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Essay

'Communication breakdown': the evolution of signal unreliability and deception

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For a signalling system to be stable, signals must confer net fitness benefits to senders and receivers, which means that some aspect of their design must correlate with a quality that receivers benefit from knowing about. However, examples abound where this correlation is complicated by phenomena commonly referred to as deception and/or signal unreliability. We argue here that unreliability and deception are notions marred with conceptual ambiguities, often used as equivalent or as catch-all terms for qualitatively different processes. Signal unreliability refers to a pattern of design–information dissociation that can arise through different processes, some deceptive and some not, with different evolutionary implications. First, nondeceptive processes that are independent of sender–receiver conflict need to be explicitly recognized if we are not to overestimate the importance of deception as a driver of signal unreliability. Second, deceptive unreliability (fuelled by sender–receiver conflict) occurs through two qualitatively different processes with potentially different consequences for signal design. 'Incomplete honesty' is inherent to most communication systems and reflects the underlying conflict between senders and receivers that share some common ground of interests. On the other hand, categorical deception by signal parasitism evolves between senders and receivers that share no common interests, as a form of deceptive signalling that is purely contingent on the presence of already existing signals. We contend that adopting a theoretical framework explicitly based on the evolutionary scenarios leading to signal unreliability has advantages over traditional schemes focusing exclusively on whether signals benefit receivers or not.

Animal signals must allow receivers to make adaptive decisions better than they would in their absence (Enquist et al., 2010; Johnstone & Grafen, 1993; but see Rendall, Owren, & Ryan, 2009). This fundamental tenet of animal communication hinges on the existence of a consistent relationship between the design of a signal and the functional information it makes available to receivers (Carazo & Font, 2010; Font & Carazo, 2010; Searcy & Nowicki, 2005). However, and even though a design/information correlation is necessary for receivers to accrue a fitness advantage from responding to signals, this leaves ample space for the evolution of deception and tells us very little about the accuracy or reliability of the information contained in animal signals.

Signal reliability is best formalized as the strength of the correlation between signal structure and the information it makes available for receivers (e.g. Hughes, 2000; Proulx, Day, & Rowe, 2002; Searcy & Nowicki, 2005). Signal reliability must hence be understood as a statistical property of a population of signals (Fig. 1), i.e. as an observed pattern of association between signal design and the information extracted by receivers. Signal unreliability results from processes that disrupt this relationship, and is hence a cornerstone notion to understand the evolution of deception, animal signals and animal communication at large. However, signal reliability/unreliability merely reflects an observed pattern of design–information association that may result from qualitatively different causal processes. Unfortunately, the distinction between these processes is rarely acknowledged explicitly in textbooks and recent reviews and too commonly skirted, when not altogether confused, in the scientific literature. We argue here that failure to discriminate between the different types of processes that may lead to signal unreliability and deception can hinder our understanding of the evolution and function of animal communication and signalling.

SIGNAL UNRELIABILITY WITHOUT DECEPTION

Signal unreliability is frequently equated with deception (Table 1), which amounts to conflating pattern and process. Signal unreliability is the result of qualitatively different processes, some

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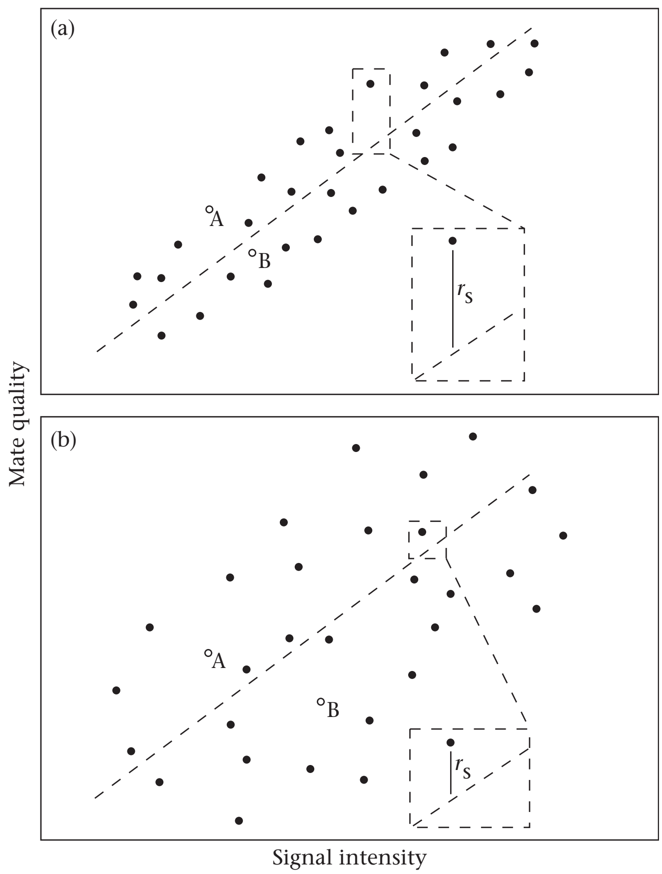

Figure 1. A hypothetical mate quality signal in which the relationship between variation in mate quality and signal structure (in our example, intensity) correlate linearly. The correlation coefficient will reflect the average reliability ($\bar{r}$) of the signalling system. If the senders' and receivers' interests overlap substantially, signalling systems will tend to exhibit high average reliability (a), while if senders' and receivers' interests diverge, they will tend to exhibit lower reliability (b). The reliability of any given signal (r_s) will be given by its residual score with respect to the fitted function. Furthermore, repeated measures of the same individuals at different times will allow estimation of both the relative reliability of an individual sender (i.e. variance of its residual scores/mean variance for all the senders in the system) and whether that individual sender is exaggerating or attenuating its signals (i.e. average residual scores significantly higher, e.g. individual A, or lower, e.g. individual B, than 0).

of which are deceptive and some not. We believe this distinction should be brought up front in analyses of animal communication if we are not mistakenly to invoke deception to explain patterns of signal reliability that can be otherwise explained.

While deceptive processes are fuelled by sender–receiver conflict (see below), signal unreliability can arise even when sender and receiver interests overlap completely. A certain degree of unreliability will always be present owing to inherent imprecision in phenotype formation (e.g. developmental noise) and to underlying imperfections in the efficacy of animal signals (Guilford & Dawkins, 1991), which include unavoidable errors during production, transmission and perception of signals (communication errors; Wiley, 1994). Signal unreliability may also arise when the receiver must pay a significant cost (e.g. in terms of time, energy or risk) in order to acquire detailed information about the quality/commodity being advertised by a signal, in which case the receiver may occasionally forgo full determination and rely on partially reliable information (Bradbury & Vehrencamp, 2011).

The distinction between deceptive and nondeceptive unreliability processes mirrors Guilford and Dawkins's (1991) distinction between signal 'efficacy' (resulting from selection pressures ensuring the transmission, reception and perception of the signal) and content-related or 'strategic' signal design (resulting from selection pressures acting on the content of the signal). Nondeceptive unreliability processes have little to do with the content of animal signals, but rather depend on the intrinsic characteristics of the communicative context in which a signal is produced, transmitted and received (i.e. on its 'efficacy' design, Guilford & Dawkins, 1991; Wiley, 1994). For example, king penguins, *Aptenodytes patagonicus*, breed in colonies of several thousand individuals, and parents that return with food for their offspring must recognize their chick using vocal cues transmitted through considerable background noise of similar spectral characteristics, and against the screening effect of hundreds of other penguins' bodies (Aubin & Jouventin, 1998). It is easy to conceive that, despite the overlapping interests of senders and receivers, recognition signals in this species will be subject to some degree of unreliability. Knowledge of the detailed characteristics of a communication system is thus required to understand and predict the reliability (and costs; Ryan & Cummings, 2005) of its signals, irrespective of whether deceptive processes occur. Furthermore, because signals measured in the animals' natural habitat are subject to environmental degradation (Bradbury & Vehrencamp, 2011), empirical field determinations of signal unreliability will almost always provide estimates of the overall reliability/unreliability of the signalling system (i.e. owing to both deceptive and nondeceptive processes). Ignoring efficacy-related

Table 1
Use of the term 'deception' (or similar) and 'signal reliability/unreliability' in recent analyses of animal communication

Source	'Deception'	'Reliability/unreliability'	A	B
Maynard Smith & Harper, 2003	Response benefits sender at the expense of receiver	Design/information correlation Unreliability used as synonymous to deception	No	No
Bradbury & Vehrencamp, 2011	Response benefits sender at the expense of receiver	Design/information correlation	Partial	Yes
Davies, Krebs, & West, 2012	Response benefits sender at the expense of receiver	Design/information correlation Unreliability used as synonymous to deception	No	No
Searcy & Nowicki, 2005	Breakdown in design/information correlation; response benefits sender	Design/information correlation	Partial	Partial
Hurd & Enquist, 2005	Sender provides unreliable/unambiguous information	Design/information correlation Unreliability used as synonymous to deception	No	No
Ruxton & Schaefer, 2011	Response benefits sender at the expense of receiver	Design/information correlation Unreliability used as synonymous to deception	No	No

We note whether such definitions explicitly make the distinction between (1) 'signal mimicry' and 'incomplete honesty' processes and (2) deceptive (i.e. content-related) and nondeceptive (i.e. efficacy-related) unreliability processes. Definitions labelled as 'partial' do not explicitly make the above distinctions, but allow for such distinctions to be made by not conflating the two processes. Most available definitions of deception tend to revolve around the idea that deceptive signals 'benefit the sender at the expense of the receiver'. However, this definition is ambiguous with respect to the costs paid by receivers, and can encompass qualitatively distinct phenomena (i.e. signal mimicry or incomplete honesty phenomena).