Journal of Comparative Psychology

Shape From Shading in Starlings (Sturnus vulgaris)

Muhammad A. J. Qadri, L. Michael Romero, and Robert G. Cook

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Muhammad A. J. Qadri, L. Michael Romero, and Robert G. Cook
Tufts University

Birds behave as if they quickly and accurately perceive an object-filled visual world. Beyond the extensive research with pigeons, however, there is a large and important gap in our knowledge about the mechanisms of object perception and recognition in other avian visual systems. The pattern of shading reflected from the surfaces of objects is one important optical feature that provides fundamental information about shape. To better understand how surface and object shading is processed by a passerine species, 5 starlings were tested with differentially illuminated convex and concave curved surfaces in 3 experiments using a simultaneous visual discrimination procedure. Starlings rapidly learned this shape-from-shading discrimination independent of varied lighting direction, surface color, and camera perspective. Variations in the pattern of lighting through experimental manipulations of camera perspective, surface height, contrast, material specularity, and surface shape were consistent with the hypothesis that the starlings perceived these illuminated surfaces as having 3-dimensional shape, similar to results previously collected with pigeons. These similarities across different orders of birds indicate that the relative shading of objects in a visual scene is a highly salient feature for shape processing in birds and is likely a highly conserved visual process that is widely distributed within this class of animal.

Keywords: shape from shading, visual perception, starling, comparative perception

One important visual property of most natural objects is that they have curved continuous surfaces that differentially reflect light. As a consequence, the patterns of lighting, shading, and shadow reflected from surfaces contain useful information about objects' shapes and locations in the environment. This type of lighting information makes essential contributions to the human perception of objects, depth, and scene layout (Gibson, 1950, 1979; Mingolla & Todd, 1986; Norman, Todd, & Orban, 2004; Ramachandran, 1988). They are also critically involved with many algorithms for machine vision and object recognition (Horn & Brooks, 1989; Zhang, Tsai, Cryer, & Shah, 1999), as well as the graphic visualization and portrayal of realistic scenes (Kniss, Premoze, Hansen, Shirley, & McPherson, 2003).

Given their reliance on vision for important activities such as flight and foraging, birds might also be sensitive to the shape

information given by differential shading, shadows, and specular highlights (shine). Prior studies with birds have employed a variety of methods, making generalization difficult, but they suggest that some of these lighting cues are used in both natural and laboratory settings (Cavoto & Cook, 2006; Hershberger, 1970; Hess, 1950; Reid & Spetch, 1998; Rowland, Cuthill, Harvey, Speed, & Ruxton, 2008; Young, Peissig, Wasserman, & Biederman, 2001).

Cook, Qadri, Kieres, and Commons-Miller (2012) recently investigated in pigeons the contributions of shading to the perception of three-dimensional (3D) smooth, curved surfaces. Their results indicated that pigeons readily use relative patterns of shading to identify the concavity or convexity of different shapes in a visual scene. The pigeons transferred a discrimination of shaded surface direction to novel perspectives of the scene, across changes in illumination, specularity, and lighting direction, as well as to novel surface shapes. When subsequently tested with videos in which the scene's lighting continuously changed, the pigeons continued to identify the shape information independent of the exact lighting at a given moment. Together, these results suggest that illumination-based information makes an important contribution when pigeons visually derive shape- and depth-based information about objects and their spatial relations in a scene.

Pigeons have been an important focus species for studies of complex perception and learning in comparative cognition (Cook, 2001a; Honig & Fetterman, 1992; Spetch & Friedman, 2006; Zeigler & Bischof, 1993). This development is more historical accident than design, as the selection of this columbiform species for early operant studies was driven primarily by considerations of pragmatism, husbandry, and availability. The intervening years of intensive study have resulted in the pigeon visual and cognitive systems being by far the best understood of any avian species. It remains an open question, however, as to whether the visual cognition of pigeons is representative of the

over 9,000 birds within this class of animal (Bock & Farrand, 1980).

Unfortunately, there is a regrettable lack of comparable research in any other bird species. Such comparative information is crucial to understanding the operation and function of vision in the behavior of birds, the evolution of this important modality, and its interaction with the processing of features in the natural visual environment. A better understanding of vision in birds generally would advance our understanding of the overarching principles by which different visual pattern-recognition systems represent the world (Marr, 1982). Our goal here was to advance the broader comparative investigation of visual processing by examining visual cognition in a passerine using the same approaches developed with pigeons. Despite being a highly successful order and extensively studied for other aspects of bird behavior, knowledge about the visual and cognitive mechanisms in passerines is decidedly limited. For this purpose, we chose to test starlings, another highly proliferative species of bird like the pigeon.

European starlings (*Sturnus vulgaris*) are a medium-sized passerine species. They are visual, diurnal, ground-feeding birds that forage for invertebrates by probing the upper soil surface or turf with their bills (Feare, 1984). Starlings have been an increasingly popular species for study, with widespread interest in their foraging and auditory behavior (Page, Hulse, & Cynx, 1989). Passeriformes and columbiformes 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 compositions of different birds has suggested that since diverging, passeriformes and columbiformes have evolved dissimilar cerebrotypes, with different relative proportions of cerebellum, brainstem, and telencephalic regions, including the relative area devoted to vision (Iwaniuk & Hurd, 2005). At least one study has suggested that starlings and pigeons may differ in their lateralization of different visual functions (Templeton & Gonzalez, 2004).

Here we investigated the perception of illumination-based visual features by this passerine species. This was done to address the serious gap in knowledge about visual cognition across different orders of birds and to understand where avian visual processing is situated within the larger set of visual pattern-recognition systems. We evaluated a working hypothesis that illumination-based cues for shape perception are a fundamental visual property for birds despite peripheral and neuroanatomic differences, and thus shape-from-shading mechanisms are common and consistent across different orders. We tested the starlings using a two-alternative, forced-choice perching task to examine their processing of the same shading-based scene stimuli tested with pigeons (Cook et al., 2012). If illumination-based information is salient to the perception of depth and shape information across birds, this hypothesis predicts that the starlings should react similarly to the pigeons across the manipulations tested here.

Experiment 1

In Experiment 1, we investigated the capacity of five starlings to discriminate the surface direction of concave and convex 3D shapes produced from differential lighting and shading. Examples of these computer-generated stimuli can be seen in Figure 1. Although synthetic, the stimuli have many of the visual character-
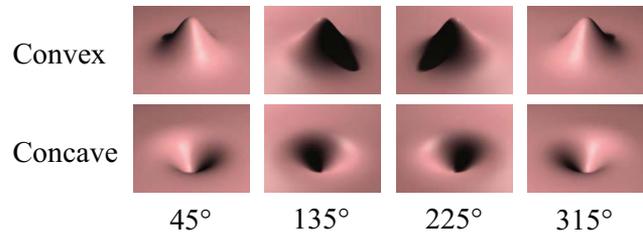

Figure 1. Examples of the convex (top row) and concave (bottom row) stimuli tested in Experiment 1. Each column illustrates a different lighting direction used to generate the shading information in the scene. These examples show the 35° camera perspective using the orange hue (see other figures for examples of the blue hue). The color version of this figure appears in the online article only.

istics experienced by birds in flight over a natural landscape. The visual elements in the image are primarily derived from their differential illumination by the lighting in this scene.

The convex stimuli appeared as hill-shaped mounds rising from the horizontal plane of a receding surface. The concave stimuli appeared as complementary depressions recessed below the plane of the surface. In any one surface stimulus, the principal source of shading and shadow was from one of four lights located off-camera at the diagonal corners of scene. The source of the lighting direction was varied among these positions to create different shading and shadowing patterns from the same surface shape. This was done to encourage the starlings to generally perceive the surface shapes rather than memorize specific illumination patterns. To further encourage the generalized recognition of the surface directions, two additional irrelevant features of the scenes were varied. Because birds experience scenes from different heights during flight, we manipulated the relative perspective of the surface shapes by rendering them from two camera viewpoints (25° or 35° above the surface). In addition, the surfaces were colored an overall blue or orange hue. Thus, 32 different stimuli were used during training.

On each trial, one concave and one convex stimulus were presented simultaneously on a computer monitor. The starlings indicated the right or left position of the correct stimulus by landing on a spatially adjacent perch that resulted in the delivery of a food reward. For three of the starlings, the convex stimulus of the pair was the correct one, whereas the concave stimulus was correct for the other two birds. The stimuli displayed within a trial were always the same in lighting direction, perspective and hue. The first phase of the experiment examined their acquisition of this shape-from-shading discrimination. The second phase investigated the birds' steady-state performance of the discrimination after learning.

If shading is a natural lighting property that is readily processed by birds, one should expect to see easy and rapid acquisition of the discrimination. That was true of the pigeons in Cook et al. (2012), who showed above-chance discrimination within just a few sessions. Further, we hypothesized, if we found that the starlings were able to reliably access surface shading to perceive shape, their learning and performance should not be strongly influenced by irrelevant variations in camera perspective, image color, or lighting direction. Finally, they should also be able to rapidly detect and

respond to this information. Pigeons, for instance, discriminated among surface directions within 500 to 1,000 ms. If the starlings' visual processing of shading were similar, a comparable time course would be expected.

Method

Animals. Five wild-caught, experimentally naïve starlings were tested. Two were females as identified by iris coloration (Kessel, 1951). They were individually housed in cages attached to each animal's testing apparatus and situated in a single common colony room on a 12-hr:12-hr light–dark (LD) cycle. The starlings were given ad libitum access to water and food prior to and between experiments; otherwise all food was obtained from experimental trials in the apparatus. The birds maintained their own weights between 85% and 100% of their free-feeding weights as determined after capture. All procedures were approved by the Tufts University Internal Animal Care and Use Committee.

Apparatus. The starlings were continuously tested in separate housing and testing live-in chambers. 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). Each chamber had two areas. One area was a wire home cage with a black plastic bottom lined with white paper-and-plastic bedding (35.5 cm wide × 46.0 cm high × 34.5 cm deep). This area contained a water dish and a wooden perch across its width. One cage wall was removed and a gray polyvinyl chloride (PVC) testing area attached (35.5 × 35.5 × 30.0 cm). The front wall of the testing area (furthest from water dishes) was made of clear Plexiglas and a liquid-crystal display (LCD) computer monitor located behind it (Dell 1908FPt; resolution: 1,440 × 1,024 pixels). In the testing area immediately in front of this monitor were three 13-cm wooden perches. The *center perch* was 20.1 cm back from the front wall and just inside the entrance to the testing area. Each trial started by triggering this perch. The two aligned *side* or *choice perches* were attached to the right and left walls of the testing area. They were 10.8 cm back from the front wall and 9.8 cm above the floor with 7.6 cm separating the interior ends of the perches. In front of each side perch was a small reward dish where food (Mazuri brand Insectivore Diet 5MK8/5MM3) was delivered from computer-controlled feeders (Coulbourn Instrument, Whitehall, PA, Pellet Feeder H14–23R) located outside of the chamber. A 28-V house light was located in the middle of the chamber's ceiling and was continuously on except during timeouts.

Each testing apparatus was programmed to conduct experimental tests from 7:30 a.m. to 7:30 p.m. each weekday, coinciding with the "on" phase of the room's light cycle. Testing continued through weekends whenever possible. During the night and any nonexperimental periods, the monitor, house light, and perch responses were turned off.

Stimulus conditions. All stimuli were 11 cm × 8 cm in size (480 × 360 pixels; landscape orientation) and generated by 3DS Max Version 7 (Autodesk, San Rafael, CA). Because these same stimuli have been technically detailed elsewhere (Cook et al., 2012), only an overview of the stimuli is provided here. The concave and convex surface shapes were created using the ripple modifier on a standard box shape to produce smoothly curved concave or convex surfaces. To provide a framework for measurement within the scenes, the peak height to surface distance of the convexity was set to 70.5 units in the software, to which we will refer as a standard value of 1 for describing the remaining metrics of the scenes.

The shading in the scenes was generated using the built-in implementation of the Blinn shader. Two surface materials were created, one consisting of blue hues and one of orange hues, and both contained a modest amount of specularity and glossiness. Two light sources illuminated the scene. The first and most important light source was from a set of four omnidirectional lights, each located in one of the four diagonal corners of the scene: the right-front (45° to the right of rendering camera's perspective), right-rear (135°), left-rear, (225°), and left-front (315°) corners. Only one of these four light sources was illuminated at a time. Their heights were 7 standard units above the surface and positioned 7 standard units from vertical midline of the surface. A second source of illumination was a dim omnidirectional light located 17 standard units above the surface, providing an even, diffuse illumination of the entire scene.

Surfaces were rendered from two different camera perspectives. These perspectives were 4.7 standard units from the scene's center at either a 25° or 35° angle above the surface. All shadows in this experiment were calculated using area shadows to provide for a more realistic soft, penumbra-like edge at shadow boundaries. All together these four factors (two surface shapes, two colors, four lighting directions, and two camera angles) resulted in a baseline set of 32 stimuli.

Procedure.

Preliminary training. To familiarize the starlings with the apparatus and the operation of the perches, the birds were first taught to use the center perch without the two side perches present. On these trials, a 2.5-cm circular, white ready signal was presented in the center of the display for 15 s. A maintained 300-ms response to the center perch (i.e., perching on the center perch) during this time caused the ready signal to be terminated and a food pellet to be delivered on a randomly selected side (initially 150 ms and then gradually increased and maintained for all perches for the remainder of the experiment). The two side perches were then added. Following a center response to the central ready signal, the signal was replaced by one of the 32 training stimuli randomly located on either the left or right side of the screen, with the starling rewarded for choosing the perch adjacent to the stimulus. Once a starling was maintaining its own weight in the apparatus exclusively from testing, visual discrimination training began.

Discrimination training. Each discrimination trial began with a center perch response to the ready signal. If a trial was not initiated during the 15-s ready signal, it was removed for 15 s and then presented again. Following a ready signal response, a concave and convex stimulus were simultaneously presented on the left and right sides of the screen (counterbalanced across trials). Except for surface direction, they were otherwise matched for camera perspective, color, and lighting direction. Their inner edges were separated by 3 cm (1.5 cm from midline) and their lower edges were 9.7 cm from the floor of the chamber (approximately even with the choice perches). For two birds, choosing the concave stimulus was correct (concave+), and for the three remaining birds, choosing the convex stimulus was correct (convex+). Correct choices were rewarded with food from the feeder adjacent to the correct choice perch. During acquisition 100% of correct

choices were rewarded, but during baseline testing this value was reduced to 85% to allow for later nonreinforced probe testing (see Experiment 2). Selecting the incorrect stimulus resulted in a 15-s dark timeout in which the chamber house light was turned off. To discourage side biases, a correction procedure was used in which incorrect responses resulted in the trial repeating, and this continued until the correct response was given. These correction trials were excluded from calculations of choice accuracy. If neither side perch was selected within 20 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 possibly "previewed," any such repeated trials were excluded from reaction time (RT) analyses.

The starlings continuously tested themselves throughout the day. Trials were organized into 96-trial blocks. Each block contained six iterations of the 16 different stimulus pairs with three trials presenting the correct stimulus on the right and three on the left side. The convex and concave stimuli of each trial were identical in color, perspective, and lighting direction. The testing order for these 96 trials was randomized in each block. Any incomplete blocks at the end of the daily testing were truncated and a new block started the next morning. Training continued until first-presentation choice accuracy was greater than 75% for two 96-trial blocks. From this point, we then collected a baseline postacquisition period of testing for 12 days.

Results

Acquisition. All five starlings readily learned this shape-from-shading discrimination. Four starlings (two in the convex+ condition and two in concave+ condition) reached criterion after only 2–3 days of training, with clear indications of learning within the first day. Counting all types of completed trials (including repeated-correction procedure trials), these four birds required a mean of 1,811 trials to reach the 75% criterion. The fifth starling needed longer to acquire the task, requiring 6,026 trials to reach criterion by the same measure. This bird showed several early periods of a strong side bias that likely interfered with learning. By the last block of acquisition, all five starlings were performing significantly above chance (50%), both evaluated as a group, $t(4) = 8.1$, $p = .001$, Cohen's $d = 3.6$ (an alpha level of .05 was used for all statistical tests), and individually (z approximation to binomial; all $z \geq 5$, all $p < .001$).

Baseline performance. During the baseline period that followed acquisition of the discrimination, the starlings completed an average of 11,942 training trials (range = 8,918–16,021). The starlings were highly accurate in discriminating the surface direction of the stimuli during these trials. Mean baseline choice accuracy for the five starlings was 94.3% (range = 91.1–96.4%). These data were then further analyzed to evaluate the influence of different stimulus factors on this discrimination.

To examine the hypothesis that the camera perspective, lighting direction, and the surface color would not affect the discrimination because the starlings were responding to the depicted shape information, we conducted a repeated-measures (RM) ANOVA (Camera Perspective × Lighting Direction × Color) using choice accuracy over the baseline period. This analysis revealed a significant main effect of camera perspective, $F(1, 4) = 13.2$, $p = .022$, $\eta_p^2 = .77$, as performance was just slightly better for the 25°

camera perspective ($M = 94.6\%$, 95% CI = [91.6%, 97.6%]) than the 35° camera perspective ($M = 93.9\%$, 95% CI = [91.3%, 96.6%]). Lighting direction, $F(3, 12) = 1.5$, $p = .268$, surface color, $F(1, 4) = 2.4$, $p = .200$, and all interactions (all $Fs < 1$, all $p > .5$) were found to be nonsignificant.

The next analyses were directed at determining how quickly the starlings discriminated the pair of stimuli on a given trial and whether this speed was influenced by the same three stimulus factors. This was motivated in part by the starlings' high accuracy, which might mask the effects of these stimulus properties on performance. Reaction time (RT) was measured as the time between stimulus onset and when the starling triggered a choice perch. For each starling, we determined the median RTs for correct trials that were completed in under 10 seconds (this excluded less than 2% of the trials; mean number of trials in RT calculations = 10,995). The average median choice RT for correct trials across birds was 1,070 ms. The same RM ANOVA (Camera Perspective × Lighting Direction × Color) as above examining median RT found no main significant effects or any interactions with this temporal measure: perspective, $F(1, 4) = .01$, $p = .915$; lighting direction, $F(3, 12) = .82$, $p = .506$; color, $F(1, 4) = .44$, $p = .542$; all interactions, $Fs < 2.4$, all $p > .1$. Despite the considerable changes these three factors created in the patterns of light in the rendered stimuli, these analyses indicate that the different sources of irrelevant variation had no measurable impact on the starlings' accuracy or speed in discriminating the concavity and convexity of the shapes in these stimuli.

Choice RT was significantly affected by choice accuracy, however. Correct responses were faster overall than incorrect responses. Median RT for correct choices was lower for all five starlings than for incorrect choices (1,562 ms; mean number of trials = 675). However, because one bird showed a consistently much larger difference (correct = 828 ms; incorrect = 2062 ms) than the other four birds, a paired t test using all five birds was not significant, $t(4) = 2.5$, $p = .066$. With this bird removed, this statistic becomes significant, $t(3) = 3.8$, $p = .031$, $d = 1.9$.

Discussion

Overall, these results indicate the starlings easily extract the convex and concave directions of the surface shape in these stimuli. They demonstrated rapid learning of the discrimination and quickly reached high levels of accuracy. Further, irrelevant variation in the stimuli related to lighting direction, color, and camera perspective had little impact on either the accuracy or the speed of their responding. These data suggest that the differential lighting from the contrasting and varied surfaces shown during training provided the starlings with reliable shape cues. Their ease in learning the task, consistently high accuracy, rapid responding, and capacity to cope with considerable irrelevant scene variation are consistent with the hypothesis that the relative shading of objects is a highly salient visual cue that is readily processed by the starling perceptual system.

The accurate perception of these shaded shapes seemed to occur quickly. Across subjects, correct choices took about 1,000 ms to make. Given that this value includes the movement time from center to side perch, the perception of the difference in the stimuli likely occurs much faster than that. Separate analyses of choice accuracy as a function of choice time suggested that accuracy

improved considerably once the starlings waited about 400–600 ms to respond (i.e., trials with choice RTs of less than 400 ms were near chance). The peck rates of the pigeons in Cook and colleague's (2012) study began to diverge at a comparable range of time. This suggests that the time course of shading processing is both rapid and similar across the two species (approximately 500–750 ms). Although the starlings' RT did not vary as a function of variation in shading among the stimuli, we did find that correct responses were consistently faster than incorrect ones. This temporal difference between correct and incorrect response distributions is also regularly observed in pigeon discriminative choice behavior (e.g., Cook, Levison, Gillett, & Blaisdell, 2005).

The critical implication from Experiment 1 was that shading appeared to be as salient a cue for starlings as had previously been found with pigeons (Cook et al., 2012). The pattern of results was highly similar across the two species. Both species quickly learned to use shading as a discriminative cue for determining the direction of a scene's surface shape. Both could do so accurately and rapidly and showed little or no effect of irrelevant scene or lighting characteristics. These similarities suggest that the perceptual shape mechanisms of both species function similarly when processing this fundamental visual feature.

Experiment 2

The goal of Experiment 2 was to test this pigeon–starling similarity by investigating how the relative salience and organization of the light and dark regions in the scenes influenced the perception of surface shape. Three different tests were conducted in this experiment. While simultaneously illuminating the nature of the discrimination learned by the starlings, these tests permitted a detailed comparison of visual performance across the two species, as pigeons had been previously tested with similar manipulations.

The first test examined the generality of the shape discrimination learned in Experiment 1. It investigated how the starlings reacted to novel, untrained changes in the camera's perspective relative to the plane of the surfaces. If the starlings had memorized the specific patterns of light and dark areas in Experiment 1, then transfer of the discrimination to these new displays should be limited. Given the well-known associative memory capacities of birds, the starlings could have simply memorized the stimuli (Cook et al., 2005). Alternatively, if the starlings had learned to discriminate the shape of the surfaces, then they should show transfer over a range of camera perspectives. As the camera's perspective becomes increasingly perpendicular to the surface, however, the 3D appearance of the shapes gradually becomes inaccessible, so the starlings' performance should decline. This pattern of results would suggest that the relative pattern of lighting mediated the starlings' discrimination.

The second test investigated the effect of varying the height and depth of the convexity and concavity of the surface shapes. If the starlings attended to shape properties, then the height of the shapes above the ground should influence the discrimination, with shapes having less implied height or depth more difficult to discriminate.

In the third test, we altered the specular highlights reflected from the surface shapes. The reflectance of different materials is a combination of both diffuse and specular components. Highly reflective materials have strong specular highlights consisting of the bright whitish points at the peak convexities and contours of

their shape. For humans, this depth cue often goes unnoticed despite its impact on perception. If the starlings discriminated shapes despite substantial alterations caused by specular modifications in the displays' relative shading, it would further support the hypothesis that the starlings were using the relative pattern of lighting to generate and recognize shape. Prior to this third test, we expanded the number, type, and combination of stimuli in training. This expansion allowed another opportunity to examine the generality of the starlings' solution to the current discrimination.

Finally, we simultaneously examined the possible contribution of shadows to the perception of shape during each of these tests. When a lighting source illuminates a scene, two types of shadows are potentially created, intrinsic and extrinsic (Knill, Mamassian, & Kersten, 1997). Extrinsic shadows are those that one object casts onto another object or surface. Our scenes contained intrinsic shadows, the shadows that an object casts onto itself. An attached intrinsic shadow is created on surface regions oriented away from the light source; this shadow is visible on the surface itself and is usually smoothly connected to areas of the object that are lit, like the dark side on a ball. A cast intrinsic shadow occurs on surface regions oriented toward the light source, but are occluded from the light source by another portion of the object. For each of the three tests, we evaluated the starlings' performance with and without the cast intrinsic shadow of the shape rendered into the scene.

Method

Animals and apparatus. The same animals and apparatus were used as in Experiment 1.

Procedure.

Variation in perspective. In this test, a series of test trials was created in which the two shapes on each trial were shown from the same novel camera perspective. Test stimuli varied the camera's angular perspective relative to the surface in 10° increments from 5° to 85°. Stimuli were generated from combinations of surface color (blue and orange), two lighting directions (45° and 225°), and with and without cast intrinsic shadows being present. This created 112 novel test stimuli: Perspective (9) × Surface Shape (2) × Color (2) × Lighting Direction (2) × Shadow Condition (2), less the 32 training stimuli that were tested.

Each of the test stimuli was randomly inserted into a 96-trial baseline block as a collection of 14 (shadow present—seven novel perspectives) or 18 (shadow absent—seven novel perspectives plus two familiar perspectives without cast shadows) nonreinforced probe trials (i.e., no outcome of any type). The starlings were well accustomed to nonreinforced trials, as the postacquisition procedure had a random 15% of baseline trials ending with no consequences after a choice. Each test trial contained two stimuli matched in configuration, except for the discriminative feature of concave or convex surface direction. Each block tested all novel perspectives with a different combination of color and lighting direction. A total of 16 of the 110-trial test blocks were conducted in which the shadows were present, followed by eight 114-trial blocks in which the shadows were removed.

Because of the continuous nature of testing, restrictions were placed on the frequency and distribution of test blocks and trials that could be conducted within a day. Test blocks were not allowed during the first 96-trial block of a day and test blocks were allowed

only when a starling's accuracy met or exceeded 80% on the previous block. Further, a new test block could not begin within 30 min of a previous test. These within-day test restrictions were used for all subsequent experiments as well.

Variation in surface height and depth. In this test, a series of test trials was conducted in which the height and depth of the convex and concave shapes were manipulated. The test stimuli were generated by varying the height and depth of the surface shape as a percentage of the standard unit (150%, 50%, 25% & 0%). These stimuli were generated using a camera perspective of 35° with both surface colors (blue & orange), all four lighting directions, and with cast shadows either being present or absent. This resulted in 128 test stimuli: Color (2) × Height/Depth (4) × Surface Direction (2) × Lighting Direction (4) × Shadow Condition (2). A collection of 16 nonreinforced probe trials was randomly mixed into a baseline 96-trial block. Each 112-trial test block tested all transfer stimuli for a single color and shadow configuration. A total of 16 test blocks (four iterations each) was conducted.

Expansion of baseline stimulus set. Prior to the third test, the baseline stimulus set was expanded to include the different camera perspectives from 15° to 85° (10° increments) examined in the first test. Training blocks remained 96 trials in size with equal numbers of camera perspectives and colors being tested, but lighting direction was now randomly selected on each trial. The starlings showed little or no decrement in accuracy with this fourfold expansion of the training set.

Variation in specularity. The third test varied the amount of reflective specularity in the material used to render the surface shapes. This was manipulated by changing the specularity parameter in the software (48, 36, 24, 12, 0; baseline value = 32). Test stimuli were tested using two lighting directions (45° and 225°),

four camera angles (35°, 45°, 65°, 85°), with both surface colors (blue and orange), and shadows present or absent. This resulted in 320 test stimuli: Levels of Specularity (5) × Surface Shape (2) × Camera Perspective (4) × Color (2) × Lighting Direction (2) × Shadow Condition (2). These test stimuli were randomly inserted as a collection of nonreinforced probe trials into the ongoing blocks of baseline trials. Each test block contained all of the specularity transfer stimuli for a single light source, surface color, and shadowing condition combination. A total of 32 (four iterations of eight block types) of these 116-trial test blocks were conducted.

Results

Variation in perspective. Figure 2 shows the mean accuracy of the five starlings as a function of camera perspective, lighting direction, and shadow condition. Overall, the birds transferred their discrimination to a substantial range of the novel camera perspectives, with perspectives below 65° supporting good to excellent transfer. With increasingly elevated camera perspectives there was a reduction in accuracy, although their lowered discrimination remained above-chance at these highest perspectives as determined by single-mean t tests across birds, 75°, $t(4) = 5.9$, $p = .004$, $d = 2.6$; 85°, $t(4) = 3.1$, $p = .035$, $d = 1.4$. Although the starlings showed good transfer across the range of these new views of the surfaces, the degree of transfer was modulated by both the direction of the lighting and presence of shadows.

These effects can be seen in Figure 2 by the greater accuracy with stimuli shown from higher perspectives that were both front-lit and also retained their shadows. A RM ANOVA (Camera Perspective × Lighting Direction × Shadow) was conducted on choice accuracy to examine this pattern. It revealed a significant
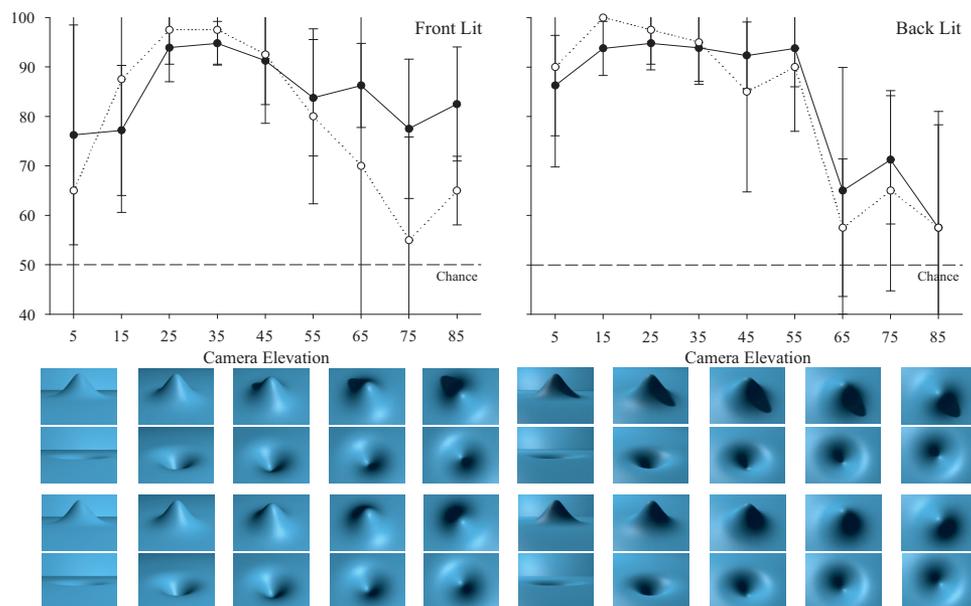

Figure 2. Mean accuracy for the five starlings as a function of camera perspective in Experiment 2 for stimuli with (filled symbols, top stimuli) and without (open symbols, bottom stimuli) shadows. Examples of the stimuli are included. Error bars indicate 95% confidence intervals. The color version of this figure appears in the online article only.

main effect of camera perspective, $F(8, 32) = 10.9$ ($p < .001$, $\eta_p^2 = .73$), reflecting the changes in accuracy noted above. Further, there were significant interactions between camera perspective and lighting direction, $F(8, 32) = 4.3$ ($p = .001$, $\eta_p^2 = .52$), as well as camera perspective and shadow $F(8, 32) = 2.7$ ($p = .048$, $\eta_p^2 = .36$). The latter interaction between camera perspective and shadow captures the increased accuracy when the shadows were available in high perspective scenes. The former interaction between camera perspective and lighting direction suggests that front-lit scenes supported better accuracy at high elevations than back-lit scenes. The remaining terms of the ANOVA were nonsignificant: lighting direction, $F(1, 4) = .1$, $p = .818$; shadow, $F(1, 4) = 2.2$, $p = .209$; interaction of lighting direction and shadow, $F(1, 4) = 6.0$, $p = .071$; and triple interaction, $F(8, 32) = 1.0$, $p = .464$.

Variation in surface height and depth. The starlings accommodated changes in surface height and depth, but showed systematic declines in accuracy with decreasing height, as shown in Figure 3. One starling, #N1, failed to respond on trials that contained height transfers and so this bird's data were not included in the analyses. As expected, the flat 0-height stimuli were not discriminable and the starlings on these trials responded at chance levels (50%; trials were randomly assigned to left and right responses; $t(3) = .95$, $p = .412$). Increases in height did not affect performance, but reductions in height caused accuracy to decrease. An RM ANOVA—Height (25, 50, and 150) × Lighting Direction × Shadowing—using choice accuracy was used to analyze the results. This analysis confirmed a significant main effect of height, $F(2, 6) = 11.7$ ($p = .008$, $\eta_p^2 = .80$), with no other main effects or interactions. The effect for height was well fit by a post hoc linear contrast testing this factor, $F(1, 3) = 19.7$ ($p = .021$, $\eta_p^2 = .87$). The remaining terms of the ANOVA were nonsignificant: lighting direction, $F(1, 3) = 3.9$, $p = .142$; shadow, $F(1, 3) = 1.2$, $p = .358$; and all interactions, $Fs < 2.6$, all $ps > .2$.

Expansion of baseline stimulus set. Accuracy from the first 20 blocks of this expanded training was analyzed. Overall, there was little impact on behavior with this fourfold increase in the number of stimuli, as choice accuracy remained high upon their introduction. With experience, all perspectives generally increased in choice accuracy, with the highest camera perspectives improving the most. A RM ANOVA (Camera Perspective × Lighting Direction × Five-Block Set) examining choice accuracy over this time was conducted. To simplify the analysis, camera perspectives were grouped into three bins—low (15°–35°), medium (45°–65°), and high (75° and 85°)—and lighting direction was grouped into front lighting and back lighting. This analysis identified a main effect of camera perspective, $F(2, 8) = 14.4$ ($p = .002$, $\eta_p^2 = .78$), as performance at low and medium camera perspectives was better in comparison to high camera perspectives, and there was also a main effect of block as accuracy increased from 84.3% to 93.0%, overall, $F(3, 12) = 5.3$ ($p = .015$, $\eta_p^2 = .57$). This analysis in addition revealed a significant interaction between camera perspective and block, $F(6, 24) = 4.4$ ($p = .004$, $\eta_p^2 = .53$), as accuracy improved more for the higher perspectives. The remaining terms of the ANOVA were nonsignificant: lighting direction, $F(1, 4) = 1.2$, $p = .336$; interaction of perspective and lighting direction, $F(2, 8) = 3.4$, $p = .087$; interaction of lighting direction and block, $F(3, 12) = 0.7$, $p = .551$; and triple interaction, $F(6, 24) = 0.4$, $p = .860$.
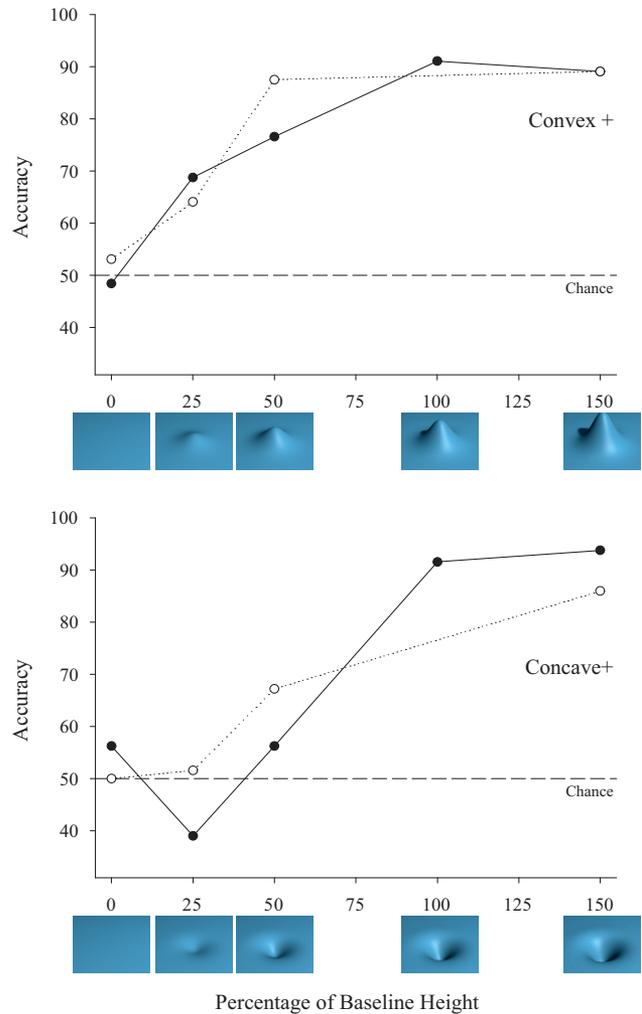

Figure 3. Mean accuracy as a function of surface height or depth in Experiment 2, shown separately for the three starlings in the convex+ assignment and the two starlings in the concave+ assignment. The filled symbols indicate responses to stimuli with shadows and the open symbols indicate responses to stimuli without shadows. The 0% height was considered ambiguous, so the assignment to correct perch was random. Examples of the shadowed stimuli are included. Error bars were omitted, as the data shown reflect the average of two birds in each condition and as such 95% confidence intervals are uninformative. The color version of this figure appears in the online article only.

Variation in specularity. As shown in Figure 4, all the starlings exhibited excellent transfer to all levels of novel specularity values. A RM ANOVA (Specularity × Camera Perspective × Lighting Direction × Shadowing) using choice accuracy confirmed that there was no significant main effect of specularity, $F(4, 16) = 1.0$, $p = .459$ or its interaction any other factor: specularity and perspective, $F(12, 48) = 0.9$, $p = .536$; specularity and lighting direction, $F(4, 16) = 3.4$, $p = .097$; specularity and shadow, $F(4, 16) = 0.8$, $p = .568$; higher interactions all $F < 1.2$, all $p > .3$. This indicates that the degree of specularity in the scenes was irrelevant to the starlings' discrimination of the stimuli. Aside from a main effect of camera perspective, $F(3, 12) = 4.1$
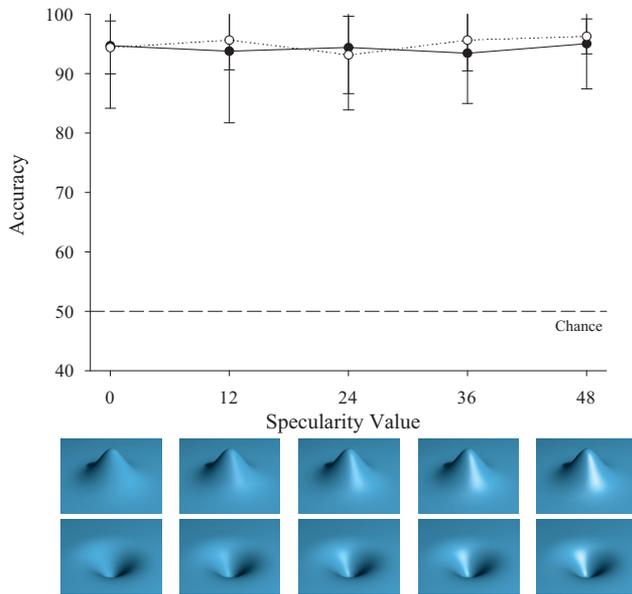
Figure 4. Mean accuracy for the five starlings as a function of specularity in Experiment 2 for stimuli with (filled symbols) and without (open symbols) shadows. Examples of shadowed stimuli are included. Error bars indicate 95% confidence intervals. The color version of this figure appears in the online article only.

$(p = .031, \eta_p^2 = .51)$, the remaining terms of the ANOVA were nonsignificant: lighting direction, $F(1, 4) = 0.02$, $p = .895$; shadow, $F(1, 4) = 0.1$, $p = .774$; interaction of perspective and shadow, $F(3, 12) = 2.9$, $p = .081$; interaction of perspective and lighting direction, $F(3, 12) = 1.7$, $p = .210$; interaction of lighting direction and shadow, $F(1, 4) = 1.1$, $p = .344$; and interaction of shadow, camera, and light, $F(3, 12) = 1.8$, $p = .198$.

Discussion

In these three tests, we varied the relative amount and location of the light and dark regions in the stimuli by varying the perspective, shape, and illumination properties of the scene. The pattern of results was most consistent with a hypothesis that the starlings perceived the shape of these scenes, as derived from the relative pattern of shading on these surfaces, independent of their past training experience. This was became evident when the starlings generalized their training to a wide range of camera perspectives and showed systematically decreasing accuracy only when shape information became unavailable because of perspective. Furthermore, decreasing the rendered height of the shape correspondingly decreased accuracy, indicating that the perceived 3D height of the shape was part of their discrimination. That both of these shape-based shading changes in the scene were effective suggests that the starlings perceived the depth and the shape of these surfaces. Given this, it is perhaps not surprising that manipulating the illumination-based properties by changing the specularity of the stimuli had no impact on the discrimination. Consequently, these experiments established that the specific distribution of light and dark pixels during training was not the direct discriminatory cue used by the starlings. Instead, it seems the starlings' visual system

was able to use the relative patterns of light and dark over a wide range of conditions to generate a perception of 3D shape. The starlings could consistently identify the concavity or convexity of the stimuli whenever it was readily visible from the relative shading information, independent of the changes of pixel-level properties caused by manipulations of perspective, height, and specularity.

The starlings' patterns of responding across these different manipulations were essentially identical to those observed in the earlier study with pigeons. Both species showed a capacity to discriminate surface shapes over a range of angular perspectives about 20–25° beyond their trained values. Increasingly perpendicular perspectives similarly caused both species to have more difficulty discriminating the shape of the surfaces. At least two reasons for this latter decline are possible. One is that the three-dimensional features for determining surface height became difficult to see as the shape of surfaces became increasingly two-dimensional (Cavoto & Cook, 2006). Birds in flight might experience similar difficulties as they move over natural objects and experience less canonical views of them. A second possibility is that there is some inherent limitation in the degree to which birds can recognize rotated 3D objects because they do not match the learned shape representation (Friedman, Vuong, & Spetch, 2009; Peissig, Young, Wasserman, & Biederman, 2000). This latter viewpoint-dependence possibility has been explored somewhat in pigeons, but not at all in starlings. Both species demonstrated a similar sensitivity to the rendered height of the shape, although the starlings appeared to show a greater sensitivity to this factor, as their performance declined sooner than observed with the pigeons. Furthermore, both species demonstrated shape invariance over changes in surface specularity. These similarities suggest that both species perceived these shape stimuli in a highly similar manner.

Finally, removing the cast shadows from the stimuli had little impact on starlings' performance over the vast majority of the conditions, except for those cases in which their presence likely added information about the shape of the stimuli. Because similar tests have not been done with pigeons, it is difficult to know if the starlings are similar or different in this aspect. In general, experiments looking at the effects of shadows with pigeons have not found a strong contribution of this factor to shape perception (Cavoto & Cook, 2006; Reid & Spetch, 1998). Previous research in humans has shown that cast shadows are more important in identifying global spatial relationships of objects in a scene than making any contribution to shape perception (Mamassian, Knill, & Kersten, 1998), although that investigation focused on the perception of extrinsic cast shadows, instead of intrinsic cast shadows, as tested here.

Experiment 3

In the previous experiments, the convex and concave shapes of the surfaces appeared to be a readily available discriminative cue, as derived from relative shading. To investigate further how shading transmits shape information was the focus of Experiment 3. This was done by evaluating the transfer of the starlings' discrimination of concavity and convexity to novel surface structures. Examining how well the discrimination

transfers to novel surfaces is an informative test for the perception of depth in these stimuli, as the degree of generalization should be influenced by the appearance and shape of the novel stimuli.

The starlings' discrimination transfer was assessed in two ways. The first was a test involving novel surface shapes tested from two of the four lighting directions (45° and 225°). One of these lighting directions provided front-lit experience and the second provided back-lit experience with the shapes. The same five shapes as previously tested with pigeons were investigated, including geometrically regular shapes and one irregular shape. These novel surface shapes varied in several fundamental aspects relative to the original sinusoidal shape, such as surface height, complexity, and axes of symmetry. Thus, any transfer should be enhanced by the similarity of the novel shapes to the original training stimulus.

Following the first test, the starlings were trained to discriminate these new shapes from the same lighting sources, and then a second transfer test was conducted using novel lighting. This involved testing these novel shapes with the two lighting directions that had not been experienced previously (135° and 315°). These novel lighting conditions rotated the light 90° from those experienced with the new shapes, resulting in a complete change in the pattern of light and dark across the surface of the new shapes. Hence, any transfer with these light-rotated stimuli would need to be mediated by the shape of the surfaces rather than any similarity to the patterns of shading experienced.

Finally, during the experiment, we expanded the nature of the testing procedures, incorporating and examining differences between the pair of stimuli within a trial. New trials were introduced in which the convex and concave stimuli also differed in their camera perspectives and/or lighting directions. Such trials further increased the demands on the starlings for recognizing the generalized shapes of the surfaces.

Method

Animals and apparatus. The same animals and apparatus were used as in Experiment 2.

Procedure.

Novel surface shapes. Five novel convex and concave surfaces were created. They were labeled bubble, mound, rectangle, sphere, and zigzag; the original shape was labeled the original sinusoid (representative examples are shown in Figure 5). These surface shapes were generated using a modified mesh box followed by a smoothing operation. The concave surfaces were 180° rotations in depth of the convex surfaces. Although some stimuli derived in this way can resist reversals in humans (Gregory, 1997), the birds' lack of natural history with these stimuli makes this an excellent technique for maintaining secondary shape characteristics while reversing convexity. The height/depth of each new surface shape in standard units was: bubble = .27, mound = .76, rectangle = 1.08, sphere = .73, zigzag = .32. These shapes were rendered using the same surface properties as the original sinusoid stimulus, using the 45° and 225° lighting directions, both blue and orange surface colors, at the 35°, 45°, 65°, and 85° camera perspectives, and both with and without shadow. This resulted in 320 test stimuli (New Surface Shapes [5] × Surface Directions [2] × Camera Perspectives [4] × Shadowing Conditions [2] × Surface Colors [2] × Lighting Directions [2]).

Novel shape transfer test. The test stimuli were inserted randomly as nonreinforced probe trials into the baseline block, which was organized in the same way as in Experiment 2. All shapes were tested in each block, from all four camera perspectives in combination with a single configuration of lighting direction, surface color, and shadow. A total of 32 116-trial test blocks were conducted in sets of eight. The first set of blue shadowed stimuli was tested, then the orange shadowed stimuli, followed by the blue unshadowed set, and finally the orange unshadowed set.
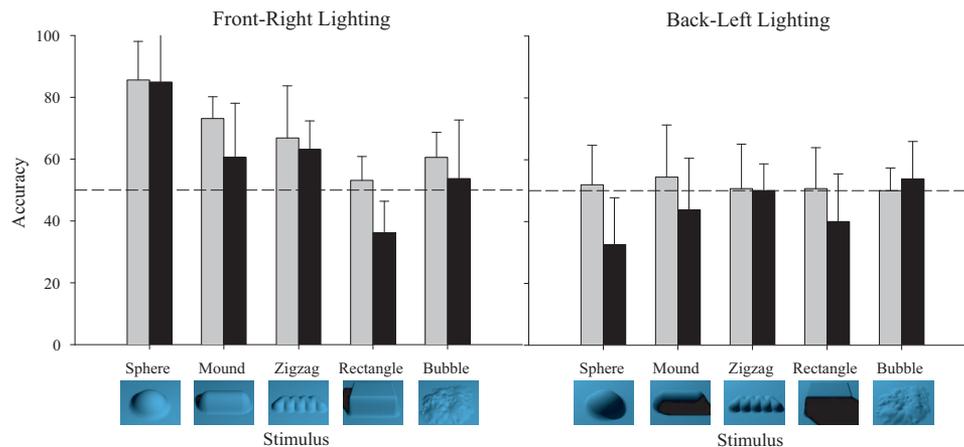

Figure 5. Mean accuracy to novel surface shapes tested in Experiment 3. The left panel shows performance on stimuli lit from the front (45° light source) and the right panel shows performance with stimuli lit from the back (225° light source). Gray bars indicate stimuli rendered from a low (35° and 45°) perspective and black bars indicate stimuli rendered from a high (65° and 85°) perspective. Examples of the shadowed, convex stimuli are included. Error bars indicate 95% confidence intervals. The color version of this figure appears in the online article only.

Incorporation of within-trial differences in baseline training. Prior to the next transfer test, we altered the baseline trials to include greater variability by allowing for differences between the left and the right stimuli in addition to surface direction. We now varied both the lighting direction and camera perspective, but not the color, between the simultaneously presented displays. To this end, camera angle (5°–85° in 10° increments) and lighting direction (45°, 135°, 225°, 315°) were *randomly assigned* for both stimuli of 64 trials (eight conducted as probe trials), with 16 additional trials remaining with stimuli *matched* for camera angle and lighting direction (eight conducted as probe trials). As a result of a programming error, starling N1 was not tested in this phase of the experiment. Finally, the 5° perspective was reintroduced during this phase of training. This phase of training lasted three weeks.

Novel shape training. After expanding the baseline training, we incorporated the five novel transfer shapes into daily testing. These new 144-trial blocks tested all stimulus conditions for the six shapes (sinusoid, sphere, rectangle, zigzag, bubble, and mound). Ninety-six randomly assigned trials (six nonreinforced probes, one of each shape) consisted of randomly selected camera perspectives and lighting directions for the two stimuli, and 48 matched trials (six probes, one of each shape) consisted of stimuli matched on perspective and lighting. For trials with the novel shapes, only the 45° and 225° lighting directions were tested in combination with the 35°, 45°, 65°, and 85° perspectives. For the original sinusoid shape, all four lighting directions and the full range of camera perspectives were tested. This new shape training lasted one week.

Novel shape lighting transfer test. Following this training, transfer tests were conducted testing the five novel shapes, but as illuminated from the two previously untested and untrained lighting directions (135° and 315°). Each 164-trial test block consisted of 144-baseline trials and 20 additional randomly inserted nonreinforced probe trials. In each probe trial, the color, lighting direction, camera perspective, and shadowing of the two display stimuli were matched, so that only the critical dimension of convexity varied. Each test block evaluated one of the new shapes at each of the four different camera perspectives and a single combination of the novel lighting directions, shadowing, and color. The first eight blocks tested the blue shadowed stimuli, the next eight tested the orange shadowed stimuli, and then this was repeated with the unshadowed stimuli.

Results

Novel shape transfer test. Overall, the starlings showed moderate transfer to the novel surface shapes. When averaged across all stimulus properties and conditions, four of the novel shapes supported significant above-chance discrimination transfer: sphere = 63.8%, $t(4) = 8.3$, $p = .001$, $d = 3.7$; mound = 58.0%, $t(4) = 3.8$, $p = .019$, $d = 1.7$; zigzag = 57.7%, $t(4) = 5.4$, $p = .006$, $d = 2.4$; bubble = 54.5%, $t(4) = 3.3$, $p = .031$, $d = 1.5$ and one showed significant below-chance transfer: rectangle = 45.0%, $t(4) = -3.7$, $p = .022$, $d = -1.6$. This confirmed that the starlings could extract surface direction from unfamiliar shapes.

The recognition of the surface direction in these novel shapes, however, was modulated by the lighting direction and camera perspective within the scene. Shown in Figure 5 is the mean transfer accuracy averaged across all five starlings for the five novel surface shapes as a function of lighting direction and perspective. It shows that discrimination transferred best when the novel shapes were illuminated from the front and presented at low perspectives. To evaluate the effects of the scene properties on transfer, a single RM ANOVA (Camera Perspective × Lighting Direction × Surface Shape × Shadow Presence) on transfer accuracy was conducted. For this analysis, camera perspective was again grouped into low (35° and 45°) and high perspectives (65° and 85°).

This ANOVA confirmed that lighting direction and camera perspective had main effects and interactions that were important to understanding the birds' transfer to the novel shapes. Of these two properties, lighting direction affected accuracy more. The ANOVA revealed significant main effects of lighting direction, $F(1, 4) = 16.2$ ($p = .016$, $\eta_p^2 = .80$), and surface shape, $F(4, 16) = 19.5$ ($p < .001$, $\eta_p^2 = .83$), and a significant interaction between the two factors, $F(4, 16) = 9.9$ ($p < .001$, $\eta_p^2 = .71$). Overall, the displays with front-lit novel shapes supported above-chance transfer, but back-lit novel shapes did not. The interaction with surface shape seems to have resulted from the front-lit sphere, mound, and zigzag supporting better transfer than either the bubble or rectangle shapes overall. The effect of lighting direction also interacted with the presence of shadows $F(1, 4) = 48.4$ ($p = .002$, $\eta_p^2 = .92$), with front-lit, shadow-containing stimuli supporting better accuracy ($M = 66.6\%$) than front-lit stimuli without shadows ($M = 61.0\%$), but the addition of shadows had no reliable effect on the more poorly performing back-lit transfer conditions.

Finally, this same ANOVA confirmed that camera perspective also influenced the degree of discrimination transfer, but to a lesser extent. This was reflected in a significant main effect of perspective, $F(1, 4) = 22.9$ ($p = .009$, $\eta_p^2 = .85$), with novel shapes shown at low perspectives supporting strong above-chance transfer ($M = 59.7\%$) relative to the same novel shapes from high perspectives ($M = 51.9\%$). The other terms of the ANOVA were nonsignificant: shadow $F(1, 4) < .1$, $p = .969$; all interaction Fs < 1.5, all ps $> .2$.

Incorporation of within-trial differences in baseline training. The next analyses examined how the within-trial mixture of lighting directions and perspectives affected the discrimination. The displays within each trial were classified relative to one another according to whether the dimensions of lighting direction and the camera perspective were *same*, *similar*, or *different*. Same trials were identified as those in which the lighting direction or camera perspective were identical (i.e., matched training trials). For the property of lighting direction, similar lighting denoted displays in which both stimuli were lit from the front or both from the back, and different lighting displays were those in which one stimulus was front-lit scene and the other back-lit. For camera perspective, similar perspective displays contained scenes whose camera elevations differed by 20° or less (e.g., similar for a 35° perspective would range from 15° to 55°), and different perspectives identified displays in which this difference was greater than 20°. Because both properties were independently and randomly selected, this classification resulted in a 3 × 3 lighting direction by camera perspective matrix.

The impact of within-trial variation on accuracy was negligible. Over all 40 blocks, the four starlings tested were just as accurate

on matched trials (96.3%) as with trials with a randomized difference in the displays, 96.0%, across-birds $t(3) = .75$. An RM ANOVA (Relative Lighting Direction × Relative Camera Perspective × 20-Block Set) examining choice accuracy revealed no significant main effects of having displays varying in lighting direction, $F(2, 6) = 0.9$, $p = .473$; camera perspective, $F(2, 6) = 2.3$, $p = .187$; or their combination, $F(4, 12) = 0.9$, $p = .504$. All remaining terms of the ANOVA were nonsignificant: block $F(1, 3) = 0.1$, $p = .752$; interaction of relative lighting direction and block, $F(2, 6) = 0.3$, $p = .730$; interaction of relative camera perspective and block, $F(2, 6) = 3.5$, $p = .099$; triple interaction, $F(4, 12) = 2.1$, $p = .142$.

Novel shape training. With the introduction of the new shapes into training, all of the starlings' discrimination of the novel shapes improved rapidly, approaching asymptotic levels of accuracy over approximately 3,200 total trials. Shown in Figure 6 is choice accuracy during training for each novel shape as a function of the number of presentations of that stimulus. Accuracy with the baseline sinusoidal shape started high and remained so over this training. Accuracy with the novel shapes in the first block was significantly above chance: $t(4) = 4.25$, $p = .013$, $d = 1.9$, as averaged across objects. Accuracy with most of the novel shapes improved quickly, except for the bubble shape, which consistently lagged behind. These differences in accuracy over training were confirmed by an RM ANOVA (surface shape, including the baseline sinusoid, by 5-block set). This revealed both significant main effects of surface shape, $F(5, 20) = 13.0$ ($p < .001$, $\eta_p^2 = .77$), and block $F(7, 28) = 10.0$ ($p < .001$, $\eta_p^2 = .71$), and a significant interaction among these factors, $F(35, 140) = 6.1$ ($p < .001$, $\eta_p^2 = .60$), as the different new shapes were acquired at different rates, and in the case of the bubble surface, supported different levels of overall accuracy. Post hoc investigation into the effect of block revealed a significant linear contrast, $F(1, 4) = 187$, $p < .001$, $\eta_p^2 = .98$, suggesting that the significant effect of block reflects learning over time.

To evaluate the efficacy of training, the final block of this training phase was separately analyzed. All surface shapes were found to support above-chance choice accuracy, all $ts(4) > 8.8$, all $ps < .001$, all $ds > 3.9$, as averaged across subjects. A one-way RM ANOVA (Shape) identified a main effect of shape, $F(5, 20) = 18.7$ ($p < .001$, $\eta_p^2 = .83$). Post hoc, Bonferroni-corrected pairwise comparisons revealed no differences in accuracy among the different shapes (overall without bubble, $M = 88.3\%$), except for the bubble surface, which supported significantly lower choice accuracy ($M = 70.2\%$) than the original sinusoid, mound, and zigzag (all $ps < .04$) and nearly so for the sphere and rectangle ($p = .06$ and $p = .08$, respectively).

Novel shape lighting transfer test. In this final test, the starlings showed good discrimination transfer for a majority of the novel shapes when the lighting was rotated by 90° (see Figure 7). All objects when lit from novel directions supported significantly above-chance accuracy, all across-birds $ts(4) > 7.7$, all $ps < .002$, all $ds > 3.4$), except for the bubble surface, $t(4) = 1.8$, $p = .146$. This transfer was not perfect, however, as accuracy was still higher for trained stimuli than the shadowed transfer stimuli, across bird RM $t(4) = 3.5$, $p = .024$, $d = 1.6$ (shadowed stimuli used for fairest comparison).

To examine how stimulus properties affected choice accuracy when the birds were tested with the novel lighting directions, we analyzed the transfer data using an RM ANOVA (Novel Lighting Directions × Grouped Camera Perspective × Surface Shape × Shadow Presence) analogous to that used in the initial novel shape transfer. This replicated main effects of surface shape, $F(4, 16) = 8.4$ ($p = .001$, $\eta_p^2 = .68$), camera perspective, $F(1, 4) = 34.2$ ($p = .004$, $\eta_p^2 = .90$), and lighting direction, $F(1, 3) = 35.0$ ($p = .004$, $\eta_p^2 = .90$), which showed that the bubble surface supported poorer performance than the other surfaces, the lower perspectives supported better performance than higher perspectives, and front-lit stimuli supported better performance than back-lit stimuli. This analysis also reported a significant effect of the shadow's presence, $F(1, 4) = 9.7$ ($p = .036$, $\eta_p^2 = .71$), a result of shadowed stimuli ($M = 78.0\%$) supporting better transfer than unshadowed stimuli ($M = 72.2\%$). In addition, the ANOVA indicated a three-way interaction between shadow presence, camera perspective, and lighting direction, $F(1, 4) = 23.7$ ($p = .008$, $\eta_p^2 = .86$), which captures the benefit of shadows for discriminating convexity and concavity in otherwise difficult or ambiguous scenes. In high perspectives with back-lit stimuli, shadowed ($M = 67.2\%$) stimuli seemed to support better performance than unshadowed ones ($M = 56.0\%$).

Three other terms of the ANOVA were found to be significant that further the preceding results: the interaction of lighting direction and surface shape, $F(4, 16) = 9.7$, $p < .001$, $\eta_p^2 = .708$; the interaction of perspective and surface shape, $F(4, 16) = 5.5$, $p = .005$, $\eta_p^2 = .580$; and the interaction of lighting, perspective, and surface shape, $F(4, 16) = 3.1$, $p = .047$, $\eta_p^2 = .434$. The remaining terms of the ANOVA were nonsignificant: interaction of shadow presence and lighting direction, $F(1, 4) = 0.4$, $p = .526$; interaction of shadow presence and perspective, $F(1, 4) < 0.1$, $p = .871$; interaction of lighting direction and perspective, $F(1, 4) = 2.0$, $p = .233$; interaction of shadow presence and surface shape, $F(4, 16) = 0.8$, $p = .521$; interaction of shadow presence, lighting direction, and surface shape, $F(4, 16) = 0.8$, $p = .506$; interaction of shadow presence, perspective, and surface shape, $F(4, 16) = 0.6$, $p = .681$; and the quadruple interaction $F(4, 16) = 1.7$, $p = .193$.
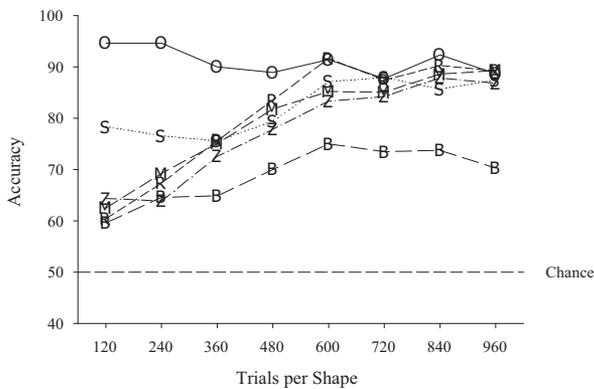

Figure 6. Mean accuracy for each object during training in Experiment 3 as a function of the total number of trials each object was presented. The symbols indicate the shape represented (O = sinusoid, B = bubble, M = mound, R = rectangle, S = sphere, and Z = zigzag).
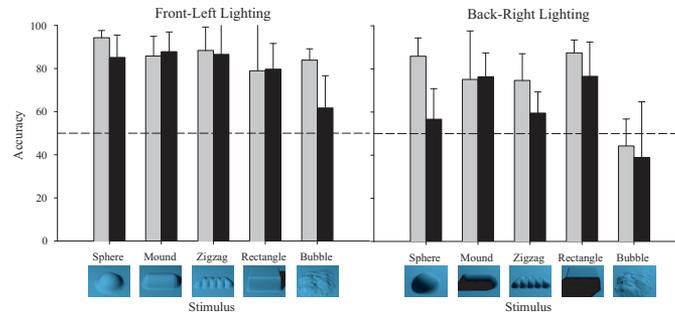
Figure 7. Mean accuracy to novel surface shapes tested in Experiment 3 following a novel 90° rotation of lighting direction. The left panel shows performance on stimuli lit from the front (315° light source) and the right panel shows performance with stimuli lit from the back (135° light source). Gray bars indicate stimuli rendered from a low (35° and 45°) perspective and black bars indicate stimuli rendered from a high (65° and 85°) perspective. Examples of the shadowed, convex stimuli are included. Error bars indicate 95% confidence intervals. The color version of this figure appears in the online article only.

Discussion

Experiment 3 revealed that the starlings were able to successfully generalize their discrimination of convexity and concavity to novel surface shapes. During novel shape transfer testing, they showed significantly above-chance accuracy upon their initial exposure to front-lit novel surface shapes, although they struggled with back-lit versions of the same stimuli. After training with the novel shapes using a subset of lighting directions, they then demonstrated excellent transfer when these shapes were illuminated from new directions. Overall, the starlings showed similar degrees and patterns of transfer to the novel shapes and the novel lighting directions as found previously with pigeons. The experiment further indicated the starlings' discriminative flexibility by revealing continued, high levels of accuracy with the introduction of new trials containing within-trial differences in lighting direction and camera perspective of the paired stimuli.

The relative degree of discrimination transfer to the different novel shapes suggests that the starlings were likely perceiving the shapes being presented in the scenes. Objects that shared more shape features with the original sinusoid stimulus supported the best transfer, and those that differed the most supported poorer transfer. The excellent transfer of discrimination to the new shapes after the lighting directions were rotated offers further support for this hypothesis. Despite changing the brightness of almost every pixel in the image, discrimination was almost as good with these newly lit shapes as with familiar lighting directions. These results evidence that the starlings did not learn the specific shading pattern during training, but had learned to discriminate the direction of the shape as transmitted by the patterns of shading. This suggests that the relative pattern of lighting in a scene is an important cue for perceiving surface shape in this passerine species.

One interesting development was that the starlings performed better on novel trials when the scene's lighting source was in front of the object rather than from behind it. This difference was also seen during perspective transfer in Experiment 2. One possible reason is that the processing of these computerized visual displays might interact with the ambient lighting in the chamber. Previous research with humans (Kleffner & Ramachandran, 1992) shows that given arrays of ambiguously shaded and reverse shaded disks (e.g., vertical light-dark gradients and vertical dark-light gradients) the scene is interpreted as having a single light source located above apparently concave and convex disks, not as having two conflicting light sources illuminating two rows of just concave or just convex disks. The starling visual system might have employed the same assumption when interpreting these stimuli and partially judged the stimuli within the context of the ambient lighting information being processed from the fixtures of the apparatus. Thus, the front-lit stimuli might be perceived more accurately because they are consistent with the chamber's ambient illumination, whereas back-lit stimuli conflict. This conflict may be overcome with experience, as it generally appeared in these experiments when new conditions were being tested. Alternatively, perhaps the information from back-lit stimuli is perceptually degraded in comparison to front-lit stimuli. Humans certainly find back-lit images harder perceptually to interpret than front-lit ones. Predator-prey interactions also evidence a possible use of differences in the direction of ambient illumination to delay recognition of either the predator (Hammerschlag, Martin, & Fallows, 2006) or the prey (Stuart-Fox, Whiting, & Moussalli, 2006). Determining the origins and generality of this possible front-lit advantage will require additional research.

General Discussion

Overall, the results of these experiments strongly imply that the starlings were seeing these stimuli as intended—as three-dimensional receding surfaces containing within them, illuminated concave or convex shapes. In three experiments, we found that starlings readily discriminated and generalized the depicted convexity of shapes in these complex, rendered, digital stimuli. Using information available from the relative patterns of shading, this *shape-from-shading* discrimination was quickly and easily acquired. Once learned, it was invariantly robust to changes in lighting direction, camera perspective, and specular highlights. The starlings readily transferred this discrimination to novel surface shapes, showing responsiveness to shape and

apparent depth information independent of any trained shading patterns. Across the experiments, whenever shape information was readily available from shading cues, the starlings performed well. When these shape cues were reduced, not visible, or eliminated, the starlings correspondingly performed more poorly. Together this evidence suggests that the relative shading within a visual scene makes an important contribution to the perception of 3D shapes of objects by this species of bird.

Two-dimensional, pixel-level accounts, such as memorizing nonform visual statistics or specific patterns of light and dark, were consistently insufficient to explain the starlings' discrimination behavior (e.g., as discriminated in Cook, 2001b). Experiments 2 and 3 drastically changed the brightness regions within the images, but the starlings continued to accurately discriminate as long as shape information was effectively transmitted. Any two-dimensional, image-based account would also lack sufficient explanation for the transfer to novel surface shapes due to the variety of shape features, including extended contour regions, internal flat areas, and localized convexity variation within the globally concave or convex objects. These changes spatially shifted critical information and altered the distribution of brightness within the scene, yet the starlings were still able to extract the convexity and concavity of these new shapes.

Cook and colleagues (2012) considered four illumination-based cues present in these stimuli for potentially extracting the shape of the objects: relative shading, contrast contours, specular highlights, and shadows. Of these cues, we argue that the starlings attended to shading, as the data suggest little if any control by contours and highlights as a result of their unreliable presence in the stimuli. Shadows also had little impact on the starlings' discrimination, only serving as a possible secondary cue when other shape information was insufficient. When compared with pigeons, these data indicate that both species process shading and perceive the shapes in these stimuli almost identically. This suggests a fundamental consistency in the basic visual cognition of these two bird species. That both species relied on the relative pattern of shading implies that perceptual shape-from-shading mechanisms are likely widely shared among diurnal terrestrial birds.

These results nicely align with and provide a mechanism for recent research examining the benefits of countershading for prey that are visually hunted by mixed species of birds (Rowland et al., 2008; Rowland et al., 2007). These controlled field studies have shown that the presence of countershading on artificial prey decreases its chances of being found by free-living avian predators. Those results in combination with our data suggest that decreased shading and shadowing may reduce visual cues related to avian predators' 3D perception of shape, making countershading an effective crypsis mechanism for prey.

The current outcomes have several implications for our understanding of the evolution and organization of visual cognition. Despite suggestions that starlings and pigeons represent different cerebrotypes (Iwaniuk & Hurd, 2005), the current research implies that basic visual information processing of these two classes are the same, suggesting that shading may represent a primitive or highly conserved perceptual feature across avian species. This raises the possibility that central visual and cognitive functions cannot afford the same plasticity to support phylogenetic, ecologically driven specializations seen in the peripheral anatomy and

neuroanatomy (Endler, 1993; Martin, 2007). Alternatively, these species could have independently converged on similar solutions because both species are diurnal terrestrial foragers with propensities for open habitats. The similar visual demands of their habitats may have resulted in similarities in vision. As a result, future investigations of an additional bird species with different visual demands, such as a columbiform or passeriform dwelling in light-dappled forests, will be revealing.

Finally, these questions can be evaluated in a larger comparative framework by comparison with mammals. Overall, our avian shape-from-shading results share similarities with established results for primates, despite large neuroanatomical differences in these classes of animals (see Shimizu & Watanabe, 2012). Both primates and birds have two visual pathways, a lemnothalamic pathway and a collothalamic pathway (Jarvis et al., 2005). For primates, the lemnothalamic pathway is the primary pathway for vision. In humans specifically, shading information is derived in the inferior temporal gyrus (Georgieva, Todd, Peeters, & Orban, 2008), which is primarily driven by activity within this pathway. In contrast, the visual organization of birds reverses the relative importance of the two pathways (Husband & Shimizu, 2001; Shimizu & Karten, 1991). The avian collothalamic pathway is dominated by the tectum and the entopallium which are the primary neural structures responsible for processing the visual world. If these visual faculties function similarly but are implemented in different neural structures, it would suggest some form of convergent evolution in visual processing over the last 200 million years.

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