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The Perception of Glass Patterns by Starlings (*Sturnus vulgaris*)

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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. Examining acquisition, steady-state performance, and the effects of diminishing global coherence, it was found that the perception of Glass patterns by five 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.

The cognitive and neural mechanisms of object perception remain a long-standing, rich, and fundamental topic for comparative investigation [e.g. 1,2]. Comparing visual cognition in birds and mammals is particularly important because they represent the two major classes of visually-dominant, mobile, social vertebrates on the planet. The pressures of muscle-powered flight over the last 250 million years of separate evolution, however, has limited the overall size and neural organization of birds in ways that are quite different from mammals [3,4]. This makes birds critical to understanding the evolution and implementation of vision in small, nuclearly-organized, collothalamie neural system in comparison to the laminar, lemnothalamie design of mammalian visual hardware. Hence, understanding visual perception and its neural substrates in these different phylogenetic classes of vertebrates is essential to developing a complete and general science of vision. Because of their small size and contrasting visual organization, birds may hold important keys to new treatments for human blindness and the engineering of visual prostheses [5,6]. Despite the unquestioned excellence of avian vision, the vast preponderance of knowledge about visual cognition in birds has come from studying a single species, the pigeon [7,8]. Because of several decades of intense focus, this readily available columbiform species is the best understood avian visual system at every level of organization from physiology to behavior.

What has not been determined is whether the pigeon is a representative model species for this large class of animals [> 9000 species, 9]. There are clear differences in peripheral visual organization among different birds that seem related to their natural histories [e.g. 10]. Further, the limited behavioral research with other bird species has frequently produced results that diverge from those found with pigeons [e.g., 11,12]. Given these discrepant results and the sheer 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 bird species is necessary [7,13].

Towards 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 [14]. **Passerines are the largest and most widespread order of birds.** Research on passerine vision has principally examined peripheral sensory mechanisms [8,10,15-17]. Thus, surprisingly little is known about how they process more complex visual information [18-22]. 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. Here we started by examining how starlings process Glass patterns.

Glass patterns are theoretically revealing stimuli created by taking a set of randomly placed dots, offsetting the dots slightly, and superimposing the transposed result on the original stimulus [23]. Humans readily perceive the global organization of such Glass patterns. Furthermore, humans detect circular or radial dot patterns more easily than translational or spiral patterns [24-26]. Similar hypersensitivity to circular information has been found when testing gratings in non-human primates [27]. It has been hypothesized that this is caused by specialized concentric form detectors that are precursors to the inferior temporal cortex processing of faces [28].

Testing Glass patterns with pigeons, Kelly, Bischof, Wong-Wylie and Spetch [25] found that pigeons differed from humans. Unlike humans, the pigeons exhibited no circular advantage, discriminating all types of Glass patterns equivalently from a random dot alternative. What is not clear is whether this comparative divergence is related to how pigeons specifically process these patterns or if it represents a class difference in how birds generally process these revealing stimuli.

To examine these comparative alternatives, five starlings were tested for their capacity to discriminate four types of Glass patterns from random dot patterns using a live-in testing procedure with a simultaneous choice discrimination. If the starlings exhibit a pigeon-like equivalence in discriminating the different stimuli, it would suggest that diurnal birds may process complex visual form information in highly similar ways. It could further imply that the pigeon model may be a representative one for the study of avian visual cognition. It would also importantly suggest that birds and mammals differ in how they process visual information. This would carry the larger implication that there are multiple computational and neural solutions to the problem of visual excellence. 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.

Methods

Ethics Statement. All procedures were approved by the Tufts University Internal Animal Care and Use Committee (protocol #M2011-21).

Animals. Five wild-caught starlings were tested (3 females & 2 males based on iris coloration). Four had served in a shape-from-shading experiment [29]. They were individually housed in cages attached to each animal's testing apparatus and housed in a single common colony room on a 12:12 LD cycle (7:00 AM-7:00 PM). The starlings maintained their own weights during testing (~85%-100% their free-feeding weights).

Apparatus. Each starling was continuously tested in its own "live-in" housing/testing chamber consisting of two areas. One area was a dark-gray PVC testing chamber (35.5 cm wide

× 35.5 cm high × 30.0 cm deep) that was attached to a wire home cage (35.5 cm × 46.0 cm × 34.5 cm). The far outside wall of the testing area was clear Plexiglas behind which an LCD monitor was located (Dell 1908; resolution of 1440×1024 pixels). The testing area had three horizontal, computerized 13-cm wooden perches parallel to the monitor. The central *ready perch* was 20.1-cm from the monitor and used to start each trial. Two lateral *choice perches* were attached to the right and left walls of the testing area (10.8 cm from monitor & 9.8 cm above the floor). A food dish in front of each choice perch delivered food (Mazuri Insectivore diet 5MK8/5MM3) from external computer-controlled feeders (Colbourn Instrument Pellet Feeder H14-23R). A centrally located houselight in the testing area 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. [25] were tested: concentric, radial, vertical, & horizontal (see Figure 1). A fifth random pattern was also tested. Stimuli consisted of small, filled white dots ($\sim .5^\circ$; 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 offset by 1.4° (center-to-center; visual angle measured from the ready perch; 200 total dots) such that they formed dipoles that followed the contour of the intended global pattern. *Tripole* and *quadrupole* local dot patterns (300 and 400 dots per stimulus, respectively) were created by re-duplicating

the original random pattern while maintaining equal inter-dot distances between successive duplications (see Figure S1 for examples). These two added patterns were included to ensure a broad coverage of possible stimulus conditions given that we were testing a new species. All local dot patterns were randomly located on each trial. These local patterns were packed into a bounding box of three different sizes subtending 22.2, 29.5, and 36.6 degrees of visual angle (see Figure S1 for examples). On each trial, the random stimulus that was paired with one of the four Glass patterns was matched for total number of dots and display size.

After acquisition, the coherence level of the 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 random stimulus and one Glass pattern stimulus to be displayed on the left and right halves of the LCD display. The side with the random stimulus was randomly determined on each trial. A correct choice was made by landing on the choice perch on the side with the random stimulus. Correct choices were rewarded with access to food. An incorrect choice, made by landing on the choice perch on the side of a Glass pattern, resulted in a 30 s timeout in which the overhead light was turned off. To discourage response perch biases, a correction procedure was used in which trials were repeated until the correct perch was chosen. These correction trials were excluded from all calculations of choice accuracy. If neither side perch was selected within 30 s of stimulus onset, the stimuli were turned off and the trial terminated. The trial was then repeated with the next ready signal

response. Because the stimuli on such trials may have been “previewed,” any such repeated trials were excluded from reaction time analyses (less than 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 AM to 2 PM and lasted until the end of the light cycle of each day (the early periods of daily testing were devoted to other visual or auditory testing). During acquisition, strings of 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, #5V=383 trials per day). A minimum of at least 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 x five coherence levels x three display sizes). These were randomly mixed into blocks that tested 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).

Results

All five starlings quickly learned the task. Two starlings showed above-chance choice accuracy in less than 400 trials (>60% in 144 successive trials), two within 800 trials, and the last one in 2300 trials. Four starlings reached the 90% accuracy criterion in an average of 3462 trials (range: 2499–5320), while the slowest bird took 8947 trials. More importantly, all starlings exhibited equivalent rates of learning with the four different Glass patterns. This can be seen in Figure 2 which shows the mean rate of acquisition for the four different Glass patterns. To adjust for the self-paced rate of testing for each bird, the results have been Vincentized to show learning as a function of the percentage of total acquisition time needed for each bird to reach criterion. A repeated measures (RM) ANOVA (Pattern x Vincentized block) using choice accuracy revealed a significant main effect of block, $F(9, 36) = 14.8$, partial $\eta^2 = .79$, but no main effect of Glass pattern, $F(3, 12) < 1$, or its interaction with block, $F(27, 108) = 1.5$ (all of these and subsequent analyses evaluated at an $\alpha \leq .05$). Examination of the median choice reaction time (RT) for correct response trials (mean median RT 1696 ms) also found no reliable differences among the different Glass patterns over this period of testing: concentric, 95% CI [583, 2734]; radial [602, 2849], horizontal [658, 2713], vertical [652, 2780].

During post-acquisition baseline testing, the starlings continued to discriminate the different Glass patterns equivalently. The last time point included in Figure 2 (labeled B) shows mean choice accuracy with the four different Glass patterns during baseline testing. Because there were no overall differences among the different Glass patterns across the starlings, Figure 3 depicts only the effects of display size and local dot pattern on choice accuracy. While overall levels of accuracy remained high, smaller displays with fewer dots in the local dot group did lower accuracy independent of the type of Glass pattern tested. A RM ANOVA (local dot pattern x display size x glass pattern) on baseline accuracy revealed significant main effects of display

size, $F(2, 8) = 22.3$, partial $\eta^2 = .85$, and local dot pattern, $F(2, 8) = 6.7$, partial $\eta^2 = .63$, and their significant interaction, $F(4, 16) = 6.8$, partial $\eta^2 = .63$. This interaction reflects how accuracy improved across display sizes more so for the denser quadrupole displays than the dipole displays. More critically, no main effect of Glass pattern or its interactions with either of these two displays factors was present over this extensive testing, $F_s < 2$, 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: concentric, 95% CI [442, 2831]; radial [400, 2892], horizontal [433, 2942], vertical [418, 2886].

Finally, Figure 4 depicts the starlings' discrimination of the dipole Glass patterns as a function of the degree 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. A RM ANOVA (Stimulus Coherence x Glass Pattern x Display size) on choice accuracy revealed significant main effects of display size $F(2, 8) = 15.5$, partial $\eta^2 = .79$, and stimulus coherence $F(4, 16) = 50.1$, partial $\eta^2 = .93$, 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 displays having an equivalent number of randomly placed dots. There were no differences in the starlings' accuracy or RT 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 inclusion of random dots. Thus, unlike humans, the starlings showed no psychological advantage for circularly-organized Glass patterns. These results do correspond, however, with those found previously with pigeons. Overall, the starlings' choice behavior across the different manipulations and measures were remarkably similar to those 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 global pattern equivalence in Glass patterns 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.

The corresponding discrimination of different Glass patterns across pigeons and starlings, despite the 70 to 120 million years since their last common ancestor [30,31] and the resulting differences in neural organization [32], suggests that their visual mechanisms remain highly similar. The one possible behavioral difference between these two bird species concerned the relative ease of learning the discrimination. All five starlings learned and did so quickly. Contrastingly, approximately one-third of Kelly and colleagues' pigeons failed to learn the basic discrimination task. Whether this reflects an important species difference or is the benefit of the greater variety in training conditions provided to the starlings is not clear. Regardless of the source, the difference between these two bird species appears relatively minor.

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 non-human primates have shown an enhanced ability to detect circular forms in similar paradigms [24], although cats and newborn chicks have shown limited evidence of possibly preferring circular organizations, too [33,34]. 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 [35,36]. Faces have components arrayed in close, circular-like areas and are likely salient, especially for highly social animals with compact, flat, forward faces. That specialized mechanisms for their perception may have evolved in humans would not be surprising [37]. The natural history and lateral-eyed facial structure of birds, however, may lend no particular importance to this type of global organization. Thus, it is possible that the starlings and pigeons attend to the global organization of Glass patterns, but do not have the same specialized mechanisms responsible for our circular preference.

That is not to say that perceiving the global patterns of dots is entirely unnatural and irrelevant for starlings. Their namesake comes from the extensive frontal pattern of whitish “stars” located on the tips of their neck and chest feathers, a pattern known to affect their social interactions [38]. Investigations of whether the global symmetry of dot stimuli designed to mimic this natural pattern, however, have produced mixed results in starlings [20,38]. Other visual features related to this specific aspect of their plumage have not been tested, however. Testing starlings in the future with dot displays arrayed more similarly to their natural chest curvature or plumage could aid in determining if 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 is one focused on the processing of spatial scale. While humans primarily rely on a global perception of the visual structure of these Glass patterns, local solutions to their

structure are possible. Because of the dot repetition used to create the pattern, Glass patterns can be discriminated from our random displays based on processing of localized dot spacing and orientation. Kelly and colleagues [25] suggested that their pigeon results reflected such attention to local information. A growing number of studies have suggested that pigeons have a strong local bias when it comes to processing hierarchical information, even when global information is available and useful [e.g., 39]. This raises the possibility that pigeons may be more strongly inclined to attend to this level of organization when processing visual objects in operant discriminations [40]. The starlings' behavior carries a possibly similar implication for that species, despite our attempts to specifically encourage and enhance control by global organization by varying the display size and the numbers of dots in the displays. 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 current 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 pay greater attention to local details or use different specialized visual features, it would be an important and fundamental difference in the visual approaches 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 tectothalamic and collothalamic neural structures is an important direction for future studies. The current results indicate that the comparative examination of visual object discrimination, recognition, and categorization by testing multiple species across a wide phylogenetic spectrum can provide important new insights to our understanding of vision and perception in human and non-human animals. A truly general theory of visual cognition should follow from such efforts.

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Figure Captions

Figure 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.

Figure 2. Accuracy during learning. Variation in accuracy from learning during the live-in procedure with the four different Glass patterns is shown across Vincentized training blocks, necessary given the variable nature of the animals' learning. The final time point (labeled B) shows accuracy during the baseline test period. Error bars indicate standard error.

Figure 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.

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

Supplementary Figure 1. Comprehensive sampling of displays used during training the starlings. The left labels indicate local group type, the top labels indicate global pattern, and the right labels indicate visual angle of the total pattern.