9-2001

# Starlings Can Categorize Symmetry Differences in Dot Displays

John P. Swaddle
*College of William and Mary*, jpswad@wm.edu

Stephen Pruett-Jones

## Recommended Citation

# Starlings Can Categorize Symmetry Differences in Dot Displays

John P. Swaddle[*] and Stephen Pruett-Jones

Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637

abstract: Fluctuating asymmetry is an estimate of developmental stability and, in some cases, the asymmetry of morphological traits can reflect aspects of individual fitness. As asymmetry can be a marker for fitness, it has been proposed that organisms could use morphological asymmetry as a direct visual cue during inter- and intraspecific encounters. Despite some experimental evidence to support this prediction, the perceptual abilities of animals to detect and respond to symmetry differences have been largely overlooked. Studying the ability of animals to perceive symmetry and factors that affect this ability are crucial to assessing whether fluctuating asymmetry could be used as a visual cue in nature. In this study, we investigated the ability of wild-caught European starlings *Sturnus vulgaris* to learn to discriminate symmetry from asymmetry in random dot patterns through operant learning experiments. The birds did not possess a spontaneous preference for either symmetry or asymmetry. The birds learned a symmetry preference, although the learning process took longer than that previously reported for pigeons *Columba livia* and was more error prone. After being trained to discriminate symmetry differences in random dot patterns, birds successfully transferred their symmetry discrimination abilities to a set of novel stimuli that they had not previously seen. This indicates that starlings can form a mental categorization of visual stimuli on the basis of a somewhat generalized symmetry phenomenon. We discuss these findings in relation to the probability that birds use fluctuating asymmetry as a visual cue.

*Keywords:* fluctuating asymmetry, perception, signals, *Sturnus vulgaris*, symmetry, operant learning.

Developmental stability reflects the ability of the genome to buffer development against a specified environmental insult to produce an intended phenotype (reviews in Zakharov 1992; Palmer 1996). The most commonly employed index of developmental stability is fluctuating asymmetry (Ludwig 1932), which represents the subtle departures from perfect symmetry in bilaterally symmetric traits. As fluctuating asymmetry is an indicator of the genome's ability to resist environmental disturbances, many researchers have examined the relations between fluctuating asymmetry and indicators of fitness (reviews in Watson and Thornhill 1994; Markow 1995; Møller and Swaddle 1997). These studies have rendered a broad spectrum of conflicting results: the asymmetry of certain traits appears related to fitness in some taxa but not others (Markow 1995; Palmer 1996). Asymmetry-fitness relationships can occur either due to increased buffering in individuals of inherently higher fitness or due to trait asymmetry directly affecting fitness (e.g., through biomechanical performance; Møller and Swaddle 1997; Sneddon and Swaddle 1999).

As asymmetry can be a marker for fitness in some organisms, Møller (1990) proposed that morphological asymmetry of exaggerated ornamental traits could be used as a direct visual cue (or signal) of quality in social and sexual encounters. Asymmetry also could act to influence behavior (e.g., mechanical performance) and so operate as an indirect signal. A number of observational studies have supported the prediction that asymmetry could be used as a cue in a range of contexts (Møller and Swaddle 1997). However, to examine the true direct visual signaling properties of fluctuating asymmetry, researchers must manipulate asymmetry (within reasonable limits determined by the natural range of asymmetry values) independent of other morphological and behavioral characters (Swaddle 1997). This form of manipulation has seldom been performed, and we are aware of only six studies that have employed such methodology (review in Swaddle 2000). In three of these cases, symmetric signals were preferred as predicted (Swaddle and Cuthill 1994a; Møller and Sorci 1998; Morris and Casey 1998); however, in the other three studies, there was no evidence for a signaling role of asymmetry (Swaddle and Witter 1995; Jablonski and Matyjasiak 1997; Tomkins and Simmons 1998). In addition, it is possible that the experiments that provide positive evidence for a signaling role of asymmetry have confounded other perceptual properties with differences in symmetry (see Shettleworth 1999).

To date, most of the evidence supporting a signaling role for fluctuating asymmetry comes from associations between the asymmetry of signaling traits and measures of individual fitness of the trait bearer (i.e., the signaler). Examining correlations between signal (fluctuating asymmetry) and signaler characteristics (fitness) ignores a vital element of any signaling system, that is, the receiver of the signal. The receiver's ability to detect, store, and recall a signal is crucial to the viability and stability of a signaling system and has largely been overlooked in studies of fluctuating asymmetry. If a receiver cannot perceive differences between symmetry and asymmetry, it does not matter how accurately asymmetry reflects fitness; an asymmetry-signaling system cannot occur.

Compared with our knowledge of symmetry perception in humans, we know relatively little about the perceptual abilities of animals with respect to symmetry (review in Swaddle 1999*b*). There is evidence that bees (Horridge 1996), some fish species (Rensch 1958; Morris and Casey 1998), and an ever-increasing number of bird species (Rensch 1958; Delius and Habers 1978; Blough and Franklin 1985; Møller 1993; Swaddle and Cuthill 1994*a*; Fiske and Amundsen 1997) can detect and respond to symmetric visual stimuli. Recently, it has been suggested that symmetry perception may be a fundamental property of most vertebrate visual systems (Osorio 1996). However, to more fully assess the plausibility of signaling by differential levels of morphological asymmetry, we need to explore the symmetry perception abilities of wild-caught animals. If these organisms cannot detect and respond to symmetry differences and are unable to learn symmetry preferences, it is highly unlikely that they could use subtle variation in signaling-trait asymmetry during natural encounters. Therefore, in this study, we experimentally investigated the ability of wild-caught European starlings *Sturnus vulgaris* to discriminate asymmetry from symmetry and to acquire, through operant learning, a generalized trait preference based on symmetry differences. Starlings have been used successfully for many behavioral investigations, including those employing operant techniques (e.g., Cuthill et al. 1990; Bateson and Kacelnik 1995), and are known to use visual morphological cues during social encounters (Swaddle and Witter 1995; A. T. D. Bennett and I. C. Cuthill, unpublished data) and, hence, are an ideal species to use when exploring the symmetry perceptual abilities of a wild bird.

## Methods

### Subjects and Apparatus

Twelve wild-caught adult European starlings of both sexes were used in this experiment. Birds were housed in a large group cage (approx. 1.2 m × 1.2 m × 1.2 m) with ad lib. food, drinking water, bathing water, and several perching sites. The housing cage was maintained at a constant 16°C on an 8L : 16D photoperiod so that birds did not undergo gonadal hypertrophy or molt. Three experimental cages (approx. 0.3 m × 0.3 m × 0.3 m) were situated in a separate room under identical environmental conditions. The experimental cages each contained an operant feeder and food trough, house light, and two stimulus pecking keys, onto which images could be back-projected by slide projectors. The feeders, house light, pecking keys, and slide projectors were controlled and monitored remotely via a PC desktop computer. The pecking keys were 15 cm apart and approximately 6 cm from the floor of the cage. The feeder was located between the two keys. A single bird was placed in each cage (hence, sessions were split into blocks of three birds at a time). When in the experimental cages, birds were visually (but not acoustically) isolated from each other. In all phases of the experiment, each bird experienced two 1-h sessions per day and were always rested for 1 h between sessions on the same day. The entire experiment was performed in two blocks of six birds; hence, six birds completed the experiment, followed by another six birds.

### Preexposure Sessions

Initially, birds experienced a series of preexposure sessions in which they learned an association between pecking at illuminated keys and receiving food through the trough. In these sessions, both pecking keys in each cage were illuminated but no image was projected onto them. The cage house light was illuminated throughout the entire experiment unless otherwise stated. When the birds pecked at either key, a food pellet (20 mg) was delivered via the feeder to the trough, and the lights on both keys were extinguished for 5 s. After this 5-s period, both pecking keys were reilluminated and the bird could receive another food pellet if it pecked at either of the keys. Throughout the study, pecks at unilluminated keys did not result in food pellet delivery. A preexposure trial was defined as one complete cycle of a bird pecking at an illuminated key, receiving a food pellet, the lights being extinguished for 5 s and then being reilluminated. A preexposure session lasted for 1 h and could comprise many trials, depending on the activity of the bird. Each bird experienced 18 preexposure sessions, two per day dispersed over a 12-d period. Birds quickly learned to peck at the illuminated keys, and the mean ($\pm$ SE) number of trials over the last six preexposure sessions was 96.57 ($\pm$ 7.80) per bird in each session.

## Prelearning Symmetry Preferences

Following the preexposure sessions, 21 pairs of symmetric and asymmetric monochromatic, random dot patterns were loaded into the slide projectors behind each of the pecking keys. Images were small, dark, square dots on a light background. Within each pair, the symmetric and asymmetric images consisted of the same number of dots (ranging from six to 18 dots per image), and the symmetric member of the pair possessed symmetry about either a vertical axis ($N = 9$), a horizontal axis ($N = 10$), or both ($N = 2$). An example of the patterns used in this study is given in figure 1. Dot displays were used because we know from previous investigations that starlings pay attention to chest plumage spot patterns during intraspecific social encounters (Swaddle and Witter 1995).

A projection schedule was constructed so that, within an experimental cage, a randomly selected symmetric pattern was displayed on one key while a randomly selected asymmetric pattern was displayed on the other. In these and all subsequent trials (see below), symmetric and asymmetric images had equal (random) probability of occurring on either left or right keys. In a similar manner to the preexposure sessions, in these prelearning sessions the birds received a food pellet if they pecked at either (symmetric or asymmetric) key. A prelearning trial was defined as the complete cycle of a bird pecking at one of the illuminated keys, receiving a food pellet, the lights being extinguished for 5 s and then being reilluminated. Birds experienced two 1-h prelearning test sessions per day for three consecutive days. Mean number of trials per session was 87.78 ($\pm 12.36$) and was similar to pecking activity in the preexposure sessions. As prelearning sessions did not reinforce differential pecking of symmetric and asymmetric keys, we could examine any preacquired or spontaneous preferences to peck at either symmetric or asymmetric images by comparing the relative proportion of pecks on the symmetric key ([symmetric pecks]/[sum of symmetric and asymmetric pecks]).

## Learning Sessions

The same visual stimuli were used in learning sessions as in the prelearning sessions. The 12 birds were randomly allocated to two treatment groups ($N = 6$ in each). Birds in the first (symmetric) group received a reinforcement food reward when they pecked at the symmetric image (i.e., the symmetric key). Pecks at the key displaying the asymmetric image (i.e., the asymmetric key) did not elicit any response from the operant feeder; however, the house light was extinguished for 5 s. Birds in the second (asymmetric) group received a food reward after pecking at the key displaying the asymmetric image. Conversely, pecks at
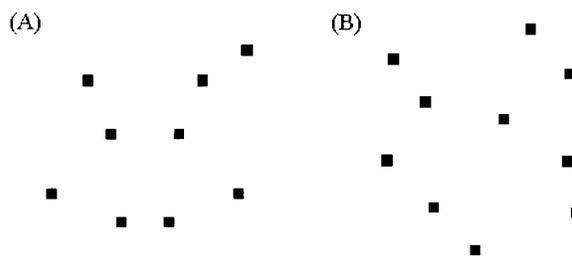


**Figure 1:** Example of the random dot patterns used as stimulus images in the experiment (refer to text for more details). *A*, Stimulus pattern that is symmetric about a vertical axis. *B*, Corresponding asymmetric pattern.

the symmetric key did not produce any response from the operant feeder, except that the house light was extinguished for 5 s. As for the previous sessions, immediately after a food pellet was delivered, the pecking key lights were extinguished for 5 s and pecks at unilluminated keys did not result in food-pellet delivery. A learning trial was defined as the complete cycle of a bird pecking at the appropriate key to elicit a food pellet (i.e., the "correct" key), the stimulus lights being extinguished for 5 s and then being reilluminated. During a learning trial, a bird could peck at the "incorrect" key (i.e., the asymmetric key for symmetry birds; and the symmetric key for asymmetry birds) many times before pecking at the correct key. For the purposes of our analyses, we examined which key was pecked first within a trial and tested for a relative preference for the correct key over the incorrect key. Bird were exposed to, on average, 16.25 ($\pm 0.71$) learning trials per 1-h session. This was reduced from the preexposure and prelearning preference sessions and could reflect the increased cognitive and perceptual difficulty of the learning trials compared with the previous nonreinforced sessions. Birds were exposed to 24 1-h learning sessions, two per day, over a 16-d period.

## Postlearning Testing

Immediately following completion of the 24 learning sessions, a new set of 21 pairs of monochromatic, random dot patterns was constructed and loaded into the slide projectors. These test stimulus patterns exhibited the same properties of the learning stimulus patterns (orientation of axes of symmetry, number of elements per stimulus) except that the dot elements were in different positions in each stimulus image compared with the learning stimuli. This allowed us to examine whether the birds had learned a preference based on a somewhat generalized symmetry property of the previous learning stimuli, as opposed to remembering individual properties of the stimuli to which

they had previously been exposed. The experimental schedule for the postlearning testing sessions was identical to the learning trials; that is, symmetry birds received food pellets for pecking at the symmetric key only, whereas asymmetry birds received food pellets for pecking at the asymmetric key. Similarly, a testing trial was defined as the complete cycle of a bird pecking at the appropriate key to elicit a food pellet, the lights being extinguished for 5 s and then being reilluminated. On average, birds were exposed to 16.36 ($\pm$1.48) trials per testing session. Birds were exposed to six 1-h learning sessions, two per day for three consecutive days. As for the learning sessions, we examined which key was pecked first within a trial and whether there was a relative preference for pecking at the correct key (i.e., symmetric key for symmetry birds; asymmetric key for asymmetry birds) as opposed to the incorrect key.

All statistical analyses were performed using Minitab (Minitab 1996), employing two-tailed tests of probability. Where appropriate, data were arcsine transformed to ensure normality.

## Results

### Prelearning Preferences

There were no initial preferences to peck at either symmetric or asymmetric keys during the prelearning sessions ($t_{11} = 0.29$, $P = .78$). The relative proportion of pecks on the symmetric key was close to 50%, as we would expect if the birds pecked keys indiscriminately to obtain food pellets (mean relative proportion of pecks on symmetric key = 49.52% $\pm$ 0.02%).

### Learning Sessions

Inspection of the learning curve indicates that birds displayed a logarithmic increase in the proportion of correct responses during the 24 learning sessions ($F = 97.03$, df = 1, 22, $P < .0001$; proportion correct responses = $0.368 + 0.240 \times \ln(\text{session})$, $r^2 = 0.815$; fig. 2). Initially, birds exhibited no relative preference to peck at either asymmetric or symmetric keys, and learning performance approached an asymptote of approximately 70% correct responses after approximately 15 learning sessions. During the latter learning sessions there was no evidence of an increase in performance, for example, there was no increase in proportion of correct responses between sessions 19 and 24 (the last six learning sessions; linear regression, $F = 0.01$, df = 1, 4, $P = .970$).

In terms of the level of symmetry/asymmetry discrimination learned during the experiment, the mean relative proportion of correct responses over the last six learning
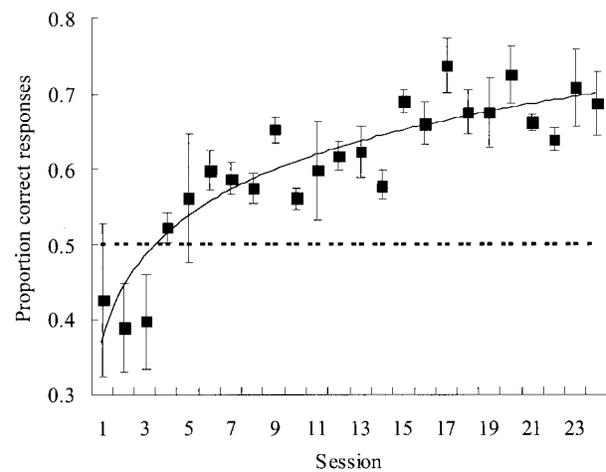


**Figure 2:** Mean ($\pm$SE) proportion of correct responses versus session during the learning phase of the experiment. A correct response was defined as a symmetry-trained bird pecking a key displaying a symmetric image or an asymmetry-trained bird pecking at an asymmetric image. See text for further methodological details. The solid dark line is a fitted logarithmic regression line, indicating a significant increase in the proportion of correct responses over time. The dashed line represents 50% preference, that is, no preference for either correct or incorrect responses.

sessions was 68.26% $\pm$ 0.02%. This level of learned discrimination is significantly different from random pecking (i.e., 50% proportion correct responses; $t = 11.85$, df = 11, $P < .0001$). There was no difference in the ability of symmetry-trained and asymmetry-trained birds to learn the correct operant task (repeated-measures ANOVA over all 24 learning sessions, $F = 0.49$, df = 23, 230, $P = .978$). In addition, there was no evidence of significant variation among birds in their performance abilities over the last six learning sessions compared with variation within-birds among-sessions ($F = 1.33$, df = 12, 5, $P = .600$). This indicates that all individuals attained a fairly consistent level of performance compared with within-individual variability.

### Postlearning Testing Sessions

Mean relative proportion of correct responses to the novel stimuli over the six testing sessions was significantly different from random pecking of the symmetric and asymmetric images ($t = 8.50$, df = 11, $P < .0001$). However, the level of performance exhibited during these testing sessions was also slightly lower than the birds' performance during the last six learning sessions ($t = 2.65$, df = 11, $P = .022$; fig. 3). The former result indicates that birds showed a significant preference for the "correct" key (i.e., symmetry birds preferred the symmetric key and asymmetry birds preferred the asymmetric key); although the
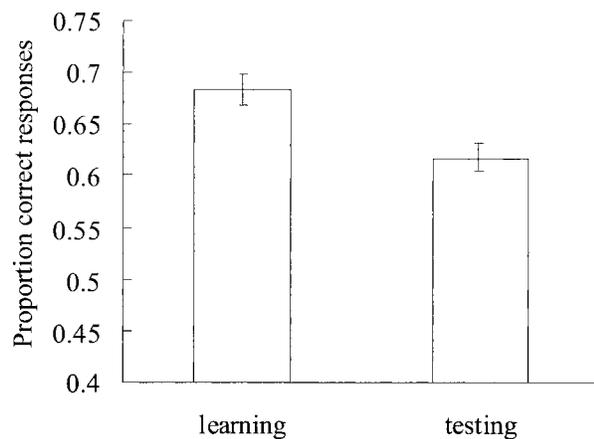
**Figure 3:** Mean (±SE) proportion of correct responses (i.e., symmetry birds pecking the symmetric key and asymmetry birds pecking the asymmetric key) during the last six learning sessions (*learning*) and the six testing sessions (*testing*) of experiment 1. Both are different from random (50%) pecking of symmetric and asymmetric keys.

level of performance was not as great as in the learning sessions. It is also worth noting that there was no change in proportion of correct responses across the six testing sessions (linear regression, $F = 0.10$, df $= 1, 4$, $P = .762$), indicating that any preference shown in these sessions was acquired before the testing trials began. In addition, we could find no evidence that orientation of the axis of symmetry of stimulus patterns (i.e., horizontal versus vertical) influenced performance in the testing sessions ($t = 0.33$, df $= 11$, $P = .75$).

## Discussion

Our findings indicate that wild-caught starlings can discriminate visual patterns on the basis of symmetry. Specifically, they can be trained to discriminate between symmetric and asymmetric monochromatic random dot patterns. Researchers have hypothesized that symmetry perception is prevalent among many taxa and that the ability to visually detect symmetry may be a fundamental property of many vertebrate (and perhaps invertebrate) visual systems (Osorio 1996; Wagemans 1996). Nonetheless, there have been few experimental studies involving nonhuman or nondomesticated animals. The study reported here on wild birds helps to redress this imbalance and further supports the notion that symmetry perception is widespread among vertebrates.

Interestingly, the 12 birds used in this experiment displayed no initial preferences (i.e., before a learned preference was acquired) for either symmetric or asymmetric stimulus patterns. Human aesthetic preferences for sym-

metry have been well documented (e.g., Bahnsen 1928; Attneave 1954; Washburn and Crowe 1988), but there is mixed evidence for spontaneous preferences in nonhuman animals (Rensch 1958; Delius and Nowack 1982; Lehrer et al. 1995). Among avian taxa, Delius and Nowack (1982) have demonstrated that domesticated pigeons *Columba livia* may, contrary to expectations, show a slight preference for asymmetric novel images. The occurrence of generalized, spontaneous symmetry preferences have been cited to explain the cases in which symmetry influences biological signaling and mate choice (e.g., Enquist and Arak 1994; Johnstone 1994; Swaddle and Cuthill 1994*a*, 1994*b*). Our data indicate that wild-caught starlings showed no spontaneous relative preference in the particular perceptual task they were set. However, our findings do not rule out the possibility that starlings could show spontaneous preferences when performing different visual perceptual tests. In a separate experiment, Swaddle (1999*a*) has shown that starlings exposed to paired-bar patterns also lack spontaneous preferences for either symmetry or asymmetry.

The change in response to the symmetric and asymmetric visual stimuli over the learning sessions clearly illustrates that starlings can learn a symmetry preference (Fig. 2). Birds reached a performance asymptote of approximately 70% accurate discrimination of symmetry from asymmetry after approximately 15 1-h trials. Previous experiments with domesticated pigeons have shown an even quicker rate of learning (Delius and Nowack 1982; Schwabl and Delius 1984). For example, Delius and Nowack reported that local bred stock of homing pigeons only require 10 daily 30-min sessions to acquire a 90% accurate discrimination of symmetric patterns from asymmetric patterns. The stimulus patterns used by Delius and Nowack were geometric monochromatic shapes, which possessed less than a 50% asymmetry (although this was not formally quantified). The stimuli used in our experiment were 100% asymmetric (for position of the elements) dot patterns and did not include easily perceived geometric structures. It has been hypothesized that regularities of elements within a visual signal can aid the perception of symmetry in humans (Wagemans et al. 1993), and, perhaps, a similar mechanism could occur in birds. In addition, perceptual performance tests performed with human subjects illustrate that the assessment of symmetry in random dot displays is often less accurate than in stimulus patterns that are composed of highly structured arrangements (Hong and Pavel 1996). Hence, the differences in stimulus images used in the previous experiments could partially account for the relatively lower performance of our wild-caught starlings compared with captive-bred domesticated pigeons. Another explanation may be that wild birds do not possess as developed an ability to

perceive symmetry as domestic birds. It could be that the data we report in this study may be more representative of responses of typical wild birds than previous studies on captive-bred pigeons.

The testing sessions provided evidence that, to some extent, symmetry preferences acquired during the learning sessions could be transferred to novel random dot stimulus patterns. Birds pecked at the correct key more often than expected by chance. However, the ability of birds to peck at the correct novel stimulus was slightly lower during the test sessions than the latter learning sessions. This may indicate that birds were not only categorizing images on the basis of symmetry differences, but also remembering detailed features of the 42 images used in the learning sessions. Pigeons are known to be able to recognize and recall a large number of complex stimulus objects in learning trials (e.g., Kirkpatrick-Steger and Wasserman 1996). However, our data indicate that birds could classify stimulus objects on the basis of symmetry and transfer this acquired ability to stimulus objects they had not previously experienced. Pigeons are known to be able to classify objects based on a wide range of visual categories (e.g., Wasserman et al. 1995; Watanabe et al. 1995; Cook et al. 1997) including symmetry (Delius and Habers 1978; Blough and Franklin 1985), therefore it is interesting that wild-caught starlings are also capable of performing a similar categorical task.

The observation that birds can categorize objects on the basis of symmetry differences and transfer this categorization to novel objects has fairly broad implications for signaling theory. This suggests that a symmetry preference acquired in one context (e.g., species recognition, foraging) could be transferred to another context (e.g., mate choice). In part, our findings provide some support for previous hypotheses that have explained the symmetry preferences quantified in prior experiments as a reflection of general symmetry preferences or preferences acquired in an unrelated context (Enquist and Arak 1994; Johnstone 1994; Swaddle and Cuthill 1994*a*, 1994*b*). In an experiment similar to those reported here, Delius and Habers (1978) also showed that pigeons can learn a general concept of symmetry, as their birds could transfer a learned symmetry preference to novel stimuli. Although our data suggest that symmetry preferences can be transferred between contexts, we suspect that this ability will vary with the psychophysical properties of the observed stimulus patterns. Symmetry differences in random dot displays, as used here, are likely to be assessed using different perceptual processes than assessment of asymmetry in tail length or badge size. Hence, we hypothesize that transfer is probably specific to the visual properties of traits in question. Therefore, it may be difficult to generalize about the prevalence of symmetry preference transfer in nature. Each case will need

to be examined with the psychophysical properties of the relevant stimuli in mind. Our data also indicate that the axis of symmetry does not influence symmetry preferences to any large degree although a preference for symmetry about a vertical axis has been often reported in humans (see Swaddle 1999*b*).

Inspection of the learning performance of birds assigned to the two treatment groups indicates that symmetry- and asymmetry-trained birds were capable of learning to the same degree and at equivalent rates. It has previously been hypothesized that learning an association with a symmetric stimulus would be easier than learning a similar association with an asymmetric stimulus (Johnstone 1994; Kirkpatrick and Rosenthal 1994). Our data indicate either that such a difference in associated learning is small or that the asymmetry- and symmetry-trained birds were performing the same perceptual task.

Importantly, our findings indicate that starlings appear to make many errors when learning to distinguish between symmetric and asymmetric stimuli. The variability among individuals during each session, even toward the latter part of the learning sessions, was reasonably large and the asymptotic performance of the starlings was only approximately 70%. Starlings commonly reach 90% performance in similar operant learning tasks (e.g., Bateson and Kacelnik 1997). The among-individual variation was equivalent to the within-individual variation in performance; therefore, it appears that individuals were making errors to the same magnitude that performance varied among individuals. This seemingly large degree of performance error, whether it was purely perceptual or additionally comprised of other cognitive inaccuracies, indicates that behavioral responses to a symmetry signal are implicitly error prone. The high levels of error have two important evolutionary implications for the structure and stability of asymmetry-signaling systems (cf. Johnstone and Grafen 1992). First, the response of the receiver may not accurately reflect the true advertising level of the signal (i.e., individual asymmetry). This would destabilize the system and also weaken the intensity of selection against asymmetric individuals. Hence, it may be unlikely that symmetry signaling is commonly used with such high levels of error. Second, receiver error could influence the signaling tactics of the signaler in that there may be little benefit for the signaler to invest in a high (very symmetric) and costly advertising level. This latter implication could help to explain why signaling structures often exhibit much larger asymmetries than nonsignaling structures. The use of operant learning experiments will also let us manipulate the relative costs and benefits associated with correctly detecting symmetry from asymmetry (through differential reward schedules), which may influence apparent levels of error. It is possible that when the relative cost to birds of

getting their selection "wrong" is greater, they will make fewer errors. The influence of relative costs and benefits may also be related to why, in some species, females use trait asymmetry when selecting mates but males do not use visual symmetry of the same traits to mediate dominance interactions (Møller 1992, 1993; Swaddle 1996). The cost to a female of choosing a poor mate may be much higher than the cost to a male of picking a fight with a dominant individual. Hence, males may make more symmetry-perception errors in dominance interactions, decreasing any relationship between social status and trait asymmetry.

It is possible that the artificial nature of the random dot displays used in this study influenced our findings and that more naturalistic cues could render different results. However, previous experiments with starlings indicate that females use chest plumage spottiness as a direct visual cue in social encounters (Swaddle and Witter 1995). We know that starlings can also detect length asymmetries in paired-bar patterns (Swaddle 1999*a*). It would be interesting to perform similar experiments using different simple and complex stimuli to thoroughly investigate the influence of stimulus properties on the symmetry perception abilities of these (and other) birds. The initial findings from this experiment indicate that starlings are capable of detecting symmetry and categorizing novel stimuli on the basis of symmetry differences, but this perceptual task is rather error prone.

## Acknowledgments

## Literature Cited

Attneave, F. 1954. Some informational aspects of visual perception. Psychological Review 61:183–193.

Bahnsen, P. 1928. Eine Unterschung über Symmetrie und Asymmetrie bei visuellen Wahrnehmungen. Zeitschrift für Psychologie 108:129–154.

Bateson, M., and A. Kacelnik. 1995. Accuracy of memory in the foraging starling *Sturnus vulgaris.* Animal Behaviour 50:431–443.

———. 1997. Starlings' preferences for predictable and unpredictable delays to food. Animal Behaviour 53: 1129–1142.

Blough, D. S., and J. J. Franklin. 1985. Pigeon discrimination of letters and other forms in texture displays. Perception and Psychophysics 38:523–532.

Cook, R. G., J. S. Katz, and B. R. Cavoto. 1997. Pigeon same-different concept learning with multiple stimulus classes. Journal of Experimental Psychology Animal Behavior Processes 23:417–433.

Cuthill, I. C., A. Kacelnik, J. R. Krebs, P. Haccou, and Y. Iwasa. 1990. Starlings exploit patches: the effect of recent experience on foraging decisions. Animal Behaviour 40: 625–640.

Delius, J. D., and G. Habers. 1978. Symmetry: can pigeons conceptualize it? Behavioral Biology 22:336–342.

Delius, J. D., and B. Nowak. 1982. Visual symmetry recognition by pigeons. Psychological Research 44: 199–212.

Enquist, M., and A. Arak. 1994. Symmetry, beauty and evolution. Nature (London) 372:169–172.

Fiske, P., and T. Amundsen. 1997. Female bluethroats prefer males with symmetric colour bands. Animal Behaviour 54:81–87.

Hong, S., and M. Pavel. 1996. Determinants of symmetry perception. Pages 135–155 *in* C. W. Tyler, ed. Human symmetry perception and its computational analysis. VSP, Utrecht.

Horridge, G. A. 1996. The honeybee (*Apis mellifera*) detects bilateral symmetry and discriminates its axis. Journal of Insect Physiology 42:755–764.

Jablonski, P. G., and P. Matyjasiak. 1997. Chaffinch (*Fringilla coelebs*) epaulette display depends on the degree of exposure but not symmetry of intruder's epaulettes. Behaviour 134:1115–1121.

Johnstone, R. A. 1994. Female preference for symmetrical males as a by-product of selection for mate recognition. Nature (London) 372:172–175.

Johnstone, R. A., and A. Grafen. 1992. Error-prone signalling. Proceedings of the Royal Society of London B, Biological Sciences 248:229–233.

Kirkpatrick, M., and G. G. Rosenthal. 1994. Symmetry without fear. Nature (London) 372:134–135.

Kirkpatrick-Steger, K., and E. A. Wasserman. 1996. What and the where of the pigeon's processing of complex visual stimuli. Journal of Experimental Psychology Animal Behavior Processes 22:60–67.

Lehrer, M., G. A. Horridge, S. W. Zhang, and R. Gadagkar. 1995. Shape vision in bees: innate preference for flower-like patterns. Philosophical Transactions of the Royal Society of London B, Biological Sciences 347:123–137.

Ludwig, W. 1932. Das Rechts-Links Problem im Tierreich und beim Menschen. Springer, Berlin.

Markow, T. A. 1995. Evolutionary ecology of developmental instability. Annual Review of Entomology 40: 105–120.

Minitab. 1996. Minitab 11 user's guide. Minitab, State College, Pa.

Møller, A. P. 1990. Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. Animal Behaviour 40:1185–1187.

———. 1992. Female preference for symmetrical male sexual ornaments. Nature (London) 357:238–240.

———. 1993. Female preference for apparently symmetrical male sexual ornaments in the barn swallow *Hirundo rustica*. Behavioral Ecology and Sociobiology 32: 371–376.

Møller, A. P., and G. Sorci. 1998. Insect preference for symmetrical artificial flowers. Oecologia (Berlin) 114: 37–42.

Møller, A. P., and J. P. Swaddle. 1997. Asymmetry, developmental stability and evolution. Oxford University Press, Oxford.

Morris, M. R., and K. Casey. 1998. Female swordtail fish prefer symmetrical sexual signal. Animal Behaviour 55: 33–39.

Osorio, D. 1996. Symmetry detection by categorization of spatial phase, a model. Proceedings of the Royal Society of London B, Biological Sciences 263:105–110.

Palmer, A. R. 1996. Waltzing with asymmetry. BioScience 46:518–532.

Rensch, B. 1958. Die Wirksamkeit ästhetischer Faktoren bei Wirbeltieren. Zeitschrift für Tierpsychologie 15: 447–461.

Schwabl, U., and J. D. Delius. 1984. Visual bar length discrimination threshold in the pigeon. Bird Behavior 5:118–121.

Shettleworth, S. J. 1999. Female mate choice in swordtails and mollies: symmetry assessment or Weber's law? Animal Behaviour 58:1139–1142.

Sneddon, L. U., and J. P. Swaddle. 1999. Asymmetry and fighting performance in the shore crab, *Carcinus maenas*. Animal Behaviour 58:431–435.

Swaddle, J. P. 1996. Reproductive success and symmetry in zebra finches. Animal Behaviour 51:203–210.

———. 1997. Experimental design and the signalling properties of fluctuating asymmetry. Animal Behaviour 54:1034–1037.

———. 1999a. Limits to length asymmetry detection in starlings: implications for biological signalling. Proceedings of the Royal Society of London B, Biological Sciences 266:1299–1303.

———. 1999b. Visual signalling by asymmetry: a review of perceptual processes. Philosophical Transactions of the Royal Society of London B, Biological Sciences 354: 1383–1393.

———. 2000. Is fluctuating asymmetry a visual signal? Pages 383–403 *in* Y. Espmark, T. Amundsen, and G. Rosenqvist, eds. Signalling and design in animal communication. Tapir Academic Press, Trondheim.

Swaddle, J. P., and I. C. Cuthill. 1994a. Female zebra finches prefer males with symmetric chest plumage. Proceedings of the Royal Society of London B, Biological Sciences 258:267–271.

———. 1994b. Preference for symmetric males by female zebra finches. Nature (London) 367:165–166.

Swaddle, J. P., and M. S. Witter. 1995. Chest plumage, dominance and fluctuating asymmetry in female starlings. Proceedings of the Royal Society of London B, Biological Sciences 260:219–223.

Tomkins, J. L., and L. W. Simmons. 1998. Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L. Animal Behaviour 56: 347–356.

Wagemans, J. 1996. Detection of visual symmetries. Pages 25–48 *in* C. W. Tyler, ed. Human symmetry perception and its computational analysis. VSP, Utrecht.

Wagemans, J., L. Van Gool, V. Swinnen, and J. Van Horebeek. 1993. Higher-order structure in regularity detection. Vision Research 33:1067–1088.

Washburn, D. K., and D. W. Crowe. 1988. Symmetries of culture. University of Washington Press, Seattle.

Wasserman, E. A., J. L. Gagliardi, B. R. Cook, K. Kirkpatrick-Steger, S. L. Astley, and I. Biederman. 1996. The pigeon's recognition of drawings of depth-rotated stimuli. Journal of Experimental Psychology Animal Behavior Processes 22:205–221.

Watanabe, S., J. Sakamoto, and M. Wakita. 1995. Pigeons discrimination of paintings by Monet and Picasso. Journal of Experimental Analysis of Behavior 63:165–174.

Watson, P. J., and R. Thornhill. 1994. Fluctuating asymmetry and sexual selection. Trends in Ecology & Evolution 9:21–25.

Zakharov, V. M. 1992. Population phenogenetics: analysis of developmental stability in natural populations. Acta Zoologica Fennica 191:7–30.

Editor: Joseph B. Travis
Associate Editor: John A. Byers