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Hidden preferences and the evolution of signals

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SUMMARY

Mechanisms concerned with the recognition of biological signals act as important agents of selection on the appearance or 'form' of signals. Recognition of a given signal form can be achieved by many equally efficient alternative mechanisms. These alternative mechanisms will be selectively neutral and subject to change by genetic drift, thus preventing the fixation of a signal form that is optimal in releasing the receiver's behaviour. Because signal form is a multidimensional trait with an almost infinite potential to vary, it is expected that some novel forms of signals always exist that elicit responses more readily than any of those signals that the receiver has experienced during its evolutionary history. The existence of such 'hidden preferences' is illustrated in simple models of recognition mechanisms based on artificial neural networks. The fundamental evolutionary instability of recognition mechanisms perhaps explains why biological signals are so variable in form, and why, in experiments, animals sometimes show greater responses to novel forms of signals than they do to familiar forms.

1. INTRODUCTION

A striking feature of many animal signals is their conspicuousness. Darwin (1871) was quick to appreciate that a problem exists in attempting to explain how such signals have evolved; conspicuous signals often involve considerable costs of production as well as attracting the attention of predators. Perhaps because Darwin viewed sexual selection as a special type of selection occurring at the time of mating, biologists have continued to place most emphasis on signals used in the context of courtship, such as the elaborate plumage of the birds of paradise, the peacock's tail, the songs of birds and the croaks of frogs.

However, it is apparent that courtship behaviour cannot claim a monopoly on striking signals. For example, aggressive interactions between animals often involve dramatic displays and colour changes. Signals used in communication between prey and predator may appear in the form of brilliant warning colours and eye-catching displays. The gaudy appearance of many flowers and fruits that attract the attention of pollinators or seed dispersers provide further examples of highly conspicuous signals. The widespread existence of elaborate signals in nature begs the question of whether there is a general theory that can be applied with equal force to all contexts in which such striking signals have evolved.

A recurring explanation in the literature for the evolution of conspicuous signals is that perceptual systems have inherent biases and respond strongly to exaggerated forms of certain stimuli. Darwin (1871), in his discussion of sexual selection, clearly recognized that if such biases exist in the nervous system of females they would undoubtedly give rise to elaborate traits in males because, as he put it, 'the males which were the handsomest or the most attractive in any manner to the females would pair oftenest, and would leave rather more offspring than other males'. Nowhere, however, did Darwin attempt to explain why such preferences arise, beyond suggesting that, in common with man, animals also possess a 'sense of the beautiful'.

The psychological effects of signals on the receiver's nervous system were also much discussed by many ethologists of the 1940s and 1950s in their analyses of immediate causation and the 'ritualization' of behaviour (summarized by Hinde (1970); receiver psychology discussed recently by Guilford & Dawkins (1991)). Comparative studies (see Huxley 1966) were carried out to show how behaviour patterns used as signals have changed during evolution, usually in such a way as to make behaviour more conspicuous or distinctive (i.e. ritualized). Evolution towards greater conspicuousness was partly explained as a result of selection acting on signals to increase their efficiency as 'releasers' of action patterns in the receiver.

More recent thinking about signal evolution has led to the conclusion that if perceptual biases exist in the receiver, selection will inevitably act on signal form in the direction of the bias (Staddon 1975; Basolo 1990; Ryan *et al.* 1990, Ryan 1991). In several theoretical models of signal evolution such biases are the central mechanism leading to the exaggeration of signals. In particular, some models of sexual selection (e.g. O'Donald 1977), assume that female preferences for more extreme forms of male display characters become established because such characters act as 'supernormal stimuli' to the female. Similarly, in

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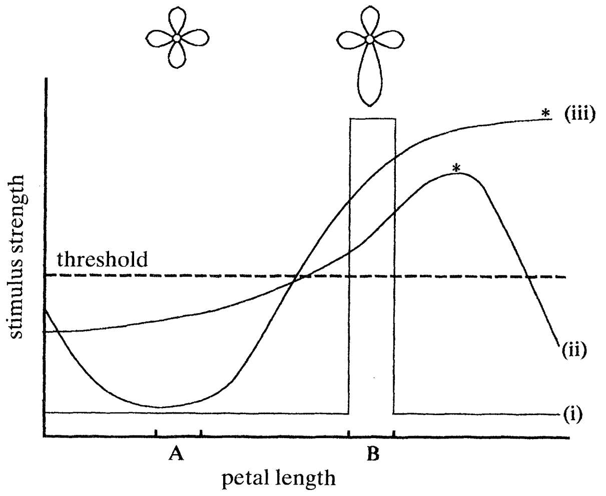


Figure 1. The level of stimulation in the hypothetical recognition cell of an insect elicited by two species of flowers which have anterior petals of different length. Only flowers of species B are assumed to be profitable for the insect to visit. Recognition is achieved and the insect visits a flower when the stimulation is above a certain threshold (dashed line). Curve (i) represents the case of perfect recognition of profitable flowers; curves (ii) and (iii) are examples of alternative recognition functions that lead to the same consequences for the insect. Curves (ii) and (iii) show, however, that hidden preferences exist (*) for flowers with more extreme petal lengths than those that exist in nature.

models of the evolution of warning coloration (Leimar *et al.* 1986), brighter colours evolve because predators that experience a distasteful prey type subsequently show stronger avoidance of more extreme forms of prey (i.e. more brightly coloured) than those previously encountered. The mechanism invoked here is the phenomenon known in learning theory as 'peak shift' (Hanson 1959).

An important omission in all these arguments, however, is the fundamental question of why such biases exist? Could the existence of such biases provide the explanation for the evolution of elaborate signals in general? These questions are explored below.

2. WHY BIASES?

It is common to find in discussions of signal evolution an idealistic view about the performance of recognition systems in animals. A frequent assumption implicit in many models is that recognition is perfect, that is the animal unerringly responds in an adaptive way to all appropriate stimuli and does not respond to all inappropriate ones.

However, in reality, perfect recognition systems will never evolve. This is because there are many more possible stimuli that may impinge on the animal's sense organs than the species is ever likely to have experienced during its evolutionary history. Modification of the recognition mechanism in the receiver has occurred only as a result of selection acting on its responses to the relatively small number of stimuli that the species has encountered. Therefore, it is impossible to predict, prior to conducting an experiment, how an animal will react when presented with a totally novel stimulus.

This conclusion has important consequences for the evolution of animal signalling systems as can be shown by the simple example illustrated in figure 1. Consider the appearance of flowers, which are signals evolved by plants to attract insects that pollinate them. Assume for the moment that there are only two species of flowers in the world, A and B; flowers of species A have short symmetrical petals whereas flowers of B are distinguished by the presence of an elongated anterior petal which forms a tongue-like lobe projecting from the corolla. Now suppose that only flowers of species B have sufficient levels of nectar to make them profitable to visit for a certain species of insect pollinator. The insect discriminates between the two species of flowers on the basis of the length of the anterior petal alone. To do this the insect's recognition mechanism reacts to all signals (i.e. anterior petal lengths) that give rise to a stimulation strength in a hypothetical recognition cell that exceeds a certain threshold and does not react to all signals which elicit stimulation below this threshold.

The function (i) in figure 1 represents an idealized situation in which perfect recognition is assumed. The insect always reacts to flowers with anterior petal lengths within the range of species B (by visiting them), but never reacts to flowers with petals outside the size range of B, including unprofitable flowers of species A. However, there is no reason that the particular function (i) should evolve. Selection will not exert any pressure on the shape of the recognition function outside the naturally occurring range of petal lengths. Given that only flowers of species A and B exist, there are many other functions, e.g. (ii) and (iii), that would prove to be equally efficient at discriminating between profitable and unprofitable flowers. There is no reason why evolution should maintain any one particular mechanism of recognition from the infinite variety of selectively neutral alternatives. In fact one might expect there to be continual changes in the shape of the recognition function due to genetic drift.

It is easy to see that this lack of stability of the recognition mechanism means that the exact form that the flowers take is also not stable over evolutionary time. If the recognition function resembles curve (ii) or curve (iii), for example, then flowers with even longer anterior petals will invade the population if they should arise by mutation. In effect, there is a 'hidden preference' for even longer petals, which is not expressed until a mutation arises. The preference is said to be 'hidden' as long as it remains 'untested' by natural selection.

The preceding example is, of course, a gross oversimplication of reality. In nature, many species of flowers exist, exhibiting great variation in petal length, shape, colour, scent and many other cues that insects may use to discriminate between profitable and unprofitable species. It is likely, therefore, that an insect's recognition mechanism has been shaped, not just by the need to distinguish two species of flowers,

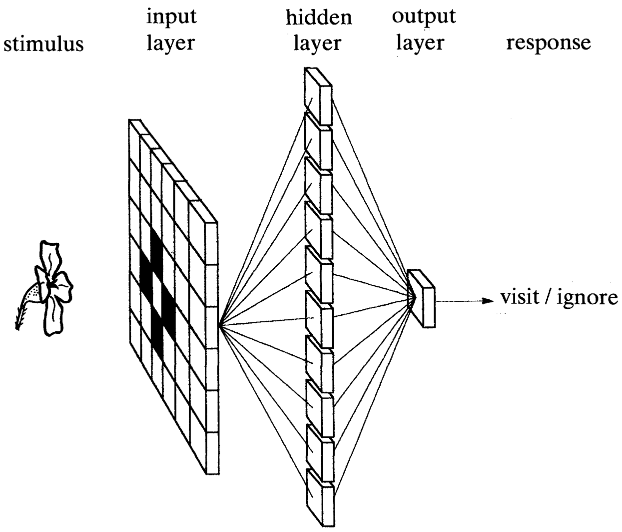


Figure 2. An artificial neural network representing the flower-recognition system of an insect. Connections lead from each cell in a given layer to all cells in the next layer to the right, but for clarity only those connections originating from one of the input cells are illustrated. By presenting patterns to the artificial retina (six × six grid of input cells) and adjusting the connection weights between cells, the network acquires the ability to discriminate between different patterns (images of flowers). Connection weights are adjusted by random mutation followed by natural selection of networks based on their performance in the discrimination task. For further explanation, refer to text.

but by the need to recognize many, and recognition of profitable flower species by insects probably depends on several dimensions of the signal occurring simultaneously in the correct configuration. However, these complications do not invalidate the general point that there is no selection on the recognition mechanism outside the naturally occurring range of flower forms experienced by the insect. Consequently, there is always the potential for novel forms of flower to arise which prove to be even more attractive to the insect than any of the familiar, profitable species.

To express this idea in more general terms, the interaction that occurs between a signaller and receiver is considered as an evolutionary game in which the signalling role tries to elicit a certain response from the receiver, and the receiving role is faced with the problem of correctly reacting to the signalling role when present in the environment. In any game of this type, a number of appearances a are available to the signalling role and a number of recognition-decision strategies r to the receiving role. An evolutionarily stable strategy, or ESS (Maynard Smith 1982), for such a game would consist of a stable equilibrium pair of strategies (a^*,r^*), where a^* is the best reply to r^* and vice versa (this ensures equilibrium). For the equilibrium pair of strategies to be stable we require in addition that if the population deviates slightly from the equilibrium then selection would return it to (a^*,r^*).

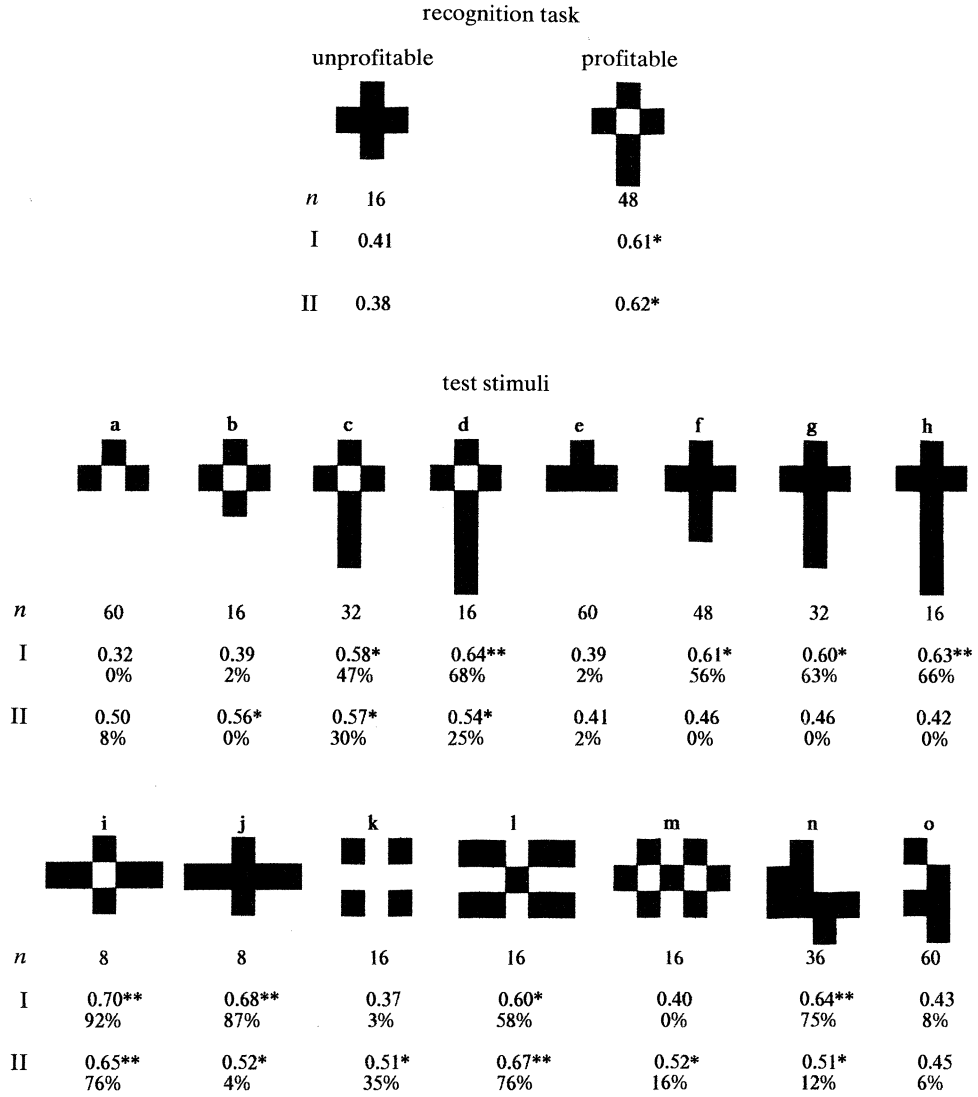
If the sets of signalling strategies and recognition-decision strategies are restricted in number such a game may have an ESS. However, in reality, the recognition of any appearance a may be achieved by many different mechanisms r_i, r_{ii} . . . r_n and there is no obvious way of reducing the number of such strategies for the purpose of evolutionary modelling. This means that an equilibrium pair (a^*,r^*) will not be stable since there are no forces that will maintain r^* from among all those r that correctly reacts to a^*. Consequently, r^* may be replaced by drift, and it follows that if the strategy space for signals is large enough a^* will no longer be the best reply to the receiver's new recognition strategy. Thus, the signal will become subject to directional selection and will change in appearance.

How close to the optimal signal (a^*) any particular appearance (a) will be, depends among other things on the rate at which the recognition-decision strategy (r) changes and the rate at which new appearances (arising by mutation) are tested by natural selection. It also critically depends on the size of the strategy space of a. In biologically realistic strategy sets, signals vary along many different dimensions and the number of possible appearances is almost infinite. For evolution to 'find' the best possible signal to use against a given recognition strategy at a given time, requires that all possible signals are tested. Clearly, it is not feasible that all possibilities can be tested within a reasonable period of evolutionary time. Moreover, the appearance of a new signal form in a population is itself likely to have selective consequences on the receiver's recognition mechanism causing further changes in its response properties. It follows that the signals which we observe animals using at any particular time will never be the 'best' possible signals to utilize and hidden preferences will always exist.

3. A MODEL OF RECOGNITION

To gain further insights into the evolution of signal form we examine below the properties of a simple model of a recognition system. The type of model used is known as an 'artificial neural network'; such networks have already found extensive applications in the field of artificial intelligence research (Caudill & Butler 1990; Eberhart & Dobbins 1990) and human psychology (e.g. Bechtel & Abrahamsen 1991). Artificial neural networks, although superficially similar to real nervous systems in their architecture, are not intended to simulate any actual biological recognition system. They are merely employed here to illustrate some principles that may be general to both artificial and biological recognition systems. Do such model systems possess 'hidden' preferences? If so, what are the likely consequences of such preferences on the evolution of signal form?

A simple artificial neural network is shown in figure 2. The network consists of a retina of six × six receptor cells, ten 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. When the network is stimulated each of the receptor cells receives input between zero and one (in the example



	unprofitable	profitable
n	16	48
I	0.41	0.61*
II	0.38	0.62*

	a	b	c	d	e	f	g	h
n	60	16	32	16	60	48	32	16
I	0.32 0%	0.39 2%	0.58* 47%	0.64** 68%	0.39 2%	0.61* 56%	0.60* 63%	0.63** 66%
II	0.50 8%	0.56* 0%	0.57* 30%	0.54* 25%	0.41 2%	0.46 0%	0.46 0%	0.42 0%

	i	j	k	l	m	n	o
n	8	8	16	16	16	36	60
I	0.70** 92%	0.68** 87%	0.37 3%	0.60* 58%	0.40 0%	0.64** 75%	0.43 8%
II	0.65** 76%	0.52* 4%	0.51* 35%	0.67** 76%	0.52* 16%	0.51* 12%	0.45 6%

Figure 3. First, a network is selected by an evolutionary process to discriminate between patterns representing symmetrical flowers (unprofitable) and patterns representing flowers with displaced anterior petals (profitable). The patterns are projected onto the artificial retina shown in figure 2 in numerous different positions and rotations (the total number denoted *n*). Below each pattern is shown the average output it elicits after repeated episodes of selection on two different networks (I and II). After selection, profitable flowers elicit an output which is above threshold (greater than 0.5), whereas unprofitable flowers elicit an output below threshold. Novel patterns (test stimuli) are then projected onto the retina and the response of the network is measured. Average output values are shown below each pattern and the percentage of projections of each pattern type that gave rise to a stronger output in the network than the profitable flower type (i.e. percentage of projections that act as 'supernormal stimuli'). For both networks, some novel patterns elicit, on average, a higher output than the profitable flowers that the networks were initially selected to recognize. *, Average response to a pattern is above threshold for a visiting response by insect. **, Average response to a pattern greater than average response elicited by a profitable flower.

which follows there are only two possible input states, 0 or 1). The output from the receptor cells equals the input. The input to all other cells, i.e. 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 is said to recognize a subset of patterns if these patterns gave rise to an activity (output) in the output cell that is greater than a certain threshold, while all other patterns that occur give rise to activities below this threshold.

In the example illustrated, the network represents the recognition system of a hypothetical insect species faced with the problem of discriminating between flowers which differ in profitability. The 'insect' was trained to discriminate between two patterns presented to its artificial retina (figure 3: recognition task), the first representing a symmetrical species of flower (unprofitable), and the second representing a species with long anterior petals (profitable). To control for the effect of overall amount of stimulation, the number of receptor cells on the retina stimulated by each of the two patterns was equal. Each pattern was projected onto the retina in numerous positions and rotations, to simulate a natural situation in which the insect may approach flowers from any direction. The insect was assumed to visit a flower when the sum of the external factor (i.e. activity in the output cell caused by the stimulus) plus the internal factor (motivational variable) reached a 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 $\sigma = 0.02$.

The network was trained by a process which is analogous to modification of the recognition mechanism that occurs over evolutionary time. Starting with some (random) vector of connection weights, each flower pattern was projected onto the retina and the activity in the output cell measured. A new network was then created by mutating some of the connection 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 (mean = 0, $\sigma = 0.1$–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 (i.e. the one in which the number of responses above threshold to profitable flowers plus number of responses below threshold to unprofitable flowers was greater). This iteration continued until the probability of an incorrect decision by the network was less than 10^{-5}.

The average output of the network to each of the two patterns after selection is shown in figure 3 (recognition task), for two examples of networks (I and II) which differ with respect to their connection weights both before and after selection. It is apparent that both of these networks evolved the ability to solve the recognition task with virtually no errors (many other networks exist that can achieve the task just as well).

After selecting the networks to solve this simple task, a series of novel patterns (test stimuli) were then projected onto the retina and the response of the output cell measured. In general, all networks tested showed a stronger response to certain patterns that they had never before experienced than to the patterns of profitable flowers that they were initially selected to react to. For network I, flower-like patterns with even longer petals (d,h,i,j) are 'supernormal', i.e. on average they elicit a higher visiting response than even the profitable flower pattern. Flower patterns with short petals (b) or with petals missing (a,e) cause the weakest response. For network II, a high contrast between the centre of the flower and petals seems, in retrospect, to be the main cue that is preferred: patterns i and l are supernormal, whereas patterns e, f, g and h all cause below threshold output in the network. Thus, both networks show hidden preferences, but the form that these preferences take differs between the networks.

It is interesting that some apparently random patterns which do not at all resemble flowers to human observers also act as supernormal stimuli to certain networks (e.g. pattern n elicits a high output in network I). Thus, irrespective of our own judgements, these networks classify such images as belonging to the category of profitable flower types. The number of random patterns that act as supernormal stimuli can be reduced if a variety of such patterns are included in the initial training phase and the networks are selected not to respond to them. However, this does not affect the general conclusion that in all biologically realistic situations some hidden preferences always exist. Only if the network is initially trained using all possible input patterns as examplars can a perfect recognition system evolve, but this is only feasible when using a very small artificial retina and by restricting the stimulus in each receptor cell to a small number of possible states (e.g. two states, 0 or 1, as in our example).

The results of this modelling exercise support our initial prediction that recognition systems are not evolutionarily stable and hidden preferences (biases) always exist. In the examples illustrated, there is bias in the mechanism favouring novel flowers with longer anterior petals (network I) or flowers with high contrast between the centre and the petals (network II).

DISCUSSION

In this paper we offer an evolutionary explanation for the existence of perceptual bias in animal recognition systems. Our explanation is centred on two fundamental premises. First, recognition of the form (or appearance) of a given stimulus can be achieved by many alternative mechanisms, and secondly, the number of possible forms of any stimulus is almost infinite. It follows, that there will always exist some novel stimuli which elicit stronger responses in the receiver than all those stimuli that the animal regularly experiences. Because biases in the recognition mechanism will evolve unseen (they will not be apparent to an observer until the animal is confronted with new stimuli), we refer to such biases as 'hidden preferences'.

Our theoretical expectation of hidden preferences is borne out, not only by the behaviour of the model recognition system which we have investigated here, but also by many empirical studies of the behaviour of real animals. The existence of 'supernormal stimuli' is well known from ethological studies on the causation of behaviour (e.g. Tinbergen 1948). Such stimuli, which elicit a much stronger response in animals than even the most effective natural stimuli, are found in many species and in many different circumstances (e.g. courtship display, incubation behaviour, feeding and aggressive behaviour) suggesting that perceptual bias is a general feature of recognition systems irrespective of behavioural context (e.g. Magnus 1958; Hailman 1967; Andersson 1982; Burley *et al.* 1982).

A phenomenon similar to the supernormal stimulus effect also appears when animals are trained to discriminate between stimuli which differ along a single dimension. If animals are rewarded when they respond to one stimulus and punished when they respond to another, their peak responsiveness after training is usually displaced along the stimulus dimension beyond the point at which they received a reward and in a direction away from the negative stimulus ('peak shift' *sensu* Hanson 1959; Mackintosh 1974).

Supernormal stimulus effects and peak shift may have a common explanation at the mechanistic level (Hogan *et al.* 1975), and have been interpreted elsewhere as a consequence of asymmetry in selection pressures (supernormality), or rewards (peak shift) along the dimension of the stimulus (Staddon 1975). When the multidimensional aspects of stimuli are considered, it is clear that the receiver, during its evolutionary history, cannot have been exposed to all possible variations in the form of any given stimulus; hence selection pressure will be asymmetrical along at least some, if not many, dimensions along which stimuli may potentially vary. It seems inevitable, therefore, that recognition systems will possess biases and that these biases may exist simultaneously in several different dimensions of stimulus.

Biases in recognition mechanisms are expected to have important consequences for the evolution of biological signals. We suggest that there will always exist an enormous potential for signallers to 'explore' the perceptual landscape of the receiver over evolutionary time. When a new form of signal arises by mutation which happens to coincide with one of the receiver's biases, it may rapidly spread to fixation in the population of signallers because of its superior effectiveness in eliciting the required response from the receiver. Over longer periods of time, selection will act on signals and tend to exaggerate them in the direction of the bias.

We have elsewhere (Enquist & Arak 1993) simulated this evolutionary process using artificial neural networks as model recognition systems. In these simulations, both the signals (i.e. patterns presented to the network) and the receivers's recognition mechanism (i.e. the network itself) are allowed to change by mutation prior to each episode of selection. The results obtained illustrate several important features of the process of coevolution of signalling and recognition strategies. First, signals that evolve always become more exaggerated than required merely for correct recognition. Second, exaggeration of signals occurs even if it involves costs for the signaller, but the extent of exaggeration is inversely related to the magnitude of such costs. Third, as signals become increasingly exaggerated there is a simultaneous decrease in the responsiveness of the receiver to signals of the original, non-exaggerated form. Finally, although the precise form of signals that evolve cannot be predicted *a priori*, selection tends to favour signals which are increasingly dissimilar in form from those signals to which a response would normally result in decreased fitness for the receiver.

In practice, it will be a formidable task for biologists to attempt to track the course that evolution has taken with respect to changes in the appearance of signals. Because recognition mechanisms are inherently unstable, traits used as signals are expected to change more rapidly during evolution than many other kinds of trait. Recent studies using the methods of phylogenetic analysis in conjunction with field studies of preference have demonstrated, in a few instances, that preferences for exaggerated signals may have existed in receivers long before the evolution of the signals themselves (Basolo 1990, 1991; Ryan *et al.* 1990; Ryan 1991; Proctor 1992). These studies perhaps offer the most convincing evidence to date that pre-existing perceptual biases in the receiver have played an important role in the evolution of signal form.

We are not suggesting that bias in the nervous system of receivers is the only factor leading to the evolution of conspicuous signals. An alternative, though not mutually exclusive, hypothesis is that conspicuousness has evolved in order to increase the probability that signals are detected by the receiver. Although there is clear evidence that properties of the transmission channel influence the form of signals that evolve in different environments (see Gerhardt (1983) for a review), the need to detect signals cannot be a sufficient explanation for conspicuousness in general. Many signals appear to be much more exaggerated than would be required merely for detection. For example, in the courtship behaviour of many species, elaborate and highly conspicuous signals are given at close range when detection by the opposite sex has already been achieved. Similarly, the loud, incessant begging calls of young nestlings, combined with a visual display of the bright colours of the gape are given only at close range, once the parent bird has arrived at the nest. In these examples (and many others), detection can be ruled out as an explanation for conspicuousness; it seems more probable that such signals have been favoured by selection because they are more likely to trigger the appropriate response in the receiver than would less exaggerated forms of the same signal.

We conclude that the mechanism that receivers use to recognize signals plays a central role in the evolution of signal form. Such mechanisms are unlikely to act as precisely-tuned filters which reject all 'inappropriate' signals, but will instead possess biases in response that cause them to accept certain novel signal forms. Certainly, it will be impossible to explain all aspects of signal form without reference to such biases. To many biologists accustomed to thinking in terms of the adaptive function of biological traits, we suspect that this conclusion will be somewhat surprising. Nevertheless, we believe the general tendency of many biological signals to evolve towards greater conspicuousness and complexity, can be partly explained as the outcome of what is essentially a non-adaptive phenomenon: the existence of hidden preferences in animal recognition systems.

It is perhaps inevitable that we should end such a discussion by returning to the most striking feature of animal signals, namely, the enormous variation and complexity of signal forms which led Darwin to postulate that animals share with humans a 'sense of the beautiful'. Since the nervous system of humans is not fundamentally different in a physiological sense from that of animals, it may be more than mere coincidence that we find attractive many of the signals which are obviously impressive to the animal receiver: the beautiful plumage of birds, the bright colours of butterflies and flowers, the complex songs of birds and whales to name but a few examples. We venture to suggest that fundamental properties of the context in which signals and recognition mechanisms coevolve, may explain not only many general features of the form of biological signals, but also some aspects of human aesthetic response towards them as well.

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