

Several alternative explanations exist for the occurrence of symmetrical signals and symmetry preferences in nature. It has been suggested that some morphological symmetries arise inevitably from developmental processes<sup>24</sup>. However, as Wallace<sup>25</sup> observed, the symmetrical body markings of wild animals are often lost or degraded in their domesticated descendants. This suggests that certain symmetries are not inescapable consequences of development, but are maintained by other selection pressures in nature.

Preferences for symmetry observed in animals might reflect symmetries in the pattern of connection between nerve cells in the brain. Such preferences may also arise because many objects in the world that animals should distinguish are themselves symmetrical (see Fig. 4). However, whether symmetry is common enough in nature to make this important as a general explanation for symmetry preference remains unclear. Finally, it has been suggested that preferences for symmetry may have evolved for adaptive reasons connected with mate choice<sup>1,10</sup>. Recent experiments on birds and insects have shown that females prefer to mate with males possessing the most symmetrical sexual ornaments<sup>1-3</sup>. Because deviations from perfect symmetry are negatively correlated with fitness in some species<sup>9</sup>, the degree of symmetry in ornaments may provide females with information about male quality. But evidence that the amount of symmetry in ornaments provides females with information does not prove that preferences for symmetry evolved for that reason. Because such preferences emerge as a by-product of selection for recognition, any benefits that females gain by mating with symmetrical males may be best considered a fortuitous effect of sensory bias.

What implications, if any, do these findings have for aesthetics? Both humans<sup>6-8</sup>, and certain other species<sup>4,5</sup>, find symmetrical patterns attractive in contexts unrelated to signalling. Such general preferences for symmetry serve no obvious function, but may result from the universal need among organisms to recognize objects irrespective of the manner in which they are encountered in the outside world. Our results suggest that in the process of learning to recognize objects, preferences can develop for particular forms that have no objective existence in nature. Such hidden preferences<sup>20</sup> are revealed only when the actual forms corresponding to them appear in nature, either through biological evolution or artistic innovation. □

## Female preference for symmetrical males as a by-product of selection for mate recognition

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**FLUCTUATING asymmetry (FA) refers to the random, stress-induced deviations from perfect symmetry that develop during the growth of bilaterally symmetrical traits<sup>1,2</sup>. Individual differences in the level of FA may influence mate choice<sup>3</sup>: in a number of species, females prefer to mate with males that have more symmetrical sexual ornaments<sup>4-7</sup>. As the degree of FA has been shown to reflect the ability of individuals to cope with a wide variety of environmental stresses<sup>2,8,9</sup>, it has been suggested that mating preferences for symmetry evolve for adaptive reasons, because the degree of FA provides honest information about male quality<sup>10,11</sup>. Here I use simple, artificial neural networks to show that such preferences are likely to arise in the absence of any link between symmetry and quality, as a by-product of selection for mate recognition.**

Female preferences for symmetrical male displays have been demonstrated in a number of species, including swallows<sup>4,5</sup>, zebra finches<sup>6</sup> and earwigs<sup>7</sup>. These preferences have commonly been explained by reference to the honest advertisement hypothesis or handicap principle<sup>12</sup>. Many sexual ornaments are thought to be expensive to produce, and are under strong directional selection. Both of these factors lead to stresses that reduce the effectiveness of developmental homeostatic mechanisms. Consequently, the level of FA in male secondary sexual traits may provide females with honest information about the developmental competence of a potential mate<sup>3,10,11</sup>. In support of this suggestion, there is evidence that the level of FA in some species is heritable and/or negatively correlated with one or more fitness measures such as viability, fecundity, and growth rate<sup>2,8,9,13,14</sup>. However, evidence that FA currently provides females with useful information regarding male quality does not prove that preferences for symmetry initially evolved for that reason.

Here I test the hypothesis that preferences for low levels of FA in males may evolve in the absence of any link between symmetry and quality, as a by-product of selection for mate recognition. I investigate the evolution of symmetry biases by examining the properties of simple, artificial neural networks trained (by a process of artificial selection) to recognize a set of patterns that exhibit varying degrees of FA. Such networks, when used in the study of sexual selection and signal evolution<sup>5,16</sup>, provide a way to examine general properties of recognition systems.

A network, representing the recognition system of a female bird, was 'trained' by artificial selection to recognize a suite of images representing a bilaterally symmetrical tail that exhibits varying degrees of FA (Fig. 1). This involved repeated mutation of the network to generate variants that differed slightly in their response to different patterns, and selection of those variants that tended to respond more strongly to the images in the training set than to random patterns. The training process thus simulates the effects of selection for mate recognition, in that it favours the ability to distinguish a specific (bilaterally symmetrical) display from other stimuli. Two different sets of training images were used: the first comprised all five of the patterns shown in Fig. 1, and the second comprised only patterns 1, 2, 4 and 5. Networks trained using the first set were thus exposed to the perfectly symmetrical tail pattern 3 during the selection procedure, whereas networks trained using the second set were not. Neither of the two training procedures gave any explicit

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advantage to network variants that favoured symmetrical over asymmetrical tail patterns. For each individual network, mutation and selection were repeated 50 times, leading to a gradual increase in the ability to distinguish tail patterns from random patterns.

To investigate whether selection for recognition gave rise to preferences for low levels of FA, I compared the response of networks to the five different tail patterns both before and after selection. If the recognition system represented by the networks was unbiased with respect to symmetry, it was predicted that each of the five tail patterns would be preferred with equal probability. Figure 2 shows the proportion of 1,000 networks that preferred each pattern (that is, responded more strongly to that pattern than to any other) at the start and at the end of training with the full set and with the partial set of tail patterns. After the first selection step, networks were no more likely to prefer one pattern than another ( $\chi^2=2.78$ , d.f.=4,  $P=0.5949$  for the full training set;  $\chi^2=0.51$ , d.f.=4,  $P=0.9728$  for the partial set). After the full selection procedure (involving 50 selection steps) had been carried out, however, the networks' preferences differed significantly from random ( $\chi^2=138.1$ , d.f.=4,  $P=0.0001$  for the full training set;  $\chi^2=156.36$ , d.f.=4,  $P=0.0001$  for the partial set), with more symmetrical tail patterns favoured over less symmetrical patterns. The perfectly symmetrical image 3 was the most frequently preferred, even by networks that had been trained using the partial set of tail patterns, and had not therefore been exposed to pattern 3 during training. The preference for symmetry in tail patterns did not, however, extend to symmetry in other images; investigation of the networks' responses to randomly generated patterns not included in either training set frequently revealed hidden preferences for asymmetrical shapes.

To examine the interaction between preferences for symmetry and preferences for greater elaboration of ornaments, I compared the networks' responses to a large set of tail patterns that were similar to those in the training set but which differed in length as well as symmetry. Figure 3 shows which of these patterns were favoured over others for networks trained using the full set of images shown in Fig. 1, and reveals that the training procedure gave rise to preferences for longer tails as well as more symmetrical tails. Differences in length between two tail patterns

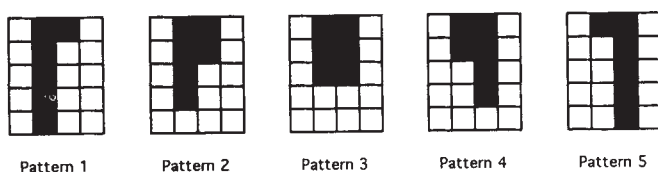


FIG. 1 Set of five tail patterns used to train networks. The neural networks themselves consist of three layers of cells: a 'retina' of  $4 \times 5$  receptor cells, five hidden cells and one output cell. Each cell in a layer connects to all cells in the next layer, and each connection is associated with a weight (ranging from  $-1$  to  $+1$ ), which regulates the strength of the signal passing between the two cells. When a network is presented with a pattern, each receptor cell receives an input of either 0 or 1. The output from these cells is equal to the input. The input to each of the hidden cells and to the output cell is a weighted sum of the outputs from all cells in the previous layer; the output from these cells is a sigmoid function of the input, specifically  $(1 + \tanh(i/2))/2$ , where  $i$  denotes the input. Networks were trained to discriminate between random images and either the full set of five tail patterns shown here, or a partial set comprising only patterns 1, 2, 4 and 5. Note that the number of receptor cells on the retina stimulated by each tail pattern is equal, so that any differences in the response to each are not due to differences in the overall amount of stimulation. Random patterns were also generated in such a way that while each receptor cell on the retina was equally likely to be stimulated by the pattern, the mean overall amount of stimulation was equal to that provided by these tail patterns. Furthermore, they were generated so that their mean level of symmetry was identical to that of the set of tail patterns.

could thus, on occasion, outweigh the effects of a difference in symmetry. For example, tail patterns with a mean length of three pixels that exhibited a low level of asymmetry were preferred to a perfectly symmetrical tail pattern with a mean length of two pixels ( $\chi^2=89.08$ , d.f.=1,  $P=0.0001$  and  $\chi^2=158.61$ , d.f.=1,  $P=0.0001$ , for the two comparisons involved). A larger difference in the level of FA, however, outweighed the effects of the bias towards greater length; a symmetrical tail pattern with a mean length of two was preferred to tail pattern with a mean length of three pixels that exhibited a high level of asymmetry ( $\chi^2=46.13$ , d.f.=1,  $P=0.0001$ , and  $\chi^2=21.78$ , d.f.=1,  $P=0.0001$  for the two comparisons involved). Although the preference for longer tails, like the preference for symmetry, extended to patterns not included in the training set, it was not open-ended. Comparing the networks' responses to symmetrical tails of different sizes, tail patterns with a mean length greater than three pixels (the length of the training images) were preferred

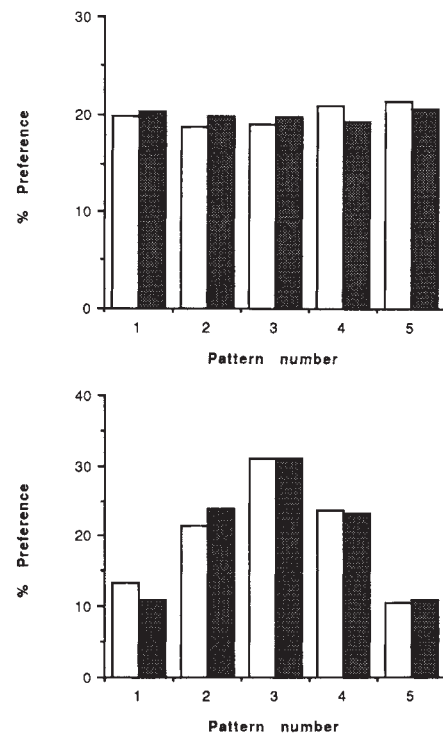


FIG. 2 Consequences of selection for recognition ability on preferences for symmetry. The selection procedure was as follows: starting with an original population of five networks each defined by a randomly generated set of weights, a new population was generated by selecting one member of the old, and replacing the other four with variants of this chosen network. The variants were created by a mutation procedure in which, with a probability of 0.05, each weight was replaced with a new, random value (evenly distributed between 0 and 1). The network chosen for replication was selected as follows: each member of the original population was scored by determining the mean value of its response to the patterns in the training set, and the mean value of its response to a set of randomly generated patterns, and subtracting the latter value from the former. The network with the highest score was then chosen. This process of mutation and selection was repeated 50 times. The selection procedure thus favoured those networks that responded more strongly to tail patterns than to random patterns (equivalent results were obtained when the selection procedure favoured networks that responded more strongly to tail patterns than to a single random pattern generated at the start of the training procedure). The graph shows the proportion of 1,000 networks that preferred each tail pattern (that is, responded more strongly to that tail pattern than to the other tail patterns) after the first selection step (top) and after the last (bottom), for both the full and partial training sets (open and shaded bars, respectively).

to shorter patterns, but a tail of mean length four was preferred to one of mean length five ( $\chi^2 = 58.98$ , d.f. = 1,  $P = 0.0001$ ).

The selection procedure probably gave rise to preferences for symmetrical tail patterns because such patterns are closer to the average of the training stimuli used. In both the full and partial training sets, the asymmetrical patterns formed mirror-reflecting pairs. As a result, the average of the training patterns, shown in Fig. 4, was itself symmetrical. Selection for recognition of the training set thus gave rise to preferences for tail patterns close to this symmetrical average. Symmetrical images that were randomly generated were not necessarily preferred, because they could diverge substantially from the average of the training stimuli.

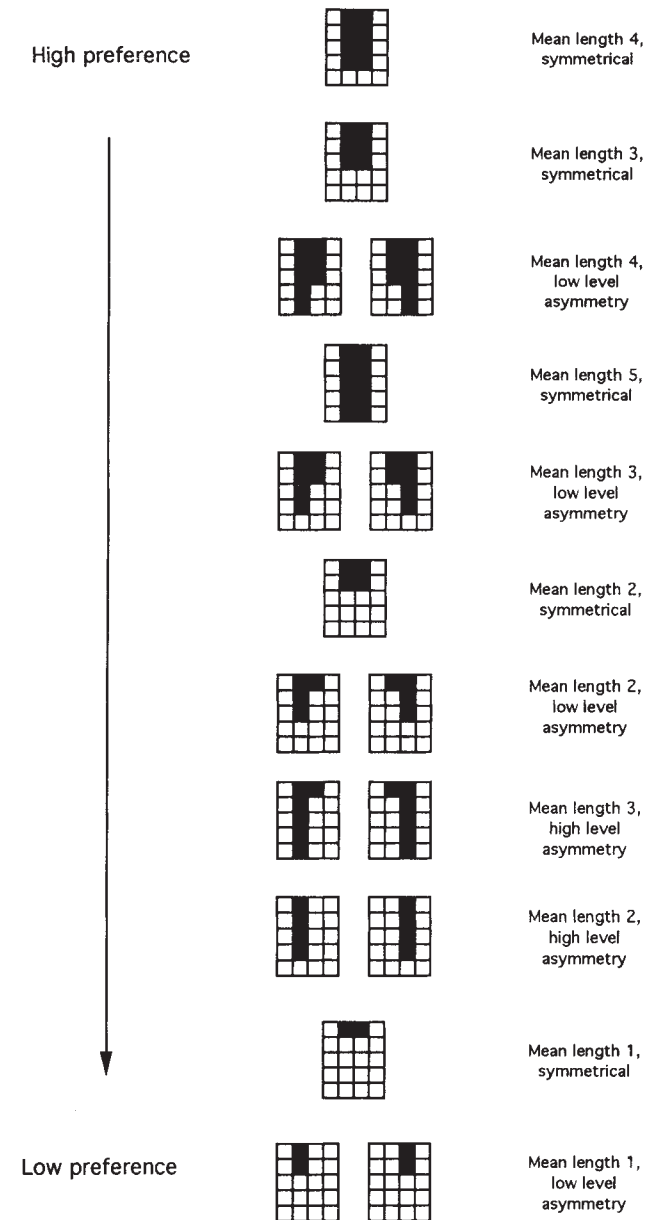


FIG. 3 Hierarchy of preference among tail patterns that vary in both length and symmetry, for networks trained using the full set of five patterns shown in Fig. 1. In a 2-way comparison, the proportion of networks that preferred any given pattern to another from the same or higher rank in the hierarchy is never significantly greater than expected by chance ( $P < 0.05$ ). At the same time, there was a significant preference for any given pattern over at least one image from each lower rank in the hierarchy.

Preferences for longer tails probably evolved because long tail patterns overlap more of the training set average. Although all the training images comprised six filled pixels in total, and thus had a mean length of three pixels, the maximum length of the asymmetrical tail patterns was greater (Fig. 1), because asymmetry involves an increase in length of one side of the tail. As a result, the average of the training patterns, shown in Fig. 4, extends beyond the mean length of three pixels to the maximum length of the most asymmetrical training patterns. Selection thus gave rise to preferences for tails of greater than normal length, which overlap more of this average. The preference was not, however, open-ended, probably because the networks tended to penalize joint filling of pixels on either side of the midline in the bottom two rows of the pattern (an occurrence that was never reinforced by the training stimuli).

Paired ornaments in nature, such as swallows' tails and earwigs' forceps, exhibit symmetrical variability just as the training stimuli did (FA being defined as deviations from symmetry that are random with respect to side, and whose population average is therefore nil). Consequently, symmetrical ornaments are closer to the population average display. The above results thus indicate that when males of a species possess paired ornaments, selection for female recognition of appropriate mates can lead to biases favouring symmetrical males. Preferences for males with low levels of FA can therefore evolve even if there is no relationship between symmetry and mate quality, and no advantage to be gained by obtaining a symmetrical partner. Moreover, such preferences may extend to a degree of symmetry that females rarely or never encounter in natural populations.

Proponents of the 'sensory exploitation' hypothesis<sup>15-21</sup> have argued that female preferences for elaborate male displays may

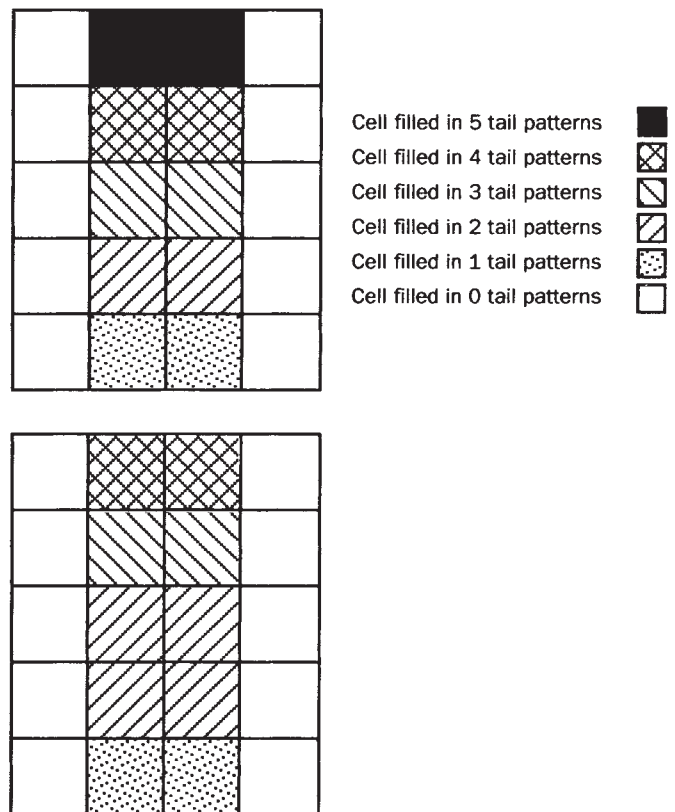


FIG. 4 Average of the training stimuli. In the case of both the full (top) and the partial (bottom) training sets, this average is symmetrical, and closer to the perfectly symmetrical tail pattern 3 than to any other tail pattern in the training set. It also extends beyond the mean length of the individual training stimuli.



often evolve for non-adaptive reasons, as a by-product of selection for other aspects of female perceptual abilities. Enquist and Arak<sup>15</sup>, for example, have demonstrated that such preferences can evolve as a by-product of selection for mate recognition. Similar explanations for symmetry biases have not, however,

been advanced. The present model shows that the sensory exploitation hypothesis is equally applicable to preferences for low levels of FA as to preferences for ornament elaboration, and that in species with bilaterally symmetrical displays, both types of preference are likely to evolve together. □

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## Cell interaction between compartments establishes the proximal–distal axis of *Drosophila* legs

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THE appendage primordia of *Drosophila* are subdivided into compartments<sup>1–4</sup> by the localized expression of transcription factors<sup>5–7</sup>. Interaction between cells in adjacent compartments establishes organizing centres responsible for generating spatial pattern and promoting cell proliferation in the developing appendages<sup>7–9</sup>. Localized expression of *hedgehog* (*hh*) in the posterior compartment of the leg imaginal disc directs expression of *wingless* (*wg*) in ventral–anterior cells and *decapentaplegic* (*dpp*) in dorsal–anterior cells near the anterior–posterior compartment boundary<sup>8</sup>; *wg* then acts to specify ventral cell fate<sup>10–12</sup> and to organize the dorsal–ventral axis of the leg<sup>13,14</sup>. Interaction between

*wg*-expressing ventral cells and dorsal cells near the anterior–posterior compartment boundary promotes axis formation in the leg<sup>14,15</sup>. Here we show that the combined action of *wg*-expressing cells in the ventral–anterior compartment and *dpp*-expressing cells in the dorsal–anterior compartment activates expression of *Distal-less*, a gene required for proximal–distal axis formation in the limbs. These results demonstrate that sequential interaction between anterior–posterior and dorsal–ventral compartments establishes the proximal–distal axis of the limbs.

Limb development in *Drosophila* requires the activity of the homeobox gene *Distal-less* (*Dll*; refs 16–19). The limbs develop from imaginal discs, specialized groups of epithelial cells which are recruited in the embryo and grow during larval development to organize the pattern of the adult appendages. Genetic studies have shown that *Dll* activity is required in the imaginal discs to promote formation of the limbs<sup>16–20</sup>. Figure 1 shows the pattern of *Dll* protein expression at three stages of development of the leg disc. In second instar and early third instar discs, *Dll* is expressed in a subset of cells in the centre of the disc epithelium (Fig. 1a). To accommodate growth during third instar, the central region of the disc epithelium adopts a highly folded arrangement. *Dll* is expressed in the central folds of the mature leg disc (Fig. 1b, c). Fate mapping studies have shown that the central folds correspond to the distal leg segments<sup>21</sup>. In the early pupal leg disc it is apparent that the domain of *Dll* expression corresponds to the distal tibia and tarsal segments of the leg (Fig.

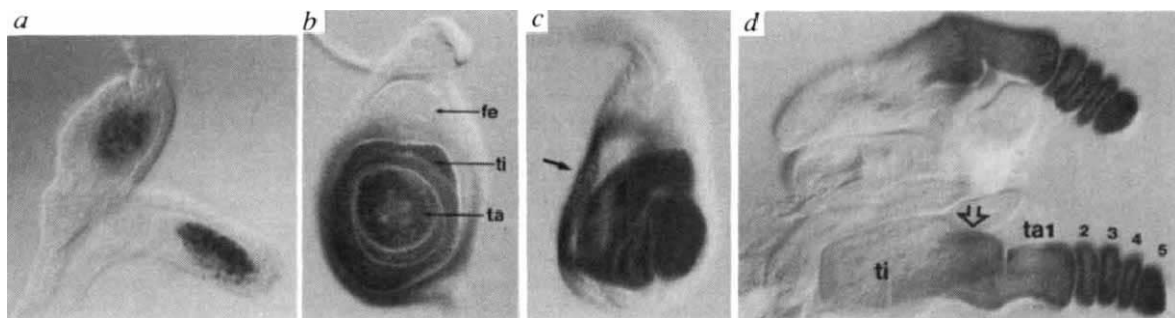


FIG. 1 *Distal-less* expression in the leg imaginal disc. a, *Dll* protein is expressed in a small group of cells in the central region of a late second instar leg disc, where the disc forms a thickened pseudostratified epithelium (visible in the lateral view). b, c, Frontal and lateral views of *Dll* expression in mature third instar leg discs. *Dll* is expressed in a central domain of the disc, corresponding to the presumptive distal segments of the leg (abbreviations: ta, tarsal segments; ti, tibia; fe, femur). In the frontal view (b), the deep folding of the disc epithelium produces a ring-like appearance to the staining. In the lateral view

(c) it is apparent that the central core of the disc constitutes a single contiguous domain of *Dll* expression. A secondary non-contiguous ring of *Dll* expression arises in the proximal femur in mid-third instar discs (arrow). The function of this domain is not known. d, *Dll* expression in everted pupal foreleg discs. The central domain corresponds to the tarsal segments (ta 1–5) and the distal part of the tibia (open arrow). METHODS. *Dll* protein was visualized in imaginal disks using antibody raised in mouse<sup>28</sup>, as described in ref. 7.