EUROPEAN STARLINGS ARE CAPABLE OF DISCRIMINATING SUBTLE SIZE ASYMMETRIES IN PAIRED STIMULI

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Small deviations from bilateral symmetry (fluctuating asymmetries) are cues to fitness differences in some animals. Therefore, researchers have considered whether animals use these small asymmetries as visual cues to determine appropriate behavioral responses (e.g., mate preferences). However, there have been few systematic studies of animals' abilities to visually discriminate such minor asymmetries. If the asymmetries cannot be discriminated, fluctuating asymmetry can not be a visual cue. Here, we report an investigation of European starlings' (*Sturnus vulgaris*) abilities to discriminate small size asymmetries. We trained starlings, through operant conditioning in a free-flight aviary, to discriminate achromatic, symmetric paired stimuli from size-matched asymmetric stimuli. By starting the learning process with a large asymmetry and progressing through sequential trials of decreasing asymmetry, we elucidated a behavioral limit to asymmetry discrimination. We found that starlings are capable of discriminating a 10% size asymmetry. There was weaker evidence for discrimination of 5% asymmetry but no evidence for signal discrimination at 2.5% size asymmetry. This level of asymmetry discrimination suggests that many size asymmetry cues in nature can be discriminated by birds. At each level of asymmetry discrimination, we also tested whether starlings could generalize their learned symmetry preference to unreinforced novel images. Consistent with previous findings, we found that starlings could generalize their symmetry preferences.

Key words: fluctuating asymmetry, size symmetry, discrimination learning, visual images, cue, aviary-based testing, food discrimination, European starlings

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Small deviations from bilateral symmetry are important cues in mediating behavioral interactions among organisms (Forsman & Herrstrom, 2004; Forsman & Merilaita, 1999, 2003; Jablonski & Matyjasiak, 2002; Mazzi, Kunzler, & Bakker, 2003; Mazzi, Kunzler, Largiader, & Bakker, 2004; Møller & Swaddle, 1997; Morris & Casey, 1998; Schlüter, Parzefall, & Schlupp, 1998; Simmons, Rhodes, Peters, & Koehler, 2004; Swaddle, 1999a, 2003; Swaddle, Che, & Clelland, 2004; Uetz & Smith, 1999). These asymmetries (termed fluctuating asymmetry) are believed to result from the inability of individuals to buffer development of their symmetric traits from environmental variables and, therefore, are considered to be an estimate of developmental instability (Ludwig, 1932; Palmer & Strobeck, 1986; Van Valen, 1962). As fluctuating asymmetry is viewed as an index of how well the genome is suited to its developmental environment, larger asymmetries may be associated with poor environments and low fitness (Jones, 1987; Møller & Swaddle, 1997; Zakharov, 1992). Therefore, a small deviation from symmetry may be a cue to low fitness in the bearer of that trait.

Even though there is broad interest in whether small deviations from symmetry are effective as visual cues, relatively little is known about whether nonhuman animals can visually discriminate minor asymmetry differences. In bird populations, average length asymmetries in display traits are commonly less than 1 to 2% (i.e., in a bilateral trait the left side of the trait is commonly 1 to 2% longer or shorter than the right; Balmford, Jones, & Thomas, 1993; Møller & Höglund, 1991). The only empirical investigations of asymmetry discrimination thresholds indicate that length asymmetries have to be greater than 2% to be reliably discriminated (Swaddle, 1999b) and that asymmetry in more complex dot patterns may be even more difficult to discriminate (Swaddle & Ruff, 2004). Investigations of perceptual limits are currently illuminating the relative importance of fluctuating asymmetry to behavioral ecology and evolutionary biology. If the small asymmetries cannot be

discriminated, then they cannot be effective cues in nature.

Many birds possess discrete plumage patches that are paired on left and right sides of the body. The size of many such paired patches has a signaling function (see review in Andersson, 1994), and they have been studied in terms of their size asymmetry properties (e.g., Dufour & Weatherhead, 1998a, b; Jablonski & Matyjasiak, 1997, 2002). However, little is known about perception of small size asymmetries in birds. A recent experiment investigated the effect of signal size asymmetry on the avoidance of conspicuous color patterns by young chickens (*Gallus gallus domesticus*) and reported that relative size asymmetries must be approximately 7.5% to be discriminated (Forsman & Herrstrom, 2004). However, close inspection of the size asymmetry data reported by Forsman and Herrstrom suggests that the size asymmetry at their threshold for discrimination was actually between 20% and 32% relative asymmetry (based on reconstructing areas from the image diameters they reported). In addition, the asymmetric stimuli were, on average, 7% smaller than the symmetric images with which they were compared. Hence, Forsman and Herrstrom's test may have confounded overall size differences with asymmetry differences, although this does not explain why the birds did not respond differentially to an asymmetry of 20%. Hence, the only preliminary data we could find in the literature indicate that chickens have difficulty discriminating a relative size asymmetry of less than approximately 20%.

Here we report the first systematic investigation of size asymmetry thresholds in a wild bird, the European starling (*Sturnus vulgaris*). Specifically, we studied whether starlings could discriminate size asymmetries in achromatic two-dimensional images in a somewhat more ecologically valid (i.e., free-flight) test situation. By training starlings to respond to large asymmetries at the start of the experiment and slowly reducing the amount of asymmetry in subsequent trials, we investigated the limits for size asymmetry discrimination (cf. Swaddle, 1999b).

Previous studies of asymmetry perception in birds have often used some derivation of an operant chamber with stimuli projected onto a small number of response keys and where the movement of the birds is limited to a small area directly in front of the stimuli (Delius & Habers, 1978; Delius & Nowak, 1982; Swaddle, 1999b; Swaddle & Pruett-Jones, 2001; Swaddle & Ruff, 2004). In nature, asymmetries are viewed in less controlled conditions (e.g., at variable angles, lighting conditions, and distances). We designed a novel experimental approach that allows birds to view multiple stimuli at one time and from multiple angles and distances. In our free-flight aviary procedure, starlings could be up to approximately 4 m from the experimental stimuli during trials. These conditions are more similar to the context of behavioral decisions that wild birds make, compared with the controlled conditions of an operant chamber. Hence, our experiment is an important first step toward more ecologically relevant testing of avian visual performance. However, we also recognize that this new methodology may have disadvantages. For example, compared with the traditional operant chamber, the aviary procedure extends the ranges of relevant variables (e.g., stimuli are viewed at a larger number of angles and distances). We also reduced the overall number of forced choices a bird made during a single learning trial, hence increasing the time frame of the experiment. In summary, our study is novel in that we are the first to experimentally investigate size asymmetry discrimination in a wild bird. Our study is also the first to attempt such an investigation with birds in a free-flight aviary.

We had two specific goals for the research reported here. First, we intended to elucidate an approximate limit for size asymmetry discrimination. Based on previous investigations with chickens (Forsman & Herrstrom, 2004), we could have hypothesized that starlings would not discriminate size asymmetries of 20% or less. However, previous data with European starlings indicate that these birds can discriminate linear asymmetries of approximately 2% (Swaddle, 1999b). Therefore, by extrapolation, we could assume that starlings will be able to discriminate a size (i.e., an area) asymmetry difference of approximately 4% and thus exceed the apparent visual abilities of chickens. However, as we also assumed that our aviary-based technique would introduce more variation in angle and distance variables than the standard method that generated this

4% prediction, we refined our prediction: starlings' asymmetry discrimination threshold will be greater than 4%. Second, we investigated whether size symmetry preferences can be generalized to novel visual cues. Previous experiments indicated that starlings and pigeons (*Columba livia*) can generalize symmetry preferences (Delius & Habers, 1978; Swaddle & Pruett-Jones, 2001). Therefore, we hypothesized that starlings would successfully generalize a size symmetry preference to a set of novel stimuli.

METHOD

Subjects

We used 13 wild-caught adult European starlings of both sexes (7 females and 6 males) in this experiment. Starlings were housed either in pairs or alone in metal wire cages (approximately 0.5 × 0.6 × 1 m) with *ad libitum* drinking water on a 8:16 hr light–dark photoperiod at a constant temperature of approximately 20 °C. There was no reason to suspect that variation in housing arrangements would affect their visual abilities in the experiment. Before experimental trials began, the starlings were deprived of their food (commercial chick crumbs) for 2 hr to promote feeding in the experimental trials. Otherwise, starlings had *ad libitum* access to food.

Apparatus

Experimental trials were conducted in a separate room (approximately 5 × 4 × 3 m) in which we marked a 1-m² grid with 100 equally spaced locations (each 100 cm²) on the floor in the center of the room. We placed two tall perches at opposite corners on the outside of the grid so that starlings could view the entire grid from approximately 1 m above the floor (see Figure 1).

Procedure

Preexposure trials. We placed clear petri dishes (5-cm diameter) that had a small food compartment to one side at 20 randomly selected locations on the grid. In four preexposure trials, all 20 of the dishes contained 3 g of the starlings' normal chick crumb food. In each of the preexposure trials, a single starling was released into the experimental
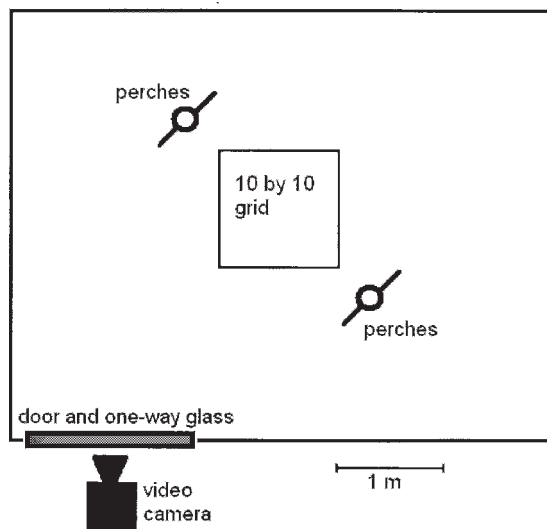

Fig. 1. Diagram of the free-flight aviary and learning grid used for the experiment. The grid was marked with 100 equally spaced locations. Starlings could perch above the grid. We recorded the starlings' activity with a video camera behind a one-way glass panel in the aviary door.

room, and we monitored its feeding activity for 40 min via a digital video camera through one-way glass (see Figure 1). Within four 40-min trials, all of the starlings had eaten from at least eight dishes within the 40-min period. Many starlings ate from more than eight dishes during this period. The subjects then progressed to the symmetry learning trials.

Symmetry discrimination learning trials. We constructed a set of 30 bilaterally symmetric images using Adobe Photoshop. The images were pairs of contiguous, achromatic images that varied in complexity from simple ellipses, triangles, and rectangles to shapes with curved edges and hollow structures (see Figure 2). Images were printed at a size of approximately 3 cm × 3 cm at 1200 dpi on white paper and laminated. A matching set of 20%-asymmetric images was produced by adjusting the size of the left and right elements so that one side (randomly left or right) was 20% larger in area than the other (i.e., one side of each stimulus was increased in size by 10% when the other side was reduced in size by 10%). However, the average size of the asymmetric images was the same as the average size of the corresponding symmetric pair. In other words, size was adjusted while keeping the aspect ratio of the images constant. The asymmetric set was

(a)

(b)

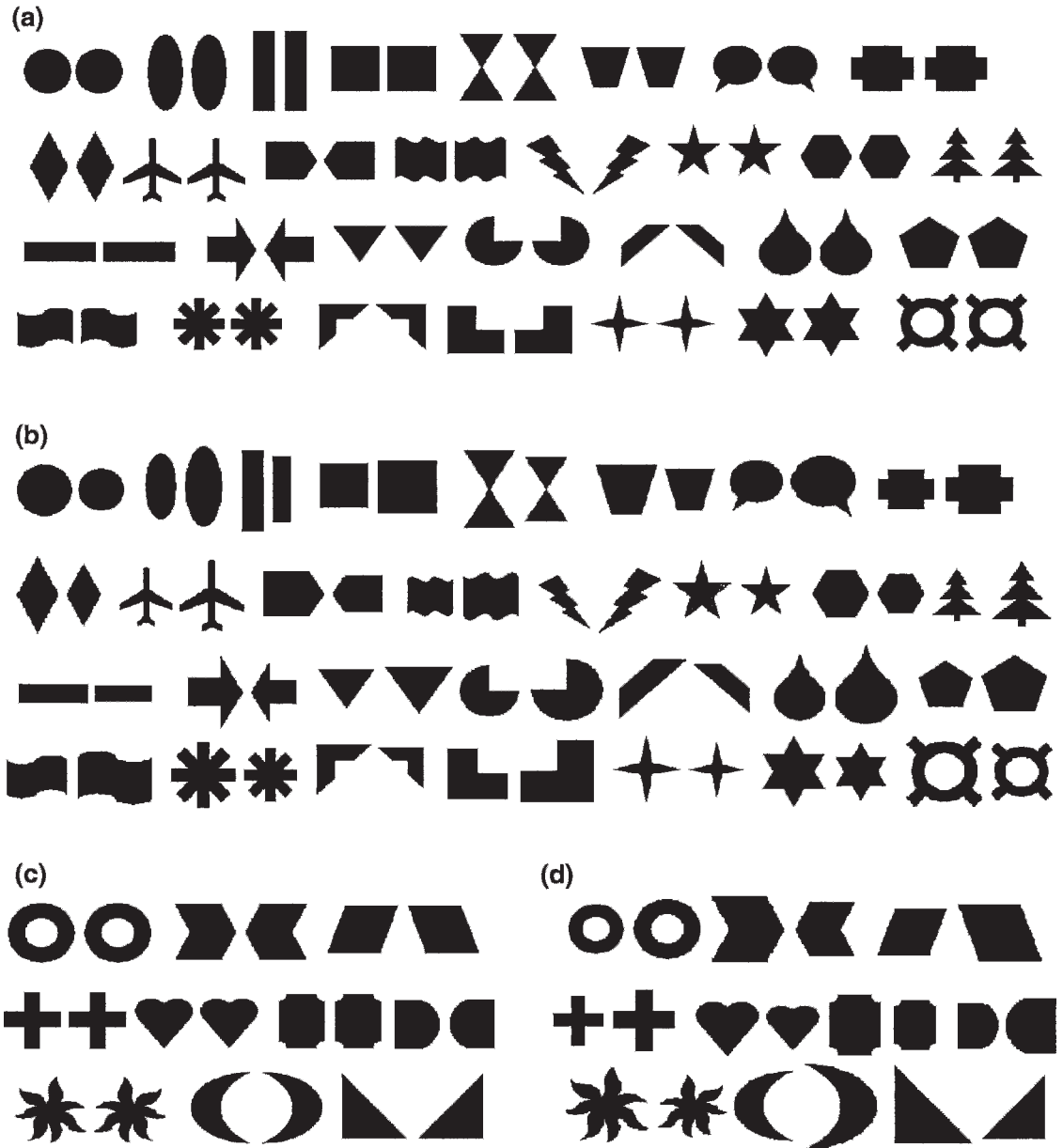
(c)   **(d)**

Fig. 2.   The stimuli used in the experiment. (a) The 30 bilaterally symmetric images used in learning trials. (b) The 30 20% size asymmetric images used in learning trials. (c) The 10 symmetric images used in test trials. (d) The 10 20% asymmetric images used in test trials.

printed and laminated in the same manner as the symmetric set. We decided to start the learning trials at the 20% size asymmetry as this was the apparent cut-off in asymmetry discrimination in a previous experiment with chickens (Forsman & Herrstrom, 2004). If starlings could discriminate 20% asymmetry, we intended to decrease asymmetry in sub-sequent trials. If they could not discriminate 20% size asymmetry, we intended to increase asymmetry in subsequent learning trials.

Throughout this article we describe the two sets of images as being ''symmetric'' or ''asymmetric''; however it is important to realize that the starlings could be judging differences in these sets according to other,

nonmutually exclusive visual cues. For example, they could be discriminating whole-image symmetry differences or could be comparing particular dimensions (e.g., height or width) or areas of two simultaneously presented images. In addition, symmetric stimuli had two elements that were identical, whereas asymmetric stimuli had two elements that were different from each other. Hence, symmetry discrimination could be described as differentially responding to same–different stimuli. We do not know what precise visual cues the starlings employed, but this limitation did not detract from our major goal of estimating the limit for discriminating between the symmetric and asymmetric sets of images. As the sets possessed geometric shapes that are well represented in birds' plumage patterns (e.g., ovals, triangles, rectangles, polygons), we considered our test relevant to symmetric and asymmetric cues in natural environments.

We chose to focus our stimuli manipulations on a vertical plane of symmetry (see Figure 2) as the majority of natural avian plumage signals possess a vertical plane of symmetry. In addition, starlings' ability to discriminate symmetry differences in achromatic dot patterns does not appear to be affected by the orientation of the axis of symmetry (Swaddle & Pruett-Jones, 2001).

We prepared two types of food. Distasteful food was prepared by spraying chick crumbs with a 15% aqueous solution of quinine hydroxide mixed with green food coloring. We used food coloring to ensure that any trace of a quinine residue was not visible to the starlings. Chick crumbs that are sprayed and dried and apparently bitter tasting are not harmful to starlings (Forsman & Merilaita, 1999; Swaddle, Che, & Clelland, 2004). Control food was prepared by spraying chick crumbs with an aqueous solution of the same green food coloring. Once the control food dried, researchers could not visually discriminate control food from the distasteful food. During the experiment, we explicitly tested whether starlings could visually discriminate control from distasteful food (see below). Throughout the learning trials, we paired control food with symmetric images and distasteful food with asymmetric images. Previous experiments had shown that the rate of learning to discriminate asymmetrical images is not affected by whether control food

accompanies symmetric or asymmetric stimuli (Swaddle, 1999b; Swaddle & Pruett-Jones, 2001).

A learning trial began by placing 10 randomly selected symmetric and 10 randomly selected 20% asymmetric images at 20 randomly selected locations on the experimental grid. We placed petri dishes containing approximately 3 g of control food over the symmetric images and dishes containing approximately 3 g of distasteful food over the asymmetric images. The images could be seen clearly through the dishes and were not obscured by the small food compartment. Hence, feeding from symmetric dishes was positively reinforced, whereas feeding from asymmetric dishes was punished.

Starlings were released one at a time into the room, and we recorded the proportion of symmetric dishes a starling fed from in a 40-min learning trial. A learning trial lasted for 40 min or until a starling had fed eight times from the dishes, whichever occurred first. We allowed starlings to revisit dishes within a trial to maintain the constant ratio of symmetric to asymmetric dishes that were available. Revisits were only recorded if the subject had searched at least one other dish on the grid before returning to the original dish location. Learning trials were conducted 3 to 5 days a week, once per day. After each learning trial, starlings were returned to their housing cages and provided with *ad libitum* food.

We adopted a criterion for discrimination learning of 75% or more feedings from symmetric dishes in three consecutive learning trials. The cumulative probability of this sequence happening by chance is less than 5%. Each starling experienced 15 learning trials unless it reached this criterion sooner. Once a starling achieved the learning criterion or completed 15 learning trials, it progressed to successive test and control trials and then to a new set of learning trials with a smaller degree of asymmetry. The decreasing steps in asymmetry were 20% (the initial condition), 10%, 5%, and 2.5%. One starling that did not meet the criterion in the 20% condition was removed from the experiment. In subsequent learning trials (employing 10%, 5%, and 2.5% asymmetry images), starlings were removed from the experiment if they did not learn within 10 trials. We adopted this stricter criterion in later learning trials as starlings

already had learned the general symmetry discrimination task, and we had positive evidence that this learning transferred to new trials (described later). Hence, each subject should not have needed the extensive 15-trial learning condition to perform the next level of task. If a starling could discriminate a smaller degree of asymmetry it should be able to do so within 10 trials (and most did), after learning the initial asymmetry discrimination task.

Test trials. Once a starling had met the learning criterion, during the next trial we tested whether performance would generalize to novel images. Test trials were identical to learning trials except that we placed 10 new symmetric and 10 new asymmetric images (see Figure 2c and 2d) at random locations on the grid. Also, we presented control food with both symmetric and asymmetric images in these 40-min test trials. As before, we recorded the proportion of feedings from symmetric versus asymmetric dishes. This procedure represented a generalization test without extinction.

Control trials. Following a test trial, each starling received a control trial. These followed the same general protocol as learning trials except that we did not place any images on the grid. We recorded the proportion of feedings from control versus distasteful food dishes. Hence, these trials were designed to test whether starlings could discriminate control from distasteful food.

Subsequent learning trials. Following completion of test and control trials, further learning–test–control trial sequences were presented employing the same procedures as described above. However, these subsequent trials used progressively lower degrees of asymmetry in the asymmetric sets of stimuli: 10%, 5%, and 2.5%. After completion of the experiment, starlings were released back to the wild at the same location they were caught.

Statistical Analyses

Although we defined a criterion for learning, we also tested statistically whether starlings had successfully learned to discriminate symmetry from asymmetry at each stage in the study. We did this by comparing the proportion of feedings from symmetric dishes in the last learning trial to the proportion of feedings from control dishes in the control trial, using a repeated-measures ANOVA.

Similarly, we tested whether any learned symmetry preference was transferred from the learning trials to the novel test images in the test trial by comparing the proportion of feedings from symmetric dishes in the test trial to the proportion of feedings from control dishes in the control trial, using a repeated-measures ANOVA. In addition, we compared the magnitude of starlings' symmetry preference to learned and novel images by comparing the proportion of feedings from symmetric dishes in the last learning trial with the proportion of feedings from symmetric dishes in the test trial, using a repeated-measures ANOVA. All ratio data were arc-sine square-root transformed to fit the assumptions of normality of ANOVA. All analyses were performed with SPSS v11 for Windows, employing two-tailed tests of probability.

RESULTS

20% Size Asymmetry Learning, Testing, and Control Trials

The per-trial proportions of feedings from control dishes for each subject for learning, testing, and control trials in the 20%, 10%, and 5% asymmetry conditions are shown in Table 1. The feeding behavior of the 13 starlings in the initial learning trial indicated no spontaneous preference for symmetric over asymmetric images (one-sample t-test against a prediction of random pecking, $t_{12} = 0.457$, $p = 0.656$). In subsequent learning trials, 5 starlings were removed from the experiment because their feeding activity dropped to low levels (i.e., they did not feed from the dishes for four consecutive trials). Therefore, the sample size was reduced to 8 starlings in the learning trials. One of the 8 starlings did not meet the learning criterion and did not progress to test, control, or further learning trials. On average (± standard error), the 7 remaining starlings took 8.6 (± 1.1) trials to reach the criterion. According to our statistical comparison of performance in learning and control trials, these starlings successfully learned to discriminate the symmetric images from the 20% asymmetric images ($F_{1,6} = 32.67$, $p = 0.001$; see Figure 3).

The learned symmetry preference generalized to novel images, as starlings were more likely to feed from the control food dishes that accompanied novel symmetric test images

Table 1

Proportion of feedings from control dishes by each subject, in the order that they entered the experiment, for all 20%, 10%, and 5% asymmetry trials during the experiment. Some starlings did not meet the learning criterion and, therefore, did not receive test or control trials at particular levels of asymmetry.

| | 20% learning trials | | | | | | | | | | | | | | |
Subject	1	2	3	4	5	6	7	8	9	10	11	12	13	20% test	control
07	0.63	0.75	0.50	0.75	0.50	1.00	0.88	1.00						1.00	0.63
03	0.38	0.38	0.63	0.25	0.38	0.63	0.75	0.75	0.75					0.38	0.25
14	0.63	0.25	0.63	1.00	0.38	0.63	0.67	0.63	0.00	1.00	0.00	0.50	1.00	na	na
20	0.63	0.75	0.75	0.75										0.75	0.63
17	0.13	0.38	0.33	1.00	1.00	0.75								0.50	0.50
43	0.75	0.75	0.63	0.75	0.63	0.50	0.88	0.75	0.75					0.67	0.43
37	0.88	0.75	0.50	0.75	0.63	0.63	0.00	0.63	0.75	0.60	0.88	0.75	0.88	0.75	0.38
35	0.40	0.50	0.50	0.63	0.88	0.88	0.75							0.67	0.50

| | 10% learning trials | | | | | | | | | | | |
Subject	1	2	3	4	5	6	7	8	9	10	10% test	control
07	0.75	0.60	0.60	0.63	0.63	0.57	0.83	0.50	0.63	0.75	na	na
03	0.50	0.25	0.88	0.63	1.00	0.63	0.63	0.88	1.00	0.75	0.75	0.50
14											na	na
20	0.38	0.50	0.75	0.88	0.75						0.50	0.71
17	0.75	0.00	0.25	1.00	0.75	0.63	0.88	1.00	1.00		0.63	0.50
43	0.60	0.75	0.88	0.75							0.50	0.38
37	1.00	0.75	0.88								1.00	0.50
35	0.80	0.00	0.14	0.67	0.33	0.50	0.50	1.00	0.50	0.50	na	na

| | 5% learning trials | | | | | | | | | | | |
Subject	1	2	3	4	5	6	7	8	9	10	5% test	control
07											na	na
03	0.50	0.50	0.50	0.38	0.50	0.50	0.50	0.38	0.50	0.71	na	na
14											na	na
20	0.88	0.00	0.50	0.33	0.50	0.50	0.75	0.50	0.71	1.00	na	na
17	0.63	0.63	0.40	0.50	0.63	0.75	0.38	0.25	0.63	0.50	na	na
43	0.63	0.50	0.50	0.71	0.75	1.00	0.50	0.80	0.83	1.00	1.00	0.50
37	0.75	1.00	0.63	0.14	0.40	0.50	0.50	0.33	0.63	0.67	na	na
35											na	na

than they were to feed from the control food dishes in the control trial ($F_{1,6} = 11.19$, $p = 0.016$; Figure 3). However, this generalized symmetry preference was significantly smaller in magnitude than that in the learning trials ($F_{1,6} = 6.58$, $p = 0.043$; Figure 3).

10% Size Asymmetry Learning, Testing, and Control Trials

Seven starlings progressed to the 10% size asymmetry learning trials. Of these, 5 successfully met the learning criterion, and they did so in an average of 6.2 ($\pm$ 1.4) trials. As before, these starlings showed a statistically significant level of learning at 10% size asymmetry ($F_{1,4} = 11.19$, $p = 0.029$; see Figure 4).

There was mixed evidence that the 5 starlings who met the learning criterion also generalized their learned symmetry preference to novel test images. Their symmetry preference in the test trial was not different from performance in their control trial ($F_{1,4} = 1.83$, $p = 0.247$). However, the magnitude of their symmetry preference in the test trial was not significantly smaller than the learned symmetry preference ($F_{1,4} = 1.22$, $p = 0.331$), contrary to the results in the 20% asymmetry comparison. The small sample size here resulted in low statistical power in both tests, and so we make no further inference from these latter two results.

5% Size Asymmetry Learning, Testing, and Control Trials

Five starlings progressed to the 5% size asymmetry learning trials. Of these, only 1
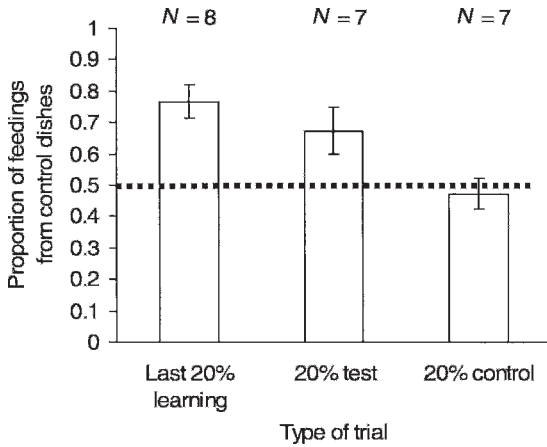
Fig. 3. Mean proportion (and standard error) of feedings from control food dishes in the last learning trial, in the test trial, and in the control trial when the task involved a 20% size asymmetry discrimination. Sample size is indicated above each bar. The dashed line indicates a 50% proportion of feedings (i.e., random feeding).
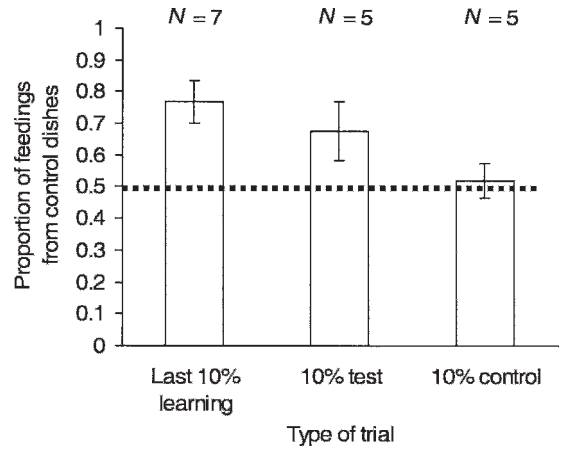
Fig. 4. Mean proportion (and standard error) of feedings from control food dishes in the last learning trial, in the test trial, and in the control trial when the task involved a 10% size asymmetry discrimination. Sample size is indicated above each bar. The dashed line indicates a 50% proportion of feedings from (i.e., random feeding).

starling met the learning criterion, and it did so in 10 trials. As we could not test statistically whether this level of learning was significantly greater than control performance in the same manner as with previous analyses, we compared performance in the last learning trial of all 5 starlings who progressed to this level with an expected control performance of random pecking at the food dishes (i.e., a 0.5 probability of eating from a control food dish) in a one-sample t-test. Given the assumption of random pecking as a baseline for comparison, this analysis indicated that the group of 5 starlings discriminated symmetry from 5% size asymmetry ($t_4 = 2.82$, $p = 0.049$).

2.5% Size Asymmetry Learning

The 1 starling that progressed to the 2.5% asymmetry learning trials did not get close to meeting the learning criterion at this level of asymmetry [(mean proportion of feedings from control food dishes over its last five trials = 0.43 ($\pm$ 0.063)].

DISCUSSION

We conclude that starlings can discriminate a difference between symmetry and 10% relative size asymmetry in achromatic, paired complex patterns. The evidence that the starlings can discriminate a 5% size asymmetry

was less conclusive — only 1 out of 5 starlings met the learning criterion at the 5% size asymmetry level. Also, the test of asymmetry discrimination at the 5% level was marginally significant ($p = 0.049$) and was based on the assumption that starlings without symmetry/asymmetry cues would peck at control food dishes at the same rate as they would peck at distasteful food dishes. This assumption was partially supported by the previous control trial performances in which the mean ratio of pecks to the two types of dishes was always close to 0.5 (see Figures 2 and 3).

Forsman and Herrstrom (2004) indicated that young chickens could not discriminate a relative size asymmetry of 20%. However, their test confounded overall size differences with symmetry/asymmetry differences. Specifically, their asymmetric stimuli were approximately 7% smaller in overall area than the symmetric stimuli. Hence, as already noted, it is somewhat difficult to interpret their data in terms of symmetry differences alone. In our test, we controlled for overall size differences by matching symmetric and asymmetric images in terms of overall area within each pair and also by having a large range of size-matched symmetric and asymmetric pairs that varied in size among pairs. In a previous test, Swaddle (1999b) showed that starlings can discriminate length asymmetries (length in

a single dimension) of approximately 2%. If this single dimension is scaled to an area (i.e., size), we could infer that starlings would discriminate an area difference of approximately 4%. This prediction fits surprisingly well with the current findings. Moreover, the correspondence in findings from the two different procedures implies that our aviary-based procedure can provide comparable information about asymmetry discrimination to that obtained with standard operant chambers, yet the aviary procedure allows more naturalistic environmental conditions.

The correspondence between the two results also suggests that traditional operant chamber procedures are relevant to interpreting visual discrimination in more natural settings. The two procedures (aviary-based and traditional operant chamber-based) are similar in that birds are trained to make behavioral choices based on the appearance of visual stimuli. Hence, both procedures are useful for probing the limits of visual discrimination and learning abilities in subjects. Yet the traditional operant chamber often forces dichotomous choices in precisely controlled conditions (e.g., timing of presentation of stimuli, lighting of stimuli, amount of food reward delivered), whereas the aviary procedure permits evaluation of multiple stimuli simultaneously in far less controlled conditions that more closely resemble natural decision-making scenarios. In future experiments, we plan to extend the aviary procedure to three-dimensional testing of asymmetry discrimination with natural visual signals and backgrounds. We also are exploring field methods of testing such discrimination ability as well.

Why do starlings have a lower threshold for discriminating size asymmetry than young chickens? It is possible that the ability to discriminate small asymmetries varies among avian species. As there is selection for the production of symmetric visual cues in some species (see reviews in Swaddle, 1999a, 2003), it is possible that there is associated selection for discriminating asymmetric cues. Although there is no evidence of preference for symmetric traits in European starlings (Swaddle & Witter, 1995) or in the wild ancestor of domestic chickens—the red jungle fowl (*Gallus gallus*) (Ligon, Kimball, & Merola-Zwartjes, 1998)—it is possible that there has been increased selection for symmetry preferences along the starling lineage compared with the chicken lineage.

It also is possible that asymmetry discrimination abilities change with age. Forsman and Herrström (2004) used 5-7 day-old chicks in their study, whereas we used adult starlings that were at least one year old. We are not aware of any study investigating a change in symmetry perception with age. We cannot realistically evaluate either hypothesis without further data. Because of low sample size, we also could not test for sex differences in asymmetry discrimination.

Our study revealed noticeable between-subject variation in learning. For example, not all starlings met the learning criterion after the same number of learning trials at a specific asymmetry level (see Table 1). One failed to learn to discriminate at 20% size asymmetry, whereas another one successfully learned to discriminate the 5% asymmetry. Such variation may be related to the aviary-based experimental design. Starlings could view the stimuli from multiple angles and distances. Some may have viewed the images from locations within the aviary that made asymmetry discrimination more difficult.

Current shape-recognition models indicate that symmetry discrimination is a low-level process that is widespread in vertebrate visual systems (Evans, Wenderoth, & Cheng, 2000; Osorio, 1996; Scognamillo, Rhodes, Morrone, & Burr, 2003; Tyler, 1996; Wilson & Wilkinson, 2002). However, relatively little is known about how minor deviations from symmetry are discriminated (Osorio, 1996; Scognamillo et al., 2003). The mechanisms underlying the discrimination of small asymmetries may not necessarily be the same visual processes involved in basic symmetry perception. Our study indicates that there may be substantial variation, both within and between species, in the discrimination of small asymmetries. Young chickens seem much worse at asymmetry discrimination than adult starlings. A recent model that correlates well with empirical measures of discrimination in humans (Scognamillo et al., 2003) suggests that vertebrate visual systems are designed to be sensitive to minor asymmetry differences of the order reported here.

Our study also indicates that learned size asymmetry preferences can be generalized to

novel stimuli—a finding generally consistent with previous reports of symmetry preference generalization in starlings and pigeons (Delius & Habers, 1978; Swaddle & Pruett-Jones, 2001). It is possible that symmetry preferences acquired in one context could affect symmetry preferences in other contexts. For example, a symmetry preference for a food item could, theoretically, affect a symmetry preference for mates. As a caveat to these generalization results, it is important to note that symmetry preferences can emerge as a by-product of birds learning to recognize novel objects when the average of the stimuli used for learning is symmetry (Jansson, Forkman, & Enquist, 2002; Swaddle et al., 2004). Since the average of the pairs of stimuli used in the learning trials was symmetry (as there were just as many left-biased as right-biased images), the generalization of a symmetry preference could result from learning to feed from food dishes placed on stimulus patterns that, when averaged, produced symmetry. Further research will be required in order to determine the soundness of this hypothesis.

Finally, we have claimed that the stimuli we used in the current study were approximations to naturally available cues and signals. Unfortunately, there are few published measurements of natural size asymmetries. Mean size asymmetries in moth-wing patterns range from 2 to 7%. However, individual asymmetry values can be much higher, up to 26% (Forsman & Herrstrom, 2004; Forsman & Merilaita, 2003). In zebra finches (*Taeniopygia guttata*), the mean asymmetry of chest bars and cheek patches is commonly around 10% (Swaddle & Cuthill, 1994; Swaddle, 2006). In chaffinches (*Fringilla coelebs*), individual epaulette asymmetry can be as large as 35% (Jablonski & Matyjasiak, 1997). Therefore, a threshold for discrimination between 5 and 10% will classify many individuals as having asymmetric traits, that is, asymmetry will be effectively discriminated.

We suggest that the threshold for size asymmetry discrimination in starlings seems low enough to indicate that size asymmetry in paired, discrete structures can be readily discriminated in nature. This is unlike the case of discrimination of length asymmetries, where many are too small to be discriminated (Swaddle, 1999b). As explained above, there is close correspondence in our estimates of starlings' abilities to discriminate area and length asymmetries, which suggests that similar mechanisms are involved in both visual tasks. However, published reports of natural avian signals indicate that length asymmetries (e.g., length asymmetries of elongated tail feathers) are far smaller than area (size) asymmetries (e.g., area asymmetries of paired epaulettes and color patches), indicating that fluctuating asymmetry in area-based signals is a more viable visual signal or cue than asymmetry in length-based cues. In addition, the size of discrete plumage and coloration patches is unlikely to have direct effects on the flight performance of birds, unlike the elongated tail feathers. So, unlike asymmetry in flight feather lengths, visual selection based on patch size asymmetry may be relatively unconstrained by the variables that affect flight. Therefore, we hypothesize that left-right asymmetry in the area of discrete coloration patches is more likely to be an effective visual cue for fluctuating asymmetry (and possibly to fitness) than the length of mechanically functional traits, such as the length of wing and tail feathers.

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