# Selection of exaggerated male traits by female aesthetic senses

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**DARWIN[1] suggested that many apparently deleterious secondary sexual characters in males, such as bright colours, elaborate ornaments and conspicuous displays, evolved as a result of female choice. Darwin never tried to explain the crucial agent of selection, that females have preferences for exaggerated male traits. Rather, he took it for granted that females of many species possess a 'sense of the beautiful', akin to the aesthetic sense in humans. The question of why such preferences evolve remains a controversial issue[2,3]. Here we report that mechanisms concerned with signal recognition possess inevitable biases in response that act as important agents of selection on signal form. The existence of such biases may be sufficient to explain the evolution of exaggerated male secondary sexual traits, and elaborate signals in general.**

To understand the evolution of exaggerated traits and conspicuous displays used by males to attract females it is first necessary to explain why females prefer such traits. In line with modern thinking in evolutionary biology, recent attempts to explain female choice focus on selection and adaptive behaviour. The problem of how females recognize conspecific males is often ignored because recognition is usually assumed to be perfect and without biases.

All but the simplest of recognition systems are unlikely to be perfect. Taking the visual system as an example, perfect recognition implies that an animal unerringly reacts to all images of the correct object (or class of objects) and never reacts to all other, inappropriate images. But a recognition mechanism can only be expected to react appropriately to those images it has been selected to identify. One cannot predict with certainty how an animal will react to new images it experiences. Many will have no effect, but because there is an almost infinite number of possible images that the retina may experience, it is expected that some of these will elicit a greater response than the particular signals to which the system has been selected to respond.

Of particular interest are stimuli that are similar to those the animal has been selected (or trained) to respond to because they may be affected by generalization. Generalization is a common property of recognition systems that involves classifying novel variations of stimuli into particular categories that the organism has experienced before. Such a property is necessary because variation in orientation, distance, light conditions and backgrounds can give rise to millions of possible images of a given object on the retina. A recognition system cannot be pre-programmed or trained to identify each such image separately.

To explore the role of the recognition in the evolution of signals, we have studied some examples of recognition mechanisms based on artificial neural networks[4,5]. Even the most simple artificial networks, consisting of a few interconnected cells, exhibit many of the properties shown by animal recognition systems: they are easily trained to classify objects and perform generalizations. Such networks provide convenient tools for uncovering general principles of recognition free from much of the complexity found in the nervous systems of real organisms.

A problem was first presented to a network representing the recognition system of a female bird (see Fig. 1 for details). The problem was for the female to recognize males of her own species in the presence of a similar sympatric species using simple visual cues. Males of the two species were identical in all respects except that conspecific males had slightly longer tails than heterospecifics.

The network was 'trained' by a procedure that mimics the process of natural selection of recognition systems that occurs over evolutionary time. The network quickly evolved the ability to distinguish images of conspecific males from heterospecific males and random patterns. Moreover, there was no single evolutionarily stable mechanism of recognition; instead it was found that many different networks, that is, combinations of connection weights, could achieve the recognition task with virtually no errors (only two examples are illustrated in Fig. 2). When the networks' reactions to new stimuli were investigated it was apparent that most stimulus patterns were not effective in eliciting a courtship response. But some stimuli were supernormal[6] (they elicited stronger responses than any of the training stimuli). Some of these stimuli bore no resemblance to the training stimuli (Fig. 2*e*), whereas others (Fig. 2*a*, *b*, *c*) appeared to be exaggerated forms of the conspecific male (longer tails, more tails and so on), illustrating the phenomenon of peak

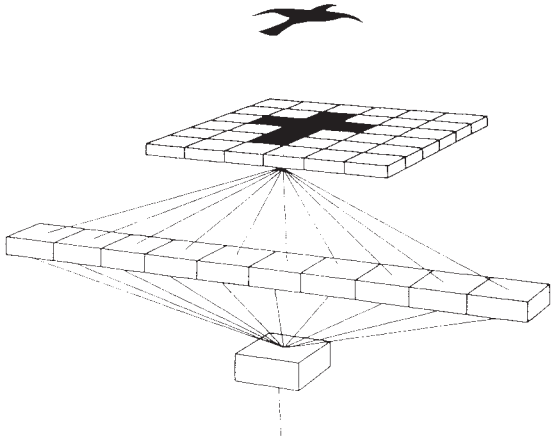


FIG. 1 A simple artificial neural network is shown which consists of a retina 6×6 receptor cells, 10 hidden cells and one output cell. Each cell in one layer connects to all cells in the next layer and to each connection a weight is associated that regulates the strength of the signal passing between cells (For clarity, only those connections originating from one of the receptor cells are illustrated). When the network is stimulated each of the receptor cells receives an input of zero or one. The output from these cells equals the input. The input to all other cells, that is cells in the hidden layer and the output cell, is a weighted sum of the output from all cells in the previous layer. The output from a hidden cell or an output cell is a sigmoid function of its net input. The network was said to recognize a subset of patterns if these patterns gave rise to an activity (output) in the output cell that was greater than a certain threshold, whereas all other patterns that occur give rise to activities below this threshold. By presenting patterns to the retina, the network can evolve the ability to discriminate between two or more groups of images. Starting with some (random) vector of connection weights, a new network was first created by mutating some of the weights. The probability of mutation for a particular connection weight was 0.1 and when a mutation occurred, an increment drawn from a normal distribution ($\sigma$ = 0.1–0.4) was added to the weight. The performance of the new network in the recognition task was then compared with the original one and the best retained. This iteration continued until the probability of an incorrect decision by the network was less than $10^{-5}$. A courtship reaction to an image was assumed to occur when the sum of external (stimulus) and internal (motivational factors reached the threshold value of 0.5. The internal factor was assumed to vary independently of the external factor and to be normally distributed with $\mu = 0$ and $\sigma = 0.02$.

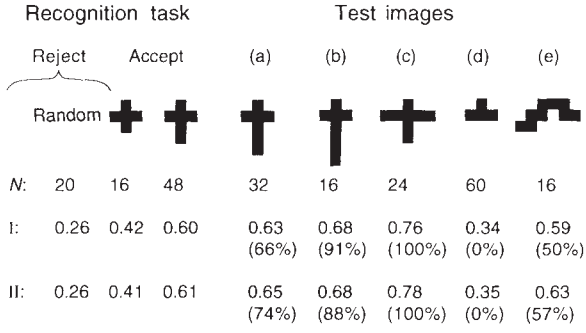
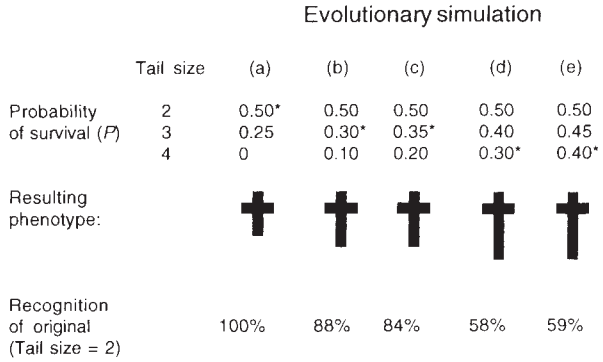



FIG. 2 The network was trained to discriminate long-tailed birds (conspecifics) from short-tailed birds (heterospecifics) and random images. The images were projected onto the retinal array in numerous positions and rotations, the total number of projections of each image type denoted by *N*. The average response to each image type after training is shown below each image for two examples of different networks (I and II) each capable of solving the recognition task. The threshold value for a courtship response is 0.5. After training, novel 'test' images are projected onto the grid and the response of the network measured. The network shows the strongest response to bird-like images with even longer tails (*a*, *b*) or longer wings (*c*) than it has been trained to recognize, but it does not react to images of birds without tails (*d*). Some fairly abstract patterns (such as *e*) also elicit a supernormal response. The figures in parentheses show the percentage of presentations of each image type that gave rise to a higher response than the image of the conspecific male.

FIG. 3 Results of a simulation in which both male tail length and the female recognition system coevolve. It was assumed that selection favours those males that elicit the strongest courtship response in females, and those females that make the fewest mistakes in choosing the correct species. In the first step of the simulation, the trained network was presented with images of 'mutant' conspecific males with various tail lengths, and the first image that elicited the strongest courtship response was selected. In the second step, the network was allowed to mutate until it discriminated between the selected males and heterospecifics with fewer errors than before. The evolutionary process was studied by repeated iteration of this procedure. The image eliciting the highest response after 100 iterations depends on the survival cost associated with increases in tail size. Longer tails evolve when there is only a weak effect of tail size on survival. As male tail length increases, females become less efficient at recognizing males with the original tail size as conspecifics. * Survival of selected form after 100 steps of simulation. Fitness = $P \times$ mating success.




shift[7]. Images of males without tails (Fig. 2 *d*) gave a weaker response than males with short tails (heterospecifics), suggesting that generalization occurs in both directions. This proves that the recognition mechanism itself exerts selection pressure on the signal; in this case, there is a 'bias' in the mechanism favouring males with longer tails.

We investigated the consequences of this bias in an evolutionary simulation by allowing both male tail length and female recognition system to change by mutation. In general, the simulation resulted in the evolution of longer tails in males, alongside a decrease in female responsiveness to conspecific males with the original tail length (Fig. 3). Exaggeration occurs even in cases when increasing tail size decreases the survival of males, but the extent of exaggeration is inversely related to survival cost. These results confirm Darwin's view[1] that traits that give an advantage in mating can evolve to such extremes that they decrease male survival. The model also demonstrates that female preference for extreme male traits can evolve simply as a consequence of the need for females to recognize males of their own species, not to discriminate between them.

It is well known that sense organs often show biases in their response to signals along certain dimensions. It follows that such biases could act as important agents of selection on the form of signals. Indeed, a few recent studies[8-11] present convincing evidence that biases in the sensory apparatus of females towards certain signals may have existed before the appearance of the same signals among males. But the question of why such biases exist has been largely ignored. Our models suggest that biases in response to signals inevitably exist as a fundamental consequence of the context in which recognition occurs. Because the number of forms that a signal can take is almost infinite, the recognition mechanism is always likely to show a greater response to some variants of the male signal not yet in existence. Such unexpressed, or 'hidden', female preferences will change continuously as a side effect of selection for improved recognition, by genetic drift (many solutions exist for a given recognition problem) and because of correlated effects[12] of selection acting on male signals. Moreover, because biases may occur simultaneously along several dimensions of the signal, selection on the recognition mechanism in one dimension may result in many dimensions of bias. Because female preferences and male traits used in signalling are very unlikely to be at equilibrium they can be expected to appear and disappear at a greater rate than would be the case for other aspects of morphology and behaviour. Although the form of male courtship signals will typically evolve away from all other stimuli that the female regularly experiences, the precise course that evolution takes will be highly unpredictable. This instability may explain the great diversity in the form of signals observed in courtship behaviour, even within single species.

Finally, the process of exaggeration described here is not confined to signals used for mate attraction; it applies with equal force to all contexts of signalling, including interspecific communication (such as warning colouration), and may offer a general explanation for the elaboration of signals that occurs during the process of ritualization[13]. It is an interesting thought that all nervous systems built for recognition may share certain general biases which result from hidden properties of the recognition system. Indeed, many elaborate signals that occur in nature are often as impressive to human observers as they appear to be to the intended recipient. Darwin's idea that a 'sense of the beautiful' is an inherent, aesthetic property of animal nervous

systems may be not far from the truth. In Darwin's own words 'When we behold a male bird elaborately displaying his graceful plumes or splendid colours . . . it is impossible to doubt that [the female] admires the beauty of her male partner'[1]. □

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# Involvement of an orthologue of the *Drosophila* pair-rule gene *hairy* in segment formation of the short germ-band embryo of *Tribolium* (Coleoptera)

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**THE segments in long germ-band insect embryos, like *Drosophila*, are all determined at syncytial blastoderm stage. This is in contrast to short germ-band embryos which show an early determination of only the anterior head segments, whereas the more posterior thoracic and abdominal segments are sequentially added after formation of a primary germ anlage (reviewed in ref. 1). Segment formation in *Drosophila* involves the pair-rule genes which define double segmental periodicities[2,3] and which have been considered to represent a special adaptation to the long germ-band type development[4,5]. *hairy* belongs to the primary pair-rule genes in *Drosophila* which are directly regulated by the gap genes, such as *Krüppel*[6–13]. We have isolated the orthologues of *hairy* and *Krüppel* from the flour beetle *Tribolium castaneum* which has a short germ type development[14]. We show here that *hairy* is expressed in several stripes at blastoderm stage and later on in two stripes in the growth zone of the developing embryo. *Krüppel* expression overlaps *hairy* stripe three and four expression, very similar to *Drosophila*. This suggests that the segment patterning mechanism that acts in an open blastoderm in *Drosophila* works in a similar way in the cellularized *Tribolium* embryo.**

To understand the potential role of pair-rule genes in short germ-band embryos, we cloned the orthologues of *Krüppel* and *hairy* from the flour beetle *Tribolium*. *Krüppel* codes for a zinc-finger protein of the $Cys_2$-$His_2$ type[15]. We have previously developed rules for the generation of polymerase chain reaction (PCR) primers to clone these type of genes[16], allowing us to obtain *Krüppel* othologues from a variety of arthropods, including *Tribolium*[16]. *hairy* codes for a transcription factor with a helix–loop–helix motif[17] allowing the design of PCR primers within conserved portions of this domain (Fig. 1). An orthologous *hairy* fragment was obtained in this way and used to clone the respective genomic region from a library[18] (Fig. 1).

Embryogenesis in *Tribolium* starts with the formation of a syncytial blastoderm (Fig. 2*a*, *b*), similar to *Drosophila*. But instead of proceeding directly with the formation of the segments, as would be typical for long germ-band embryos like *Drosophila*, it forms first a germ anlage (Fig. 2*c*, *d*). This germ anlage includes the gnathal segments and a growth zone from which the remaining segments are formed (see legend to Fig. 2*e*, *f*).

The expression pattern of *Krüppel* and *hairy* in *Tribolium* was analysed by whole-mount *in situ* hybridization[19]. The first expression of *hairy* is seen at early blastoderm stage (Fig. 3*a*) in two circumferential stripes. These stripes move towards posterior (Fig. 3*b*) and lose their dorsal expression, but remain ventrally expressed in the region of the germ rudiment (Fig. 3*c*). A new expression domain of *hairy*, formally the third stripe, forms now at the posterior end of the embryo (Fig. 3*b*, *c*). In *Drosophila*, the third and the fourth *hairy* stripes lie within the region of the *Krüppel* expression domain[10,11]. Analysis of *Krüppel* expression at this stage indicates that the same is true for *Tribolium*. The first expression of *Krüppel* is seen at the posterior end, preceeding the expression of *hairy* in the same region (Fig. 3*d*). As shown in Fig. 2, the amnion folds in this region and grows towards the anterior. At the same time, cell proliferation occurs at the posterior end of the germ rudiment. The effect of these separate growth and cell movement processes is that the cells which were at the posterior end at blastoderm stage will become part of the central region of the early germ band, where

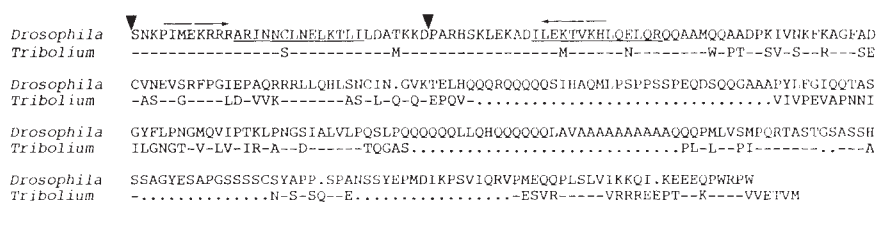


FIG. 1 Protein sequence comparison (single-letter amino-acid code) between the *hairy* orthologues from *Drosophila* and *Tribolium*. Dashes denote identities, dots denote insertions/deletions. The positions of the introns in both species are denoted by arrowheads, the helix regions of the helix–loop–helix motif are underlined and the arrows indicate the positions of the PCR primers. The *Drosophila* sequence (numbering according to ref. 17) starts with codon 33 (position 1,611), directly after the first intron. The *Tribolium* sequence is derived from a genomic clone and shows an intron at the same position, the first exon of *hairy* in *Tribolium* could not yet be identified. *Drosophila* shows another intron after codon 65 which is also present in *Tribolium* (531 base pairs long). The sequence comparison shows that not only the helix–loop–helix motif is conserved, but also several additional regions within the coding region, suggesting that a true orthologue was obtained. There is, in contrast, a clear divergence in the regions of high cryptic simplicity[24], for example the glutamine and alanine stretches, which has similarly been noted in interspecific comparisons between other genes[24,25].

METHODS. A fragment of *hairy* from *Tribolium* was amplified by PCR[26] using the following primers CCTATIATGGAGAA(A,G)(C,A)G(A,C,G,T)(A,C)G and ATGCTTGAC(A,G)GTCTT(C,T)TC(A,C,G,T)A (corresponding to positions 1,621–1,640 and 1,905–1,886 in the *Drosophila* sequence, ref. 17) and cloned into an M13 vector as described[16]. The fragment was then used to screen a genomic library of *Tribolium*[18] and the sequence of the coding region was obtained. The fragment used for the *in situ* hybridization experiments included the whole region shown, apart of the first four and the last 20 amino acids.