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60 YEARS OF ANIMAL BEHAVIOUR

Anniversary Essay

Receiver psychology: a receiver's perspective

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The elaborate design of animal signals is challenging to explain. In 1991, Guilford and Dawkins published their iconic paper on 'receiver psychology' in *Animal Behaviour* (**42,** 1–14), and proposed that the ways in which animals detect, discriminate and learn about relevant stimuli in their environment would have a significant influence on signal evolution. In this essay, I review the impact of this paper on the study of animal communication, and in particular how highlighting the tactical design of animal signals has been important in changing the way in which we think about and study animal signals. Although there has been some recent criticism of receiver psychology, I think it continues to be a powerful approach that generates exciting areas for future research.

Reading Guilford & Dawkins's (1991) paper, 'Receiver psychology and the evolution of animal signals', quite simply changed my life. This may sound rather unlikely, but let me explain. I first read the paper as a final-year undergraduate student; I had become hooked by the study of behaviour and particularly fascinated by the evolution of animal signals. The paper was so totally different from the other papers that I had been reading on animal communication that it immediately captured my attention and interest. I was fascinated by their ideas, and it became clear to me that I wanted to go on to study the evolution of animal communication. Consequently, at the end of my undergraduate degree, I went to do a Ph.D. with Tim Guilford and Marian Dawkins. Reading this paper inspired my first career choice (had I known what that was back then), and the paths that my research has subsequently followed.

But Guilford and Dawkins's paper hasn't just affected my own research; it has had a significant and lasting impact on how researchers study animal communication. When the paper was published, the evolution of communication was a 'hot topic' in animal behaviour, with discussions and debates predominantly centred around two key questions. The first was, quite simply: what is a signal? To the uninitiated, defining what a signal is might seem to be a rather trivial matter. However, it was, and continues to be, a major challenge for researchers: there is still no single agreed definition, and definitions vary between researchers (e.g. Hauser 1996; Maynard Smith & Harper 2003; Searcy & Nowacki 2005). Problems tend to revolve around the information content of a signal: for example, does the signal have a meaning to the receiver, and what kind of information does it contain? While I'm not going to dwell on these issues in depth, particularly given the continuing discussions in the literature (Rendall et al. 2009; Carazo & Font 2010; Owren et al. 2010; Scarantino 2010; Scott-Phillips 2010; Ruxton & Schaefer 2011), it's important to realize that this was also a major point of discussion in the early nineties.

Other questions that were dominant in the literature at that time were: are signals honest, and if so, what selection pressures maintain their honesty? While the answer to these questions might seem pretty straightforward to modern students of animal behaviour,

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Zahavi's (1975, 1977) idea that animal signals could be 'handicaps' was only just starting to become widely accepted, with the publication of Grafen's (1990) model in the previous year demonstrating that a signal's reliability could be stabilized through its cost to the signaller. Now, it is perhaps hard to imagine a time when the handicap principle was not an accepted model for studying animal communication and sexual selection, but when Guilford and Dawkins published their paper, data to support it were still lacking.

This period of defining, debating and discussion was clearly focused on how signals provided information to receivers and how that information could be reliable. It was against this backdrop that Guilford and Dawkins's paper on receiver psychology was published. They realized that the diversity of signals, the different types of signals that animals produced, could not be readily explained by only thinking about the information content of a signal. What they described as an 'extraordinary diversity' of signal designs across species had to be explained by other mechanisms. They proposed that we could only fully understand signal design by knowing how signals were perceived and processed by signal receivers. They coined the phrase 'receiver psychology' to encompass the cognitive mechanisms in signal receivers that process incoming information and could potentially influence signal evolution. In doing so, they not only identified an alternative set of selection pressures that could significantly influence signal evolution, they also provided a new terminology and framework to study the different selection pressures acting on animal signals.

INTRODUCING STRATEGIC AND TACTICAL DESIGN

For the first time, Guilford and Dawkins made a clear distinction between selection pressures acting on the content of the signal, which they called the 'strategic design', and those acting on the efficacy of the signal, which they called the 'tactical design'. The strategic design was defined as being how natural selection acted on a signal in order that information was provided to a receiver. In contrast, the tactical design was how the signal was designed to get the information across to the receiver; this is often referred to as 'signal efficacy' (e.g. Hebets & Papaj 2005). We can think about these two different aspects of signal design as being 'what a signal is designed to do' and 'how a signal is designed to do it'. As Guilford and Dawkins pointed out, arguments about the strategic design dominated the study of animal communication; the tactical design of animal signals had been much neglected.

The clarification that both strategic and tactical design existed in animal signals should not be underestimated. Prior to the publication of this paper, what we would now call strategic and tactical design had been pretty much viewed in isolation from one another. While research on the strategic design was focused on big evolutionary questions about the functional aspects of signals, studies of signal efficacy predominantly considered signal detectability, where the effects of the physics of the environment or the neural circuits of receivers could be measured. For example, birdsong was shown to be well adapted to its environment: features such as narrow frequency range (e.g. great tits, *Parus major*: Hunter & Krebs 1979) and slower repetition of elements (e.g. rufous-collared sparrows, *Zonotrichia capensis*: Nottebohm 1975) enhanced the successful transmission of song in dense habitat by reducing attenuation and degradation (Wiley & Richards 1978). Signals were also known to be well tuned to the sensory systems of their receivers, such as the visual waving displays of the male water mite, *Neumania papillator*; the displays stimulate females' visual systems, which are designed to detect and capture prey (Proctor 1991). Studies of strategic and tactical design were thus focused on questions that were not readily integrated, with detectability sometimes even being seen as a constraint rather than a selection pressure acting on signals (Krebs & Davies 1987).

Guilford and Dawkins's explicit classification of strategic and tactical design in the evolution of animal signals provided a way to integrate these two approaches in a clear framework. Detectability could now be seen in the broader context of the many cognitive mechanisms that could be important for signal evolution. Defined as being 'how easily a signal could be perceived as distinct from its background', detectability was just the first stage of signal processing by receivers. Tactical design was not just about how animals' sensory systems detected stimuli, but also how they processed information in order to make a decision about how to respond and behave. Detectability therefore joined a family of selection pressures that Guilford and Dawkins argued could have a significant effect on signal evolution in conjunction with selection for signal reliability. 'Receiver psychology' was the term that they introduced to capture neatly this category of selection pressures, and Guilford and Dawkins argued that the ways in which receivers detect, discriminate, learn and remember signals are all important selection pressures in signal evolution.

Their distinction between strategic design and signal efficacy enabled different selection pressures to be identified and studied. Nowhere is this more evident than in the study of multicomponent signals. Multicomponent signals are those that contain more than one component in at least one sensory modality (signals given in multiple sensory modalities are often referred to as 'multimodal'; Partan & Marler 1999; Rowe 1999). Multicomponent signalling is commonly found across the animal kingdom; for example, a survey of 73 bird species compiled from *Stokes Nature Guides* revealed that 92% of bird species had at least one display that contained two or more components in different sensory modalities (Hebets & Papaj 2005). However, when Guilford and Dawkins's paper was published, hardly anyone was asking the obvious question: why are so many animal signals multicomponent?

Guilford and Dawkins not only asked the all-important question but showed how receiver psychology provided an answer: multiple components could enhance the efficacy of a signal. They were particularly interested in the extreme situation in which an additional component in a signal display might not have any informative value to the receiver but could enhance the detectability, discriminability or memorability of another signal component that provided information and to which the receiver predominantly responded. Multicomponent signals are a perfect study system for investigating the interaction between strategic design and signal efficacy because it is possible to identify components that could have evolved under different selection pressures. This is perhaps best demonstrated in a system that I know well: aposematic signalling.

For more than a century, the widespread multicomponent nature of warning displays has been recorded by naturalists, with many aposematic prey combining conspicuous warning coloration with other display components, most notably the production of odours or sounds upon attack (e.g. Carpenter 1938; Rothschild 1961; Blest 1964; Eisner et al. 1974; C. Rowe & C. G. Halpin, unpublished data). Since visually hunting predators readily avoid aposematic prey on the basis of their warning coloration (e.g. Brower 1960; Gittleman & Harvey 1980), what could the function of these sounds and odours be?

One idea was that the sounds and odours could enhance predators' abilities to learn to associate the warning coloration with the prey's defences (Claridge 1974; Rothschild et al. 1984). Therefore, while the warning coloration would play a clear strategic role of warning the predator of the prey's toxicity, the sounds and odours would have a purely tactical function. This can be easily tested, since it is possible to control and manipulate components of