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Visual signalling by asymmetry: a review of perceptual processes

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Individual levels of asymmetry in traits that display fluctuating asymmetry could be used as visual signals of phenotypic (and perhaps genotypic) quality, as asymmetry can often be negatively related to fitness parameters. There are some data to support this hypothesis but the experimental protocols employed have commonly resulted in asymmetries far larger than those observed in nature. To date, there has been little consideration of the ability of animals to accurately discriminate small asymmetries (of the magnitude observed in the wild) from perfect symmetry. This is key to assessing the plausibility of the asymmetry-signalling hypothesis. Here, I review the perceptual processes that may lead to the discrimination of asymmetry and discuss a number of ecologically relevant factors that may influence asymmetry signalling. These include: signal orientation, distance of trait elements from the axis of symmetry, trait complexity, trait contrast and colour, and the behaviour of both signaller and receiver. I also discuss the evolution of symmetry preferences and make suggestions as to where researchers should focus attention to examine the generality of asymmetry-signalling theory. In highly developmentally stable signalling systems the magnitude of asymmetry may be too small to be detected accurately and reliably, hence asymmetry signalling is unlikely to have evolved in these situations.

Keywords: fluctuating asymmetry; developmental stability; symmetry perception; signalling theory; sexual selection

1. INTRODUCTION

There has been much recent interest in the role of fluctuating asymmetry (Ludwig 1932) in evolutionary biology as the minor differences between left and right elements of bilaterally symmetrical traits may be intimately related to fitness parameters (reviews in Watson & Thornhill 1994; Palmer 1996; Møller & Swaddle 1997). Møller (1990) suggested that these small asymmetries could be used as signals of phenotypic (and perhaps genotypic) fitness in social and sexual encounters. There is a growing body of observational data to support this hypothesis. However, relatively few studies have altered the asymmetry of traits and monitored subsequent behaviour to examine the true signalling properties of asymmetry independent of other confounding individual parameters. These studies provide a range of data, some of which indicate a preference for symmetry (Møller 1992; Grammer & Thornhill 1994; Fiske & Amundsen 1997), whereas others do not (Oakes & Barnard 1994; Swaddle & Cuthill 1995; Kowner 1996). However, these experiments have confounded manipulations of asymmetry with extraneous factors (e.g. flight performance, trait size, colour pattern, trait averageness) that may also influence behaviour and alter the dynamics of the signalling system.

When visual asymmetry of signalling traits has been manipulated independently of other confounding factors, the evidence indicates that asymmetry can be an effective signal (Møller 1993, 1995; Swaddle & Cuthill 1994*a*; Bennett *et al.* 1996; Swaddle 1996; Uetz *et al.* 1996 but see Ligon *et al.* 1998). However, these studies employed techniques that have resulted in asymmetries larger than those commonly observed in nature. To date, only five studies have employed experimental manipulations that have resulted in asymmetry values representative of the magnitude found in unmanipulated populations. First, Swaddle & Cuthill (1994*b*) found that female zebra finches, *Taeniopygia guttata*, prefer males with symmetrical chest bar plumage. The role of chest bars in the signalling strategy of male zebra finches is not clear, hence these data must be interpreted with caution when assessing the signalling properties of fluctuating asymmetry. Recently, Morris & Casey (1998) have shown that female swordtail fish, *Xiphophorus cortezi*, prefer to associate with males that have symmetrical numbers of vertical bar markings on their flanks. In a closely related species, these bar marks appear to have a signalling function in intra- and interspecific social encounters (Morris *et al.* 1995). In contrast, asymmetry does not appear to be used as a signal in European starlings *Sturnus vulgaris* (Swaddle & Witter 1995), chaffinches *Fringilla coelebs* (Jablonski & Matyjasiak 1997) or the earwig *Forficula auricularia* (Tomkins & Simmons 1998). Therefore, the relative paucity of evidence currently available suggests that the direct role of fluctuating asymmetry in visual signalling is not clear and remains

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an issue of considerable contention (e.g. Balmford *et al.* 1993; Palmer 1996).

The supportive evidence most often cited for asymmetry signalling relates some relationship between intrinsic properties of the signaller and the signaller's phenotypic display of developmental instability. Individuals with low asymmetry in traits that display fluctuating asymmetry often experience fitness benefits (reviews in Watson & Thornhill 1994; Møller & Swaddle 1997). However, signalling theory dictates that for us to fully assess the plausibility of the asymmetry-signalling debate we must also thoroughly investigate the ability of the receiver to accurately detect, respond and remember the level of the signal, i.e. the trait asymmetry (cf. Swaddle 1997*a*). This is a crucial element that has been largely overlooked.

Therefore, in this paper I review the literature related to the visual perception of symmetry and discuss this in terms of the asymmetry-signalling debate. In particular, I suggest that, in vertebrates, bilateral asymmetry may be used more commonly as a signal than other forms of asymmetry. I review the perceptual processes that may lead to symmetry detection and discuss how the characteristics of signalling traits may influence asymmetry signalling. I comment on how behaviour of both signaller and receiver may influence asymmetry signalling. As asymmetries in nature are often small (commonly less than 1% of trait size in ordinary morphological traits, but can be larger in signalling traits), I discuss the perceptual thresholds for asymmetry detection and the implications of these thresholds for signalling theory. Finally, I theorize as to how a preference for symmetry may arise independently of an association with fitness. The majority of studies investigating the perception of symmetry have been performed on human subjects, therefore the reader should assume that my discussion refers to human vision unless otherwise stated. Caution must be applied when attempting to draw general conclusions from human studies and when applying them to other animal systems. As we know relatively little about non-human symmetry perception many of the predictions that I make concerning the visual abilities of animal 'receivers' are speculative and have not been investigated empirically. I hope that this review will help to stimulate such research and forge links between perceptual psychology and evolutionary biology.

2. SYMMETRY AS A SIGNAL

Symmetry is a representation of self-similarity most commonly defined in terms of a structure (or part of a structure) being subjected to three forms of Euclidean transformation to give four major forms of symmetry (Weyl 1952). (i) Reflectional symmetry (often referred to as bilateral or mirror symmetry) is where a structure is reflected across a plane of symmetry. (ii) Rotational symmetry occurs when a structure is rotated around a point of symmetry. (iii) Translational symmetry refers to the situation where a structure is moved a distance parallel to a plane but its orientation is not altered. (iv) Glide-reflection is a combination of reflectional and translational symmetry, i.e. a structure is reflected in a plane and then moved a distance parallel to that plane. For the purposes of this review I shall only refer to the first three forms of symmetry, as glide-reflection is a composite form.

When most people discuss the perception of symmetry they refer to bilateral (i.e. reflectional symmetry) and overlook the other forms of symmetry. There is some justification for this approach in terms of the perceptual elements of signalling theory. Through a series of investigations, several groups of investigators have suggested that in humans, bilateral symmetry is more readily detected and processed than the other two major forms of symmetry transformation: rotational and translational (review in Wagemans 1996). Julesz (1971) first indicated that bilateral symmetry is assessed more quickly than translational or point-reflection (i.e. rotation about 180°) symmetry. Subsequently, it has been demonstrated that symmetries created by rotation around 90° and 180° are more difficult to detect than symmetries created by mirror reflection (Royer 1981) (although relative response to rotation around smaller angles has not yet been investigated). Additionally, Fitts *et al.* (1956), Corballis & Roldan (1974), Bruce & Morgan (1975) and Baylis & Driver (1994, 1995) have compiled evidence to indicate that bilateral symmetry is more readily detected than translational symmetry. Hence, in higher vertebrates (as the experiments cited above were performed on humans), you may expect a relative prevalence of bilaterally symmetrical signalling structures to have evolved compared with those that display rotational or translational symmetry. It is doubtful that these putative perceptual generalizations apply to invertebrate taxa; especially as many insect taxa appear to respond to radial symmetry of floral signals (Møller & Eriksson 1995).

Bilateral symmetry is more prevalent in vertebrates than other forms of symmetry and most of the signalling structures reported in the recent literature have displayed bilateral symmetry as opposed to the other forms of symmetry. Radial symmetry is common in many forms of flowering plant (and invertebrates) and bilateral symmetry is believed to have evolved from radially symmetrical ancestors resulting in most higher angiosperms displaying bilateral symmetry. It has been claimed that bilateral symmetry of floral traits may contain relatively more information than radial symmetry (Davenport & Kohanzadeh 1982). If information is related to the 'novel' surface area of the flower, any degree of symmetry repeats information as elements of the flower are repeated. Bilateral symmetry reflects half of the flower in one axis, hence half of the flower is novel. Floral radial symmetry most commonly occurs in angles less than 180° (e.g. three-, four-, and fivefold radial symmetry), therefore relatively less of the area of the flower is unique. Hence, bilaterally symmetrical flowers could possess more 'informational content' (Davenport & Kohanzadeh 1982), although this is purely a theoretical argument and there are no data to support this notion. These considerations could indicate that bilateral symmetry may be relatively more important to the general discussion of signalling issues in floral traits. However, in instances of rotational symmetry an element can be repeated two, three, four or more times, and could potentially render more information concerning developmental instability than the two mirrored elements present in bilateral symmetry. Hence, radial asymmetry may be an equally (or perhaps more) important feature of a signal as bilateral symmetry in some flowering plants. This implies that perception of radial symmetry may be important in many insect taxa as they are commonly 'receivers' of floral signals.

For the purposes of this review, I have emphasized studies that have focused on bilateral symmetry, as most of the recent publications have reported observations and experiments in vertebrate taxa. Nevertheless, I have not ignored rotational and translational symmetry, as these features may have perceptual mechanisms in common in many visual systems.

3. MECHANISMS OF SYMMETRY PERCEPTION

Numerous processes that underlie symmetry perception have been proposed, but there is a general lack of agreement on a unitary theory that explains how the visual system detects and responds to symmetrical patterns. The empirical studies suggest that symmetry perception is a complex process that may involve a series of mental computations and transformations. Hence, early theories suggested that the visual system undergoes two or more procedural steps to ascertain symmetry properties. For example, Palmer & Hemenway (1978) suggested that, first, an axis of symmetry is selected by a crude, but rapid, analysis of the orientation of elements within the pattern. Second, after the axis is established, a more detailed comparison of the two halves is performed. Similar separation of visual processing into fast, pre-attentive assessment followed by slower point-by-point (see below) pattern matching has been invoked by other researchers (e.g. Julesz 1971; Bruce & Morgan 1975; Foster 1991).

This form of model has been criticized on a number of levels (see Wagemans 1996). In particular, Royer (1981) pointed out that the initial (pre-attentive) phase of symmetry perception is the most problematic element to explain, as it is more likely to reflect the functional architecture of the neural system and influences other forms of cognitive and perceptual processes (e.g. Driver *et al.* 1992). As the general property of symmetry can be assessed by the human visual system very quickly (in less than 100 ms in some instances) (e.g. Julesz 1971; Hogben *et al.* 1976; Carmody *et al.* 1977; Barlow & Reeves 1979; Locher & Nodine 1989; Wagemans *et al.* 1991, 1993), it is difficult to explain how the pre-attentive phase accomplishes this in such a short period of time. It is possible that only part of an image is processed (e.g. Barlow & Reeves 1979) or that elements within an image are pooled in some way to form a shape whose symmetry is assessed (cf. Jenkins 1983). If only part of an image is processed, the remainder of the pattern would be assumed to show equal levels of symmetry (Tyler 1996). This is a similar process that we commonly use to recognize everyday objects, i.e. we complete the picture without inspecting all of its parts—a form of non-sensory completion (Kanisza 1976). If elements are pooled to form a larger feature, this introduces another step in the pre-attentive process that makes it more difficult to explain performance reported in several experiments (see discussion in Wagemans 1996).

These considerations led many researchers to suppose that symmetry detection was an intrinsic, fundamental property of the human visual system. Detection of symmetry may be an implicit corollary of how the visual system encodes and processes information (e.g. Barlow & Reeves 1979; Royer 1981; Palmer 1982; Pashler 1990; Foster 1991; Locher & Wagemans 1993; Wagemans *et al.* 1993; Tyler & Miller 1994; Osorio 1996). Recently, Wagemans *et al.* (1993) have proposed a computational model in which the visual system detects groupings of elements (initially by random) within a display (they termed this 'bootstrapping') to form a 'mental' shape. In a bilaterally symmetrical pattern, the direction and orientation of these groupings predicts the next most likely group of elements to be found; so the visual system searches for a similar shape in the predicted direction. As the random processing of elements is converted into a systematic processing of the image, the visual system can quickly ascertain whether the groupings are in the same orientation and, hence, assess general symmetry properties. The essence of the Wagemans *et al.* (1993) model is that symmetry is more readily detected when pairwise correspondence of points is supported by regularity in higher-order structures.

Tyler & Miller (1994) have suggested that the local pattern vector at the focus of attention (i.e. the fovea) may be used to form a template, which is matched to pattern vectors at other localities on the retina. The term 'local pattern vector' refers to the specific response profile of local detectors, hence a match between two locations implies that there is a correspondence between these two elements (i.e. some form of symmetry).

Osorio (1996) has proposed a general model for symmetry detection that is based on low-level categorization of phase relations in the spatial harmonics across elements that comprise an image (cf. Morrone & Burr 1988). Symmetry detection based on the phase relationships of spatial frequency components has previously been suggested (Julesz & Chang 1979; Delius & Nowak 1982). This form of detection mechanism has also been suggested to explain edge and line detection by the vertebrate visual system (Morrone *et al.* 1986) and, hence, is an attractive suggestion for the general detection of symmetry across a wide range of taxa. The basic principle behind this theory lies in examination of the properties of the sine function of the harmonics when the harmonics of each element are in phase or congruent. An 'edge' is detected if the harmonics are in phase (or congruent) at zero crossings (i.e. 0° or 360°), whereas a 'line' is detected if phase congruence occurs at peaks or troughs (i.e. 90° or 270°). A bilaterally symmetrical pattern, under this analysis procedure, appears as a line of no specific contrast (refer to Osorio (1996) for further details). Through development of a working model, Osorio demonstrated that an array of filters, operating on elements across an entire image, can use spatial phase information to determine axes of symmetry. He also proposes that similar mechanisms could operate in less complex visual systems and may explain the prevalence of symmetry perception in some insect taxa (Lehrer *et al.* 1994; Giurfa *et al.* 1995).

In summary, there is consensus that symmetry detection is a fundamental property of the human visual system, and perhaps a number of other vertebrate visual systems, that develops early during ontogeny (Bornstein *et al.* 1981). The precise mechanisms underlying the process of symmetry detection is not known, although more recent models can explain most of the reported empirical data (e.g. Wagemans *et al.* 1993; Tyler & Miller 1994; Osorio 1996). It is likely that there are not specific symmetry detectors, rather that symmetry perception is a concomitant of how the visual system encodes and processes information.

(a) *Animal symmetry perception*

Compared with our knowledge of human vision, relatively little is known about the ability of non-human animals to perceive and respond to symmetry. Honeybees, *Apis mellifera*, can be quickly trained to detect and respond to the general property of symmetry (Hertz 1929, 1933; Free 1970; Giurfa *et al.* 1995; Horridge 1996). Additionally, bees can discriminate between patterns that possess bilateral as opposed to rotational symmetry (Horridge 1996). I am aware of only three studies of symmetry perceptual abilities in fishes, which indicate that some fishes (*Carassius* and *Macropodus*; *Poecilia reticulata*; *Xiphophorus cortezi*) can detect symmetry (Rensch 1958; Sheridan & Pomiankowski 1997; Morris & Casey 1998, respectively). Pigeons, *Columba livia*, can distinguish symmetry from asymmetry (Zentall & Hogan 1975; but see Morgan *et al.* 1976) and conceptualize the general concept of symmetry (Delius & Habers 1978; Delius & Nowak 1982). Additionally, it appears that chickens (*Gallus gallus*; Rensch 1958, 1973), barn swallows (*Hirundo rustica*; Møller 1993), zebra finches (Swaddle & Cuthill 1994*a*,*b*; Bennett *et al.* 1996), bluethroats (*Luscinia svecica*; Fiske & Amundsen 1997), jackdaws (*Corvus monedula*) and carrion crows (*Corvus corone*; Rensch 1958, 1973) can perceive symmetry properties. There is also some evidence that two species of monkey can detect symmetry (Rensch 1958).

The published data appear to indicate that a wide range of taxa can detect symmetry and that some non-human taxa, especially birds, have developed symmetry discrimination abilities at least of the order of that described for humans (Schwabl & Delius 1984). Therefore, it seems relevant to discuss the human vision literature when considering the purported visual capabilities of a number of animal groups. At several fundamental levels, birds and non-human mammals may have similar (or perhaps better) abilities to detect and respond to symmetrical visual stimuli than humans. However, I should also reiterate the caveat that readers should be aware that most of the data discussed have not been collected from non-human animals and that extrapolation beyond the human visual system should be done with caution.

4. TRAIT CHARACTERISTICS AND ASYMMETRY SIGNALLING

A review of the literature indicates that a number of fundamental properties of a display (or signal) may influence the way in which symmetry is perceived. These factors could be viewed as elements that 'amplify' the asymmetry signal (cf. Hasson 1989, 1990) and, hence could be favoured by selection mechanisms. In the following section I postulate as to how (i) orientation of the axis of symmetry, (ii) distance of traits elements from the axis of symmetry, (iii) trait complexity, and (iv) trait contrast and colour may affect asymmetry signalling.

(a) *Orientation of the axis of symmetry*

In humans, it has been claimed that symmetry about a vertical axis is more salient than symmetry about any other axis (Mach 1959; Rock & Leaman 1963; Goldmeier 1972; Rock 1973; Corballis & Roldan 1975; Fox 1975; Barlow & Reeves 1979; Fisher & Fracasso 1987). Explicitly, there are data to indicate a hierarchy in ease of detection so that symmetry in a vertical plane is easiest to detect, followed by horizontal symmetry and then diagonal symmetry (Palmer & Hemenway 1978; Barlow & Reeves 1979; Royer 1981). However, there are studies that contradict this simple relationship (e.g. Fisher & Bornstein 1981; Jenkins 1983; Pashler 1990; Corballis & Roldan 1975), indicating that there may not be a structural bias in the neural filters that process symmetrical patterns (cf. Mansfield 1974; Mansfield & Ronner 1978).

Pashler (1990) found that informing subjects of the orientation of symmetry in test stimuli increased perceptual performance in terms of speed and accuracy of detection. This could imply that subjects are capable of altering their frame of reference in terms of the orientation of the axis of symmetry to the most likely orientation that they will experience (Shepard & Metzler 1971). In light of this, Wenderoth (1994) exposed subjects to stimuli that varied in the orientation of the plane of symmetry ranging from horizontal to vertical and several intermediate diagonal orientations. Wenderoth found that subjects responded best to stimuli whose plane of symmetry was orientated at the mean angle for the frequency distribution of the whole population of presentations, i.e. they focused on the most likely angle of orientation. This evidence of 'attentional selectivity' further implies that the influence of axis orientation on perception is not reliant on a bias in the neural array of orientation detectors (Chaudhuri 1990). In several cases, symmetry about a vertical axis is most easily detected, but the mechanism underlying this bias is not clearly understood.

The fundamental differences in the manner in which humans perceive bilateral symmetry in different orientations may have implications for the ways in which other animal species perceive and respond to symmetry information. Although there is little known concerning orientation effects in other taxa, there is some evidence that honeybees respond quicker to bilateral symmetry in a vertical plane as opposed to a horizontal plane (Lehrer *et al.* 1995; Horridge 1996). This is similar to what we see in humans. In general, we may expect selection pressures to favour the evolution of asymmetry-signalling traits with a vertical axis of symmetry, especially in organisms that primarily orientate their visual field about a vertical axis, i.e. in a similar manner to humans.

(b) *Distance from the mid-line*

The ability to perceive symmetries is not only reliant on the orientation of the axis of symmetry, but also the spacing of the elements within the stimulus object (Corballis & Roldan 1974). A number of studies have indicated that symmetry is most readily assessed in a narrow strip centred around the axis of symmetry (Julesz 1971; Bruce & Morgan 1975; Barlow & Reeves 1979; Jenkins 1982). This may also be related to symmetry being most easily perceived at the point of fixation (Barlow & Reeves 1979; Saarinen 1988; Locher & Nodine 1989). However, Wenderoth (1995) and Barlow & Reeves (1979) have also indicated that proximity to the edge of a pattern is an important feature in symmetry detection. Hence, features close to the centre and close to the outside edge of a pattern that is reflected across an axis of symmetry are most readily assessed in terms of their symmetry.

These findings could suggest that asymmetry signalling would be most effective in traits that are close to or span the body axis, or in traits that define the outer edges of the overall shape of an organism. In traits that span the body axis, central elements (i.e. those around the axis of symmetry) may be more effective as a signal than other parts of the trait. To date, there have been no studies to explore this relationship in non-human animal systems. These observations also predict that asymmetry signalling is least likely to occur in traits where left and right elements are not visible simultaneously, such as coloration patches on either side of fishes (but see Sheridan & Pomiankowski 1997; Morris & Casey 1998).

(c) *Trait complexity*

In general, many researchers have predicted that symmetry will take longer to assess in more complex stimuli (see Baylis & Driver 1994), presumably as more elements within patterns need to be processed by the visual system to assess the symmetry of more complex structures. However, this relationship is not necessarily straightforward as there is growing evidence that elements within patterns can be grouped together into smaller subunits of perceptual comparison between left and right sides (e.g. Tapiovaara 1990; Baylis & Driver 1994). If elements are closer together, then symmetry (if present) is detected quicker (Corballis & Roldan 1974).

Trait complexity may also influence the manner in which symmetry information is extracted from visual stimuli. The symmetrical properties of relatively simple patterns with low spatial frequencies may be extracted globally and may not make specific requirements on points of fixation to determine the symmetrical relationships of elements within the patterns (Julesz 1971). Whereas, a point-by-point (or group-by-group, where points are pooled together) comparison may be required when assessing the symmetry of more complex patterns that have higher spatial frequencies (Julesz 1971; Bruce & Morgan 1975; Palmer & Hemenway 1978; Zimmer 1984).

This could mean that in simple structures, intrinsic display properties such as distance from the mid-line may not influence symmetry detection as much as in complex ornaments. Therefore, it could be predicted that the asymmetry of simple structures, such as ornament length, could be assessed at larger distances from the axis of symmetry than for complex structures such as multi-coloured or patterned elements. The two experiments that have demonstrated symmetry perception in the traits on opposite sides of fishes (i.e. left and right elements are not simultaneously visible) have studied relatively simple structures: colour spots (Sheridan & Pomiankowski 1997) and vertical bar patterns (Morris & Casey 1998). It may be that complex ornaments involved in asymmetry signalling may be more likely to occur close to the plane of symmetry. And colour patches far from the axis of symmetry (but not at the edge of a visible pattern) are less likely to be used as an effective and reliable signal. Interestingly, red epaulettes in male red-winged blackbirds, *Agelaius phoeniceus*, do not appear to signal asymmetry information (Dufour & Weatherhead 1996). And left and right components of this trait are a relatively large distance from the mid-plane, whereas the asymmetry of the complex plumage chest bars of zebra finches is a signal and this plumage area spans the axis of symmetry (Swaddle & Cuthill 1994*b*). Of course, these two studies are not directly comparable as they employed very different methodologies and the relative magnitude of asymmetries also differed. However, listing these examples serves to demonstrate that predictions concerning asymmetry signalling and distance from the mid-plane could be tested by conducting both within- and among-species experiments that manipulate asymmetry to similar magnitudes using common, standardized methods.

It also appears that symmetry detection in humans is quicker if the object contains elements that are composed of angles and lines, as opposed to simple dots (Corballis & Roldan 1974). The difference between dots and lines is also evident when subjects are asked to discriminate small asymmetry from perfect symmetry: when stimuli are composed of more regular features, asymmetry discrimination is enhanced (Hong & Pavel 1996). This may mean that symmetry in discretely shaped patches of coloration, such as chest stripes in male zebra finches, may be more easily assessed than more diffuse spot patterns, such as the spotty chest plumage of female starlings, *Sturnus vulgaris* (cf. Swaddle & Witter 1995).

(d) *Trait contrast and colour*

Zhang & Gerbino (1992) have explicitly shown that the relative contrast of elements within a stimulus pattern influences symmetry perception. In their study, they varied the contrast of elements (dots) between left and right sides of symmetrical dot patterns. Contrast asymmetry negatively influenced the process of assessing morphological asymmetry, i.e. symmetry was less readily detected in the symmetrical pattern that contained a contrast asymmetry. This implies that contrast and colour asymmetries will also be important when assessing symmetry in nature along with simple pattern matching (see also Tyler *et al.* 1993). Therefore, when researchers assess asymmetry of signalling traits they should not only measure the morphological asymmetry but also the contrast and colour asymmetry of left and right sides.

5. BEHAVIOUR, CULTURE AND ASYMMETRY PERCEPTION

Behaviour of the signaller and receiver may influence asymmetry detection. A series of investigations have repeatedly demonstrated that viewing a symmetrical pattern at an increasing angle (or skew) decreases the ability to detect the symmetry (Gerbino & Zhang 1991; Wagemans *et al.* 1991, 1992, 1993; Locher & Smets 1992; Szlyk *et al.* 1996). Therefore, in systems where asymmetry signalling has evolved we may expect to see behavioural adaptations that minimize these skew effects. These may include a synchronization of movement between signaller and receiver or, alternatively, a lack of movement by both parties that enhances the probability that the signal is orientated perpendicular to the eyes of the receiver.

As described above, there are a number of trait features that can aid symmetry perception, hence we could expect behavioural adaptations to maximize these features and potentially amplify the signal. For example, we could expect symmetrical signalling traits to be held in a vertical orientation to the eyes of the receiver and signallers to avoid habitats of sharply varying light intensity. In this respect, there is some evidence of behavioural modification that could enhance symmetry perception. When bees land on a bilaterally symmetrical flower they orientate their body to the axis of symmetry (Jones & Buchmann 1974). This could be to maximize balance or to enhance symmetry perception.

There may also be some cross-cultural differences in the perception of symmetry. Human societies choose, use and learn different types of symmetries preferentially (review in Washburn & Crowe 1988). When testing for symmetry perception in humans it may be important to take these differences into account as some societies are better at detecting bilateral symmetry, some rotational symmetry and other translational symmetry. For example, Bukusu (West Kenyan) children are less capable of reproducing rotated objects than Scottish children, but they are equally efficient at reproducing images that have been vertically reflected (Bentley 1977). It has been suggested that symmetry preferences are learned (Paraskevapoulo 1968) and that education differences may account for some of the cross-cultural differences seen in symmetry preference. Hargittai (1992) has indicated that the Japanese culture may dislike exact symmetry more than conventional Western culture. Symmetry appears as being too perfect for Japanese liking: it is too unnatural and sterile. It is possible that non-human animals could also show some elements of cultural variation in their symmetry perceptual abilities and preferences, although any effects of cultural differences would be expected to be much weaker than in humans and are not likely to influence the presence–absence of symmetry preferences. Cultural variation in symmetry perception could be tested by examining perceptual performance of species that have been geographically separated, or by experimentally exposing developing animals to different forms of symmetry–asymmetry cues. This could be an overcomplication of an already complicated issue, but could, I feel, be an issue worthy of consideration.

6. PERCEPTUAL THRESHOLDS AND ACCURACY

Is symmetry a canonical property that is exaggerated by the visual system (cf. Freyd & Tversky 1984)? In other words, do our visual systems interpret a near-symmetrical image as a perfectly symmetrical image? In a number of experimental studies, objects that are distorted from perfect symmetry by a set degree are perceived as being symmetrical as reliably as true symmetrical stimuli (e.g. Julesz 1971; Barlow & Reeves 1979; Jenkins 1983). However, the human visual system also has the ability to discriminate perfectly symmetrical patterns from those with some degree of asymmetry (Barlow & Reeves 1979; Jenkins 1983). Experimental investigations of the perceptual thresholds of discriminating small degrees of asymmetry from perfect symmetry are generally lacking from the literature, so it is not possible to put an exact figure on the magnitude of relative asymmetry that is 'perceivably' different from zero asymmetry (see below). Hong & Pavel (1996) report a recent experiment in which subjects were required to discriminate between perfectly symmetrical images and those that possessed small degrees of asymmetry. Their data indicate that humans can discriminate an asymmetry of no less than 1.5% when the display is highly structured but only about 3% when the display comprises a random dot display. The issue of perceptual thresholds is an integral component in assessing the plausibility and generality of much of the asymmetry-signalling literature. As the asymmetries that are measured in nature are so small (commonly less than 1% of trait size), it may not be possible to discern asymmetry from perfect symmetry (Swaddle 1997*a*).

The only evidence I am aware of which could be interpreted as indicating a perceptual threshold for discriminating asymmetry from perfect symmetry in non-human animals comes from a bar length discrimination experiment performed on pigeons by Schwabl & Delius (1984). In their experiment, pigeons were exposed to 'long' and 'short' white bar patterns on a dark background. Pigeons were trained to discriminate between the two categories at initial length differences of approximately 46% and 23%. In subsequent trials the difference in length between the two bars, which could be interpreted as a length asymmetry, was reduced to approximately 4% and 2%. Pigeons could still reliably distinguish between long and short bars, implying that in an asymmetry discrimination task they could perceive a 2% relative asymmetry as being different from perfect symmetry. This exceeds the apparent perceptual abilities of humans, who possess a threshold for bar length discrimination at approximately 4% length difference (Ono 1967). Schwabl & Delius (1984) did not interpret their data in terms of symmetry detection and it should be noted that the evidence their study provides is indirect, but valuable nonetheless.

These data imply that pigeons have a perceptual threshold for asymmetry discrimination at approximately 2% asymmetry. In many published reports of relative asymmetry values this could mean that the majority of the population are perceived visually as symmetrical, as mean asymmetry is often less than 2% of trait size. In the two studies that have unequivocally demonstrated a signalling role for asymmetry, the relative difference between symmetrical and asymmetrical signals was larger than this putative 2% threshold level: approximately 10% in Swaddle & Cuthill's (1994*b*) zebra finches and approximately 21% in Morris & Casey's (1998) swordtail fishes. For asymmetry to be an effective signal it must be used as a selection criterion for discriminating among individuals. Hence, if the majority of individuals are categorized as symmetrical, asymmetry will have little discriminatory ability and its use as a signal must be in doubt when traits display high developmental stability. Signalling traits do tend to display greater levels of fluctuating asymmetry than traits under stabilizing selection (Møller & Pomiankowski 1993), but trait asymmetry could still be too small for many visual systems. As it is not possible to extrapolate from Schwabl & Delius's (1984) single study on a single species, a detailed study of perceptual thresholds for asymmetry discrimination in relation to the population distribution of trait asymmetry values is required before we can fully assess the generality of asymmetry-signalling theory. It is also fair to remark at this point that a small morphological asymmetry could become magnified into a large behavioural asymmetry (e.g. birds with small wing and tail asymmetries have reduced flight performance; Evans *et al.* 1994; Swaddle 1997*b*) and this could provide a plausible mechanism for asymmetry discrimination in some systems (further discussion in Møller & Swaddle 1997). However, for the purposes of this review I am restricting my comments to the direct visual assessment of morphological trait asymmetry.

Pigeons have greater visual acuity for length discrimination than humans, so could asymmetry discrimination abilities be better in birds than mammals? The visual system of birds appears to be superior in a number of other features, for example, pattern-recognition orientation invariance (Delius & Hollard 1995), ultraviolet colour detection (Bennett *et al.* 1996, and references therein), polarization plane discrimination (Delius *et al.* 1976) and hue discrimination (Emmerton & Delius 1980). Therefore, asymmetry signalling could be more prevalent in avian as opposed to mammalian signalling systems. To date, there have been too few studies performed with non-avian taxa to comment on this suggestion.

For a signal to be effective, it must be both discriminable and memorable (Guilford & Dawkins 1991). Hence, if symmetry is detected it must also be coded and stored at some cognitive level. Even if symmetry (and hence asymmetry) is perceived at a lower level, e.g. as a by-product of edge and line detection (Delius & Nowak 1982; Osorio 1996), organisms would still have to store some memory of the symmetry of other signals to make among-signal discrimination possible. Therefore, it is not only imperative to study asymmetry discrimination, but also the manner and efficiency in which visual asymmetry information is stored and recalled by cognitive processes.

Assigning an accurate threshold value to asymmetry discrimination is 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 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 (not just from perfect symmetry but also from varying levels of asymmetry) and investigating factors that influence this discrimination, are vital in assessing the role that asymmetry may play in any signalling system.

7. EVOLUTION OF SYMMETRY PREFERENCES

It is possible that a preference for symmetrical objects has evolved independently of any association between symmetry and fitness. Aesthetic symmetry preferences have been observed in humans (e.g. Bahnsen 1928; Attneave 1954, 1955) even if the symmetry is not complete (Eisenman & Rappaport 1967; Eisenman & Gellens 1968; Szilagyi & Baird 1977; Howe 1980). There is also some evidence for aesthetic symmetry preferences in birds and insects (e.g. Rensch 1957, 1958; Lehrer *et al.* 1994; but see Delius & Nowak (1982) for slight preference for asymmetry in pigeons). Hence, researchers have begun to focus on the evolutionary origins of a preference for symmetry.

Several artificial neural network models have been developed to help explain how a preference for visual symmetry could evolve (Enquist & Arak 1994; Johnstone 1994; Bullock & Cliff 1997). Enquist & Arak's (1994) model suggested that symmetry preferences may have evolved as a concomitant of a process to detect patterns irrespective of orientation, distance or position. This could imply that detection of small asymmetries could be masked, as varying orientation or skew will most likely introduce a certain degree of perceptual asymmetry (cf. Wagemans *et al.* 1991, 1992). However, Enquist & Arak's model does show some sensitivity to small asymmetries, i.e. of the order of magnitude observed in biological traits that display fluctuating asymmetry. There has been some debate in the literature as to whether the artificial selection regime employed by Enquist & Arak influenced the preference for gross symmetry that they observed and that their model does not actually generate or maintain complex symmetry (Cook 1995; Dawkins & Guilford 1995; Bullock & Cliff 1997). The neural network model proposed by Johnstone (1994) employed a training regime in which trait averageness and symmetry co-varied so that the most average traits were also the most symmetrical. As Johnstone notes, the strongest response was elicited by the most average of all signals presented, which were also the most symmetrical (see below). To further highlight the importance of trait averageness, Johnstone also demonstrated that symmetrical traits further from the population mean size were not preferred.

Osorio (1996) has proposed that his model of symmetry detection by categorization of relative phases of spatial harmonics predicts that there should be an intrinsic preference for symmetrical images, as symmetry increases the proportion of axial points detected by the visual system. Osorio suggests that this relationship could be interpreted as somewhat similar to asymmetry creating a 'blurring' or 'kinking' of a physical line. Hence, it is possible that symmetry preferences are hard-wired into the visual system as a by-product of other visual functions: in this case as a by-product of edge and line detection by spatial phase. Enquist & Arak (1994) also suggest that the visual system has become hard-wired for symmetry preferences, perhaps as a result of experiencing a high frequency of symmetrical objects in nature, although this may be a difficult evolutionary hypothesis to test.

Swaddle & Cuthill (1994*b*), Johnstone (1994) and Enquist & Johnstone (1997) have proposed that symmetry preferences might have evolved because symmetry is the 'average' signal expression in traits that display fluctuating asymmetry. As fluctuating asymmetry shows a normal distribution centred around zero, symmetry must be the most common and average signal. The specific mechanism they proposed was that of 'prototyping', which can be viewed as a form of generalization procedure. It is thought that humans form a mental prototype that is an average (or summation) of previous signals against which they compare a novel signal. Several studies have indicated that these prototypical representations are preferred over more extreme signals (Strauss 1979; Bomba & Siqueland 1983; Younger 1985; Quinn & Eimas 1986; Younger & Gotlieb 1988; Langlois & Roggman 1990). As prototypes for traits that show fluctuating asymmetry will be symmetrical, it could be predicted that symmetrical (average) signals should be preferred. There is also evidence from the comparative psychology literature that this form of generalization procedure occurs in pigeons (e.g. Kalish & Guttman 1957; Blough 1969) and some insect species, e.g. *Drosophila melanogaster* (Dill & Heisenberg 1995). Therefore, as symmetry should always be the average and most common signal in traits that display fluctuating asymmetry, a preference for symmetry could arise through established psychological processes. It has subsequently been demonstrated that this form of mechanism can give rise to a preference for symmetry in an artificial simulation (Enquist & Johnstone 1997). Additionally, this process of template storage involves cortical activity and so may operate independently of any lower-level symmetry preference mechanism.

Overall, symmetry preferences could have developed independently of an association with fitness parameters, although little is known about preferences for perfect symmetry over small asymmetries. The models discussed above may only explain (in part) the evolution of a gross preference for symmetry and hence the evolution of symmetrical signals. Their contribution to the apparent preference for symmetry over minor asymmetry requires further theoretical and empirical investigation. In light of this, I think it is relevant that Julesz (1971) showed that slightly imperfect symmetrical (i.e. mildly asymmetrical) patterns of dots are preferred over arrangements that have exact mathematical symmetry. To the naked eye, the preferred dot arrangements still appear symmetrical; their degree of asymmetry is very subtle but detectable enough to render these patterns more attractive. The perceptual processing of subtle asymmetries of the order found in traits that display fluctuating asymmetry may not fall within traditional categories of symmetry perception and may differ greatly among taxa depending on the perceptual thresholds for asymmetry discrimination.

8. CONCLUSIONS

Compared with our knowledge of the human visual system, we know relatively little about symmetry perception in non-human animals. We also do not know whether the discrimination of small asymmetries from perfect symmetry employs similar perceptual processes as detection of symmetry *per se*. For example, Palmer & Hemenway (1978) showed that discriminating perfect symmetry from patterns with slight asymmetry took 24 s, which is much longer than studies report for the perception of symmetry itself. This implies there is some additional processing or cognitive element involved when discriminating a small asymmetry. Asymmetry discrimination may be more complicated than the failure to find symmetry and may involve some aspects of mental storage and pattern matching (cf. Swaddle & Cuthill 1994*b*; Enquist & Johnstone 1997).

Perhaps the most pressing area to which our attention should be focused is that of perceptual thresholds and accuracy of asymmetry discrimination. In traits where asymmetry is too small, i.e. in traits with a high degree of developmental stability, asymmetry signalling simply is not viable. But we do not know what is too small unless we get a more accurate estimate of the perceptual thresholds in operation. The data collected so far indicate that birds may have asymmetry detection abilities on a par with (or perhaps slightly better than) that of humans. So it may be useful for researchers to use the figures I have highlighted in this review as a first indicator of whether asymmetry signalling is viable in their study system. If most of the population of trait asymmetry scores falls below a nominative 2% relative asymmetry threshold, direct visual signalling by fluctuating asymmetry is not likely to occur.

The accuracy with which animals can detect and respond to asymmetry is also a fundamental area that needs to be explored further. As the asymmetries are commonly small and the variation among individuals may be difficult to perceive, the frequency of errors of perception may have a great influence on the evolution and signalling tactics of the signaller. Extraneous factors not directly involved with the phenotypic expression of the signal, such as orientation, skew or lighting, may also influence asymmetry discrimination and introduce significant levels of misinterpretation and perceptual error.

The preceding review of factors that may influence symmetry perception also raises the general question of whether we are measuring the correct 'perceptual currency' when assessing the asymmetry of signalling traits. For example, we do not know that two-dimensional length of the outer tail feathers of a barn swallow is the only important asymmetry measure that comprises that particular signal. There may be other differences in feather breadth, shape, orientation and angle that may also be important elements of the signal. Therefore, we should explore different, more perceptually relevant currencies of asymmetry (e.g. Zabrodsky & Algom 1996) when applying asymmetry-signalling theory to evolutionary and ecological questions. This issue may be particularly important when assessing the asymmetry of complex traits such as coloration patches.

In summary, I hope to have brought attention to the complexity of asymmetry signalling and made useful suggestions as to what factors of a potential signal may influence the perception of asymmetry. This may help researchers to focus their efforts on systems where asymmetry signalling is more probable and illustrate that asymmetry cannot be a universal signal if asymmetry values are too small to be perceived. There are certain features of a trait that can enhance (or amplify) asymmetry discriminatory performance and hence should be favoured by sexual selection if asymmetry signalling occurs. These include (i) vertical orientation of the plane of symmetry (in higher vertebrate species); (ii) close proximity of left and right elements to the mid-line of the body (i.e. the axis of symmetry); (iii) composition of elements within a trait to form geometrical lines and shapes; and (iv) homogeneity of trait contrast and colour. A thorough empirical test of these predictions is needed before the generality of asymmetry signalling can be fully assessed.

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