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Is Fluctuating Asymmetry a Visual Signal?

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Abstract

Fluctuating asymmetries are the small, random deviation from perfect symmetry that occur during the development of otherwise symmetric traits and are a measure of developmental stability. It has frequently been claimed that fluctuating asymmetry is related to aspects of fitness, as asymmetry is an indicator of how well the genome can buffer developmental processes against perturbations from the environment. As asymmetry could be related to fitness, it has been further proposed that animals could use fluctuating asymmetry as a signal or cue to reveal fitness-related information to conspecifics (and perhaps heterospecifics). In this study I present a literature review which indicates that asymmetry is inconsistently related to both parameters. In some taxa, asymmetry can be related to fitness and be an effective signal; however, in other taxa fluctuating asymmetry is clearly not related to either aspects of fitness or signalling. In many cases, fluctuating asymmetry may be too small and inconspicuous to be detected as a visual signal and I discuss a number of symmetry perception parameters that may influence the receiver-psychology of symmetry-signalling and hence influence the efficacy of any symmetry-signalling system.

*In particular I present a number of empirical results from visual perception experiments with European starlings *Sturnus vulgaris*, which indicate that symmetry detection and discrimination is particularly error-prone, hence reducing the probability that fluctuating asymmetry could be used as an effective signal in this species. The general role of perceptual processes and their influence on signalling by fluctuating asymmetry is discussed.*

Fluctuating asymmetry is a measure of developmental instability. Specifically, fluctuating asymmetries are the small, random deviations from perfect bilateral symmetry that occur during the development of traits that we would normally describe as being symmetric (Ludwig 1932; Van Valen 1962). These asymmetries can arise for a number of reasons that can be conveniently grouped into two categories. First, there are a number of genetic factors that can increase levels of asymmetry. These include intense inbreeding, incorporation of mutant genes into the genome, recent episodes of hybridization that splits up previously co-adapted gene complexes, and perhaps extreme homozygosity in some taxa (Møller & Swaddle 1997). Second, there is a whole suite of environmental factors that can disrupt developmental processes to increase asymmetry. Such factors include temperatures that are too high or too low, nutritional stress (e.g. low food availability, or poor quality diet), high parasitic infection and chemical pollution (most commonly reported for aquatic species in polluted waterways) (Møller & Swaddle 1997). In summary, fluctuating asymmetry is a reflection of how well the genome can buffer developmental processes against environmental perturbations, and particular genotypes are better at buffering development than others.

Fluctuating asymmetry and fitness

As fluctuating asymmetry is an indicator of how well the genotype is coping with environmental conditions, researchers have investigated associations between asymmetry and fitness parameters to examine whether asymmetry could be a marker for fitness. In a number of cases, individuals with low asymmetry can have significant fitness advantages, and a recent meta-analysis has revealed that there is a relatively small, but significant, negative relationship between asymmetry and fitness measures (Leung & Forbes 1996). In this study I have conducted a further review of this literature, incorporating all of the studies cited by Leung and Forbes as well as ones not included and more recent references (excluding studies on human subjects). These studies are summarised in Table 1.

As can be seen from my literature review (reported on the basis of published species accounts, $N = 74$), there are inconsistent relationships between asymmetry and fitness measures (survival, fecundity, growth rates, body condition, parasitic infestation) among taxa. This is especially true when considering data from correlational and observational studies of asymmetry; only 52% of published correlational studies report the predicted negative relationship between asymmetry and fitness. The percentage of species accounts reporting the predicted negative relationship is much greater in studies where asymmetries have been induced experimentally (approximately 94% of cases). This is, perhaps, not surprising as many of the experiments reported have disrupted developmental stability through fairly gross environmental manipulation away from optimal developmental

Table 1. Review of non-human species accounts of the relations between fluctuating asymmetry and aspects of fitness (survival, fecundity, growth rates, body condition, parasitic infestation). Study results are summarised as follows: -ve, individuals with low asymmetry have a fitness advantage. No effect, no relationship between asymmetry and fitness. +ve, individuals with greater asymmetry have a fitness advantage. Correlations refers to correlational studies. Experiments refers to studies in which trait asymmetry has been manipulated in some manner or the experiment was performed under standardised conditions. In many of these experiments, the asymmetry was induced by environmental disturbance. Reference numbers are given in the footnote along with an indication of how many species were assessed within each study. If species numbers are not given, one species was studied. Only one study is included for each species account, but multiple citations are given if there are conflicting data for the same species.

	-ve	No effect	+ve	N
Correlations	30	22	5	57
Experiments	16	1	0	17
TOTAL	46	23	5	74

Notes to table 1.

Correlations -ve effect: 1, (Danzmann et al. 1986); 2, (Pankakoski 1985); 3, (Gest et al. 1986); 4, (Brault & de Oliveira 1995); 5, (Agnew & Koella 1995); 6, (Parsons 1962); 7, (Downhower et al. 1990); 8, (Chenuil 1991); 9, (Zakharov et al. 1991); 10, (Møller 1996b); 11, (Forbes et al. 1996); 12, (Møller et al. 1996); 13, (Stockley et al. 1996); 14, (Novak et al. 1993); 15, (Parker & Leamy 1991); 16, (Packer & Pusey 1993); 17, (Markowski 1993); 18, (Wolf et al. 1986); 19, (Zvereva et al. 1997); 20, (Bonn 1996); 21, (Escós et al. 1997); 22, (Reimchen 1997); 23, (Vrijenhoek 1994); 24, (Schall 1996); 25, (Saino & Møller 1994); 26, (Markusson & Folstad 1997); 27, (McKenzie & O'Farrell 1993); 28, (Somarakis et al. 1997); 29, (Roldan et al. 1998); 30, (Simmons 1995).

Correlations no effect: 8; 26; 31, (Björklund 1996); 32, (Møller 1994); 33, (Arcese 1994); 34, (Leung & Forbes 1997); 35, (Windig et al. 1994); 36, (Dufour & Weatherhead 1998b); 37, (Wiggins 1997); 38, (Forbes et al. 1996); 39, (Hoffmann et al. 1998); 40, (Polak 1997b) 4 spp.; 41, (Schandorff 1997); 42, (Vøllestad & Hindar 1997); 43, (Arnqvist et al. 1997); 44, (Hoikkala et al. 1998); 45, (Kimball et al. 1997); 46, (Carrascal et al. 1998).

Correlations +ve effect: 16; 22; 36; 47, (Suchentrunk 1993); 48, (Campbell & Emlen 1996).

Experiments -ve effect: 49, (Bagchi et al. 1989); 50, (McKenzie & O'Farrell 1993); 51, (Møller et al. 1995b); 52, (Møller et al. 1995a); 53, (Møller 1996a); 54, (Swaddle & Witter 1994); 55, (Swaddle 1996); 56, (Swaddle 1997); 57, (Ueno 1994); 58, (Naugler & Leech 1994); 59, (Thornhill 1992a); 60, (Zvereva 1997); 61, (Polak 1993); 62, (Folstad et al. 1996); 63, (Campbell et al. 1998); 64, (Beardmore et al. 1960).

Experiments no effect: 65, (Wardhaugh et al. 1993).

conditions. In sub-optimal conditions we should expect negative effects on fitness, as the optimality of developmental conditions is often determined by fitness effects.

The most generalised conclusion that I can draw from this literature review is that fluctuating asymmetry can be a marker for fitness in some systems and that the relationship between fitness and asymmetry is taxon- and trait-specific. This is a conclusion that other reviewers have previously reached (Markow 1995; Palmer 1996; Clarke 1997, 1998).

Fluctuating asymmetry and visual signalling

As fluctuating asymmetry can be a marker for fitness, it is possible that morphological asymmetry could be used a direct visual signal or cue of fitness in some systems (Møller 1990). This prediction has generated great interest in studies of fluctuating asymmetry and developmental instability, particularly in relation to sexual selection. In the eight years since Møller (1990) first hypothesised that asymmetry of secondary sexual traits could be used as a cue in mate choice, there have been at least 194 non-human species accounts relating some aspect of visual signalling (mostly indirect measures) to morphological fluctuating asymmetry. I have summarised these studies in Table 2.

Table 2. Review table of number of non-human species accounts relating some aspect of visual signalling to magnitude of trait fluctuating asymmetry. Study results are summarised as follows: -ve, individuals with low asymmetry are preferred or are inferred to do better in a signalling context. No effect, no relationship between asymmetry and signalling parameters. +ve, individuals with greater asymmetry are preferred or are inferred to do better in a signalling context. Correlations refers to correlational studies. Experiments refers to studies in which trait asymmetry has been manipulated in some manner. Natural range experiments refers to experimental studies that have performed asymmetry manipulations within a reasonable morphological range set by natural data sets for that particular species and have not confounded manipulations with other variables, such as behaviour, size or signal intensity. Note the large proportion of correlational studies (approximately 92%) and the relative paucity of species that have been investigated under experimentally controlled conditions. Reference numbers are given in the footnote along with an indication of how many species were assessed within each study. If species numbers are not given, one species was studied. Only one study is included for each species account, but multiple citations are given if there are conflicting data for the same species.

	-ve	No effect	+ve	N
Correlations	58	113	3	174
Experiments	5	5	1	11
Natural range experiments	3	2	0	5
TOTAL	66	120	4	190

Notes to table 2.

Correlations -ve effect: 1, (Møller & Eriksson 1995) 8 spp.; 2, (Eriksson 1996) 2 spp.; 3, (Harvey & Walsh 1993); 4, (Córdoba-Aguilar 1995); 5, (Radesäter & Halldórsdóttir 1993); 6, (Møller & Zamora-Muñoz 1997); 7, (Simmons 1995); 8, (Otronen 1998); 9, (Thornhill 1992b) 2 spp.; 10, (Thornhill 1992a); 11, (Thornhill & Sauer 1992); 12, (McLachlan & Cant 1995); 13, (Allen & Simmons 1996); 14, (Liggett et al. 1993); 15, (Markow 1987); 16, (Markow & Ricker 1992); 17, (Møller 1996b); 18, (Kodric-Brown 1997); 19, (Karino 1997); 20, (Sheridan & Pomiankowski 1997); 21, (Rintamäki et al. 1997); 22, (Forkman & Corr 1996); 23, Hasegawa (1995); 24, Borgia (1985); 25, (Møller 1993b); 26, (Wauters et al. 1996); 27, (Arcese 1994); 28, (Møller et al. 1996); 29, (Roldan et al. 1998); 30, (Møller & Höglund 1991) 3 spp.; 31, (Møller 1992) 9 spp.; 32, Córdoba-Aguilar (1997); 33, Malyon & Healy (1994); 34, (Tomkins & Simmons 1995b) 2 spp.; 35, (Balmford et al. 1993); 36, (Carrascal et al. 1998); 37, (Norry et al. 1998).

Correlations no effect: 1 2 spp.; 16 3 spp.; 18; 21; 30 12 spp.; 31 5 spp.; 34 23 spp.; 35 41 spp.; 38, (Jennions

1998b); 39, (Tomkins & Simmons 1995a) 5 spp.; 40, (Hunt & Simmons 1997); 41, (David et al. 1998); 42, (Amqvist et al. 1997); 43, (Ueno 1994); 44, (Brown 1997); 45, (Hoikkala et al. 1998); 46, (Polak 1997a); 47, (Taylor, M. I., Turner, G. F., Robinson, R. L. & Stauffer, J. R., unpubl. data); 48, (Brooks & Caithness 1995); 49, (Ryan et al. 1995); 50, (Veiga et al. 1997); 51, (Orland 1996); 52, (Fiske et al. 1994); 53, (Dunn 1994); 54, (Savalli 1995); 55, (Dufour & Weatherhead 1998a); 56, (Hoysak & Ankney 1996); 57, (Stockley et al. 1996)

Correlations +ve effect: 16, 34, 35.

Experiments -ve effect: 58, (Møller 1995); 59, (Møller 1993a); 60, (Fiske & Amundsen 1997); 61, (Swaddle & Cuthill 1994b); 62, (Schlüter et al. 1998).

Experiments no effect: 38; 62; 63, (Ligon et al. 1998); 64, (Jennions 1998a); 65, (Markow & Sawka 1992).

Experiments +ve effect: 66, (Oakes & Barnard 1994).

Natural range experiments -ve effect: 67, (Morris 1998); 68, (Møller & Sorci 1998); 69, (Swaddle & Cuthill 1994a).

Natural range experiments no effect: 70, (Swaddle & Witter 1995); 71, (Jablonski & Matyjasiak 1997).

As can be seen from this large body of literature, there is a general lack of consensus as to whether asymmetry is used as a visual signal. A recent meta-analysis of the influence of fluctuating asymmetry on sexual selection processes suggests that symmetry does play an important role (Thornhill & Møller 1998), but the review I have performed here incorporates a broader range and number of studies and also focuses on the differences between correlational and experimental studies. The correlational studies summarised above can only provide indirect evidence for any relationship between asymmetry and signalling. It is probable that in many of the signalling systems studied, asymmetry is either correlated with another signalling feature or that the asymmetry itself is not directly assessed. Therefore, correlational studies will tend to over-estimate the occurrences in which asymmetry is used a signal. Nevertheless, the majority of species examples (approximately 65%) indicate that morphological asymmetry does not function as a visual signal.

To confirm a signalling function, experimental manipulation of signalling structures are needed. Despite the large number of such studies, I could find only five in which asymmetry has been manipulated independent of other signalling features (trait size, signal intensity, behaviour) and the resulting experimental asymmetries have fallen within a natural range of asymmetry. In these '*natural range*' experiments, three studies have indicated the predicted negative relationship (symmetric individuals are preferred) for zebra finches *Taeniopygia guttata* (Swaddle & Cuthill 1994a); swordtail fish *Xiphophorus cortezi* (Morris 1998); and model flowers attracting insect pollinators (Møller & Sorci 1998). However, the remaining two studies have demonstrated that signalling trait asymmetry in European starlings *Sturnus vulgaris* (Swaddle & Witter 1995) and chaffinches *Fringilla coelebs* (Jablonski & Matyjasiak 1997) do not influence intra-specific competitive encounters.

Although only five natural range experiments have been reported, it is interesting that the three which support the predicted negative relationship have examined signalling in the context of mate preferences and sexual selection. On the other hand, the two studies in which asymmetry has no effect have examined signalling in the context of social dominance. This could indicate that symmetry signalling is context-specific and is related to

the relative benefit of accurate discrimination of the signal (Swaddle 1999). In cases of mate choice the benefit of getting a high quality mate may outweigh the cost of choosing a poor quality mate. The relative cost of inaccurately assessing individuals in social dominance interactions may be much smaller. Interestingly, where the benefits/costs of dominance interactions have been experimentally manipulated, symmetric individuals became relatively more dominant when the benefits of social dominance were increased (Swaddle & Witter 1994; Witter & Swaddle 1994).

Receiver-psychology of symmetry-signalling

The preceding review of the symmetry-signalling literature indicates that there is extreme heterogeneity among the data reported. In some cases, asymmetry can be used as a signal, whereas in others cases asymmetry appears unimportant. Most of the evidence commonly cited (and the majority of studies included in table 2) to support the notion that asymmetry can be used as a signal reports correlations between trait asymmetry (i.e. the signal) and some property of the signaller (Møller & Pomiankowski 1993; Watson & Thornhill 1994; Møller & Swaddle 1997). A vital element of any signalling system has been largely over-looked by researchers interested in assessing asymmetry signalling: the receiver's ability to detect, discriminate and respond to the asymmetry signal (receiver-psychology) (Guilford & Dawkins 1991). Without reliable detection of the asymmetry signal and accurate discrimination among natural asymmetry levels it is hard to envisage that signalling by fluctuating asymmetry could occur (Swaddle 1999). A central issue is thus the perceptual ability of organisms to discriminate symmetry from asymmetry. For the remainder of this manuscript I will focus on symmetry perception and its role in symmetry-signalling, as this has seldom been discussed in the literature.

Visual perception of symmetry

Compared with our knowledge of human visual symmetry perception, we know little about how well animals detect and respond to symmetry. In the following section I will indicate features of the human visual system that may be relevant to how other animals perceive symmetry, and discuss the implications of this for symmetry signalling.

Human symmetry perception

Human visual symmetry perception has been studied for over a hundred years and a review of the processes involved is presented elsewhere (Swaddle 1999). Here, I will briefly discuss features of symmetry perception that could act to either amplify or attenuate a symmetry-signal.

- (i) Most researchers agree that symmetry perception is a fundamental property of the human visual system and decoding of visual information (Wagemans et al. 1993; Tyler & Miller 1994; Osorio 1996).
- (ii) Bilateral symmetry is more readily detected than rotational or translational symmetry (Wagemans 1996). This could imply that asymmetry differences may be easiest to detect in traits with bilateral symmetry.

- (iii) Symmetry is easiest to detect about a vertical axis compared with symmetry about horizontal or diagonal axes (Palmer & Hemenway 1978). If this is similar for other animals, asymmetry differences should generally be easiest to discriminate in signalling structures with a vertical axis of symmetry.
- (iv) Symmetry is most easily assessed in the pattern area closest to the axis of symmetry (Jenkins 1982). Therefore, symmetry-signalling may be more prevalent where traits span the axis of symmetry rather than left and right elements appearing a large distance apart on either sides of the body.
- (v) Geometric patterns aid symmetry perception (Baylis & Driver 1994). Hence, asymmetry differences may be most easily assessed in complex traits composed of regular geometric shapes.
- (vi) Contrast and colour asymmetry can influence the assessment of morphological symmetry (Zhang & Gerbino 1992). Therefore, when assessing asymmetry, contrast and colour differences may also be important. This is not only relevant to the organisms involved in the signalling system, but also to researchers quantifying asymmetry in scientific studies.

Non-human symmetry perception

There are a number of features of non-human visual systems that appear to parallel our knowledge of the human visual system. I have summarised these below.

- (i) Symmetry perception appears widespread among many taxonomic groups. There is experimental evidence to indicate that species of bees, fish, birds and primates can perceive and respond to symmetry (Swaddle 1999).
- (ii) Symmetry perception may be a fundamental property of the vertebrate visual system and a corollary of how vertebrates detect edges and lines within structures (Osorio 1996).
- (iii) Bees can discriminate bilateral from rotational symmetry (Horridge 1996).
- (iv) Pigeons can learn a general symmetry preference (Delius & Habers 1978; Delius & Nowak 1982).

INVESTIGATIONS OF RECEIVER-PSYCHOLOGY OF SYMMETRY-SIGNALLING

As can be seen from the preceding section, we know rather little about how animals detect and respond to symmetry and asymmetry differences. Therefore, in the following section I will present four fundamental areas of research in which I feel we need to investigate symmetry perception further. These areas are supported with some empirical data that I have collected from studies of wild-caught European starlings. The methodological details and full data will be presented elsewhere (Swaddle, J. P. & Pruett-Jones, S., unpubl. data).

Do organisms exhibit a general symmetry preference?

General symmetry preferences have been invoked as an explanation for some of the symmetry preferences observed in the experiments summarised earlier in this manuscript (Enquist & Arak 1994; Johnstone 1994; Swaddle & Cuthill 1994a,b). If organisms have a pre-disposed preference for symmetry (over asymmetry) or have acquired a symmetry

preference in a specified context and can transfer that preference to another context, then signalling via fluctuating asymmetry may have evolved indirectly as a by-product of some other function. There is generally a lack of evidence that organisms display a strong predisposition toward symmetric objects, although there have been very few studies (Rensch 1958; Delius & Nowak 1982; Lehrer et al. 1995).

My experimental studies with starlings also indicate that birds do not show a spontaneous or pre-acquired preference for symmetric objects. By presenting symmetric and asymmetric pairs of monochromatic random dot patterns to starlings in a 2-key Skinner box, I could compare spontaneous preferences to peck (chose) at either symmetric or asymmetric images. Although birds showed a high degree of key-pecking, there was no relative preference for either symmetric or asymmetric patterns (figure 1) (Swaddle, J. P. & Prutt-Jones, S., unpubl. data).

Figure 1

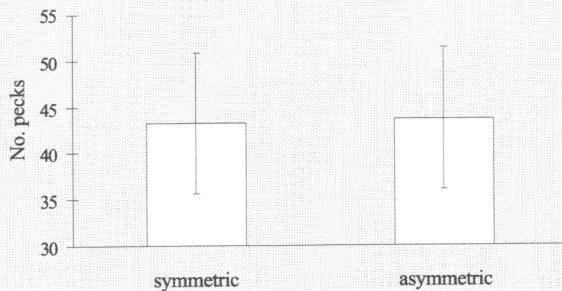


Figure 1. Mean (\pm S.E.) number of pecks at symmetric and asymmetric random dot patterns presented to starlings ($N = 6$) over 10 1hr trials in a 2-key Skinner box. There is no difference in number of pecks on symmetric or asymmetric keys ($t = 0.09$, $df = 5$, $P = 0.93$).

Figure 2

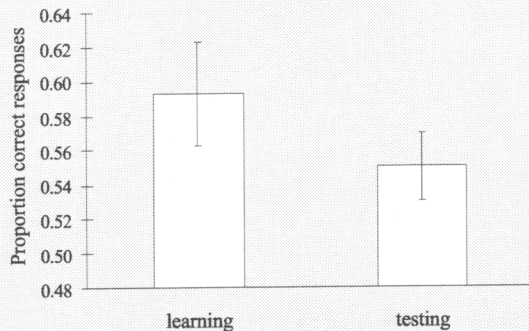


Figure 2. Mean (\pm S.E.) proportion of 'correct' responses (i.e. correct discrimination of symmetry from asymmetry) during the last 10 learning trials (exposure to learning images) and the 10 testing trials (testing on novel images). There is no significant difference ($t = 1.51$, $df = 5$, $P = 0.19$), indicating that there was some transfer of the general ability to discriminate symmetry from asymmetry. However, performance with the novel images (testing) was not quite significantly different from random (50%) pecking

at symmetric and asymmetric images ($t = 2.23$, $df = 5$, $P = 0.076$), indicating that the generalized symmetry discrimination was not strong.

Can organisms acquire generalised symmetry detection?

In a similar manner to the previous question, if organisms can acquire a symmetry preference and transfer that preference to another context, symmetry preferences in mate choice may have evolved through indirect mechanisms. This can be viewed as a 'generalised' symmetry preference and has been demonstrated to some degree in captive-bred pigeons (Delius & Habers 1978).

My experiments with wild-caught starlings show mixed evidence for the capacity to acquire a generalised symmetry preference. Over a series of 76 1hr learning trials, birds were trained by operant-conditioning (using food rewards) to discriminate between symmetric and asymmetric random dot patterns. Half of the birds received food rewards if they pecked at the symmetric images, while the other birds were rewarded if they pecked at the asymmetric images. After acquisition of the task (successful discrimination by symmetry) birds were tested for symmetry discrimination abilities on a novel set of images that they had not previously been exposed to. The birds did not completely transfer their pre-acquired preferences, but there was an indication that they could do this to some extent (figure 2) (Swaddle, J. P. & Pruett-Jones, S., unpubl. data).

Is reception of an symmetry-signal error-prone?

Asymmetry discrimination may be a difficult perceptual task to perform, as indicated by the relatively low levels of performance shown in the starling experiments described above. Therefore, I postulate that there may be a relatively high degree of error associated with the perceptual and cognitive elements involved in detecting asymmetry, discriminating various levels of asymmetry and responding appropriately to the asymmetry signal. Errors of reception have two important implications (Johnstone & Grafen 1992). (i) The response of the receiver may not accurately reflect the true advertising level of the signal (i.e. individual asymmetry). This would de-stabilise the system and also weaken the intensity of selection against asymmetric individuals. (ii) Receiver-error could influence the signalling tactics of the signaller in that there may be little benefit for the signaller to invest in a high (very symmetric) and costly advertising level. Empirical data from my starling experiments indicates that there is a large degree of among-individual variation in ability to reliably discriminate symmetry from asymmetry, even when asymmetry is very large compared with asymmetries observed in nature (figure 3) (Swaddle, J. P. & Pruett-Jones, S., unpubl. data).

Perceptual thresholds?

Perhaps the most important issue is that of perceptual thresholds for asymmetry discrimination, i.e., what magnitude of asymmetry can be discriminated from symmetry? There is very little data relevant to this question. Indirect evidence from a study on pigeons suggest that these birds are able to discriminate at best a 2% relative asymmetry (e.g. left side of trait is 2% larger than right side) from zero asymmetry (Schwabl & Delius 1984). Many of the asymmetries observed in nature may be too small to be discriminated from zero asymmetry. For example, mean trait asymmetry for signalling structures in birds

have been reported as approximately 1.9 to 3.5% of trait size (Møller & Höglund 1991; Balmford et al. 1993).

Fluctuating asymmetry is characterised by a normal distribution of signed asymmetry scores (Palmer & Strobeck 1986), although it is predicted that distributions could be more leptokurtic. Receivers will select individuals on the basis of unsigned asymmetry scores; hence individuals will be chosen from a truncated half-normal distribution. It is, therefore, straightforward to see that mean relative asymmetry will have to be substantially greater than 2% for the receiver to be able to discriminate among the majority of individuals in the population based on signal asymmetry. This illustrates the importance of receiver psychology in assessing the signalling role of asymmetry and may help to explain discrepancies among studies in this highly disputed field of research. In species where the mean population relative asymmetry is low in relation to the ability to perceive asymmetry, symmetry-signalling is not likely to have evolved.

Figure 3

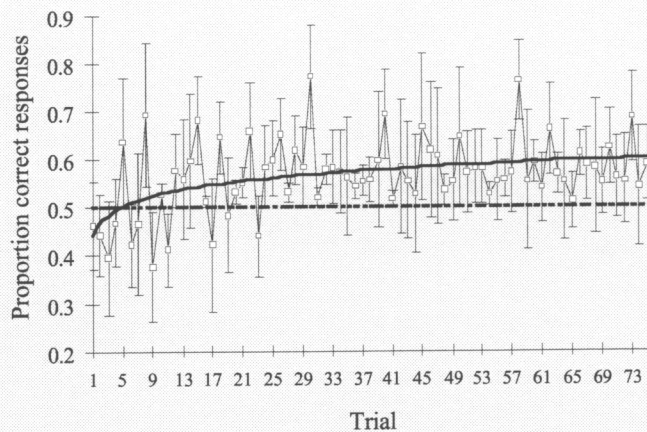


Figure 3. Mean (\pm S.E.) proportion of 'correct' discrimination of asymmetry from symmetry versus trial where birds received operant food rewards upon correct discrimination. The solid dark line is a fitted logarithmic regression line indicating a significant increase in the proportion of correct responses over time. The dashed line represents 50% preference, i.e., no preference for either correct or incorrect responses. The large error bars indicate among-individual variation in performance.

It also important to point out that all of the experiments in which the signalling role of asymmetry has been investigated have either studied traits with far greater asymmetries than 2% or manipulated asymmetries to extremely large degrees (commonly 20-30%). The smallest experimentally-induced asymmetry comes from a study of chest plumage asymmetry on mate preference in zebra finches, which resulted in a relative asymmetry of approximately 10% (Swaddle & Cuthill 1994a).

Conclusions

The question posed in the title of this manuscript was 'Is fluctuating asymmetry a visual signal?' The answer to this question is not clear and I doubt if it is possible to generalise among signalling systems. There is clear evidence that asymmetry can influence some signalling systems, and symmetric individuals are sometimes preferred in mate choice situations. However, there is also compelling evidence to indicate that fluctuating asymmetry does not influence signalling systems in other situations.

Why is there variation in the importance of fluctuating asymmetry as a visual signal? As the relationship between fluctuating asymmetry and fitness parameters appears to be taxon- and trait-specific, it seems likely that symmetry-signalling should also be similarly specific to certain signalling systems. In addition, we know very little about how symmetry/asymmetry is perceived and detected by visual systems. Without a more complete knowledge of the receiver-psychology of symmetry-signalling it is very difficult to draw any general conclusions. It is probable that many asymmetries observed in nature will be too small to play a direct visual signalling role, and that asymmetry perception of large asymmetries is likely to be error-prone. These features reduce the probability of fluctuating asymmetry being an effective and reliable signal. Perceptual studies in humans also illustrate that signal trait features could act to amplify or interfere with an asymmetry signal, and the relative role of these features will vary among taxa and traits. Therefore, I urge researchers to study these perceptual parameters within the context of individual signalling systems.

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