeons differ in their processing of circular versus linearly organized Glass patterns. To test whether this comparative difference is characteristic of birds as a phylogenetic class, we investigated for the first time how a passerine (starlings, *Sturnus vulgaris*) discriminated multiple Glass patterns from random-dot stimuli in a simultaneous discrimination. By examining acquisition, steady-state performance, and the effects of diminishing global coherence, it was found that the perception of Glass patterns by 5 starlings differed from human perception and corresponded to that established with pigeons. This suggests an important difference in how birds and primates are specialized in their processing of circular visual patterns, perhaps related to face perception, or in how these highly visual animals direct attention to the global and local components of spatially separated form stimuli.

Keywords Comparative cognition · Visual perception · Glass pattern · Starling · *Sturnus vulgaris*

The mechanisms of object perception remain a long-standing and fundamental topic for comparative investigation (e.g., Fujita, Tanaka, Ito, & Cheng, 1992; Hubel & Wiesel, 1962). Comparing visual cognition in birds and mammals is particularly crucial because they represent the two major classes of

visually dominant, mobile, social vertebrates on the planet. Understanding visual perception and its neural substrates in these different phylogenetic classes is essential to developing a complete and general science of vision. The pressures of muscle-powered flight over the last 250 million years of separate evolution has limited the overall size and neural organization of birds in ways that are different from mammals (Husband & Shimizu, 2001; Jarvis et al., 2005). This makes birds critical to understanding the evolution and implementation of vision in small, nuclearily organized, primarily collothalamal neural system in comparison with the larger, laminar, primarily lemnothalamal design of mammalian visual hardware. Despite the unquestioned excellence of avian vision, the vast preponderance of knowledge about avian visual cognition comes from a single species, the pigeon (Cook, 2001; Zeigler & Bischof, 1993). Because of decades of intense focus, this readily available columbiform species is the best understood avian visual system from physiology to behavior.

What has not been determined is whether the pigeon is a representative model species for this large class of animals (>9,000 species; Bock & Farrand, 1980). There are clear differences in peripheral visual organization among different birds that seem related to their natural histories (e.g., Martin, 2007). Furthermore, the limited previous behavioral research with other bird species has frequently produced results that diverge from those with pigeons (e.g., Forkman, 1998; Vallortigara, 2006). Given these discrepancies and the paucity of information from other bird species, testing the generality and representativeness of the dominant pigeon model with a broader examination of visual cognition in other birds is necessary (Cook, 2001; Emery, 2006).

Toward that goal, we have recently begun evaluating visual cognition in the European starling (*Sturnus vulgaris*). Starlings are a common, highly visual, diurnal, ground-feeding passerine species (Feare, 1984). Passerines are the

Electronic supplementary material The online version of this article (doi:10.3758/s13423-014-0709-z) contains supplementary material, which is available to authorized users.

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largest and most widespread order of birds. Consequently, understanding how a passeriform species processes various fundamental components of visual objects is an excellent starting point for a broader comparative examination of avian visual cognition. Research on passerine vision has principally examined peripheral sensory mechanisms (Dolan & Fernández-Juricic, 2010; Endler, Westcott, Madden, & Robson, 2005; Hart, 2001; Jones, Pierce, & Ward, 2007; Martin, 2007; Zeigler & Bischof, 1993). These have revealed that starlings and pigeons are relative similar in the horizontal extent of their monocular and binocular visual fields (Martin, 1986). There are differences, however, in the distributions of cones across the eyes and in their contrast sensitivity function, at least as measured using an electroretinogram (Ghim & Hodos, 2006; Hart, Partridge, & Cuthill, 2000). One study has suggested that starlings and pigeons may differ in their lateralization of different visual functions (Templeton & Gonzalez, 2004). Lastly, a multivariate analysis of the brain compositions of various birds has suggested that since diverging between 70 to 120 million years ago (Brown, Rest, Garcia-Moreno, Sorenson, & Mindell, 2008; Chojnowski, Kimball, & Braun, 2008), passeriformes and columbiformes have evolved dissimilar cerebrotypes, with different relative proportions of cerebellum, brainstem, and telencephalic regions, including areas known to process vision (Iwaniuk & Hurd, 2005). Surprisingly little is known about how starlings cognitively process more complex visual information, especially in comparison with other birds (Bennett, Cuthill, Partridge, & Lunau, 1997; Cook, Qadri, Kieres, & Commons-Miller, 2012; Qadri, Romero, & Cook, *in press*; Swaddle, Che, & Clelland, 2004; Templeton & Gonzalez, 2004). Here, we started by examining how starlings process Glass patterns.

Glass patterns are theoretically revealing stimuli created by taking randomly placed dots, offsetting them appropriately, and superimposing the transposed result on the original stimulus (Glass, 1969). Humans readily perceive the global organization of the resultant Glass patterns. Furthermore, humans detect circular or radial Glass patterns through random noise more easily than translational or spiral patterns (Kelly, Bischof, Wong-Wylie, & Spetch, 2001; Wilson & Wilkinson, 1998). A similar hypersensitivity to circular information has been found testing gratings in nonhuman primates (Gallant, Braun, & Van Essen, 1993). It has been hypothesized that this is caused by specialized concentric form detectors that are precursors to the inferior temporal cortex processing of faces (Wilson, Wilkinson, & Asaad, 1997).

Testing Glass patterns with pigeons, Kelly et al. (2001) found that they differed from humans. Unlike humans, pigeons exhibited no circular advantage, discriminating all types of Glass patterns equivalently from their random-dot alternative. What is not clear is whether this comparative divergence is limited to pigeons or, instead, represents a class difference between birds and primates generally.

To examine these comparative alternatives, five starlings were tested for their capacity to discriminate four types of Glass patterns from the random-dot pattern tested by Kelly and colleagues (2001), using a simultaneous choice discrimination in a live-in testing procedure. If the starlings exhibit a pigeon-like equivalence in discriminating the different Glass patterns, it would suggest that diurnal birds may generally process complex visual form information in similar ways. It would further imply that the pigeon may indeed be a representative model for studying avian visual cognition. Most important, it would suggest that birds and mammals differ in how they process visual information, carrying the larger implication that multiple computational and neural solutions for visual excellence exist. If the starlings show a primate-like pattern of results, on the other hand, it would suggest that a broader comparative psychology of avian visual cognition is necessary and that at least some avian and mammalian species may have converged upon similar computational solutions to visual perception, despite their considerably different evolutionary history and contrasting neural organizations.

Method

Animals

Five wild-caught starlings were tested (3 females and 2 males). Four had served in a shape-from-shading experiment (Qadri et al., *in press*). They were individually housed in a single room on a 12:12-h light:dark cycle (7:00 a.m.–7:00 p.m.). The starlings maintained their own weights during testing (~85%–100% their free-feeding weights). All procedures were approved by the Tufts University IACUC.

Apparatus

Since details for this apparatus have been reported elsewhere (Qadri et al., *in press*), only the critical details are outlined here. Each starling was continuously tested in its own “live-in” housing/testing chamber consisting of a home cage and a testing area without any divider. One wall of the testing area was clear Plexiglas, behind which an LCD monitor was located (Dell 1908; resolution of 1,440 × 1,024 pixels). The testing area had three horizontal, computerized 13-cm wooden perches parallel to the monitor, one central *ready perch* (20.1 cm from the monitor) that was used to start each trial and two laterally positioned *choice perches*. A food dish in front of each choice perch collected food (Mazuri Insectivore diet 5MK8/5MM3) from external computer-controlled feeders (Coulbourn Instrument Pellet Feeder H14-23R). A centrally located houselight was on continuously, except during timeouts. The chambers were arranged on shelves so that the birds could not see each other, although vocalizations and

other activities were audible. Room ventilation masked noises from outside the colony room.

Stimuli

Four types of Glass patterns modeled after those used in Kelly et al. (2001) were tested: concentric, radial, vertical, and horizontal (see Fig. 1). Kelly and colleagues' fifth random pattern, consisting of randomly placed dots, was also tested in order to permit the best comparison with pigeons. Stimuli consisted of small, filled white dots ($\sim 0.5^\circ$; using the distance between the center perch and the monitor as viewing distance) on a black background. The first week of training had briefly included trials testing black dots on white backgrounds, but these were eliminated once it became clear that they supported consistently poorer performance for all starlings.

Three local dot patterns were used to create the global patterns. Traditional *dipole* Glass patterns consisted of an array of 100 randomly placed dots with a duplicated array of dots offset by 1.4° (center-to-center; visual angle measured from the ready perch; 200 total dots) forming dipoles that followed the intended global pattern. *Tripole* and *quadrupole* local dot patterns (300 and 400 dots per stimulus, respectively) were created by reduplicating the original random pattern while maintaining equal interdot distances between successive duplications (see Fig. S1). All local dot patterns were randomly located on each trial. These local patterns were packed into three different display sizes subtending 22.2° , 29.5° , and 36.6° of visual angle (see Fig. S1 for examples). These variations extending Kelly and colleagues' (2001) stimuli were added to ensure a broad coverage of conditions, given that we were testing a new species, and to encourage global processing.

After acquisition, the coherence level of dipole-composed Glass patterns was varied from 20 % to 100 %. Coherence values corresponded to the number of dipoles that followed

the contour of the global pattern. Thus, a 20 % coherence condition for any Glass pattern would have 20 randomly placed dipoles oriented according to the global rule and the remainder of the dots randomly placed.

Experimental testing

Each trial was triggered by the starling landing on the ready perch for 300 ms when the 2.5 cm ready signal was on. This resulted in one Glass pattern stimulus and one random stimulus (matched for number of dots and visual angle) to be displayed on the left and right halves of the display (randomly determined on each trial). A correct choice, made by landing on the choice perch in front of the random stimulus, was rewarded with food. An incorrect choice, made by landing on the choice perch on the side of a Glass pattern, resulted in a 30-s dark timeout. To discourage response perch biases, trials were repeated until the correct perch was chosen. These repeated trials were excluded from all calculations of choice accuracy. If neither side perch was selected within 30 s of stimulus onset, the stimuli were removed, and the trial was repeated. Because the stimuli on such trials may have been "previewed," these trials were excluded from reaction time analyses ($<2.5\%$ of trials).

The starlings continuously tested themselves throughout the day, with each bird determining its own rate of testing. This experiment was conducted in counterbalanced blocks of trials that started between 10 a.m. and 2 p.m. and lasted until the end of the light cycle of each day (the early periods of daily testing were devoted to other unrelated testing). During acquisition, 72-trial blocks were composed of equal numbers of trials testing the four Glass patterns at the three display sizes and three local set sizes. Unfinished blocks at the end of a day were truncated. Acquisition continued until the starling reached a criterion of 90 % accuracy over 360 successive trials. A baseline period was conducted following acquisition. Due to the nature of self-paced testing, each starling completed a different number of trials during this baseline period. The starlings performed, on average, 310 trials per day (individual birds #1O = 343, #2R = 242, #3S = 157, #4U = 423, #5 V = 383 trials per day). A minimum of 21 days of baseline testing was collected from each bird.

Finally, we then tested the starlings with multiple levels of stimulus coherence. Five levels of coherence values (20 %, 40 %, 60 %, 80 %, and 100 % coherent) were tested using just the dipole displays (60 trials per block; four Glass patterns \times five coherence levels \times three display sizes). These were randomly mixed with trials built from the two other local patterns (24 additional trials). These 84-trial blocks were tested until all combinations of coherence and patterns had been tested a minimum of 150 times with each bird (the least productive starling, #3S, only completed 50 trials with each configuration).

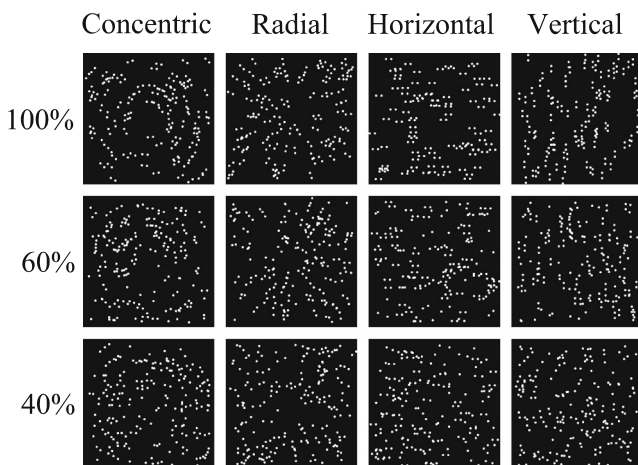


Fig. 1 Examples of the four Glass patterns tested with the starlings. These examples represent displays constructed from 100 dipoles. The central location of each dipole was randomly generated on each trial

Results

All five starlings quickly learned the task. Two starlings showed above-chance choice accuracy within fewer than 400 trials (>60 % on 144 successive trials), two within 800 trials, and the last one by on 2,300 trials. Four starlings reached the 90 % accuracy criterion in an average of 3,462 trials (range: 2,499–5,320), while the slowest bird took 8,947 trials. More important, all starlings exhibited equivalent rates of learning with the four Glass patterns. This can be seen in Fig. 2, which shows the mean rate of acquisition for the different Glass patterns. A repeated measures (RM) ANOVA (Glass pattern \times block) using choice accuracy revealed a significant main effect of block, $F(9, 36) = 14.8, p < .001, \eta^2_p = .79$, but no main effect of Glass pattern, $F(3, 12) < 1$, or its interaction with block, $F(27, 108) = 1.5, p = .072$ (all analyses evaluated at $\alpha \leq .05$). Examination of the median choice reaction time (RT) for correct response trials (mean median RT: 1,696 ms) also found no reliable differences among the different Glass patterns over this period of testing: concentric, 95 % CI [583, 2,734]; radial [602, 2,849], horizontal [658, 2,713], vertical [652, 2,780].

During postacquisition baseline testing, the starlings continued to discriminate the different Glass patterns equivalently. Since there were no overall differences among the different Glass patterns across the starlings, Fig. 3 depicts only the effects

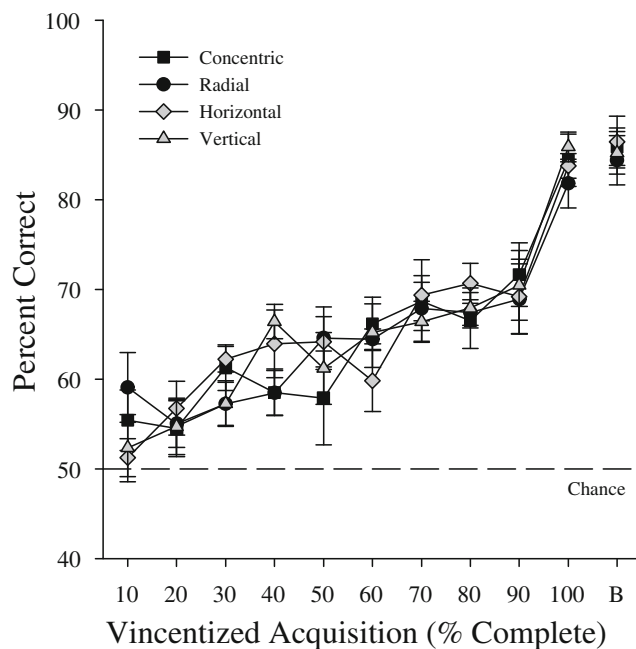


Fig. 2 Accuracy during learning. All starlings learned during the live-in procedure with the four different Glass patterns. To adjust for the self-paced rate of testing and learning for each bird, the results have been Vincitized to show learning as a function of the percentage of total acquisition time needed for each bird to reach criterion. The final time point (labeled B) shows accuracy during the baseline test period. Error bars indicate standard error

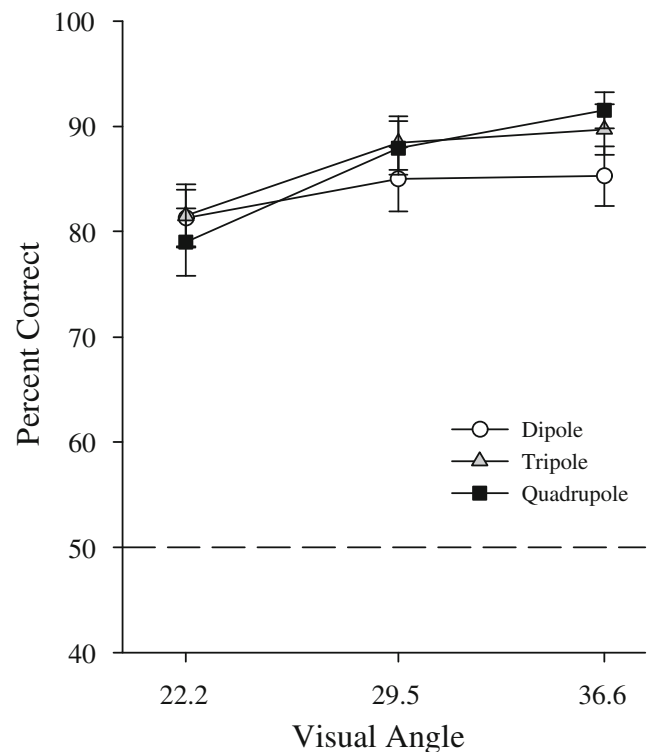


Fig. 3 Accuracy during the baseline test period. Accuracy is displayed as a function of display size and type of local dot pattern. Error bars indicate standard error

of display size and local dot pattern on choice accuracy. While overall accuracy remained high, smaller displays with fewer dots in the local dot group did reduce accuracy independently of the type of Glass pattern tested. An RM ANOVA (local dot pattern \times display size \times Glass pattern) on baseline accuracy revealed significant main effects of display size, $F(2, 8) = 22.3, p = .001, \eta^2_p = .85$, and local dot pattern, $F(2, 8) = 6.7, p = .019, \eta^2_p = .63$, and their significant interaction, $F(4, 16) = 6.8, p = .002, \eta^2_p = .63$. This interaction reflects that accuracy improved across display sizes more so for the denser quadrupole displays than for the dipole displays. More critically, no main effect of Glass pattern, $F(3, 12) = 2.1, p = .156$, or its interactions with either of these two displays factors $F_s < 1.5, p_s > .225$, was found, indicating that the global pattern did not affect the starlings' accuracy regardless of the display conditions tested. Comparable statistical examinations of median correct RTs also found no differences among the Glass patterns.

Finally, Fig. 4 depicts the starlings' discrimination of the dipole Glass patterns as a function of stimulus coherence. Overall, choice accuracy linearly and significantly declined with decreasing stimulus coherence for all Glass patterns, $r^2_s \geq .973$. Unlike in humans, no advantage for any of the Glass patterns emerged at any level of coherence. An RM ANOVA (stimulus coherence \times Glass pattern \times display size) on choice accuracy revealed significant main effects of display size $F(2, 8) = 15.5, p = .002, \eta^2_p = .79$, and stimulus

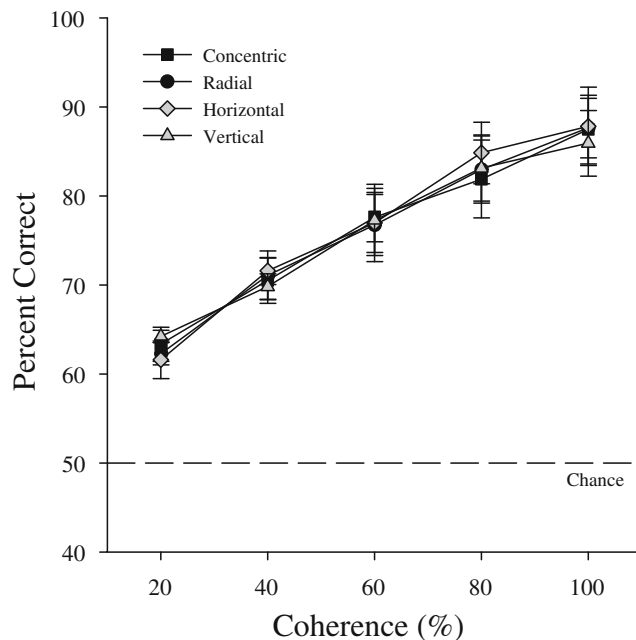


Fig. 4 Accuracy for each of the Glass patterns as a function of stimulus coherence during testing. Error bars indicate standard error

coherence, $F(4, 16) = 50.1$, $p < .001$, $\eta_p^2 = .93$, but no significant main effect or interactions with the different types of Glass pattern.

Discussion

These experiments revealed for the first time that starlings can discriminate Glass patterns from comparable random displays. The starlings' accuracy and RT did not vary across the four different Glass patterns as tested over a wide set of display conditions. This equivalence was true during acquisition, after learning, over different display sizes, across different local dot patterns, and through progressive degradations of the global patterns by the addition of random noise. Thus, unlike humans, the starlings showed no psychological advantage for circularly organized Glass patterns. These results do correspond, however, with those previously found with pigeons (Kelly et al., 2001). Overall, the starlings' choice behavior across the different manipulations and measures was remarkably similar to that of pigeons. This comparative correspondence across these different orders of birds indicates that their visual mechanisms for processing these patterns of spatially distributed elements were similar, if not identical. This carries the larger implication that Glass pattern equivalence may be a widely shared feature across this phylogenetic class of animal (although testing other contrasting bird orders would be helpful). This further suggests that birds may differ fundamentally from primates in the visual mechanisms underlying the grouping and integration of separated local and global information.

Despite the 70 to 120 million years since their last common ancestor (Brown et al., 2008; Chojnowski et al., 2008) and the resulting differences in neural organization (Iwaniuk & Hurd, 2005), this correspondence in the discrimination of Glass patterns among birds suggests that the visual mechanisms of these two species are highly similar. This suggests that the specific mechanisms underlying visual processing in birds is likely phylogenetically old and potentially resistant to substantial changes to their organization (Gutiérrez-Ibáñez et al., 2014). Alternatively, this similarity could indicate convergent evolution resulting from their similar visual ecologies. Both species are diurnal and primarily ground-feeding, although they search for different types of food. Testing a third bird species that occupies a different niche would be informative. Localizing these behavioral results to brain functions in regions that have remained relatively static or have differentially evolved between these species would also be informative (Iwaniuk & Hurd, 2005). Assuming that global perception is involved, the avian tectum, which processes information across a wide array of visual angles (Jassik-Gerschenfeld & Guichard, 1972), is likely a critical locus for the processing of these displays. One possible behavioral difference between these two bird species concerns the relative ease of learning the discrimination. All five starlings learned quickly. Contrastingly, approximately one third of Kelly and colleagues' pigeons failed to learn the basic task. Whether this reflects a critical species difference or is the benefit of the greater variety in training conditions provided to our starlings is unclear. Regardless of the source, any difference between these two bird species appears relatively minor, as related to the processing of these stimuli.

The larger difference between humans and birds in their relative discrimination of circularly and linearly organized Glass patterns can be considered from two perspectives. One alternative is that this is an indication that circular organizations are important to only one of these classes of animals. So far, only humans and nonhuman primates have shown an enhanced ability to detect circular forms in similar paradigms (Wilson & Wilkinson, 1998). One hypothesis has suggested that this circular form advantage in humans results from the specialized processing of face-like information in the precursors to the fusiform face area (Wilkinson et al., 2000). Faces have predictable components arrayed in close, circular-like areas and are likely salient, especially for highly social animals with compact, flat, forward faces. Therefore, specialized processing mechanisms in primates would not be surprising (Kanwisher & Yovel, 2006). The natural history and lateral-eyed facial structure of birds, however, may lend no particular importance to this organization. Thus, the pigeons and starlings may attend to the global form of the Glass patterns but lack the specialized mechanisms responsible for our circular benefit.

Perceiving the global organization of dots is not, however, entirely unnatural and irrelevant for starlings. Their namesake

is the extensive frontal pattern of whitish “stars” located on the tips of their neck and chest feathers, a “dot” pattern known to affect their social interactions (Swaddle & Witter, 1995). Investigations of global symmetry perception of dot stimuli designed to mimic this natural pattern, however, have produced mixed results in starlings (Swaddle & Pruett-Jones, 2001; Swaddle & Witter, 1995). Other visual features related to this aspect of their plumage are yet untested. Testing starlings with dot displays arrayed more similarly to their natural chest curvature or plumage could aid in determining whether and how specialized global shape or pattern detectors evolved in these animals.

An alternative to this visual specialization account of the comparative difference in Glass pattern perception considers the effect of spatial scale. While humans primarily rely on globally perceiving these Glass patterns, local solutions to their structure are possible. By attending to areas smaller than the full Glass pattern, like just the top-right region of each stimulus, the stimuli can be discriminated without truly “seeing” the global pattern, as Kelly and colleagues (2001) suggest about their subjects. Increasingly, studies have suggested that pigeons have a strong local bias when processing hierarchical form information, even when global information is available and useful (e.g., Cavoto & Cook, 2001). The starlings’ performance carries a possibly similar implication, despite our attempts to specifically encourage and enhance control by global organization by varying display features. It is premature to conclude that starlings are as locally biased as pigeons until a wider variety of conditions and tasks have been investigated. The present results, however, raise the distinct possibility that a local bias in the processing of visual information may be a general property of avian cognition.

If birds attend more to local details or use different specialized visual features, it would be a meaningful and fundamental difference in the visual mechanisms of these two classes of highly visual vertebrates. How such potential differences in visual cognition between mammals and birds are specifically tied to their different underlying lemnthalamic and collothalamal neural structures is an important direction for future studies. The present results indicate that the comparative examination of visual object discrimination, recognition, and categorization by testing multiple species across a wide phylogenetic spectrum can provide new insights to our understanding of vision and perception in human and nonhuman animals. A truly general theory of visual cognition should follow from such comparative efforts.

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