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Review Paper

Avian psychology and communication

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The evolution of animal communication is a complex issue and one that attracts much research and debate. 'Receiver psychology' has been highlighted as a potential selective force, and we review how avian psychological processes and biases can influence the evolution and design of signals as well as the progress that has been made in testing these ideas in behavioural studies. Interestingly, although birds are a focal group for experimental psychologists and behavioural ecologists alike, the integration of theoretical ideas from psychology into studies of communication has been relatively slow. However, recent operant experiments are starting to address how birds perceive and respond to complex natural signals in an attempt to answer evolutionary problems in communication. This review outlines how a psychological approach to understanding communication is useful, and we hope that it stimulates further research addressing the role of psychological mechanisms in signal evolution.

Keywords: cognition; perception; receiver bias; discrimination learning; memory; operant

1. INTRODUCTION

Animal communication is a long-established tool in the study of animal cognition. For example, the different alarm calls of vervet monkeys (*Cercopithecus aethiops*) reveal how they discriminate among different predators (Seyfarth *et al.* 1980); the dance of the honeybee (*Apis mellifera*) has been successfully used to investigate how honeybees navigate (e.g. Michelsen *et al.* 1992; Esch *et al.* 2001); and verbal communication has been important in the investigations into the cognitive abilities of both birds and mammals (Ristau 1991; Pepperberg 2000). However, there is now a growing interest in the reverse question: how does animal cognition affect communication?

Communication systems, whether evolved or man-made, can be thought of as having two components. The first is the information carried in the signal: signals function by transmitting information from a signaller to a receiver. In studies of animal communication, research tends to focus on what function the signal has evolved to perform, answering questions about what the signal communicates and how the reliability of the system is maintained. This functional aspect of signalling has been called the 'strategic' component of the signal (Guilford & Dawkins 1991).

However, there is a second important component to communication: the 'tactical design', or the form of the signal (Guilford & Dawkins 1991). The information emitted is in some sense only half of the story since the signal also has to be received by another animal, and the transmission properties of the environment as well as the sensory and perceptual properties of the signal receiver will influence the ease with which a signal is received (Endler 1992; Dawkins 1993). Guilford & Dawkins (1991, 1993) coined the term 'receiver psychology' to refer to the psychological mechanisms of the animal receiving a signal that could influence signal evolution. Their idea was that the principles of learning and memory generated in psychological experiments could be directly applied to communication systems: making information easier to detect, discriminate, learn and remember by receivers would probably increase the success of a signal, and would be selected for.

Although Guilford and Dawkins originally reflected upon how well studied psychological mechanisms could influence signal evolution, there are also findings and ideas stemming from behavioural studies that are important in understanding the role of receiver psychology in natural signalling systems. We review what is now known about the role of avian psychology in the evolution and design of communication. We have chosen to focus on birds, since they are a popular group for studying both psychological learning rules and the behaviour of communication, and therefore constitute an excellent group in which to consider this issue.

The first section reviews the learned and unlearned psychological biases that could promote the evolution of novel signals, and lead to the conspicuous and exaggerated signals commonly found in birds. The second section investigates how understanding more about avian psychology could help solve the question of why many avian displays are so complex (e.g. Zuk *et al.* 1992; Møller & Pomiankowski 1993; Rowe 1999; Andersson *et al.* 2002). Although there still tends to be a division between studies of tactical and strategic selection pressures in signal evolution, displays that have easily recognizable components may make it easier to study these two elements together within a single signal. In fact, the integration of psychological ideas into signalling studies has been slow, and in our final two sections, we review how psychological methods and ideas can be more widely adopted in communication research. We will discuss the future of this research area and ask whether psychological processes can ever be fully integrated into behavioural research in avian communication.

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2. AVIAN PSYCHOLOGY AND THE DIRECTION OF SIGNAL EVOLUTION

Since the introduction of the 'handicap principle' (Zahavi 1977; Grafen 1990), research in animal communication has been dominated by questions of signal cost and reliability: for example, why are signals so extravagant, and how can signals be reliable indicators of quality? This has meant that explanations of signal evolution based on psychological mechanisms have been largely overlooked at the expense of theory based on information transfer and cost. What these strategic models fail to explain fully is the diversity of signal form, and this is perhaps best explained by perceptual and psychological processes in receivers (Guilford & Dawkins 1991; Dawkins 1993).

Probably the best-known psychological process that can foster signal evolution is that of 'sensory bias' or 'receiver bias', where signals evolve to 'exploit' pre-existing perceptual or cognitive preferences in receivers (see Endler & Basolo (1998) and Ryan (1998) for detailed reviews). Mate-choice experiments, where females choose males on the basis of their visual or acoustic signals (or both), show that they can have preferences for signals that have not yet evolved in conspecific males. For example, female least auklets (*Aethia pusilla*) prefer males with white crests similar to those of two closely related species (*A. cristatella* and *A. pygmaea*) despite conspecific males being naturally crestless (Jones & Hunter 1998). In an even more extreme case, female zebra finches (*Taenopygia guttata*) have been found to prefer males with synthetic and unnatural traits, choosing, for example, males with red-coloured leg rings (Burley *et al.* 1982) or white feathers glued to their crowns (Burley & Symanski 1998). While these examples show how females can show a preference for novel traits, other biases seem to be open-ended, potentially leading to the continuous exaggeration of a male trait. Female red-shouldered widowbirds (*Euplectes auxillaris*) have an increased preference for males with increasingly longer tails, even when males exhibit tails that are exaggerated far outside their natural range (Pryke & Andersson 2002). Taken together, these studies show that there are two effects of sensory biases: the emergence of entirely novel signals and the exaggeration of existing traits. It is not clear whether these two effects can arise from the same bias, but it seems that a visual preference for red, for example, could lead to selection for novel red traits and their subsequent exaggeration.

Female songbirds can also have biases that would promote the evolution of the male song repertoires commonly found in many songbirds (Catchpole & Slater 1995): in some species where males have only a single song type, females have been found to have a preference for repertoires over single song types (Searcy 1992; Collins 1999). In the case of the common grackle (*Quiscalus quiscula*), phylogenetic evidence suggests that the female preference is ancestral, and that males appear actually to have lost repertoire behaviour (Gray & Hagelin 1996). Female zebra finches also show a preference for male repertoires, but males continue to produce a single song despite this seeming advantage to song complexity (Collins 1999). This suggests, as does the study of the common grackle, that although females' biases for complex males traits can exist, there are costs or limitations that offset the benefits to males for producing repertoires, and that biases measured in the laboratory will not always lead to exaggerated traits in natural populations. When traits do become exaggerated, they are likely to be costly to the signaller in terms of either increased predation or energetic investment, and this may lead to the signal evolving to indicate male quality reliably when a certain degree of expression is reached (Burley & Symanski 1998). This makes it difficult to assess whether signals have arisen through a visual bias or selection for reliable information in many signals since in each case the signal will eventually correlate with male quality. It is also impossible to know how many bird species harbour hidden preferences for novel or exaggerated signals, but they could be widespread since they have also been found in other taxa such as frogs, spiders and fishes (see Ryan (1998) for review). These latent biases that exist for size and colour could therefore be responsible for the initial evolution and consequent exaggeration of a considerable number of visual signals.

The biases could result from general perceptual and psychological processes, or because they have evolved for another function, for example in food or habitat choice. A recent experiment on five species of bowerbirds found that the colours that males choose for their bower decorations correlate with the colours that females choose during foraging (Madden & Tanner 2003). These colours are therefore attractive to females either because they have an unlearned preference for these colours and are more likely to detect or select them, or possibly through a learned preference due to the association between the coloration and food reward. This latter idea cannot be ruled out of this study, but regardless of knowing the exact mechanism, the experiment shows how receiver biases stemming from foraging behaviour could explain some of the very rich nature of avian visual signals.

The idea of sensory bias in the evolution of sexual signals originated in the behavioural literature (Basolo 1990; Ryan & Rand 1990; Ryan *et al.* 1990), but it is complemented by ideas and studies firmly rooted in experimental psychology. At the simplest level, neural network models show that biases can arise from general recognition processes in receivers that can potentially explain the evolution of symmetrical and exaggerated traits (Enquist & Arak 1993, 1994; Arak & Enquist 1993; Johnstone 1994; Hurd *et al.* 1995). Both these types of signal are thought to indicate male quality, with symmetry being an outward measure of developmental stability and 'good genes' (Møller 1990). These models have been criticized for their simplicity in that they are unlikely to capture real properties of visual recognition systems (Cook 1995; Dawkins & Guilford 1995); furthermore, slight procedural changes can also significantly alter the outcome (Bullock & Cliff 1997). Although possibly artefacts, the results from these models have been important in demonstrating that general recognition rules can produce signals previously thought to evolve solely through selection for reliability.

Another potentially important psychological mechanism that could also drive signal exaggeration is that of 'peak shift'. Psychologists have found that when birds learn a discrimination task where the rewarded and the non-rewarded stimuli differ along a single dimension (e.g. colour), they show a preference for novel stimuli that are exaggerated versions of the positive stimulus (Spence 1937; Hanson 1959). In terms of animal signals, this increased preference for a novel stimulus over the positively rewarded stimulus suggests that when signals have to be learned, an emergent preference could select for increasingly exaggerated signals (see Guilford & Dawkins (1991, 1993) for further description and discussion). Peak shift is different from sensory bias since it cannot explain the evolution of novel traits, but only the exaggeration of traits when the signal has to be learned.

A good example where this might happen is in the evolution of warning signals of unpalatable insects because birds have to learn to discriminate between palatable and unpalatable prey. Since palatable prey are generally cryptic to avoid predation (e.g. being brown or green), unpalatable insects should evolve conspicuous signals to increase the birds' abilities to discriminate between them (Guilford & Dawkins 1991). In fact, there is currently no conclusive evidence on whether or not peak shift works in the same way for negatively reinforced signals such as insect warning colours, as with positively reinforced signals (but see Gambarale & Tullberg (1996), where peak shift was not specifically identified as the mechanism). However, in a recent experiment, Jansson & Enquist (2003) used chickens (*Gallus gallus domesticus*) discriminating between coloured stimuli presented on touchscreens to show that birds can select for signals exaggerated along a colour dimension. They negatively reinforced a set of three blue or green stimuli and rewarded the chickens for pecking at one of three stimuli that varied in the degree of colour difference from the negative stimulus set. The chickens' responses to the rewarded stimulus set showed that they preferred to peck at the more distinct colour, which in an evolutionary process would lead to more distinct coloration in the positive signal. This experiment shows that a peak shift effect could potentially account for the exaggeration of colourful signals through the process of discrimination.

Another type of signalling system where peak shift may therefore be important is in the evolution of sexually selected traits. Sexual signals of parents are often learned or 'imprinted' when birds are young, to enable species and mate recognition (see ten Cate & Vos (1999) for a recent review). Therefore, as a by-product of sexual imprinting, peak shift could also enhance sexual signals by young birds learning to discriminate either between parents or even between mates of their own and different species (Weary *et al.* 1993; Owens *et al.* 1999; ten Cate & Vos 1999). This area has received little attention in the sexual selection literature and, to our knowledge, there has been no direct test of this relatively simple idea.

Sometimes birds need to associate different signals with the same outcome, such as recognizing the songs from a single individual or the colour patterns of several unpalatable insect species. In these cases, we would predict convergence among signals (Enquist & Johnstone 1997), because psychological experiments clearly show that birds trained to associate two stimuli that differ along a single dimension with a reward will subsequently prefer intermediate signals by the process of generalization (Kalish & Guttman 1957). Therefore, in systems where a signal is learned, generalization could even be a restraining force in the evolution of exaggerated signals since the average population expression of that signal could produce the maximum response from receivers. We know relatively little about how birds learn, generalize between, or even categorize natural signals (see Hausberger & Cousillas (1996) and Horn & Falls (1996) as examples of categorization of acoustic signals), but it may not necessarily be as we might initially expect.

For example, a recent study of Müllerian mimicry tested the widely held assumption that predators find it easier to learn two patterns the more similar they are (Müller 1879). In fact, great tits (*Parus major*) initially learned to avoid two aposematic visually dissimilar prey types at the same rate as two visually identical types (Rowe *et al.* 2004). These data suggest that when birds learn to avoid two aposematic prey types they are able to generalize between them in very crude terms, i.e. by avoiding conspicuous prey, and that it is only later in the learning process that birds begin to learn individual patterns. That there is apparently little cost to dissimilar-looking aposematic species in the learning process begs the question of where the selection for Müllerian mimicry originates, but it could be in the way that the animals categorize and remember the patterns (Speed 1993, 1999, 2000) or costs of recognition errors (MacDougall & Dawkins 1998). These processes have yet to be explored in relation to aposematism and mimicry, or indeed in any signalling system, but they could have more of an impact on the evolution of visual warning signals than previously thought. It is clearly important to test how birds recognize and remember signals since these processes are as likely to be involved in signal evolution as learning and discrimination are. Understanding the evolution of avian signals through receiver psychology is not just restricted to studies of sensory biases since general psychological processes are likely to be just as important and deserve further investigation.

3. AVIAN PSYCHOLOGY AND SIGNAL COMPLEXITY

Signal complexity is a common feature of avian communication systems; in fact, it is difficult to think of a signal that is a simple cue varying in just a single dimension. Complexity can be seen within a sensory modality, such as the patterning of a colourful signal, or through the increase in the number of signals in other sensory modalities, such as using calls and colour together in a display; these have been termed 'multicomponent', and 'multimodal' signals when components are in different sensory modalities (Partan & Marler 1999; Rowe 1999). There is both theoretical and empirical evidence that components of complex signals can independently transmit information to receivers (e.g. Zuk *et al.* 1992; Møller & Pomiankowski 1993; Johnstone 1995, 1996; Kilner *et al.* 1999; Andersson *et al.* 2002; Papeschi & Dessi-Fulgheri 2003). However, because of what we know about how birds perceive complex stimuli from psychological studies, this may be more common in multimodal than in multicomponent signals (Rowe 1999). However, there is also accumulating evidence that signal components are not perceived independently, and that interactions can occur between signal components that could increase the efficacy of the intended message (e.g. Rowe & Guilford 1996; Møller *et al.* 1998; Rowe 2002; Leonard *et al.* 2003).

These signals are then ideal for studying the relative roles of strategic and tactical selection pressures in signal evolution.

The role of many signal components in displays is often unknown, and there is the temptation in behavioural studies to concentrate on only the most conspicuous component, or to try and explain each component independently from the other. However, these approaches may miss the way in which components have evolved to work together in signal transmission (Rowe 1999). For example, it has been suggested that the patterns and stripes on ornamental tails act to 'amplify' females' abilities to judge tail length, an important factor in mate choice in some species (Hasson 1989, 1991). Although there has been no direct test of this idea in birds, melanin spots of male guppies (*Poecilia reticulata*) enhance the degree to which females accurately judge males based on the orange carotenoid patches in their patterns (Brooks & Caithness 1995; Brooks 1996). Therefore, possessing a non-informative signal component as part of a display could enhance the perceptual precision or accuracy of signal reception in birds but, to our knowledge, there has been no empirical attempt to measure either of these benefits.

In a related idea, Guilford & Dawkins (1991) suggested that potentiating displays could exist, where signals in one sensory modality specifically enhance the strength of learning about another component in a different sensory modality. In particular, this suggestion was made in relation to warning signals, where sounds and odours could promote the learned avoidance of the conspicuous pattern (Claridge 1974; Rothschild *et al.* 1984), although potentiation could occur in any multicomponent signal that involves learning. There is now evidence that sounds can enhance the ability of foraging birds to learn to discriminate between rewarded and non-rewarded prey types on the basis of colour, although this could be due to changes in attention rather than any potentiating effect (see Rowe (2002) for further discussion). The role of attention in avian communication systems is often overlooked, but it could play an important role in the evolution of signal complexity. For example, the begging calls of nestling tree swallows (*Tachycineta bicolor*) seem to play a role in directing parents' attention to their postural begging display (Leonard *et al.* 2003), while extra feather ornaments in combination with movement may enhance the attention that females pay to male signals (Marchetti 1993; Hausmann *et al.* 2003). While these two examples are more about how an additional signal component might direct attention towards other components of a display, it could also increase the perceptual accuracy and precision of the information received.

It is important to realize that psychological interactions between avian signal components mean that we should take a more 'gestalt' view of avian displays (Rowe 1999). Studies of insect warning coloration, sexual signals and chick begging displays all reveal that a bird's response to a display cannot be assumed to be the sum of signal components (Rowe & Guilford 1996; Møller *et al.* 1998; Leonard *et al.* 2003). What is needed to help understand complex avian signals are studies that consider multiple components in an integrated way; it is not enough to make predictions from general psychological theory since the responses to a specific signal may be very different (Rowe 1999).

A recent example of this type of approach is from an experiment on California quail (*Callipepla californica*), which found that the combination of multiple plumage ornaments of males explained more of the variation in female choice than when considering each separately (Calkins & Burley 2003). Females may therefore be taking a composite measure of all plumage ornaments rather than relying on each separately. This type of study is invaluable in helping us to understand what happens in real signalling situations. Future studies need to recognize that focusing on just a single component of a display is likely to miss the broader picture in terms of why the signal is so complex and why it has evolved. The only comprehensive approach to understanding the evolution of complex signals and the relative importance of strategic and tactical selection pressures in signal design is by measuring each component of a display, seeing how traits correlate with each other and with signaller quality and how they vary across the population, and by measuring receiver responses to single and multiple traits.

4. PSYCHOLOGICAL TECHNIQUES IN COMMUNICATION RESEARCH

It was the hope of Guilford & Dawkins (1991, 1993) that psychologists and neurobiologists would incorporate evolutionary ideas into their work, while at the same time behavioural biologists would recognize the importance of avian psychology in understanding communication. While writing this review, we have been surprised to find that there has been relatively little crossing over between the two fields. This may be due to their differences in approach and experimental methods. In experimental psychology, birds perform laboratory-based experiments that use artificial stimuli, such as lights and tones, to generate and test theories of learning, memory, recognition and categorization. However, animal behaviour, and behavioural ecology in particular, focuses on the behaviours of a wide range of species and attempts to understand both the proximal and evolutionary mechanisms behind them. Despite this continuing disparity, it is possible to apply not only psychological theories to communication, but also to use psychological techniques to study the cognitive abilities of birds in relation to communication. Operant experiments are a common way that psychologists investigate birds' perceptual and cognitive abilities by rewarding or punishing birds with respect to decisions they make based on the stimuli they are exposed to. Although they predominantly use tones and lights, it is possible to replace these with more natural stimuli to test birds' behavioural responses to signal components.

One area where this method has been successfully employed is in birdsong research, where it has been possible to separate the components of a signal that birds might use to discriminate between different songs, such as pitch, relative pitch and song length (e.g. Cynx 1995; Weisman *et al.* 1998; MacDougall-Shackleton *et al.* 1998; Sturdy *et al.* 2000; Beckers *et al.* 2003). It has also been useful in determining how they might categorize them so as to recognize conspecifics or even identify individuals (e.g. Horn & Falls 1996; Gentner & Hulse 1998, 2000;

Gentner *et al.* 2000; Beckers & ten Cate 2001), as well as looking at the effects of early experience on perception and preferences (e.g. Chaiken *et al.* 1997; Njegovan & Weisman 1997; Riebel & Slater 1998; Riebel 2000). These studies are useful because they reveal the sensory capabilities of birds while eliminating problems of motivational changes and constraints of the breeding season (Gentner & Hulse 1998; Beckers *et al.* 2003; Phillmore *et al.* 2002). However, care must be taken when interpreting these results, since contextual cues found in the wild that could either aid or hinder discrimination are not available to the birds; the results should therefore be validated in a natural system.

Operant conditioning has been used to study visual as well as acoustic signals in birds, and this approach has yielded interesting results in relation to the issue of symmetrical signals. There are now studies that have investigated the biases and perceptual issues surrounding the question of whether birds use symmetry as a signal of quality. Several studies suggest that it is unlikely that birds use symmetry as a signal at all: starlings (*Sturnus vulgaris*) find it difficult to perceive differences in symmetry at levels similar to those of natural signals (Swaddle 1999), and both pigeons and starlings find it hard to learn discriminations based upon symmetry (Huber *et al.* 1999; Swaddle & Pruett-Jones 2001). One study suggested that chickens (*Gallus gallus*) have an unlearned preference for symmetry when trained on a range of asymmetric stimuli (Jansson *et al.* 2002). However, despite using potentially useful methodology (Forkman & Enquist 2000), the interpretation of the results suffers from the same criticism as earlier models (Enquist & Arak 1994; Johnstone 1994), in that the preference could be for the average stimulus rather than for symmetry *per se*. Therefore, although these operant studies question the likelihood of symmetry being a useful signal, they also highlight how the training regimes used in operant experiments can potentially cause bias in the results and interpretation.

In another experiment on the perception of insect warning signals, pigeons (*Columba livia*) were trained to discriminate between slides of flies and wasps, and then their responses to slides of hoverflies that mimic the wasp pattern to varying degrees were measured (Dittrich *et al.* 1993). In general, when birds were rewarded with food for pecking at flies and punished for pecking at wasps, responses decreased with increasing pattern similarity to wasps as perceived by human observers, but interestingly some patterns that humans thought were very different from wasps were treated as very similar by the birds. The study was criticized for using slides as stimuli that may not fully capture the colour patterns as birds see them (Cuthill & Bennett 1993), but a similar result was found with real specimens under naturally lit conditions (Green *et al.* 1999). In this case, there was no reason to think that the training set biased the result (although it remains a possibility), and the results are an important reminder that birds may have different perceptual and psychophysical abilities from our own, and the way we see avian signals may not be exactly how birds see them.

Although there are relatively few such operant experiments testing perceptual and psychological processes with natural signals, they are important because their results contribute to signalling theory and help us to understand the limits that might constrain signal evolution. There are potential problems of extrapolation to Nature with these studies (which can be levelled at any laboratory experiment, since they must abstract elements of natural systems), but these studies certainly earn their place in integrating and even generating psychological ideas relevant to signal evolution. In addition, this approach could also be used to model the evolution of signals using avian receivers. The recent study of colour signal exaggeration (Jansson & Enquist 2003) is a simple example, but more powerful evolutionary techniques such as the use of genetic algorithms could be used to generate realistic variation and heritability in signals upon which receiver psychology could act (Bond & Kamil 1998, 2002). There are potential problems in the species used, what sex they are, subjects' previous experiences, and what training stimuli are used in relation to the interpretation of results, but this technique is likely to be an invaluable tool in modelling the effects of receiver psychology in signal evolution.

5. CONCLUSIONS

There are many new research themes in the overlap between psychology and evolution, such as evolutionary psychology (Buss 1995; Daly & Wilson 1999; Barrett *et al.* 2002), cognitive ecology (Real 1993; Dukas 1998; Healy & Braithwaite 2003) and cognitive ethology (Ristau 1991; Jamieson & Bekoff 1996; Allen & Bekoff 1997). While evolutionary psychology investigates plausible explanations for modern human behaviour, both cognitive ecology and cognitive ethology attempt to explain the adaptive nature of psychological and neurological processes underlying animal behaviour, especially in relation to the social and natural environment in which they have evolved. However, the idea of receiver psychology has taken the opposite view, in that it considers how the neurological and psychological processes of an animal can shape its environment by acting on the signals of other animals. Although we have been encouraged by the progress made in understanding the potential selection forces exerted by avian psychology on signal evolution and design, it seems to us that this perspective has not been widely appreciated in studies of communication.

There have been important steps forward: behavioural studies have uncovered inherent psychological biases in birds that could explain the evolution of novel signals, and have also found that the processes of learning and discrimination can lead to exaggerated visual traits. In addition, the way that birds perceive and process signals is beginning to be appreciated as an important selective force in complex signal evolution. However, despite these advances, psychological studies are very much in the minority when compared with studies of information content and reliability of animal signals. Obviously both factors influence signal evolution, but it is still surprising that there is little integration of ideas and findings. One area where this might be important is in complex displays: many studies continue to look at single traits in isolation, when in fact there are now abundant studies suggesting that consideration of the entire display, including interactions between components, is crucial. Studying these displays in their entirety will also provide information about how strategic and tactical selection pressures operate in signalling systems, and how they combine to make an effective signal.

This leads to a final question of whether the continuing divide between 'strategy' and 'tactics' is useful in communication research, and whether psychology will ever be fully integrated into studies of communication (Johnstone 1998; Andersson 2000). In some sense, because of the continuing low number of psychological studies compared to those researching signal strategy and cost, the division is useful since it highlights psychological processes that might otherwise be overlooked. Alternatively, this may not continue to be a useful dichotomy. The receiver's role in communication can be summed up as the perception and assessment of information, and studying the psychological or informative parts of a signal separately ignores the interaction of the two in producing adaptive behaviour in receivers. Although this review has not covered issues associated with the decision-making process, there are certainly psychological issues behind information perception that should also be considered in the future. For example, there is relatively little work (especially experimental) in the area of receiver error, where the ability of birds to judge information correctly could affect signal form (Johnstone & Grafen 1992; MacDougall & Dawkins 1998). Receiver error may also be subject to Weber's law, which states that where discriminations between stimuli or intervals of time differ by a fixed amount, the discrimination becomes increasingly difficult with increasing stimulus size. This law has been fruitfully applied in other areas of avian behavioural ecology (e.g. Bateson & Kacelnik 1995), but in communication it could be an important contributor to perceptual error in large signals (Meck 1997; Shettleworth 1999), perhaps even maintaining variation in extravagant sexual traits. We think this integration of what are essentially the psychophysics of perception and the assessment of information will make it difficult to maintain the distinction between strategic and tactical design in the future.

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