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Limits to length asymmetry detection in starlings: implications for biological signalling

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Fluctuating asymmetry has received considerable recent attention in evolutionary biology as these small developmental asymmetries can be related to biological fitness and, hence, could be used as a visual cue (or signal) of quality among individuals. The ability of signal receivers to detect and respond to small asymmetries is a fundamental assumption of the symmetry-signalling hypothesis, but has not been experimentally investigated. In this study I have investigated the perceptual threshold to detect and respond to paired-bar length asymmetry in a common bird, the European starling *Sturnus vulgaris*, by means of operant-learning techniques. The threshold indicates how large the length asymmetry must be to be reliably discriminated from symmetry; birds could not detect an asymmetry of 1.25%. In nature, many asymmetries can be smaller than 1.25%, hence this initial study suggests that caution should be used when trying to invoke symmetry-signalling in natural populations.

Keywords: fluctuating asymmetry; operant conditioning; sexual selection; signalling; starling; symmetry perception

1. INTRODUCTION

Fluctuating asymmetries are the small, random deviations from perfect bilateral symmetry that occur during the development of symmetric traits and can reflect the extent to which the genome buffers development against environmental stressors (Ludwig 1932; Møller & Swaddle 1997; Palmer & Strobeck 1986). As asymmetry can reveal how well the genome is coping with environmental conditions during development, researchers have looked for associations between fluctuating asymmetry and aspects of biological fitness (reviews in Markow 1995; Leung & Forbes 1996; Møller & Swaddle 1997; Clarke 1998). As asymmetry is related to fitness parameters in some cases (but not others; Leung & Forbes 1996), it has been suggested that individual expression of fluctuating asymmetry could be used as a cue or signal of fitness during sexual and social encounters (Møller 1990). It has also been claimed that asymmetry could be used as a general viability cue (or signal) in other visually mediated behaviours (e.g. foraging, predator–prey interactions; Møller & Swaddle 1997). There is some experimental evidence to support a signalling hypothesis: females prefer symmetric males over asymmetric males as potential mates (Swaddle & Cuthill 1994; Morris & Casey 1998). However, there are also examples in which asymmetry does not play a signalling role (Swaddle & Witter 1995; Tomkins & Simmons 1998), hence signalling by fluctuating asymmetry is an issue of considerable recent debate among evolutionary biologists (Markow 1995; Palmer 1996; Møller & Swaddle 1997).

When addressing the potential signalling function of fluctuating asymmetry, most researchers have investigated relationships between signal production (i.e. the asymmetry) and intrinsic properties of the signaller (e.g. aspects of fitness and/or mating success) (Møller & Swaddle 1997). The ability of the signal receivers to detect and respond to these small asymmetries (commonly less than 1 or 2% relative difference between left and right sides) (Møller & Pomiankowski 1993; Palmer 1996) has been largely overlooked and yet is fundamental to assessing the plausibility of the whole signalling hypothesis. Therefore, in this study I have experimentally investigated the threshold for detection and behavioural response to one class of asymmetry (length asymmetry in paired bars) by means of operant-training techniques in the European starling *Sturnus vulgaris*. Starlings use visual cues to regulate social dominance hierarchies: females with spottier chest plumage are more dominant (Swaddle & Witter 1995), although the asymmetry of this chest plumage does not appear to influence social standing. The ability of starlings to discriminate symmetric visual stimuli from asymmetric stimuli will not only reveal how large asymmetries have to be to be detectable, but also shed light on the resolution power of the avian visual system for discriminating among degrees of length asymmetry (i.e. levels of the signal) and, hence, the potential signalling resolution power of fluctuating asymmetry to indicate differences among individuals. The avian visual system is believed to be superior to that of other taxa with regard to a number of important features, such as visual acuity, stimulus size discrimination and hue discrimination (Hodos 1993). Therefore, a threshold of asymmetry detection in birds could be a 'best-case' indication of generalized bar-length asymmetry detection abilities in other vertebrates.

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2. METHODS

(a) *Subjects, apparatus and pre-exposure*

I used six wild-caught adult starlings (three males and three females) in this experiment. Birds were housed in a large metal cage (approximately 1.5 m × 1.5 m × 1.5 m) with ad libitum food, drinking and bathing water on an 8 L:16 D photoperiod and at a constant 16 °C. I acclimatized the birds to two-key Skinner boxes through a series of 14 1 h pre-exposure sessions (two per day) in which birds quickly learned to associate pecking at illuminated keys with obtaining a food reward. A single bird was placed in each Skinner box throughout all sessions in this experiment. The Skinner boxes were situated in a separate room, but under identical environmental conditions. Each box (28 cm × 26 cm × 30 cm) consisted of a motorized food-pellet dispenser and trough and two pecking keys (2.5 cm diameter), onto which images were back-projected by slide projectors. The feeder and trough were situated between the two pecking keys. All responses of the birds pecking at the keys and operation of the slide projectors and feeders were logged and controlled by a desktop computer. Blank images were projected onto both keys during pre-exposure sessions. If the bird pecked at either illuminated key, a food item was delivered through the feeder and the stimulus lights were extinguished for 5 s and then re-illuminated constantly until another key peck was made. Pecks at un-illuminated keys did not produce any response from the operant feeder. During the last four pre-exposure sessions, birds received an average of 32.38 (s.e.m. = 4.88) food items per 1 h session through pecking at illuminated keys.

(b) *Asymmetry detection sessions*

Immediately after pre-exposure, I trained the birds (through positive reinforcement by food rewards) to discriminate between symmetric and asymmetric images that were projected onto the pecking keys by slide projectors. The stimulus images used in this experiment were sets of 40 symmetric and 40 asymmetric monochromatic, vertical paired-bar patterns (dark bars on a light background). Left and right elements of each bar were 3 mm apart. In 20 of the asymmetric images the left bar was longer than right, in the other 20 the right bar was longer than the left. The images within both sets of symmetric and asymmetric images were of the same overall mean bar size and varied between 0.5 and 2.0 cm, in gradations of approximately 0.08 cm, giving 20 overall mean bar lengths in each set of symmetric and asymmetric stimuli. There were two stimulus patterns (in symmetric and asymmetric sets) at each mean bar length so that within the asymmetric set one image could possess a longer bar on the right and another could possess the longer bar on the left side while maintaining the same overall bar length.

In the initial 24 learning sessions, asymmetric images possessed a 10% asymmetry (i.e. one side of the paired bar was 10% longer than the other). Within each trial of each session, one of the 40 symmetric images (randomly selected) was displayed on one key (randomly left or right) while one of the 40 asymmetric stimuli (randomly selected) was projected onto the other key. Three of the birds were trained to peck at the symmetric key; the remainder were trained to peck at the asymmetric key. If a bird pecked at the correct key (i.e. the symmetric key for symmetric-trained birds, and vice versa), the stimulus lights were extinguished and a food pellet was presented to the bird. If a bird pecked at the inappropriate key, the operant apparatus did not respond. A trial was defined as the complete cycle of a bird pecking at the correct key, receiving a food item, the lights being extinguished and then re-illuminated after 5 s with the keys displaying another pair of randomly selected symmetric and asymmetric images. Hence, depending on the activity of the individual bird, a 1 h session could consist of many trials. Birds learned to discriminate symmetric from asymmetric images in these sessions (see below).

Immediately after completion of the 10%-asymmetry sessions, birds were further exposed to blocks of ten 1 h sessions in which the asymmetry of the asymmetric images was altered in the following order: 5%, 2.5%, 1.25%, 10% and 1.8% (i.e. ten sessions at 5% asymmetry were followed by ten at 2.5% asymmetry, and so on). These trials followed the same protocol as above and were designed to identify a threshold asymmetry below which the birds could no longer reliably discriminate asymmetry from symmetry. New sets of 40 asymmetric images (of the same overall size as above) were used in each of the 5%, 2.5%, 1.25%, 10% and 1.8% asymmetry sessions; hence asymmetric stimuli were novel in these trials. Every effort was made to focus the bar images as sharply as possible when projected onto the pecking keys. At all stages of the study, two operant sessions were performed for each bird per day. Birds were always rested for at least 1 h between sessions.

All statistical analyses were performed on Minitab (Minitab Inc. 1994) employing two-tailed tests of probability throughout.

3. RESULTS AND DISCUSSION

The birds learned to discriminate between symmetric and asymmetric images over the initial 24 1 h (10%-asymmetry) learning sessions. They showed a logarithmic increase in their ability to discriminate between asymmetry and symmetry ($F_{1,22} = 48.21$, $p < 0.00001$, $r^2 = 0.687$; proportion of correct responses $= 0.448 + 0.667\ln(\text{trial})$) (figure 1). I defined correct discrimination as the bird pecking at the correct key in the first peck within a trial. There was no difference in this logarithmic learning response between birds that were trained to peck at symmetric keys and those that were trained to peck at asymmetric keys ($F_{23,92} = 0.54$, $p = 0.955$). This refutes the suggestion that animals may find it easier to learn an association with a symmetric stimulus object than with an asymmetric object (Johnstone 1994; Kirkpatrick & Rosenthal 1994), although sample sizes were small in this experiment.

Discriminatory performance did not vary across the last ten sessions of the initial 24 10%-asymmetry learning sessions (mixed-model repeated-measures ANOVA $F_{9,45} = 0.36$, $p = 0.946$), hence performance over these sessions was averaged to examine the extent of asymmetry detection achieved during this learning phase. Comparing performance with random pecking of left and right keys, the birds exhibited a consistent ability to correctly discriminate the 10%-asymmetric images from the symmetric images ($t = 6.61$, $p = 0.0012$) (figure 2).

When asymmetry was reduced to 5% and further to 2.5%, birds still exhibited reliable discrimination between symmetric and asymmetric images (5%-asymmetry: $t_5 = 4.51$, $p = 0.0063$; 2.5%-asymmetry: $t_5 = 6.61$, $p = 0.0012$; figure 2). However, birds could not accurately discriminate the 1.25%-asymmetric stimuli from the symmetric patterns ($t_5 = 0.03$, $p = 0.98$). To examine whether birds had merely habituated to presentation of

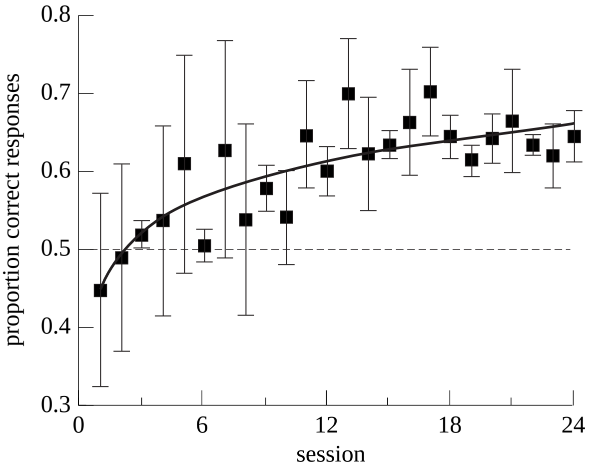

Figure 1. Mean (s.e.m.) proportion of correct discrimination between asymmetric and symmetric images during the 10%-asymmetry learning sessions. There was a significant logarithmic increase in performance across the sessions, as indicated by the solid curve ($F_{1,22} = 48.21$, $p < 0.00001$, $r^2 = 0.687$; proportion of correct responses = 0.448 + 0.667ln (session)). The dotted line indicates 50% random pecking at either left or right key.

stimuli and were no longer responding to perceptible asymmetry differences, I exposed birds to a further ten sessions in which a new set of 10%-asymmetric stimuli were presented. Asymmetry-detection performance immediately returned to prior learning levels and birds accurately discriminated these 10%-asymmetric stimuli from symmetric images ($t_5 = 6.73$, $p = 0.0011$; figure 2). This series of trials indicates that the starlings display a threshold response to decreasing asymmetry and do not respond to asymmetries of 1.25% (or less).

To explore the asymmetry-detection threshold between 1.25% and 2.5%, I presented 1.8%-asymmetry images in a further series of ten 1 h sessions immediately following the 10%-asymmetry test sessions. Pecking performance in these sessions indicated that birds can accurately discriminate 1.8%-asymmetry from symmetry ($t_5 = 6.75$, $p = 0.0011$). An apparent threshold for asymmetry detection below 1.8%-asymmetry is consistent with a previous study on pigeons (*Columba livia*), in which the birds could discriminate bar-length differences of 2% under operant protocols similar to those used here (Schwabl & Delius 1984). However, it should be noted that the pigeon experiment did not explicitly explore the influence of bar-length symmetry on perceptual performance. The data I have presented in this study indicate that wild-caught starlings have a threshold for bar-length asymmetry discrimination between 1.8% and 1.25%. If similar forms of asymmetry present in nature (e.g. tail-length differences) are smaller than this threshold value, it is not likely that asymmetry could be used as a direct visual cue or signal in these features. It may also be relevant that the studies that have shown conclusively that animals can pay attention to naturalistic biological symmetry have all manipulated asymmetry to values well above the perceptual threshold implied by this study: 10% asymmetry in chest plumage of male zebra finches (*Taeniopygia guttata*) (Swaddle & Cuthill 1994), 21% in bar patterns of male swordtail fish (*Xiphophorus cortezi*) (Morris & Casey 1998).

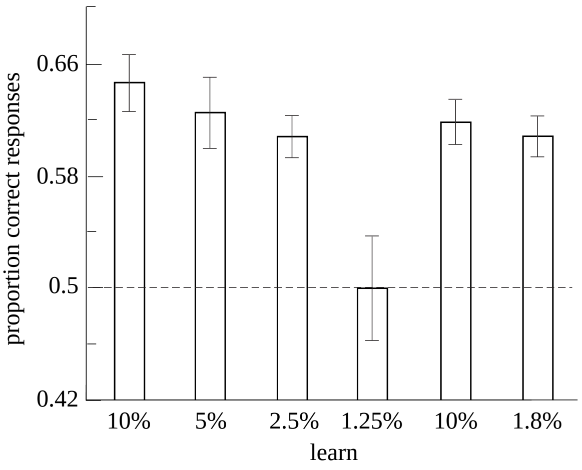

Figure 2. Mean (s.e.m.) proportion of correct discrimination during the last ten 10%-asymmetry learning sessions (10% learn), the ten 5%-asymmetry sessions (5%), the ten 2.5%-asymmetry sessions (2.5%), the ten 1.25%-asymmetry sessions (1.25%), the ten 10%-asymmetry test sessions (10%) and the ten 1.8%-asymmetry test sessions (1.8%). The degree of correct discrimination of symmetry from asymmetry did not differ between 10% learn and 5% sessions (one-sample *t*-test on within-individual differences in performance, $t_5 = 1.66$, $p = 0.16$); 10% learn and 2.5% sessions ($t_5 = 1.27$, $p = 0.26$); 10% learn and 10% test sessions ($t_5 = 1.25$, $p = 0.27$); or 10% learn and 1.8% sessions ($t_5 = 1.32$, $p = 0.24$). However, birds made significantly more errors during the 1.25% sessions than in the 10% learn sessions ($t_5 = 3.26$, $p = 0.022$). Birds did not alter in discriminatory abilities across the ten 5% sessions ($F_{9,45} = 0.58$, $p = 0.809$), 2.5% sessions ($F_{9,45} = 0.85$, $p = 0.575$), 1.25% sessions ($F_{9,45} = 0.58$, $p = 0.802$), 10% test sessions ($F_{9,45} = 0.63$, $p = 0.764$), or 1.8% sessions ($F_{9,45} = 1.69$, $p = 0.120$), indicating that asymmetry-detection abilities had been acquired before these sessions began and that asymmetry–symmetry preferences were transferred among stimulus sets.

As asymmetry necessarily arises from one side of a trait being larger (in this case longer) than the other, it is possible that birds could discriminate among visual cues on the basis of maximum (or minimum) length of either side of the trait assessed. This is a methodological problem that has confounded many studies of fluctuating asymmetry (see, for example, Oakes & Barnard 1994; Fiske & Amundsen 1997; Jennions 1998). Here I have separated length from asymmetry by presenting random selections of asymmetric and symmetric patterns for each trial within a session. Nevertheless, it is still possible that birds could base their preferences on maximum (or minimum) lengths of the four bars that they view in a trial, as asymmetric patterns tend to have a greater probability of possessing both longest and shortest bars. I have tested for this explicitly by re-analysing the 1.8%-asymmetry data with respect to a preference for the longest bar observed within a trial (identical results are obtained for preference for the shortest bar). There is no evidence for a preference for the longest bar ($t_5 = 0.88$, $p = 0.42$; proportion of correct responses = 47.1% ± 0.3). However, birds could still employ some form of irregularity detection mechanism other than multidimensional 'symmetry' detection to discriminate among the patterns. The outline of a symmetric paired-bar pattern is a rectangle, whereas the outline of an asymmetric pattern appears more irregular and lopsided. Perhaps birds solve the discrimination task by detecting rectangular irregularity? They could also use this mechanism in nature to resolve asymmetry differences. We do not know what precise mechanism is used and whether this mechanism varies among stimulus patterns; therefore there is a need to study symmetry detection in many contexts and with different visual stimuli and forms of asymmetry (see below).

It is possible that in natural conditions, the visual signalling role of fluctuating asymmetry could be either amplified or attenuated by additional morphological or behavioural traits (Hasson 1989; Swaddle 1999). The stimulus images that I employed in this study were of homogeneous colour and contrast, comprised simple geometric shapes, and were aligned in a vertical plane of symmetry; left and right components were situated close together, the images were stationary and both symmetric and asymmetric stimuli were presented in the same plane to the observer. These stimulus properties, based on our knowledge of human symmetry perception, strongly favour the detection of symmetry from asymmetry and could be viewed as amplifier properties themselves (Swaddle 1999). Hence, the 1.25% threshold indicated by this study is likely to be a 'best-case' estimate of the visual signalling threshold for bar-length asymmetry detection in most natural conditions. In highly aerial species, small morphological asymmetry could influence flight performance (Thomas 1993; Swaddle 1997), hence asymmetry could be an indirect cue in such species.

In addition, the stimulus images were viewed by the starlings at close proximity. Video observations indicated that the birds were maximally 10–12 cm from the images during discrimination events, but often closer than this. By extrapolating correct discriminatory performance at 1.8%-asymmetry in the smallest image at a distance of 10 cm, an upper estimate of starling performance suggests they can discriminate an asymmetry difference of approximately 0.1 mm at 10 cm distance, which is similar to reported visual acuity in pigeons (Macko & Hodos 1985). If starlings resolve asymmetry differences by means of visual acuity, the apparent similarity between the systems of the pigeon and the starling suggests that the bar-length threshold figure illustrated by this study may have some generality among avian species, although more species, obviously, need to be investigated.

Fluctuating asymmetry is characterized by a normal distribution of signed asymmetry scores centred at zero, but can exhibit more leptokurtic frequency distributions (Palmer 1996; Palmer & Strobeck 1986). Visual signalling-selection will act upon unsigned asymmetry and hence draw individuals from a truncated half-normal distribution. If mean unsigned asymmetry values are close to 1.25% most individuals (approximately 65%, assuming a normal distribution) will fall below the threshold for asymmetry detection and be perceived as 'symmetric'. In addition, of the remaining individuals in the population that are perceived as 'asymmetric', approximately 85% of those individuals will be perceived as equally asymmetric owing to a presumed visual resolution of 1.25% asymmetry. Hence, mean unsigned asymmetry would have to be much greater than 1.25% for the visual system to be able to discriminate among most individuals within a population. Therefore, if birds attempt to discriminate among visual cues by using perceptual mechanisms similar to those employed during discrimination tasks in this experiment, many length asymmetries in nature could be too small to be detected and there would be little resolution among signalling levels.

Perceptual thresholds for asymmetry detection are also important in that the reliability and accuracy with which a receiver can assess small asymmetries is crucial to the signalling tactics of the signaller. In any error-prone signalling system, the response of the receiver depends on the perceived level of the signal rather than on the true signalling level itself. Additionally, with error-prone signalling it is possible that one level of advertising could be perceived as being many different advertising levels (Johnstone & Grafen 1992). Therefore, estimating the accuracy to which asymmetry can be discriminated, and investigating factors that influence this discrimination, are vital in assessing the role that asymmetry may play in any signalling system. In this study, birds reached an asymptote of performance at approximately 65% correct discrimination; this result appears more error-prone than general signalling models usually account for. It is possible that the context and relative benefits of the reward schedule used in this particular experiment could alter performance, but 65% is still surprisingly low and indicates that symmetry-signalling may be inherently error-prone. Pigeons appear to reach a much higher level of performance (80–90% correct discrimination) when performing visual tasks in operant experiments (see, for example, Schwabl & Delius 1984), as do starlings performing a range of tasks in operant conditioning paradigms (see, for example, Bateson & Kacelnik 1997). Therefore, the data from my study indicate either that discriminating among the symmetry classes of paired-bar patterns was particularly difficult and error-prone, or that starlings in particular find this task difficult. A comparative approach may be useful in addressing this question.

This study provides the first experimental demonstration of perceptual thresholds for any form of asymmetry detection and indicates limits to which symmetry-signalling can be inferred or invoked in similar bar-length discrimination tasks for other avian systems. I wish to highlight that in many cases asymmetries may be too small for symmetry-signalling to be viable and that researchers should pay heed to the ability of their study subjects to discriminate among levels of asymmetry. The plausibility (or generality) of signalling by fluctuating asymmetry is further reduced by the often weak relations exhibited between morphological asymmetry and recorded fitness parameters (Markow 1995; Leung & Forbes 1996; Palmer 1996; Møller & Swaddle 1997; Clarke 1998). Even if we assume that the phenotypic expression of asymmetry is highly related to (heritable or non-heritable) fitness benefits (which will often not be a safe assumption to make), in many populations the asymmetry cue (or signal) of most individuals could be too small to be detected and the perceptual limits of asymmetry-discrimination will result in poor resolution of differences among individuals with notable asymmetric traits.

It is possible that species that use fluctuating asymmetry as a visual cue have better symmetry-detection capabilities than indicated here and there could be selection for such capabilities. However, for selection to act on the perceptual processes involved in symmetry–asymmetry discrimination, the symmetry differences must have been discriminable in an ancestral state. A wider, comparative approach may shed light on this and is beyond the scope of the present experiment. The context in which the threshold indicated by this study was measured may also be of importance; birds experiencing greater benefit of correctly discriminating between symmetry and asymmetry (and/or increased cost of getting the task wrong) may perform to a different level. However, as the data indicate a threshold response to symmetry detection, even if the magnitude of responses is altered a similar threshold figure would be indicated. The form of the stimulus pattern and the type of asymmetry present may also influence performance. Birds may exhibit a different apparent symmetry detection threshold when discriminating asymmetries in random dot patterns or shape differences than that indicated by the bar-length differences (as shown here). It is likely that birds could use different perceptual processes in assessing the asymmetry of these different tasks and only by a thorough examination of responses to a range of stimuli using a range of reward protocols will we be able to address the broad issue of general symmetry detection. This experiment represents a start in this process and also demonstrates the kind of valuable contribution that perceptual psychology techniques can make to evolutionary biology, in particular to the study of animal communication. It is only through assessment of both the properties of the signal and the psychology of the receiver that we will be able to fully evaluate the plausibility and generality of any hypothesized signalling system.

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