Some General Comments on the Evolution and Design of Animal Communication Systems

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SUMMARY

Animal communication systems have evolved so that individuals can make decisions based upon the behaviour, physiology or morphology of others. Receiving mechanisms probably evolve to increase the efficiency and reliability of information reception whereas signals probably evolve to increase the efficiency of communication and reliability of manipulation of the receiving individual to the benefit of the emitter. The minimum requirement for clear reception suggests that any study of the evolution and design of communication systems must consider the factors that affect the quality of the received and processed signal. Critical information is needed about how the signal is generated and emitted, how it fares during transmission through air, water or substrate, how it is received and processed by the receiver's sensory and cognitive systems, and the factors which affect the fitness consequences of alternative ways of reacting to the information contained in the signal. These should allow predictions about the kinds and forms of signals used by animals signalling under known conditions. Phylogenetic history, and the geological time a clade spends in different signalling environments, will also affect signal evolution, and hence the success of predictions about signal design. We need to use methods of many different biological fields to understand the design and evolution of signals and signalling systems.

1. INTRODUCTION

Animal communication systems have evolved so that individuals can make decisions based upon the behaviour, physiology or morphology of others, through the use of signals. Signals are changes in the environment caused by one individual (the emitter) which can convey information to another (the receiver, figure 1). Receiving mechanisms probably evolve to increase the efficiency and reliability of information reception while signals probably evolve to increase the efficiency of communication and reliability of manipulation of the receiving individual to the benefit of the emitter. The interests of the emitter and receiver need not coincide, even within species (figure 1; Otte 1974; Dawkins & Krebs 1978; Guilford & Dawkins; Wagner 1992), but the reception of the signal must be clear enough to allow the receiver to make a behavioural or physiological decision. We can consider signals as consisting of two components, content and structure or design (figure 2), and these roughly correspond to the strategy and efficacy of a communication system (Guilford & Dawkins 1991).

The minimum requirement for clear reception suggests that any study of the evolution and design of communication systems must consider the factors which affect the quality of the received and processed signal. Critical information is needed about how the signal is generated and emitted, how it fares during transmission through air, water or substrate, how it is received and processed by the receiver's sensory and cognitive systems, and the factors that affect the fitness consequences of alternative ways of reacting to the information contained in the signal. Some of the factors that affect signals, and hence constrain or bias the direction of evolution of signals and signalling systems, are summarized in table 1. These should allow predictions about the kinds and forms of signals used by animals signalling under known conditions (Endler 1992).

2. SIGNAL GENERATION

The first step in signalling is to generate and emit the signal (table 1). The physics, biophysics and chemistry of producing signals can have strong effects on what sorts of signals that can be emitted. As a result it may be physically impossible, or energetically very costly, for signals to evolve in particular directions, yet relatively easy to evolve in other directions. There have been a number of interesting studies of the functional morphology of signal generation (Ewing 1989; Font & Rome 1990; Boppré & Vane-Wright 1989; Löfstedt, this symposium), but the evolutionary implications of signal emitter design have rarely been considered (Löfstedt, this symposium).

If it is possible but expensive to produce a signal, then the time, place, and age of signalling will be biased or constrained by trade-offs between present and future fitness. Such trade-offs have been relatively well-studied by life-history theorists, and there are some good examples from frog call energetics (Elmberg

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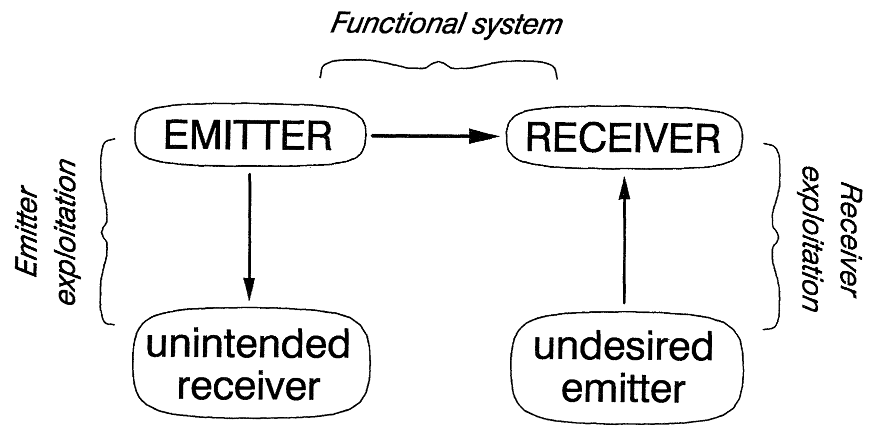

Figure 1. Basic elements of a communication system (after Otte 1974). The emitting individual generates the signal and transmits it to the receiver. An individual can be both an emitter and a receiver, and networks of emitters are found in species such as frogs and crickets. There are two forms of exploitation in which: (i) the emitter is taken advantage of by an unintended receiver (eavesdropping); and (ii) the receiver is 'fooled' by an undesirable emitter (for example, Batesian mimicry).

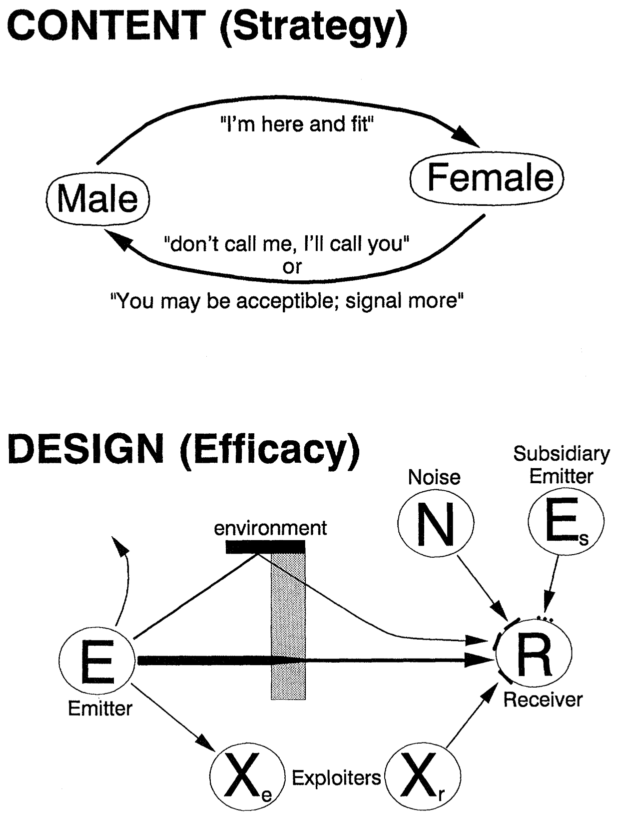

Figure 2. Basic components of the design of a signalling system. Mate choice is used as an example, but the principles apply to other signalling systems. The content of a signal is the information it contains about the signaller (whether true, misleading or false) and is effected by the evolution of communication strategies in the species of interest. The physical structure of the signal evolves to increase the efficacy of the transmission of the message between emitter and receiver. Emitters (E) should try to emit in the right direction, and during environmental conditions which minimize absorption, distortion and interference, and minimize reception by emitter exploiters (X_e) such as predators or signal-homing parasites. Receivers (R) should receive under the best conditions for reception, and avoid or filter out noise and competing signals from subsidiary emitters (E_s) and receiver exploiters (X_r) such as Batesian mimics or males with inferior genes.

& Lundberg 1991; Pough & Taigen 1990; Pough *et al.* 1992; Taigen & Wells 1985; Wells & Taigen 1989). There is also some evidence that singing can be very costly to birds (Reid 1987). Methods of reducing energy expenditure in signal emission can not only include the design of the emitting structures, but also singing behaviour. For example, it is possible that a varied repertoire in birds reduces fatigue, allowing singing for longer than if the same song elements were used; different song elements use different suites of muscles, so some can rest when the song elements change (Lambrechts & Dhondt 1988).

In addition to fitness or life-history trade-offs, timing, intensity, and form of signals can be affected by other environmental factors. For example, if a pheromone consists of components of different volatilities, the ratio of the emitted components would vary with temperature, so selection would favour emission at the temperature which yields the most stimulating component mix for the receiver. Spatial and temporal variation of predation, climatic and microenvironmental conditions favours signals which are emitted at the places, times and environmental conditions which maximize emission and transmission to the intended receivers and minimize transmission to exploiters (Endler 1991, 1992).

The direction of evolution of signal generation can be environmentally biased in another way. For example, some environmental factors do not directly affect the signals, but do affect the evolution of the breeding system. If this causes breeding to be limited to a small range of environmental conditions, then this will bias the evolution of signals and signalling behaviour to work better under those more specific conditions. For example, if breeding habitat is only available during brief times, as in desert frogs and toads (Sullivan 1989), then the specific environmental conditions at those times are the ones which generate evolutionary bias, rather than all conditions experienced during the animal's lifetime.

The strategic component of signalling can also bias the direction of evolution of the form and timing of emitted signals. There will be a trade-off between how

Table 1. *Factors affecting signals during communication, and therefore biasing the direction of evolution*
(There is no correspondence across rows in this table.)

signal generation and emission	transmission through the medium	signal reception and processing	decisions based on the perceived signal
biophysical limits to form and intensity	background noise	biophysical and biochemical limits to reception	other signals
	interfering signals		choice time wasted
energetic limits	attenuation	sensory adaptive state and attentiveness	reasons for choice
biochemical limits	blocking	need to be attentive	need for choice
energy storage	absorption	need for alerting signals	predator risk
timing and location: predation short season best place and time	reflection and refraction	short reception time	parasite risk
	distance	other signals	physiological state
environmental effects on emission	spectral properties	noise	quality of signal
information content versus clarity	temperature	jamming	quality of different signal components: purity value to receiver value to emitter
	self-interference	signal reception rate	
information density or rate	information density	information processing rate	
genetic variation	timing and location	pattern recognition needs	signal channel use

much information which can be encoded in a signal and how clear the information is when information content of a signal is near the upper limit set by noise and processing ability. For example, as the complexity of a frequency modulation increases the more difficult it may be to prevent the introduction of noise during the generation, emission, and transmission of the signal. A similar problem may arise if the information density or the rate of transmission is too high. An overly complex colour pattern may be difficult to produce and may not signal foraging ability or effective defenses (aposematism) as well as a simpler pattern (Guilford 1986, 1988). A high rate of transmission of sound, pheromones or motion, may be much more difficult to achieve than a lower rate, and the latter will be achieved with less added noise. In coevolutionary systems such as that of Müllerian and Batesian mimicry, the design of the signals of other species will also affect selection on the form of the signal (Endler 1988; Guilford 1988).

Finally, even if it is physically or chemically possible to produce a more effective signal in a given environment, there may not be enough genetic variation for the signal to evolve to its optimum form (Löfstedt, this symposium).

3. TRANSMISSION OF THE SIGNAL THROUGH AIR, WATER OR THE SUBSTRATE

The second step in communication is the transmission of the signal through the medium (table 1, figure 2). Signals should evolve to minimize the effects of background noise and interfering signals from other species. Selection also favours signals that experience less attenuation, blocking, absorption, reflection, refraction and other distorting effects of the transmission medium. Intensity falls off with distance, and it may fall off at different rates for different components of the signal (olfaction) or different carrier frequencies (vision, hearing, electroreception). Some of these distorting effects are temperature-dependent. If the same signal arrives at slightly different times from different parts of the medium (for example reverberation in sound, or reflections near the air–water interface), then a poorly designed signal can interfere with itself. All of these effects will be exacerbated if the signal has a high information density, or when information is transmitted at a high rate. A fair amount is known about the effects of the environment on the quality of transmitted signals (Ewing 1989; Endler 1992; Römer 1993; Römer & Lewald 1992), but the implications of signal distortion for the evolution of signal design are only just beginning to be considered (Endler 1992; Römer & Lewald 1992).

As in the case of signal emission, signalling behaviour can evolve to minimize environmental constraints on signal transmission by favouring signalling during times and places at which distortion and attenuation are minimized. Selection can not only work directly to minimize environmental effects, but also indirectly through selection on the place and time of communication. For example, predation or shortlived microenvironmental conditions may favour breeding under precise conditions which are limited enough to favour specific signals which transmit better during these times and places. It is possible that explosive breeders and microhabitat specialists may have on average more predictable signal design than more continuous breeders and microhabitat generalists.

4. SIGNAL RECEPTION AND PROCESSING

Once the signal reaches the receiver, it has to be received and processed (table 1). As in signal generation, there are biophysical, biochemical, and energetic limits to signal reception, and these will affect the evolution of both signals and receptor design (Endler 1992; Löfstedt, this symposium; Römer, this symposium; Ryan & Rand, this symposium).

A given receptor does not always transduce signals into neural outputs in the same way, and what can and cannot be received is dependent upon the current adaptive state of a given receptor. (This is not to be confused with evolutionary adaptation; physiological adaptation takes place on a scale of hours whereas evolutionary adoptation takes place over many generations.) For example, if an animal is in a microenvironment with high light intensity, its visual system will be light-adapted, and it will be less effective at distinguishing between darker than lighter colour pattern elements. But if it is in a dark microenvironment it will be dark-adapted, and less able to distinguish between lighter than between darker colour pattern elements. This can be important in species which live in vegetation where there is a great deal of spatial variation in light intensity. If the dark-adaptation is even greater, there will be no colour vision. Similarly, if a class of odours is common in an environment, it may be difficult to receive a pheromone or chiromone in the same class. Changing the time and place of signalling may allow a species to increase its sensitivity to conspecific signals, but reduce the ability of exploiters (figure 1) to utilize the signal. Of course there may be additional constraints. For example, if a shift in signal reception time or location causes a shift in the ambient temperature during reception, then this may change the ease of reception of olfactory signals.

Even if the sensory system is in an optimal state of adaptation for signal reception, the receiver may not pay any attention to the signal, perhaps because it is doing something else. For example, if a receiver is searching for predators or prey, it may not be attentive to conspecific signals. Attentiveness is a neglected but potentially important part of signal evolution (Guilford & Dawkins 1991). The need for attentiveness may evolve because the brains of species in a given clade can only process so much information at a time, or because there are significant fitness costs to being simultaneously but only partially attentive to a wide variety of different signals.

If the need for attentiveness is strong, then alerting signals will probably evolve. These signals serve only to attract the receiver's attention, so are subject to fewer constraints than the 'main' signal. Alerting signals are usually simpler in form, often of greater intensity, more rapid, and of shorter duration than the 'main' signal. Presumably this reflects the balance between getting the receiver's attention and avoiding attracting the attention of predators, parasites, or unintended conspecific receivers (such as rivals). But the significantly different form of alerting signals places an additional burden on the design of receivers and the brain in processing these signals, so both the alerting and 'main' signals may reflect a compromise in the signal and receptor design so that both function well.

Given that an emitter wants to minimize the reception of its signal by unintended receivers, it will probably only signal for brief times, and at specific times and places. If the time for signal reception is short, then there might not be enough time to receive the signal accurately, as a result of limits to attentiveness, rate-limiting mechanisms of reception, and speed of signal processing by the brain. This may bias the direction of evolution of both signals and signal receptors. The presence of other signals in the environment such as congeners, mimicking predators (as in fireflies), and even undesirable conspecifics, may favour the evolution of filters in the receptors to minimize interference during reception in the sensory channel. If ambient noise has reasonably predictable properties, then noise may also be filtered out, or behaviour may evolve to favour listening positions and times (as well as signalling times) which minimize the effects of background noise (Endler (1992) and references therein). Some species (for example, electric fish and some orthopterans) actively sing at the same frequencies and times as conspecifics in an effort to 'jam' and interfere with their signals, reducing the rival's potential reproductive success. No filtering can avoid this problem, but it may favour the evolution of receiver behaviour which can minimize the confusing effects of jamming.

For any given sensory system, there will be a physical upper limit to how fast a signal can be received, and owing to biophysical and biochemical limits in nerve transmission and synapse function, there will be limits to how fast a signal can be processed. So if there is a constraint on transmission time, but a lot of information needs to be transmitted, not all of it will be received or processed properly. This may favour the use of multiple channels or sensory modes, or favour the evolution of signal forms which are easier to receive and process quickly. For example, it may favour visual over auditory signals, or a mixture of both rather than only one.

One way to reduce the effects of noise in communication is to 'expect' a signal of a certain form, that is, have a filter which only lets the signal through, or a template which recognizes signals of a certain form. The simplest version of this is frequency tuning, as in amphibian auditory systems (see examples in Fuzessery (1988), Zakon & Wilczynski (1988)). Filters can be more complex, allowing only certain frequencies of sound, certain colours, or certain chemical signals to elicit a response by receptors.

On a still more complex level, pattern recognition may be a very important component of signal reception or decision-making (see, for example, Karplus & Algom (1981)). The mechanisms of pattern recognition may place severe restrictions on the kinds of signals which can be sent as well as the rate at which they can be sent, received, processed and recognized. Some signal forms and sensory modes may yield more evolutionary potential for diversification and bias than others, but this is essentially unexplored. Arak & Enquist's (1993, this symposium) neural network models of mate choice and recognition are fascinating examples of some of the phenomena which can arise in any system in which learning is important. If a system learns to recognize some signals, it will automatically have the ability to recognize other signals which do not necessarily exist in the population (Arak & Enquist 1993, this symposium). This could bias the direction of evolution of both signals and the recognition system in specific directions (Endler & McLellan 1988; Endler 1989, 1992; Basolo 1990; Arak & Enquist 1993, this symposium). The interesting and important thing about neural network models is that different lineages initially trained to recognize the same signals may by chance acquire templates which work for the same starting signals, but can recognize very different signals which are not present in any population. The result could be rapid divergence of signals and recognitions systems (Arak & Enquist 1993, this symposium). The ability to recognize unknown (or untrained) patterns could result in pre-existing biases or preferences for different and novel signal traits, and bias the direction of evolution of the signals and receptors, as well as the behaviour used in signal emission, transmission and reception (Endler & McLellan 1988; Endler 1989, 1992; Basolo 1990).

5. DECISIONS BASED UPON THE PERCEIVED SIGNAL

Once a signal is received and perceived, there are many factors which can influence how it is used by the receiver to make a decision about subsequent behaviour or physiological changes (table 1, figure 2). These factors can bias the direction of evolution of all aspects of signalling systems. Compared with the factors outlined in the first three columns of table 1, the behavioural and evolutionary dynamics of perceived signals is reasonably well known (see Otte 1974; Dawkins & Krebs 1978; Lande 1981; Pomiankowski 1988; Guilford 1986, 1988; Grafen 1990*a*,*b*; Guilford & Dawkins 1991; Dawkins & Guilford 1991; Johnstone & Grafen 1992; and the papers in the second half of this symposium). Consequently, I will only briefly outline some of the less frequently considered factors here (table 1).

Useful signals must be discriminated from useless signals. For example, the presence of congeneric signals may cause divergence in the signals, receptors, signal processing, and signalling behaviour (including location of signal emission and reception) of the two species. Less reliable signals should also be discriminated against, and this may result in rapid evolution of signal systems in some sensory channels compared to other channels. Exploitative signals must also be discriminated against.

Behaviour as well as signal design should evolve to minimize reception by the wrong receivers ('eavesdropping'; figures 1 and 2; Otte 1977). The problem of 'eavesdropping' is a fascinating one, and applies even within species (McGregor, this symposium). Sometimes evolution to avoid signalling exploitation can take surprising turns. Cicadas are subject to parasitoid attack by Sarcophagid flies. The flies differentially attack males and are attracted to the cicadas' courtship song. So the flies exploit the cicadas. In addition, the fly larva destroys the cicada's sound generation organ. This prevents attraction of other flies, which reduces the chance of two larvae in the same host (Soper *et al.* 1976). In this case the fly behaviour prevents further exploitation of the cicada's signals. Presumably there is selection to prevent eavesdropping on host behaviour and host signals. With the exception of studies of mimicry and warning signals, the dynamics of two-species signalling system evolution has not been investigated theoretically.

The time needed for making a decision on the basis of a single signal, or choosing among conspecifics emitting different signals, may take time away from doing other things, such as scanning for predators or foraging. These trade-offs may constrain or bias the direction of evolution of both the form and content of signals, as well as the associated signalling and receiving behaviour. The time taken for the choice, or perhaps the number of channels of information (within and between sensory modes) may be greater for decisions which have larger lifetime fitness consequences than for decisions which have only minor implications for survival and reproduction. For example, if dangerous predators are common, mate choice may be more limited, simpler, or even random, but if predators are weak or uncommon and food is plentiful, perhaps criteria for mate choice will be complex and assessed in detail. On the other hand, if a 'good genes' or direct benefit sexual system is present, then assessment of signals may be complex and detailed even in the presence of high predation intensity. In the latter case, perhaps different sensory channels will be used than those used by the most dangerous predators.

The physiological state of a receiver may affect decisions about when and where to be available to receive signals, when and where to be attentive to signals, and the time it takes for signal-based decisions. For example, a hungry receiver may be less attentive and may be less discriminating than a sated receiver, because it wants to finish the decision quickly and get back to foraging. Alternatively, a hungry receiver with heritable poor foraging ability may wish to spend more time on the choice of a mate to ensure better offspring by direct or indirect benefit sexual selection. In either case, hunger or other physiological states may affect the number of sensory channels used. This will also affect the success and failure rates of different kinds of signals and different signalling behaviour of the emitters. If, say, different places within a given species' geographic range differ enough in food availability, then the average physiological states of high-food and low-food populations may be different, and so may evolve different signals, signal behaviour, and signal-receiving behaviour. If this went far enough, subspecific differentiation and even speciation could result.

The form and timing of the signals themselves will be affected by the balance between different selective factors. For example, traits favoured by sexual selection will also attract predators (Endler 1978, 1983, 1991; Tuttle & Ryan 1982) and parasitoids (Cade 1975, 1981, 1984; Soper *et al.* 1976), resulting in signals which are compromises between the selective factors. Compromises may also be made in signalling behaviour, for example aggregations of singing male crickets attract more parasitoids than isolated males, but more females come to aggregations. But females attracted to aggregations are themselves more likely to be subject to parasitization than those going to single males. As a result, there may be alternative male strategies which differentially balance these selective factors, and no net advantage to calling in groups or singly (Cade 1981). Geographical variation in predation intensity may result in geographical variation in many aspects of signal systems, as in the predation–sexual selection system in guppies (Endler 1978, 1983). Geographical variation in the sensory abilities and behaviour of predators can also affect the signals of aposematic animals (Endler 1988).

The quality of the signal will also affect decisions. For example, if it is difficult to receive and process a signal in a given sensory mode, then others will be used more frequently, both by receiver and sender. If the receiver makes decisions on the basis of a comparison among several signals, then sensory channels and signal components which exhibit more variation among competing signallers will be favoured at the expense of the less variable channels. Even if the emitted signals are very different, if a channel is very noisy, then it may take much effort (time and energy) to distinguish among the emitters, or may even be impossible, so other channels or more variable signal components will be used instead.

In the previous discussion, I was intentionally vague about what I meant by signal 'quality'. Signal quality has two components, clarity and value, which roughly correspond to Guilford & Dawkins' (1991) efficacy and strategy, and the forgoing arguments apply to both components. A signal component may be low in quality because it is difficult to receive and process (efficacy), or because it gives false or misleading information about the emitter (strategy). If a signal component or channel is low quality in either sense, other components or channels will be favoured. Given that the interests of signallers and receivers may not be identical, the value of any given signal may vary significantly between emitter and receiver, and among receivers differing in physiology or genotype. This makes decision making on the basis of signals more difficult than it would be purely on the basis of the clarity of reception. As the suite of predators, parasites, and food availability characters varies geographically, so too will decisions based upon the signals, affecting the evolution of the signals as well as the receivers. The evolutionary dynamics of signal value or strategy are interesting and complex (Kodric-Brown & Brown 1984; Guilford & Dawkins 1991; Dawkins & Guilford 1991; Grafen 1990*b*; Johnstone & Grafen 1992; and papers in the second half of this symposium).

An emitter sending signals through different sensory channels or modes (such as vision and hearing) will send different information among the channels. The channels will also differ in their ability to send the same basic information about the emitter, and in their cost to the emitter to generate and display. High quality signals should be favoured by natural selection (including sexual selection and selection in other communication systems), whereas low quality signals will either be disfavoured or drift if variation in them cannot be discriminated by the receivers. As a result, there may be rapid evolution of signal systems in some sensory channels compared to others. For example, if it is difficult to recognize and assess vocal signals, but visual signals are easier, then visual signalling may evolve faster than auditory signalling. But if, say, environmental conditions are different in a different place, and favour auditory signalling, then sound systems may evolve faster than visual ones. A similar argument can be made for visual and olfactory communication in Lepidoptera (Vane-Wright & Boppré, this symposium). Of course different sources, such as predators, conspecifics, and prey, may be most easily perceived in different channels, so the balance of which channels are used for which purposes may reflect the relative importance of the modes of all signals received. Table 2 outlines some of the costs and benefits of signalling in different sensory channels, but it must be remembered that even within channels, different components of signals will have their advantages and disadvantages. For example, in visual systems, movement may be better than colour or pattern under some conditions (such as low light intensity), pattern contrast (dark and light) might be better under others (high predation), and colour contrast better under still other conditions (colour-blind predators). The trade-off between different sensory modes and different signal components within modes is essentially unexplored.

6. SENSORY BIASES, THE DIRECTION OF EVOLUTION, AND PHYLOGENY

The evolution of a communication system involves three suites of traits, the signals, the sensory and cognitive systems used to receive the signals, and the behaviour associated with the signalling. A shift in one of these will have fitness consequences for the other two, and so we would expect them to coevolve (figure 3). This has been considered most thoroughly with respect to sexual selection, so I will use this as an example.

If there is variation among males in their emitted signals, then those males which produce signals which are most efficient in stimulating the female's sensory systems will have an advantage over other signals

Table 2. *Some advantages and disadvantages of signaling in different sensory modes*

mode	advantages	disadvantages
vision	very fast many channels (motion speed and direction, brightness, hue, chroma, polarization, etc.) high information transfer rate line of sight (predation, rivals)	line of sight necessary (e.g. courtship) ambient light dependent (except bioluminescence)
hearing	very fast several channels (frequency, amplitude, etc.) medium to high information transfer rate	mixes with noise easily cannot hide from predators or parasites
electroreception	similar to hearing, but smaller frequency range	similar to hearing, but more noise, and attenuates faster than sound depends upon salinity and conductance
olfaction	many channels very specific signals directly related to foods and physiology; good fitness indicators	slow probably expensive to emit many specific receptors needed low directional control in emission poor directionality for tracking
contact (touch and taste)	fast possible direct indicator (as olfaction) high information in temporal and touch and taste pattern	close range only (and predation risk) not as fast or as high information transfer rate as in vision or hearing

(Alexander 1962; Barlow 1977; West-Eberhard 1979, 1984; Burley 1985; Endler & McLellan 1988; Endler 1989, 1992; Basolo 1990; Ryan & Rand 1990, this symposium; Ryan 1991). This is known as 'sensory exploitation' (figure 3, shaded) because the male signal characteristics can be thought of as exploiting (or manipulating) the female's sensory system (Ryan & Rand 1990, this symposium; Ryan 1991). Given that a sensory system can have biophysical properties which are independent of evolutionary history, it is possible that these properties may actually bias the direction of evolution of signals. It is also possible that pre-existing biases may exist in the brain, for similar reasons. In fact these properties may result in pre-existing biases for male traits which only evolve after the origin of the sensory or cognitive biases (Basolo 1990). Arak & Enquist's (1993, this symposium) neural network models provide a possible mechanism for such pre-existing biases: whatever a neural network happens to learn may incidentally produce biases for signals which do not yet exist, or do so only in a different population or species. So evolving to recognize one signal may generate a pre-existing bias for a completely new signal. As soon as the variation in the signal is perceived by the bias, relative finesses of all signallers in the population will change, and natural and sexual selection will favour that new signal form, and the system will evolve in that direction.

Compared with other aspects of the evolution of signal systems, the evolutionary interactions of female preferences and male traits is relatively well-studied, and needs no discussion here (see Lande 1991; Pomiankowski 1988; Grafen 1990*a,b*). However, almost all attention has been paid to the content or strategy of the signals, and very little to the factors which affect the clarity or efficacy of the signals (exceptions include Ryan 1991; Ryan & Rand, this symposium; Endler 1991).

Given that a signal works best for the environmental conditions and receptors which have favoured it, this places constraints and biases on the signalling

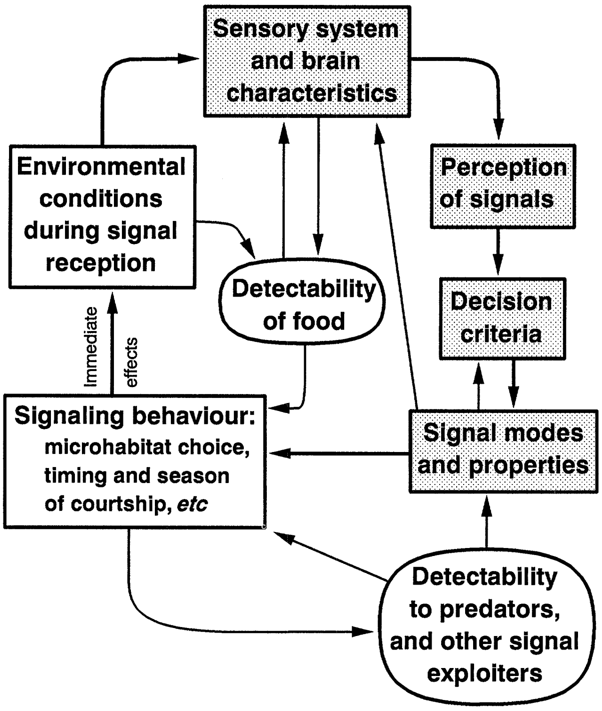

Figure 3. Sensory drive; processes that bias the direction of evolution (after Endler 1992). The shaded components make up sensory exploitation (Ryan 1991). Arrows indicate evolutionary effects, except where noted. For example, sexual selection is often modelled as a reciprocal interaction between decision criteria (female choice criteria) and signal structure (male traits). Other interactions are possible but are not shown for clarity. See Endler (1992) for details.

behaviour to maintain the match. If some males consistently signal under environmental conditions, times, or places which yield a poorer female response, then these males will be at a disadvantage compared with males signalling at the best times, places, and conditions. (This will be true even if the content of the signal is misleading; for example, mimicry may work best under some environmental conditions and not others.) This favours behaviour specific to specific habitats and microhabitats, and perhaps also specific microclimates, etc. This may cause microhabitat specialization not only in signalling behaviour, but also in other aspects of the animal's life-history, especially if the best signalling conditions and places are rare, and only associated with specific habitats. This in turn may favour habitat and microhabitat specificity (figure 3; Endler 1992).

If microhabitat specificity evolves, then this may mean that much time is spent in characteristic sets of environmental conditions. These would favour sensory systems which would work best in those conditions, as well as receive signals under those conditions. Therefore habitat specificity could bias the direction of the evolution of sensory systems (Lythgoe 1979; Endler 1991, 1992). Habitat specificity as well as specialized conditions for detecting prey or other food, and detecting predators, will also affect the rate and direction of the evolution of sensory systems (figure 3), as well as which channels will be used (as in table 2).

The evolution of sensory systems will affect which signals are easiest to receive, easiest to distinguish, and easiest to base decisions on, and this will have effects on the evolution of the signals and the signal behaviour, with subsequent evolutionary effects on the sensory systems (figure 3). A change anywhere in this cycle of interactions will affect the entire system, so we can say that sensory systems, signals, and signalling behaviour evolve together. The direction of this joint evolution will be set by the biophysical and energetic conditions of signal emission, environmental conditions which favour clarity of reception, neural conditions which favour the processing of certain kinds of signals or signal components, and the strategies behind signal emission, detection, discrimination, and decision-making. This process may be called 'sensory drive' for brevity (Endler & McLellan 1988; Endler 1989, 1992; figure 3).

Sensory drive should mean that groups of unrelated species living in similar conditions should use similar signals and senses, and that many of the general properties of their signalling systems should be predictable from a knowledge of these conditions (Lythgoe 1979; Endler 1991, 1992, 1993). But because signals, signalling behaviour, receptors, and signal processing evolve together, there will also be constraints on the rate and direction of evolution simply because a change in any component affects the others.

Historical accidents might affect the direction of sensory drive. For example, if the phylogenetic history of a given group of species (clade) was entirely within a particular habitat and set of environmental conditions, then this may favour the development of particular sensory systems and modes, and the loss or reduction of others (tables 1 and 2). As a result, even if one or more species in this clade suddenly invades a novel habitat, it may not be able to evolve the predicted suites of traits, and the subsequent direction of evolution may be in the direction of the next best mode of communication. On the other hand, new sensory conditions may allow the sudden evolution of very different signal structure with resulting evolutionary changes in behaviour and sensory systems. The sequence or history of environmental conditions that a clade experiences will probably be unique to that clade, and perhaps different enough from others to make general predictions difficult to test. On the other hand, if the mean time (generations) spent in each set of environmental conditions were known, a time-weighted average of the conditions might predict the direction of sensory drive. If this were not known, or only partially known, the history may seem random. Finally, if the sensory system changes for other reasons (such as detecting new prey), this may also favour new signals and signalling behaviour which would not be expected on the basis of environmental conditions alone (figure 3). Possible examples, and a discussion of phylogenetic effects, are found in Basolo (1990, 1991), Ryan & Rand (this symposium) and Vane-Wright & Boppré (this symposium).

7. GENERAL OR SPECIFIC EXPLANATIONS?

Two frequent reactions to the list of factors (tables 1 and 2) which can affect the evolution of signalling systems are: (i) there are so many factors that we will never be able to understand any system; and (ii) this approach will never yield any generalities, because it implies that every system is unique. I think that both appraisals are completely wrong.

Although there are indeed many factors to consider (tables 1 and 2), not all will be important in any one system. It is up to us to consider the biology of whatever systems upon which we work and address those aspects which seem to be most likely to be of major importance. For example, in my study of signalling to mates and minimal signalling to predators in guppies, I concentrated on the ambient light spectrum, the reflectance spectrum of each colour pattern element (and backgrounds), the transmission spectrum of water, and some general measures of visual abilities to predict conspicuousness to predators and mates (Endler 1991) and mating success (J.A. Endler & A.E. Houde, unpublished data). The strategic decision rules and dynamics of the system are also in line with what one can predict from various kinds of sexual selection theory (Endler 1983; Houde & Endler 1990; Kodric-Brown 1989; Nicoletto 1991). It is indeed possible that there are a number of other factors which affect guppies (tables 1 and 2), but in spite of this we have a good understanding of the system. The same can be said for Ryan's work on Tungara frogs (summarized in Ryan, this symposium). Complexity and the presence of multiple factors should not be equated with impracticality.

The degree of detail required to understand a given system does imply that there is a danger of complete understanding of a single system with no implications for other systems. But this is a general criticism of all of biology, and is not limited to the study of signal evolution. We must not fall into the trap of not seeing the forest for the trees. The problems in communication outlined in tables 1 and 2 have been repeatedly solved by millions of species, and these factors are based upon standard principles of biophysics, biochemistry, neurobiology, and behaviour. Consequently there should be a great deal of regularity in the design and form of signals, and this should be predictable from a knowledge of the signalling environment, signalling behaviour, and neurobiology. There is a good deal known about optimal signal design in sound and visual signalling, and these yield some general predictions which are independent of any one species (see references and detailed discussion in Endler (1992)). Table 3 gives a sampling of the kinds of general predictions which can be made about signal design. There are obviously many more possible predictions about signal design and content. Although each species is unique in the factors of table 1 which it experiences, the only uniqueness is in the combination of these factors and their relative importance. Each factor is associated with a suite of predictions about how signals, signalling behaviour, signal reception and processing should evolve. So, general predictions require a knowledge of how these factors combine in each species as well as how the most important factors work. By analogy, the factors in table 1 should be regarded as words, and we need to know the grammar and meaning as well.

8. WHAT QUESTIONS SHOULD BE ASKED ABOUT THE EVOLUTION OF SIGNALLING SYSTEMS?

To get a reasonably complete understanding of the evolution of signals, receptors, and signalling behaviour, it is useful to concentrate on the following nine questions.

1. How much of the signal can we predict from a consideration of structural design, and how much from strategic considerations? Unfortunately, most previous studies have only dealt with the latter.
2. What can be signalled? What kind of information about the signaller can be received and perceived? For example, there has been a lot of work on fitness indicators in indirect benefit models of sexual selection, but we still know little or nothing about what is being indicated and how it can be indicated.
3. What kinds of information does the receiver want to receive? What information is of value in decision making to the receiver? Presumably information which increases its expected lifetime fitness. And can this information be obtained from the signals?
4. What kinds of information does the emitter want the receiver to receive and act upon? What can be transmitted clearly or deceptively?
5. What is the trade-off between random, environmentally biased, and intended error rates in reception, perception and decision making? Does natural selection affect type I and type II errors (choose when bad and not choose when good) differently?
6. Are different kinds and modes of signals used for different kinds of information transfer?
7. Do different kinds of signals vary in their effectiveness in eliciting a response of decision in the receiver?
8. Do different kinds of signals vary in their relative costs and benefits to receiver and emitter? How often do the interests of receiver and emitter differ, even within species?
9. What accounts for the origin and the maintenance of signals and signalling systems? Origin and maintenance do not necessarily result from the same processes (Endler & McLellan 1988).

Table 3. *Sampling of the kinds of predictions which one can make from a consideration of the biology, biophysics, and neurobiology of signalling*

1. Use frequency modulation in channels that attenuate at random in time
2. Use multiple channels where there is much noise and much information to transmit during a short period of time
3. Use channels and signal components within channels which maximize the clarity of emission, transmission, reception and processing speed, and the decision speed of the receiver
4. Use channels and signal structure which maximizes the probability of a decision that increases the fitness of the emitter and receiver, allowing for possible conflicts of interest among emitters and receivers (figure 2)
5. Use signalling behaviour which improves reception of the signals. If the interests of emitter and receiver coincide, use behaviour which maximizes clear reception and minimizes decision speed by the receiver. If the interests diverge, then emitters should signal under conditions and with signals which maximize signal processing, decision time and error rates, while receivers should receive under conditions (and use channels) that minimize processing time, decision time and error rates
6. Use sensory systems which improve reception of and discrimination between signals

Finally, and probably most importantly, it is valuable to ask just what we are trying to explain in a study of the evolution of communication systems. Are we interested in:

1. The evolution of signals generally? Specifically? Or in the diversity of signals?
2. The content, structure, or both aspects of signals?
3. The evolution of sensory and cognitive systems?
4. The evolution of signalling behaviour?
5. The joint evolution of signals, signalling behaviour, sensory and cognitive systems (sensory drive, figure 3)?
6. Explaining specific or general patterns of variation?
7. Species recognition and speciation?

Our aims will have a profound affect on which aspects of signal evolution should be studied, and in what detail. We are only just beginning to appreciate the richness of biological phenomena involved in the evolution of communication, and it will take all of our biological skills and knowledge to understand it.

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