

Avian Visual Cognition: Shape from Shading in the European Starling (*Sturnus vulgaris*)

An honors thesis for the Department of Psychology

Muhammad A. Qadri

Tufts University, 2010

Abstract

“Shape from shading” is the ability to integrate the pattern of light reflected by a surface and with light source information to derive the object's structure. This study explores this ability in five European starlings (*Sturnus vulgaris*), a model passerine species previously used once in our lab (Khan, 2009). The focus of the current study was to follow the experiments from Cook, Commons-Miller, Kieres (2009) where this ability was studied in pigeons. This study used an operant chamber in a closed-economy feeding system which used perching as the response behavior. The study established that starlings are able to discriminate concavities from convexities and, using transfer tests to categorically similar stimuli, confirms that the starlings are responding to concavity and convexity.

Introduction

Regardless of having an ability for binocular vision, animals can still use monocular shape cues to learn about their environment (Cavoto & Cook, 2006). Commonly known monocular cues are occlusion and parallel line convergence, but subtler cues are also present. The current study focuses on one specific monocular shape cue: shading information. When light strikes an object, the light reflects off the object to an observer. Because of the near-microscopic texturing of the object, the light reflects diffusely off the object, which results in the parts of the object nearest to the light source being brighter than those furthest from the light source, creating shading. Thus, by integrating shading information with knowledge of the source of the light, shape can be discernible even on a smooth surface with few, if any, other visual cues.

Abilities in humans

Many studies and experiments have been performed on the human ability to use shading as a depth cue. Experiments so far suggest several aspects about the usage of shading information in visual perception. Several lines of research have established that it is a fairly primitive depth cue (Yonas, Kuskowski, & Sternfels, 1979; Ramachandran, 1988; Kleffner & Ramachandran 1992). It can be used as a primary feature in a visual search task and as a figure-ground separator, indicating that it is processed early in the visual system (Kleffner & Ramachandran, 1992). The appearance of flashing discs being interpreted as a moving item is contingent upon coherence and consistency in the shading information (Kleffner & Ramachandran, 1992). However, there are data that support the possibility that more complex processes and perceptions can affect the shape perception. For example, viewing a mask mold lit from above, as a result of humans' strong ability to see faces, the mental lighting shifts so that the face is convex, not concave (Ramachandran, 1988). Hence, images are perceived to be

internally consistent, such that there is only one functionally bright light source. Though humans do have the ability to use shape from shading, it has a very weak signal; studies that used both sharp contrast lines (edges) and shape from shading as cues found that the strength of the discrimination was better when edges were present (Ramachandran, 1988). Additionally, a neural network model showed that when training a relatively simple network, an internal layer of nodes develops that is differentially activated to straight lines at various orientations, mimicking area V1 in the human brain (Lehky & Sejnowski, 1997). However, at least one patient with neurological damage has shown that edge processing and shading processing are dissociable tasks (Humphrey, Symons, Herbert, & Goodale, 1996).

Abilities in nonhumans

Shading is believed to be a salient visual cue in the rest of the animal kingdom because of the prevalence of countershading, the lighter underbelly of many creatures (Kiltie, 1988; Ruxton et al. 2004). Experiments on shape from shading on members of the animal kingdom so far is limited to primate vision and pigeon vision, and much of which is still unpublished. Earlier comparative studies looked at primates' abilities to group visually concave and convex stimuli, finding that where humans had a stronger ability with a vertical gradient versus a horizontal gradient, chimpanzees had a stronger ability to discriminate horizontal than vertical gradients (Tomonoga, 1998). Beyond that, not much research has been devoted to exploring this line of visual perception.

However, experiments have shown other animals being differentially affected by shading, which is found in the countershading literature. In an experiment looking at the selective advantage of countershading, Edmunds and Dewhirst (1993) created four categories of green-colored pastries: dark green, light green, countershaded (dark top, light bottom) and reverse countershaded (light top, dark bottom). One hundred of these were then randomly distributed in

an unmarked 10×10 grid setting on a lawn for about seven hours, and this was repeated for seven total instances of predation. Predation by wild birds was measured by the number of pastries taken or pecked. In this experiment, it was seen that countershaded prey were taken significantly less than their dark counterparts. The birds most frequently seen attending to the lawns were “house sparrow (*Passer domesticus*), chaffinch (*Fringilla coelebs*), starling (*Sturnus vulgaris*), blackbird (*Turdus merula*), song thrush (*Turdus philomelos*), robin (*Erithacus rubecula*), dunnock (*Prunella modularis*), blue tit (*Parus coeruleus*) and great tit (*Parus major*)” all of which are of the order *Passeriformes*. More literature in this field, however, simply establishes or refutes whether countershading is preferable for the prey, but does not explore the factors affecting the perception of the predators.

The work with pigeons is essentially a summary of Cook et al. (2009) plus an addendum of tests that are still unpublished. Pigeons were tested in a go/no-go discrimination with smooth, concave and convex stimuli, the same as described below. The conditions were counterbalanced for convexity across birds, and they were able to learn the discrimination within 200 – 300 trials. Using non-reinforced probe trials to test the feature space, the pigeons showed the ability to transfer to new camera angles of the same stimulus, the same curve without cast shadows (but preserving shading), different heights of the structure, and different shapes entirely. The discrimination fell when the camera angle was too high (almost vertical) or when the height of the curve was flat or near-flat. Further tests were done on the same subjects where both the baseline and the transfer stimuli were rotated 180°, and the pigeons responded to the previously convex stimuli as concave, and vice versa.

Closed economy system

A big consideration while conducting this thesis work was that the apparatus should be setup such that all the food that each starling receives comes from performing the task. This is

called a closed economy system. Previous research involving starlings focused on daily energy expenditure (DEE) and behavioral adaptations to food scarcity (Wiersma, Salomans & Verhulst 2005; Bautista et al., 1998). Wiersma, Salomans and Verhulst's research (2005) showed that when placed in conditions in which foraging for food succeeded with a low probability, the starlings have an increased DEE, likely the result of the extra energy needed for foraging. Previous research indicated that DEE actually went down, which matches the theory that the birds must conserve energy (Bautista et al, 1998). The difference was explained as the result of a fixed versus variable ratio of reinforcement; in a fixed ratio, the starlings have a reduced DEE and in a variable ratio, they have an increased DEE (Wiersma, Salomans & Verhulst, 2005). This experiment showed that starlings also lose a considerable amount of weight and reduce their dormant energy consumption, allowing them to maintain their levels of increased DEE.

The current study

The current study is focusing to expand the shape from shading research from the columbiforme order to the passerine order. Countershading experiments have shown that passeriforms are sensitive to shading, and thus it should be possible to not only demonstrate the ability in starlings, but also to explore what factors affect it. Although the current setup can be informative about the cognitive workload of the task with respect to food pressures, the current study will not address the closed economy system and the questions it poses.

Subjects

Five wild-caught male starlings were used as subjects. All five were previously in a physiological experiment looking at stress responses, and then used in the pilot of this experiment in which the task was the same as the pigeons' task. The birds were housed in individual cages with attached operant chambers. The exact setup will be discussed later. All the

birds were given free access to water, but all food was provided from the task, using BioServe® dustless precision pellets, 45mg rodent grain-based diet delivered from a Colbourn Instrument Pellet Feeder controlled via a relay switch from Phidgets, Inc.. Given this closed-economy system, no deprivation was necessary in testing.

Apparatus

Each bird's home cage was divided between two areas. One area 35.5 cm wide×46.0 cm high×34.5cm deep was the traditional home cage with metal wire sides and top and plastic bottom, containing a water dish and a 1.75 cm thick perch (home perch). The wall opposite the water was removed and lead to the testing area, which was 35.5 cm wide×35.5 cm high×30.0cm deep, and had a clear, 0.6 cm plexiglass wall opposite the opening. Three 13.0 cm perches (input perches) were installed in the chamber, one in the center (center perch) by the opening, and two perches (side perches) built into the walls. In front of each side perch was a trough that caught food dispensed from the feeder on either side of the chamber. The center perch, which is located 4.1 cm above the floor of the chamber, can be depressed to 2.9 cm above the floor, but the microswitch to which the perch is connected emits a small click at 3.2 cm above the floor, which indicates that the computer can now sense that the perch is depressed. Similarly, the side perches are 9.8 cm from the floor, register at 7.0 cm, and stop at about 5.1 cm. A perch is only registered as being active when the switch was depressed for a fixed time. On the other side of the clear plexiglass is a Dell 1908 FPt LCD monitor on which the stimuli were presented on the 1440×1024 resolution screen. The apparatus began to run experiments from 7:00 AM EST to 7:00 PM EST, with no variation in the light cycle. During the "night," the monitors and houselight were all turned off, but the computers themselves were still running.

Apparatus Task

The chamber is designed for a forced-choice two alternative task. A trial was initiated by activating the center perch when a white circle 1.8 cm in diameter (the warning signal) was visible on the screen. The warning signal was then replaced with one or two stimuli placed in front of the perches. The starling then has to activate a side perch to indicate its choice. The default background for the warning signal and the inter-trial and inter-session screens was black.

Phase I - Training

Part One - Perch-Food Association

Prior to exposure on the discrimination task, the starlings were first conditioned to sit on the input perches in return for food reward. Initially, the two side perches were removed so that only the center perch was available for use. The warning signal was visible for 15 seconds, then disappeared for 2 seconds, and this cycle continuously repeated. A perch was activated by depressing the switch for 150 ms. If the center perch was activated when the warning signal was visible, the starling was reward with one food pellet on a randomly selected side. If the starling activated the center perch when the warning signal was invisible, then the warning signal was kept invisible until the starling left the center perch. Once the starling was able to maintain its baseline weight, it was then moved to part two.

Part Two - Two Perch-Food Association

In part two of training, the starlings were given one of the two side perches (native perch). For three of the starlings, the native perch was on the left side, and for the remainder, the native perch was on the right. The starling was then required to land on the center perch when the warning signal was visible, and then to activate the side perch when the stimulus appeared on the screen in front of it. The stimuli used were the same as in the experiment (see below), and

only the positive stimulus was shown. The positive stimulus was counterbalanced across the groups of native perches, so that one one of the subjects had a native left perch and was training with the convex stimulus, and another had a right native perch and was training with the convex stimulus, etc. Once the starlings were able to perform this task adequately, the native perch was then removed and the opposite perch (secondary perch) was placed in the chamber. The task, however, remained unchanged; the warning signal was followed by the positive stimulus being placed in front of the only available perched. This part was considered finished when the bird was able to maintain its weight close to the baseline.

Phase II - Discrimination

Stimuli

The stimuli used in this task were the same as those from Cook et al. (2009) and Khan (2009). The images were blue or peach continuous surfaces rendered in 3ds MAX with a "ripple" object constrained to show only one concavity or one convexity of the same shape. The camera was angled at 25° or 35° at a fixed distance. This surface was then lit with one default spot light facing downward centered above the curve with a wide, diffuse light, and one additional light placed in four possible locations with respect to the camera: the rear-left, front-left, front-right, and rear-right (See Figure 2).

Task

For this phase, all three input perches were placed in the chamber. A trial began by landing on the center perch while the warning signal was visible, which was then replaced by two 11 cm × 8 cm stimuli located 2.8 cm from the edges of the screen. One stimulus was positive (S+) , and one was negative (S-). Activating the perch in front of the positive stimulus resulted in food reward, but activating the perch in front of the negative stimulus resulted in a timeout with a

black screen and no houselight. If the warning signal was not activated, it disappeared for 15 s, and if any perch was depressed, the warning signal would not appear. If neither choice perch was activated within 20 s of stimulus onset, the trial would be repeated. The trials were composed such that every block of 32 trials had 16 left-positive and 16 right-positive trials, and those were randomly distributed throughout the set.

During acquisition, certain biases were expected to show up and were controlled for when they appeared. The primary concern was a side-bias; each starling would have a stronger association of reward for the native perch than the secondary perch, and when given the choice between the two perches, they consistently chose a single perch. This behavior was modulated by increasing the timeout interval. Initially set to 3 s, the starling was able to continue receiving its reward by simply proceeding through trials on the order of 1,000 times each day without consideration for timeout. This timeout was then extended to 15 s, resulting in more discriminatory behavior. However, for two of the birds, this was not effective; thus, a correction procedure was introduced. If the starling received an incorrect trial, the trial would be repeated until the starling responded correctly. Once the discrimination behavior was observed, the correction procedure was removed and the birds maintained discrimination.

There were additional hiccups for various birds. For one bird, Dick, who was the bird used in the prototyping of these chambers, he had developed a different response pattern: inactivity. At that point in the experiment, the starling was not required to finish the trial or repeat unfinished trials, but introduction of that restriction was as effective as the above-stated correction procedure. Some birds were accidentally activating perches by hitting them or swiping at them during movement, so the perch activation time was increased from 150ms to 300 ms. Lastly, as a result of the developing nature of the apparatus, many initial clogs and feeder failures

disrupted discrimination learning, but careful, controlled manipulations of the feeding route and regular maintenance of the system minimized these.

Results

All five birds showed the ability to discriminate the baseline stimuli. For four of the birds, this was seen very soon after beginning the discrimination or upon the introduction of a correction procedure. In the second of set of 96 trial sessions, all five birds, on average were significantly above chance at 57% ($t(4) = 2.89$, $p < .05$), and this significance was maintained as the accuracy continued to rise after that (See Table 1; See Figure 2). A five factor ANOVA of the first ten sessions of acquisition based on session, stimulus color, camera angle, front-back lighting, and left-right lighting reconfirmed that there was a main effect of session ($F(9,36)=9.31$, $p < .05$), and revealed no main effects for color, camera angle, or light directionality (See Table 2). The ANOVA revealed a significant interaction between color and front-back lighting during this acquisition phase ($F(1,4) = 9.89$, $p < .05$); the blue, front-lit stimulus has higher overall discrimination during acquisition than a red, front-lit stimulus, but the blue, back-lit stimulus has lower overall discrimination during acquisition than a red, back-lit stimulus. No other interactions were found.

Once the five starlings had reach a steady state, the data was reanalyzed to see if there were any trends in discrimination of the learned task. Steady state was defined as beginning at the first 32-block session after a perfect session, and 180 sessions were used. All trials with multiple presentations of the stimulus were removed. No main effect of stimulus color, camera angle, or light directionality or interactions thereof were found (See Table 3).

Phase III - Experimentation

Experiment One - Novel Camera Angles and Removal of Shadows

Stimuli

In order to determine that the starlings had generalized the discrimination to concavity and convexity, and that they did not simply memorize the exemplars from each category, the stimuli were systematically changed, and the starlings' abilities to transfer to the novel stimuli were analyzed. The transfer stimuli are the same as the first sets of transfer tests in Cook et al. (2009), where the same curved surface as the baseline stimuli was used but the camera angle was varied. The camera angles tested were those from 5° to 85° in 10° steps, in both colors and lit from the four baseline light positions. In addition to this, the shadows cast by the surface onto the ground behind it was removed from the stimulus, leaving only the actual shading information of the object as input for the discrimination.

Task

After the birds exhibited their abilities to learn the task, they were tested with non-reinforced probe trials of transfer stimuli to observe their responses to various aspects of the shaded surface. Probe trials were clustered to be only in "probe sessions," which were only run if the bird's accuracy in its previous session was above 85% and there were at least 30 minutes between the last probe trial and the beginning of the session. For transfer trials, the side of the positive stimulus was randomly assigned, and probe trials were evenly and randomly distributed among the regular trials throughout the whole session. Unlike with the pigeons, none of the baseline sessions contained probe trials because this task was a decision task; by the time a response is made, the bird has reached a decision, so regularly removing reward was unnecessary. Additionally, we speculate that of the regular baseline trials, some trials end up

being perceived as unrewarded due to either occasional feeder failure or starling inattention, which results in the non-reinforced probes being treated like a regular occurrence. For each set of stimuli, four probe trials were collected per condition per bird. However, in the middle of the transfers to novel camera angle, one starling was lost due to an unrelated foot injury, but the data were kept and analyzed for that bird.

Results

The data show that the starlings were able to discriminate the stimuli regardless of the novel camera angles, and this ability was preserved despite the removal of the cast shadow. The starlings maintained greater than 90% accuracy for the 15°-45° camera angles, greater than chance ability for 5° and 55°, and near discrimination from 65° to 85° (See Figure 3). This same trend was seen when the shadow was removed (See Figure 4). In order to obtain stronger results from the ANOVA by using the data of the lost starling, one ANOVA was used to analyze the data just with the shadow, and another was used to analyze the full with and without shadow data. The first ANOVA reveals a main effect of both camera angle and front-back lighting direction ($F(8,32) = 4.335$, $p < .05$; $F(1,4) = 11.623$, $p < .05$), and no other main effects or interactions (See Table 4). The lighting direction indicates that the stimuli lit from the front were more discriminable than the ones lit from the rear. Visually, the camera data are grouped into three areas: high, medium, and low accuracy. The high accuracy area is from 15° to 45°, medium accuracy has 5° and 55° stimuli, and low accuracy are the 65° to 85° stimuli (See Figure 3). This is confirmed by some of the pairwise T-tests, but the amount of variability limits the reported significance of other T-tests (See Table 5). The second ANOVA, which is a four-factor anova incorporating shadow, reveals no significant effect of shadow ($F(1,3) = 8.461$, $p = 0.06$), still reports a significant effect of camera angle ($F(8,24) = 4.128$, $p < .05$), but shows no other significant effects (See Table 6). However, there are interactions between camera angle and

lighting direction ($F(8,24) = 5.881$, $p < .05$), a result of the fact that the front-lit stimuli are discriminable at the 55° and 65° camera angles. Finally, the second ANOVA also reports a significant interaction between color, shadow, and lighting direction which is present because although the accuracy fell overall when shadow was removed, in the case of shadowless stimuli, the red, back-lit stimulus discrimination was significantly better than the red, front-lit stimulus while the opposite was the case for the blue stimuli, but for shadowed stimuli, lighting from the front resulted in better discrimination regardless of color ($F(1,3) = 13.810$, $p < .05$).

Experiment Two: Novel Stimuli - Variations in Height

Task

Having determined that the starlings are capable of discriminating the concavity and convexity of the stimuli, the factors contributing to this discrimination were explored. Several options presented themselves, but the most logical first step was changing the amount of shading information by reducing the curvature of the shape. This was equivalent to changing the height of the curved surface used in the stimuli. The heights tested were 0% (flat), 25%, 50%, and 150% of the original curve's height; the stimuli were blue, with a 25° and 35° camera angle, and lit from all four corners, the same as presented in the Cook et al. (2009).

Results

Varying the height of the curved surface changed the ability of the starlings to determine the concavity of the displayed stimuli. The 0% and 25% height stimuli had near-chance accuracy, at 53% and 46% percent correct respectively, but the 50%, 100%, and 150% height showed preserved discrimination, with 66%, 82%, and 78%, respectively (See Figure 5). However, of these, only the 100% height had a significant deviation from chance ($t(3)=5.034$, $p<.05$). The height data were analyzed using a four-factor ANOVA based on height, camera

angle, front-back, and left-right lighting direction. This ANOVA revealed a main effect of height ($F(4,12) = 3.744, p < .05$), and an interaction between height, camera, and front-back lighting ($F(4,12) = 3.839, p < .05$; See Table 7). This interaction appears to be the result of an interaction between camera angle and front-back lighting which disappears when the object is flat. Pairwise T-tests of the different heights do not indicate any of the heights being statistically significantly different from the others (See Table 8).

Discussion

The current study was conducted to test the hypothesis that starlings, and passerine species in general, can use shading information to determine shape. The starlings have shown that they are able to discriminate the concave and convex stimuli at a rate comparable to that of the pigeons used in Cook et al. (2009). That the group showed significant deviation from chance within 180 trials is a reflection of the saliency of convexity and the simplicity of the shape from shading task. The second and third experiments confirm that it is convexity that the starlings are using for the discrimination, because they showed the ability to transfer correctly to non-identical but categorically similar novel stimuli.

The correction procedure used during acquisition was likely an indicator of a problem experimentally, not with the task or the starlings' abilities themselves. Experimentally, a correction procedure can be used for many reasons. For example when the subject consistently activates the choice key in a trial without attending to the stimuli, a correction procedure would be to repeat a wrong trial until the subject responds correctly. Thus, the correction procedure can be construed as a form of punishment, or a consequence of incorrect behavior, designed specifically to eliminate a behavior so that other actions are possible for the subject to use. In the current study, the system had been designed at that point such that a starling could make two hops, one to start the trial and one to indicate a decision, and either eat or not eat in a very quick

time span, reducing the need for discrimination. By introducing the correction procedure, we forced the starlings to attend to the stimuli on the screen in order to receive further nutrition. However, it is very unlikely that this is a reflection of the starlings' abilities to discriminate convexity from concavity, and instead we theorize that the repeated behavior is an attempt at maximizing reward while minimizing action. Supporting this view is the behavior of Dick, who initially only responded to positive stimuli on his native perch; repeating the trial forced him to fly to his secondary perch in order to continue with the session, which he adjusted to rapidly.

Since the starlings were able to take this baseline discrimination and transfer the discrimination to nonidentical but categorically similar stimuli, we assert that the starlings are able to perceive the property of convexity from the two-dimensional image of a shaded, three-dimensional object. Of the dimensions of the stimuli that we varied, lighting direction, color, camera angle, and height, only height and camera angle provided strong evidence of having response control. Varying the camera angles resulted in varied discrimination. Camera angles within 10° to the baseline values of 25° and 35° resulted in the best discrimination. Since these stimuli were closest to the baseline, they differed the least from those values, so it is not surprising that their discrimination was high. Values 20° from baseline resulted in partial discrimination; the percent correct on average was not near chance but were clearly different from the baseline values. This can be the result of novel stimuli effects, since the images are now significantly deviating from the baseline. Additionally, visible in the 5° stimuli is the actual background of the image, which should have been a solid color similar to the stimulus, but as a result of inconsistencies in the original experiment, a few had a curved backdrop with a dark black region behind it. This could explain the decrease in the starlings' and pigeons' activities regardless of the prevalence of monocular depth cues available at the 5° camera angle.

One interesting result of this experiment is the significance of lighting. Although it did not have a significant effect by itself, it had an interaction with color in acquisition and an interaction with camera angle in the transfer test. This was unexpected because no interactions were noted in Cook et al. 2009 (as cited in Khan, 2009). It is possible that the color-light interaction is simply experimental error since we do not see this effect during the steady state, or the transfer to novel camera angles. However, in the camera-light interaction, it seems as though lighting the image from the front allowed for discrimination when the camera angle caused ambiguity in the shape of the stimulus; the starlings had a higher percent correct with the 55° and 65° front-lit stimuli than their back-lit counterparts. This is likely the result of the visible shadow cast when the object is lit from the front. Removal of the shadow took away this advantage, leading to the interaction seen in the no-shadows portion of that experiment.

The fact that the curved surface's height affects the discrimination is not surprising, because reducing the shape results in reduced shading effects. Thus, a flat or near-flat surface cannot be determined to be convex or concave. However, the other conditions which contained a reasonable height should have been discriminable. The lack of a significant deviation from chance can be a result, in part, of the reduced power of the experiment as a result of losing one of the starlings. Additionally, the pairwise T-tests from the ANOVA show no significant differences between any of the conditions. However, assuming that there is a height below which all stimuli are mostly indistinguishable and above which mostly all stimuli are distinguishable, then seeing that 25% is visually distinct from 50% breaks the dimension space into those two groups. 0% and 25% height likely do not allow for discrimination, but 50% to 150% height do. Again the effect of cast shadows appears in this data. The three-way interaction was likely the result of the fact that with flat stimuli, no cast shadows are possible, and so it cannot be used as a subtle cue for directionality. However, with the stimuli that contained structure of actual height,

the shadow had a differential effect; some angles must make it difficult to integrate the shadow information with the shading information to come to a decision.

Although these tests do show some gradation and ranking of stimuli discernability, this experiment is restricted by the range of the response measure that we used. Percent correct is limited at its highest by 100%, and we encounter responses in this area frequently, resulting in a ceiling effect. Thus, there might be effects of the various dimensions, like color or lighting, but the response measure used in combination with the starlings' abilities mask any such possibilities. If a response measure were used that had less of a hard limit, relationships between the stimuli dimensions might be better discernible.

A less bound measure that might help rank the stimuli dimensions, for example, is the average response time for the stimuli. A quicker response time could be correlated with stronger or more accessible cues, possibly revealing the varying effects of the stimuli dimensions. An ANOVA for correct, single-presentation trials after full acquisition showed that across both camera angles, both colors, front-back lighting, and left-right lighting, the response time is not significantly different (See Table 9). However, an interaction between camera angle and lighting was found to be significant; although the response times of the front-lit stimuli are slower than the backlit stimuli, whereas the back-lit 35° stimulus had a faster response time than its 45° counterpart, the front-lit 35° stimulus had a much slower response time than its 45° counterpart ($F(1, 5) = 15.30, p < .05$). This is likely the result of interference from a secondary monocular depth cue: shadow. The front-lit stimuli cast a much more noticeable shadow than the back-lit stimuli, and this shadow is more noticeable in the former case. However, this is not indicative of a factor aiding in the shape from shading task but instead an indicator of the number of monocular depth cues available in reality. Altogether, this suggests a uniformity between these stimuli dimensions.

One of the big goals of this experiment was to begin the exploration of the cognitive processes of starlings as compared to pigeons in an analogous shape from shading experiment. Most critical in this comparison is recognizing the differences between the two forms of the experiment. The pigeon experiment was a go/no-go task where the pigeon got reinforced possibly multiple times for pecking at the lone, visible stimulus during the trial, and all information was collected via nonreinforced probes. In contrast, the starlings see two images and are reinforced once per image after the decision is made by the perching response. The big question is about what the bird learned; clearly they are under stimulus control, but what question are they resolving? Which is the concave or convex stimulus? Which is the more concave or more convex stimulus? Since the image sets were always paired, could there have been a specific interaction between the images. Unfortunately, the current data do not allow for disambiguating which of these is the case. However, the current form of the experiment is sufficient to resolve the issue, and continuation of the experiment is all that is necessary.

To determine whether the starlings are controlled by relative convexity, the solution would be to show two shapes of differing convexity as controlled by surface height and observing if the starlings simply move to the more convex object or indiscriminately choose either object. Indiscriminate choice would be indicative of responding to the convexity of a single object, whereas discriminate choice would suggest that the birds are actually attending to a single stimulus' convexity. Similarly, the solution to the stimulus pairing issue would be to mismatch the images in terms of stimuli dimensions while leaving the combination of convexity and concavity within a trial. Maintained discrimination would indicate that the convexity is the primary control, and loss of the discrimination would be suggestive of image interaction.

Another possible question is about whether the starling task is comparable to the pigeon task focuses on the point of not just the task differences, but the perceptual differences. The

pigeons viewing a lone stimulus only had to deal with one light source relative to one image. The pigeons could treat it as one plane, possibly like a wall, and one object. However, the starlings have more options for how to interpret the two images on the screen. First, aside from the black space between the two images, there is little or nothing to say that they are not, in fact, one image with an occluder. Given that the light source and surface color match for the two stimuli, the starling could interpret the two images as one continuous surface. However, a moment's thought will reveal that this condition does not per se confound the experiment. There are no properties of continuous items that would attending to the concavity at different ends of the object.

Further testing is clearly necessary, but not just to disambiguate the current study's results, but to elaborate them further. The pigeon research has already laid out a floorplan for the upcoming research: camera angle acquisition, specular highlight variability, systematic removal of visual information, ability to transfer to novel stimuli, flipping images to observe effects of assumed lighting and orientation, and finally ability to acquire novel shapes. However, in addition to these, further tests are available to explore the same question of importance of shading to monocular depth perception. For example, global normalization of the image so that ranges of color values are normalized to their central range, resulting in a topographical delineation of areas of the stimulus where the darkest and lightest areas match those of the regular stimuli, but the image appears much blockier. This used to be a more common task for humans before the proliferation of 16 bit color in computers. There are four dimensions along which the topographical shading along two dimensions: domain, range, density, and uniformity. Allowing for a limited domain would result in a partially full-resolution stimulus, and a partially topographical map. Limiting the range would change the amount of brightness between the brightest value and the darkest value of the domain, allowing for only brightnesses greater than 50%, for example. The density of the mapping is a measure of how many shades are needed for

the starlings to perceive a shape. Lastly, the uniformity of the mapping means that some part of the color spectrum will be globbed into a topographical group, while another smaller portion would be grouped into a similarly sized topographical group. Varying these four dimensions would allow the experiment to explore the perceptual components of lighting and shading perception in the starling visual system.

The current study confirms that the starlings are able to be brought under the stimulus control of shaded convex and concave surfaces. The transference of the differential responses to novel but categorically similar stimuli confirms that the convexity of the stimuli is the cue. Future experiments are needed to further confirm that the cue being used is shading, and then to determine what aspects of shading are critical for the discrimination and how those components interact. The apparatus developed for this experiment makes possible many future decision based experiments for the starlings, and it can facilitate further studies into closed economy systems involving a cognitive processing payload as well as auditory studies in the passerine species.

References

- Bautista, L. M., Tinbergen, J., Wiersma, P., & Kacelnik, A. (1998). Optimal Foraging and Beyond: How Starlings Cope with Changes in Food Availability. *The American Naturalist*, 152(4), 543-561.
- Cavoto, B. R., & Cook, R. G. (2006). The contribution of monocular depth cues to scene perception by pigeons. *Psychological Science*, 17(7), 628-634.
- Cook, R., Commons-Miller, N., & Kieres, A. (2009 March). *Shape from Shading in Pigeons*. Presentation at the Comparative Cognition Conference, Tampa, FL.
- Edmunds, M., & Dewhirst, R. A. (1994). The survival value of countershading with wild birds as predators. *Biological Journal of the Linnean Society*, 51(4), 447-452.
- Humphrey, K. G., Symons, L. A., Herbert, A. M., & Goodale, M. A. (1996). A neurological dissociation between shape from shading and shape from edges. *Behavioural Brain Research*, 76(1-2), 117-125.
- Khan, N. (2009). *The Use of Shape from Shading by the European Starlings (Sturnus vulgaris)* (Unpublished senior honors thesis). Tufts University, Medford, MA.
- Kiltie, R. A., Countershading: Universally deceptive or deceptively universal?, *Trends in Ecology & Evolution*, 3(1), 1988, 21-23.
- Kleffner, D. A., & Ramachandran, V. S. (1992). On the perception of shape from shading. *Perception & Psychophysics*, 52(1), 18-36.

- Lehky, S. R., & Sejnowski, T. J. (1988). Network model of shape-from-shading: Neural function arises from both receptive and projective fields. *Nature*, 333(6172), 452-454.
- Mingolla, E., & Todd, J. T. (1986). Perception of solid shape from shading. *Biological Cybernetics*, 53(3), 137-151.
- Ramachandran, V. S. (1988). Perception of shape from shading. *Nature*, 331(6152), 163-166.
- Ruxton, G. D. , Speed, M. P., Kelly, D. J. , What, if anything, is the adaptive function of countershading?, *Animal Behaviour*, 68(3), 2004, 445-451.
- Tomonaga, M. (1998). Perception of shape from shading in chimpanzees (pan troglodytes) and humans (Homo sapiens). *Animal Cognition*, 1(1), 25-35.
- Wiersma, P., Salomans, H. M., Verhulst, S. (2005). Metabolic adjustments to increasing foraging costs of starlings in a closed economy . *The Journal of Experimental Biology*, 208, 4099-4108 .
- Yonas, A., Kuskowski, M., & Sternfels, S. (1979). The role of frames of reference in the development of responsiveness to shading information. *Child Development*, 50(2), 495-500.

Table 1

T-tests for deviation from chance during acquisition

Session	Accuracy	t(4)	p
1	51.93%	1.378	0.240
2*	57.31%	4.563	0.010
3*	78.11%	3.042	0.038
4*	80.60%	3.441	0.026
5*	85.36%	3.996	0.016
6*	84.12%	4.049	0.015
7*	84.62%	4.311	0.013
8*	82.00%	3.742	0.020
9*	86.00%	4.150	0.014
10**	84.19%	5.787	0.004

Table 2

Main Effects and Interactions on Percent Correct for All Five Birds During Acquisition

Significance	Effect	Analysis of Variance
***	Session	F(9, 36)= 9.313, p < 0.001
	Color	F(1, 4)= 0.348, p = 0.587
	Camera	F(1, 4)= 5.280, p = 0.083
	Front-Back Lighting (FBL)	F(1, 4)= 1.857, p = 0.245
	Left-Right Lighting (LRL)	F(1, 4)= 0.184, p = 0.690
	Session × Color	F(9, 36)= 0.693, p = 0.710
	Session × Camera	F(9, 36)= 0.998, p = 0.459
	Color × Camera	F(1, 4)= 0.186, p = 0.688
	Session × Color × Camera	F(9, 36)= 0.367, p = 0.944
	Session × FBL	F(9, 36)= 0.928, p = 0.513
*	Color × FBL	F(1, 4)= 9.885, p = 0.035
	Session × Color × FBL	F(9, 36)= 0.633, p = 0.762
	Camera × FBL	F(1, 4)= 3.129, p = 0.152
	Session × Camera × FBL	F(9, 36)= 0.674, p = 0.727
	Color × Camera × FBL	F(1, 4)= 1.210, p = 0.333
	Session × Color × Camera × FBL	F(9, 36)= 1.584, p = 0.157
	Session × LRL	F(9, 36)= 1.595, p = 0.154
	Color × LRL	F(1, 4)= 6.279, p = 0.066
	Session × Color × LRL	F(9, 36)= 1.573, p = 0.161
	Camera × LRL	F(1, 4)= 0.653, p = 0.464
	Session × Camera × LRL	F(9, 36)= 0.706, p = 0.700
	Color × Camera × LRL	F(1, 4)= 2.432, p = 0.194
	Session × Color × Camera × LRL	F(9, 36)= 0.780, p = 0.636
	FBL × LRL	F(1, 4)= 0.000, p = 0.986
	Session × FBL × LRL	F(9, 36)= 1.705, p = 0.124
	Color × FBL × LRL	F(1, 4)= 0.091, p = 0.778
	Session × Color × FBL × LRL	F(9, 36)= 0.690, p = 0.713
	Camera × FBL × LRL	F(1, 4)= 0.498, p = 0.519
	Session × Camera × FBL × LRL	F(9, 36)= 1.036, p = 0.432
	Color × Camera × FBL × LRL	F(1, 4)= 0.134, p = 0.733
	Session × Color × Camera × FBL × LRL	F(9, 36)= 0.814, p = 0.607

Table 3

Main Effects and Interactions on Percent Correct of All Five Birds during Steady State

Significance	Effect	Analysis of Variance
	Color	$F(1, 4) = 1.123, p = 0.349$
	Camera	$F(1, 4) = 1.123, p = 0.349$
	Front-Back Lighting	$F(1, 4) = 3.136, p = 0.151$
	Left-Right Lighting	$F(1, 4) = 0.421, p = 0.552$
	Color \times Camera	$F(1, 4) = 0.515, p = 0.513$
	Color \times FBL	$F(1, 4) = 2.853, p = 0.166$
	Camera \times FBL	$F(1, 4) = 0.246, p = 0.646$
	Color \times Camera \times FBL	$F(1, 4) = 0.112, p = 0.755$
	Color \times LRL	$F(1, 4) = 0.409, p = 0.557$
	Camera \times LRL	$F(1, 4) = 0.411, p = 0.556$
	Color \times Camera \times LRL	$F(1, 4) = 0.033, p = 0.865$
	FBL \times LRL	$F(1, 4) = 0.108, p = 0.759$
	Color \times FBL \times LRL	$F(1, 4) = 0.379, p = 0.571$
	Camera \times FBL \times LRL	$F(1, 4) = 0.098, p = 0.770$
	Color \times Camera \times FBL \times LRL	$F(1, 4) = 7.623, p = 0.051$

Table 4

Main Effect and Interactions for Five Birds in a Transfer Test to Novel Camera Angles

Significance	Effect	Analysis of Variance
	Color	FBL(1, 4) = 0.002, p = 0.966
	Camera	FBL(8, 32) = 4.335, p = 0.001
	Front-Back Lighting (FBL)	FBL(1, 4) = 11.623 , p = 0.027
	Color \times Camera	FBL(8, 32) = 1.066, p = 0.411
	Color \times FBL	FBL(1, 4) = 0.000, p = 0.988
	Camera \times FBL	FBL(8, 32) = 1.268, p = 0.294
	Color \times Camera \times FBL	FBL(8, 32) = 0.693, p = 0.695

Table 5

Pairwise T-tests of Different Camera Angles from the Transfer to Novel Heights

Camera Angle	5	15	25	35	45	55	65	75	85
5		0.138	0.077	0.078	0.125	-0.067	-0.221	-0.217	-0.246
15			-0.060	-0.060	-0.013	-0.204	-0.358	-0.354	-0.383
25				0.000	0.048	-0.144	-0.298	-0.294	-0.323
35					0.047	-0.145	-0.299	-0.295	-0.324
45						-0.192	-0.346	-0.342	-0.371
55							-0.154	-0.150	-0.179
65								0.004	-0.025
75									-0.029

Entries are differences between the estimated marginal means. Bolded entries are significant ($p < .05$). Note that the greyed out boxes are either redundant or irrelevant.

Table 6

Main Effects and Interactions of Stimuli Dimensions on Accuracy for Transfer to Shadowless Stimuli

Significance	Effect	Analysis of Variance
	Shadow	$F(1, 3) = 8.461, p = 0.062$
	Color	$F(1, 3) = 1.024, p = 0.386$
**	Camera	$F(8, 24) = 4.128, p = 0.003$
	Front-Back Lighting (FBL)	$F(1, 3) = 1.551, p = 0.301$
	Shadow \times Color	$F(1, 3) = 0.000, p = 0.989$
	Shadow \times Camera	$F(8, 24) = 1.168, p = 0.357$
	color \times Camera	$F(8, 24) = 1.439, p = 0.231$
	Shadow \times Color \times Camera	$F(8, 24) = 0.604, p = 0.765$
	Shadow \times FBL	$F(1, 3) = 2.197, p = 0.235$
	Color \times FBL	$F(1, 3) = 0.643, p = 0.481$
	Shadow \times Color \times FBL	$F(1, 3) = 13.810, p = 0.034$
***	camera \times FBL	$F(8, 24) = 5.881, p = 0.000$
	Shadow \times Camera \times FBL	$F(8, 24) = 0.953, p = 0.494$
	Color \times Camera \times FBL	$F(8, 24) = 1.152, p = 0.367$
	Shadow \times Color \times Camera \times FBL	$F(8, 24) = 0.198, p = 0.988$

Table 7

Main Effects and Interactions on Accuracy of Stimuli Dimensions in Novel Height Transfers

Significance	Effect	Analysis of Variance
*	Height	$F(4, 12) = 3.744, p = 0.034$
	Camera	$F(1, 3) = 0.001, p = 0.981$
	Front-Back Lighting (FBL)	$F(1, 3) = 1.349, p = 0.329$
	Left-Right Lighting (LRL)	$F(1, 3) = 1.286, p = 0.339$
	Height \times Camera	$F(4, 12) = 0.384, p = 0.816$
	Height \times FBL	$F(4, 12) = 0.414, p = 0.796$
	Camera \times FBL	$F(1, 3) = 0.471, p = 0.542$
	Height \times Camera \times FBL	$F(4, 12) = 3.839, p = 0.031$
*	Height \times LRL	$F(4, 12) = 1.948, p = 0.167$
	Camera \times LRL	$F(1, 3) = 0.044, p = 0.847$
	Height \times Camera \times LRL	$F(4, 12) = 1.012, p = 0.439$
	FBL \times LRL	$F(1, 3) = 0.589, p = 0.499$
	Height \times FBL \times LRL	$F(4, 12) = 0.384, p = 0.816$
	Camera \times FBL \times LRL	$F(1, 3) = 0.885, p = 0.416$
	Height \times Camera \times FBL \times LRL	$F(4, 12) = 1.767, p = 0.200$

Table 8

Pairwise T-tests of Different Heights Relative to Baseline from the Transfer to Novel Heights

Relative Height	0	25	50	100	150
0		-0.07	0.13	0.29	0.25
25			0.2	0.36	0.32
50				0.16	0.13
100					-0.04
150					

Entries are differences between the estimated marginal means. Bolded entries are significant ($p < .05$). Note that the greyed out boxes are either redundant or irrelevant.

Table 9

Main Effect and Interactions on Response Time of Stimuli Dimensions during Steady State

Significance	Effect	Analysis of Variance
	Color	$F(1, 5) = 4.510, p = 0.087$
	Camera	$F(1, 5) = 0.327, p = 0.592$
	Front-Back Lighting (FBL)	$F(1, 5) = 2.640, p = 0.165$
	Left-Right Lighting (LRL)	$F(1, 5) = 3.179, p = 0.135$
	Color \times Camera	$F(1, 5) = 1.710, p = 0.248$
	Color \times FBL	$F(1, 5) = 0.768, p = 0.421$
*	Camera \times FBL	$F(1, 5) = 15.304, p = 0.011$
	Color \times Camera \times FBL	$F(1, 5) = 0.298, p = 0.609$
	Color \times LRL	$F(1, 5) = 3.585, p = 0.117$
	Camera \times LRL	$F(1, 5) = 0.231, p = 0.651$
	Color \times Camera \times LRL	$F(1, 5) = 6.467, p = 0.052$
	FBL \times LRL	$F(1, 5) = 6.428, p = 0.052$
	Color \times FBL \times LRL	$F(1, 5) = 0.712, p = 0.437$
	Camera \times FBL \times LRL	$F(1, 5) = 4.796, p = 0.080$
	Color \times Camera \times FBL \times LRL	$F(1, 5) = 0.249, p = 0.639$

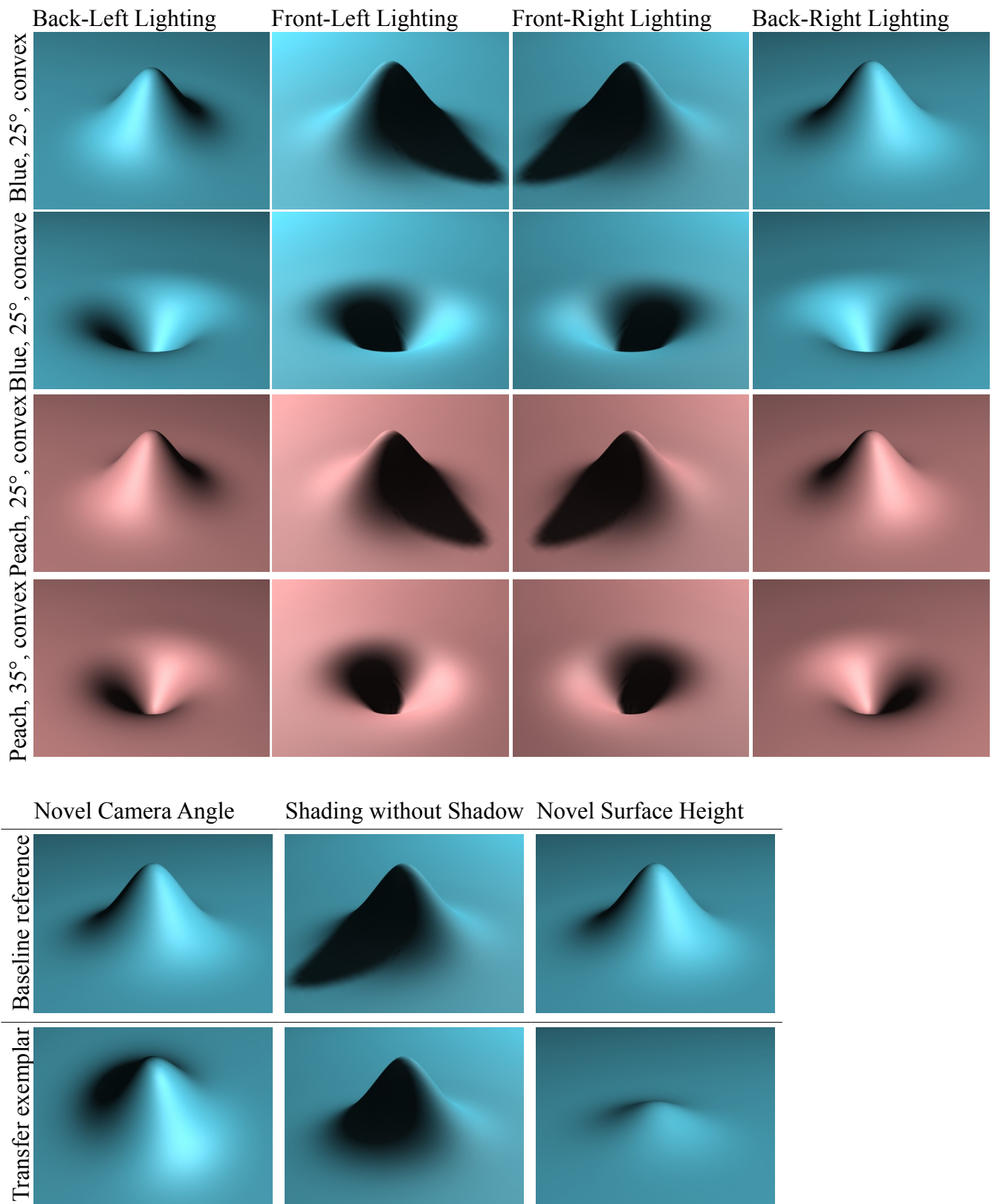


Figure 1: Stimuli used in Cook et al. (2009), Khan (2009), and the current study illustrating the difference in coloring, camera angle, light source direction, and height.

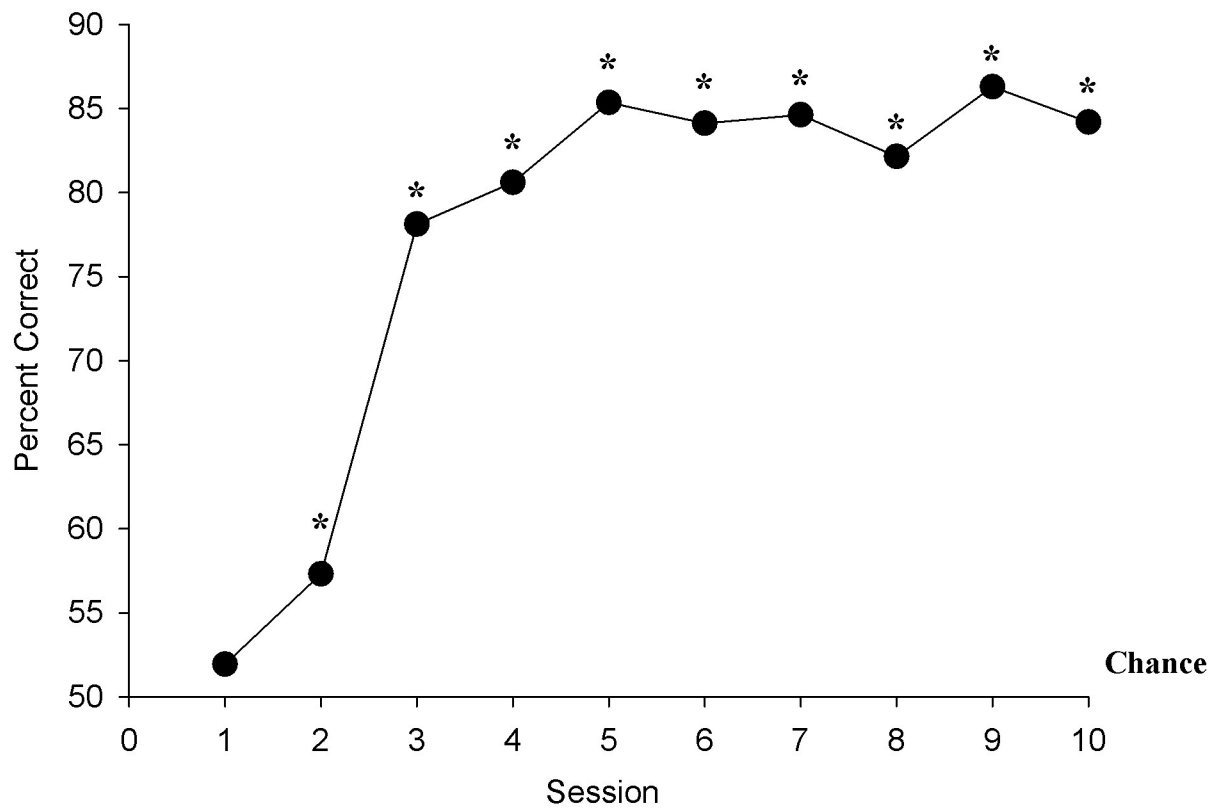


Figure 2: Average percent correct for five birds during the acquisition of the shape from shading task. The asterisks indicate significant difference from chance behavior (located at the axis).

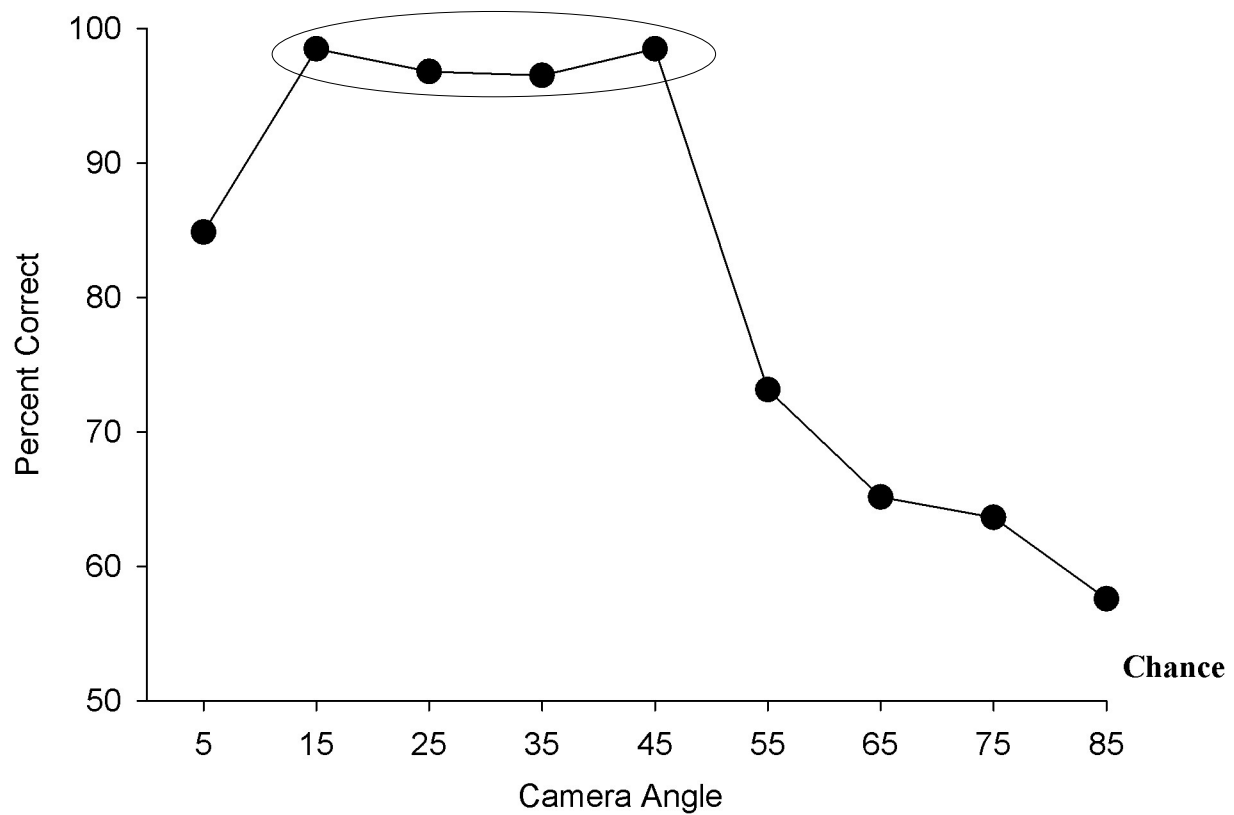


Figure 3: Average starling performance for five birds on transfer tests to new camera angles. Baseline data were at 25° and 35°. Circled data points are those that are significantly different ($p < .05$) from the 55° camera angle as reported by pairwise T-tests. Chance is the lower axis.

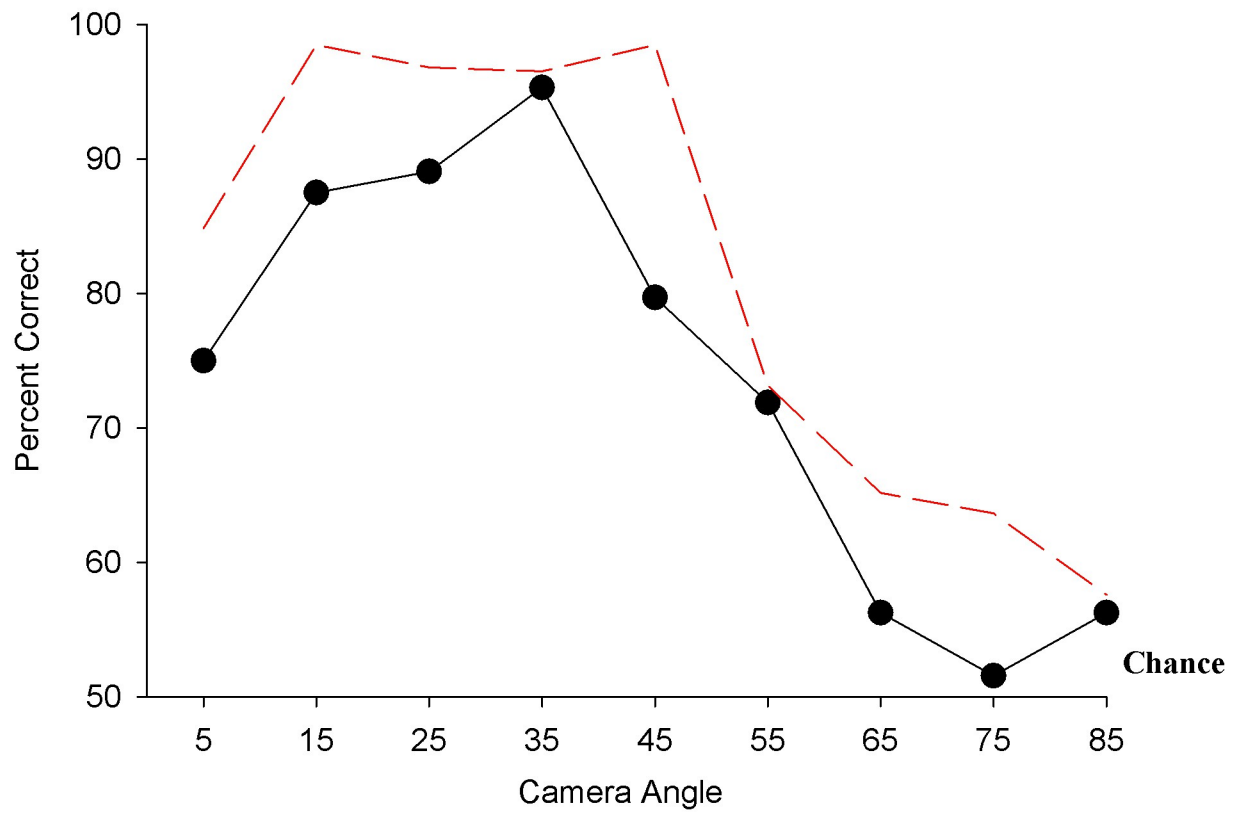


Figure 4: Average accuracy by four starlings on transfer to stimuli without shadows. The dotted red line is the plot from the previous figure, showing the accuracy with shadows. There was no significant effect of shadow reported in the ANOVA. Chance coincides with the lower axis.

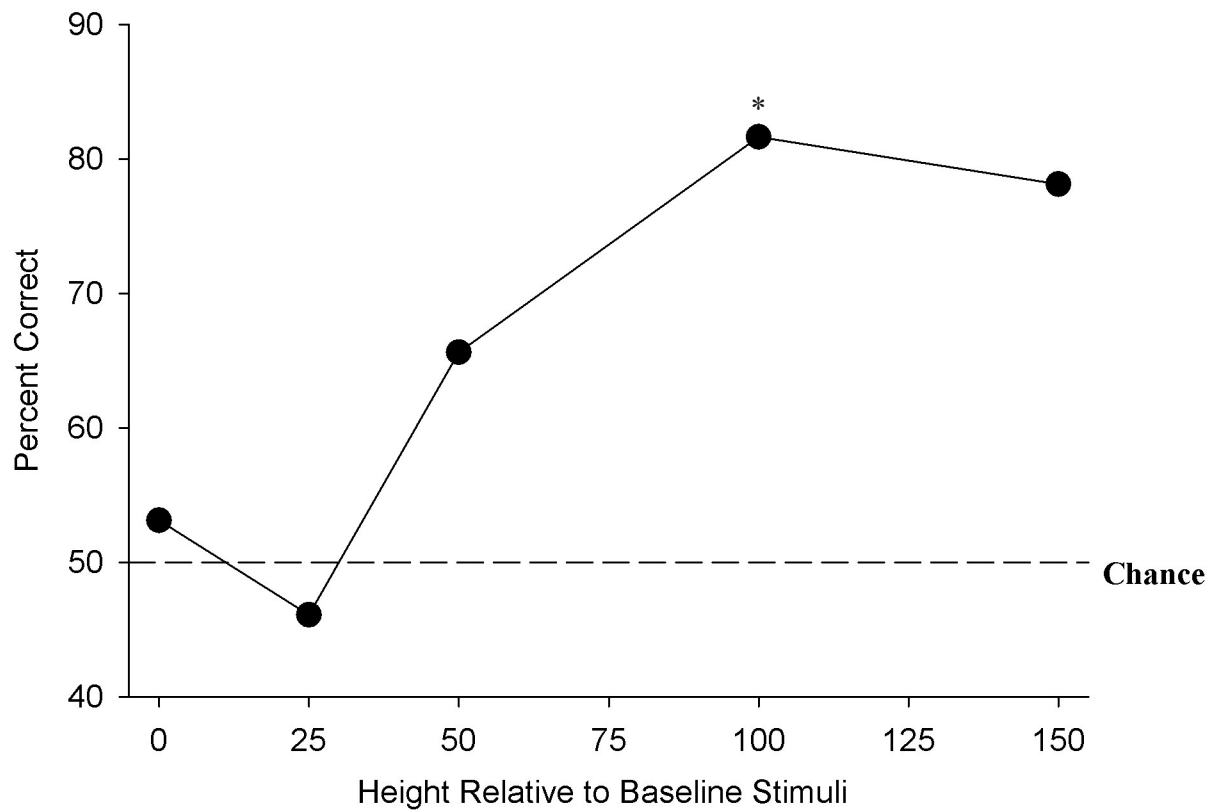


Figure 5: Average accuracy for four birds on transfer tests to convexities and concavities of different heights. The asterisk indicates significant deviation from chance.