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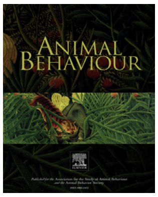

Receiver tolerance for imperfect signal reliability: results from experimental signalling games

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This paper presents an alternative approach to studying signaller–receiver interactions. The conventional approach focuses on signal reliability; instead, we focus on receivers' willingness to tolerate imperfect reliability (receiver tolerance). Both approaches aim to explain what promotes and maintains communication. We define receiver tolerance as following a signal in the face of reduced reliability. We used experimental signalling games with blue jay, *Cyanocitta cristata*, subjects to demonstrate whether uncertain environments generate receiver tolerance for imperfect reliability. Many models of signalling games ignore environmental certainty or predictability, but this certainty is a key part of understanding receiver tolerance. For example, low environmental certainty should increase tolerance since receivers are more uncertain about which action to take. We also tested whether signallers exploit receiver tolerance by signalling dishonestly. The results show that receivers are more likely to heed signals when environments are uncertain. Moreover, signallers are sensitive to this receiver tolerance and, when signallers and receivers have opposing material interests, low environmental certainty promotes dishonest signalling and high certainty restricts it. Our results highlight the usefulness of an approach emphasizing receiver tolerance and demonstrate the critical importance of environmental certainty for signaller–receiver interactions.

The literature of animal communication emphasizes signal reliability. Reliability is thought to present a problem, since signallers can often gain from dishonesty, but reducing reliability should destabilize signaller–receiver interactions. Maynard Smith and Harper (2003, Preface) called this problem of reliability 'the central problem for evolutionary biologists interested in signals'. A huge literature exists on this 'problem of reliability' and the mechanisms that potentially prevent dishonesty (e.g. Maynard Smith, 1991; McGraw, Hill, & Parker, 2005; Polnaszek & Stephens, 2014; Reby & McComb, 2003; Zahavi, 1975; and see Searcy & Nowicki, 2005). The problem of reliability arises because if a signaller reduces the reliability of its signal, the receiver may stop attending to the signal, so that the signal–response equilibrium becomes unstable. The problem of signal–response stability is, therefore, jointly a problem of signaller reliability and receiver tolerance for imperfect reliability (or simply 'receiver tolerance'); even though the determinants of the receiver's willingness to follow imperfectly reliable signals are seldom addressed. Notice that we conceive of reliability as a continuous variable, so that a signal can be partially reliable. Receiver tolerance, then, measures the extent to which a receiver follows a signal in the face of reduced reliability. Receiver tolerance need not be an error; as we explain below, it can pay to follow a partially reliable signal.

Our paper offers two experiments focused on receiver tolerance. These experiments seek to understand the conditions under which receivers are tolerant of imperfect reliability (i.e. the causes of receiver tolerance) and demonstrate the effects of receiver tolerance on signaller–receiver interactions (i.e. the consequences). To frame these experiments, we develop a simple model that asks when a receiver should follow a partially reliable signal.

Imagine that a receiver faces a binary choice (say accept or reject, for concreteness) and it observes a partially reliable signal that indicates the correct action (meaning the one with the highest payoff) with probability q. An unreliable signal has a $q = 0.5$ (it is just random noise), and a perfectly reliable signal has a $q = 1$ (it correlates with the correct action perfectly). Suppose, next that reject is the correct response with probability p (here termed environmental certainty). If $p = 1$, then the environment is certain and reject is always the correct action; if $p = 0.5$, then the environment is uncertain and the correct action is a 50/50 gamble. Thus, as the parameter p varies from 0.5 to 1 it measures the receiver's certainty about the environment. When $p = 0.5$, the receiver is

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completely uncertain about how to act, and when $p = 1$, receivers can be certain that the correct action is to reject.

Clearly, the signal is most valuable to the receiver when it is most uncertain about the appropriate action. It follows that receivers can benefit even from an unreliable signal when environmental certainty is low. The higher the certainty, the more reliable a signal must be to merit the receiver's attention. Figure 1 shows this logic graphically: more ‘signal-following’ space when environments are unpredictable, less when predictable (adapted from the flag-model of receiver behaviour: McLinn & Stephens, 2006). For example, when $p = 0.5$, following a perfectly reliable signal ($q = 1$) or a mediocre signal (say $q = 0.6$), both lead to the correct action more often than acting without the signal (because $q > p$). Alternatively, when environmental certainty is high, receivers should only follow extremely reliable signals. Therefore, the certainty of the environment should constrain the set of strategies available to signallers, and whether they can use complete honesty (i.e. perfect reliability), dishonesty, or something in between (we develop a model to explore this idea at length in the Supplementary material).

In natural signalling problems, certainty refers to a receiver's prior information about behaviourally relevant states. If, for example, 90% of males are high quality, then female receivers can be relatively confident about the quality of a particular signalling male; at the other extreme, if only 50% of males are high quality, then female receivers will be relatively uncertain about the quality of a signalling male. More generally, certainty, and its polar opposite uncertainty, reflects the variability in the prior distribution of the states that animals ‘signal about’, whether these states are differences in patch richness, male quality, motivation to fight, or hunger. If there are only two possible states, as in our experiment, the base rate p is sufficient to describe this uncertainty. In more complicated situations, with many possible states, one could use variance or the Shannon index (e.g. Shannon, 1948) to measure uncertainty.

Signallers should use receiver tolerance as an opportunity to influence receivers to make decisions that benefit themselves; this means signalling reliably when signallers and receivers agree on the best outcome, but decreasing reliability when conflict exists. The ability of signallers to capitalize flexibly on receiver tolerance depends on the assumption that signallers are sensitive to their influence over receivers. Our first experiment tests this assumption by showing the extent to which signallers exploit a unilaterally tolerant receiver (i.e. one that always follows signals). We expect signallers to change their signalling strategy in response to this receiver tolerance and opportunistically reduce reliability when conflict exists. Second, we test the hypothesis that unpredictable environments cause receivers to tolerate imperfectly reliable signals, which in turn allows signallers to signal dishonestly and exploit this tolerance. We expect the level of environmental certainty to modify receiver tolerance, and thus change whether signallers can signal dishonestly without causing the receiver to ignore signals.

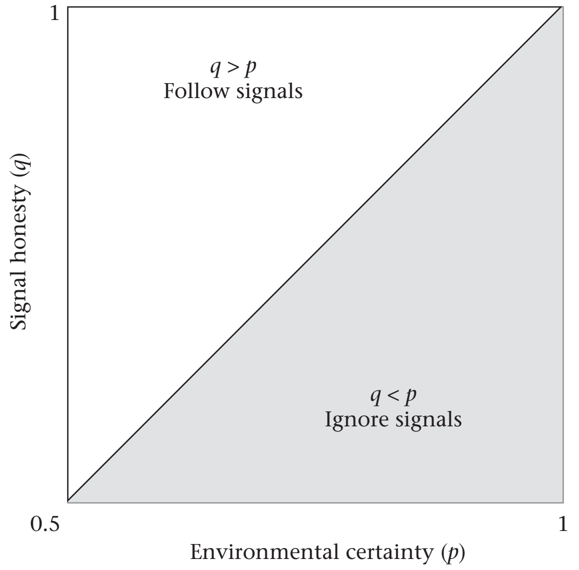

Figure 1. Relation between signal reliability (q) and environmental certainty (p). Receivers should only follow signals when $q > p$. There is more signal-following space (indicated by the white area) in uncertain environments (when p is near 0.5). Almost no signal-following space exists in certain environments (when p is near 1).

This set of two experiments placed pairs of captive blue jays, *Cyanocitta cristata*, in adjacent operant chambers (Fig. 2), where they played a signal–response game. The signaller used positional signals to indicate to the receiver which of two perches was rewarded with food. Using this design, we explored signalling equilibria achieved by learning in a novel laboratory situation. This is an atypical approach because most studies have focused on signals in natural contexts, where equilibria are maintained across generations and the interaction between genes and experience is typically undefined. Importantly, though, our methodology allows precise control over theoretically important variables. For example, we can precisely control environmental certainty by manipulating the probability that each of two perches is rewarded with food. We can also manage the incentives of signallers and receivers by regulating food rewards; creating conditions of mutual benefit or conflict.

GENERAL METHODS

Definitions: Honesty and Reliability

It is rather straightforward to measure the reliability of signallers' actions (e.g. signal A is consistently given in state A). It is less clear whether reliability is the equivalent of honesty, or if a lapse in reliability is dishonest (rather than an ‘honest mistake’) (Bradbury & Vehrencamp, 2000; Wiley, 1994). As such, we use the following definitions to identify signaller actions as honest or dishonest (although other definitions exist, we follow Polnaszek & Stephens, 2014; Searcy & Nowicki, 2005). First, the receiver must have a history of responding to signal S with action A. The action of a signaller is then ‘honest’ if it gives signal S when action A is in the best interest of the receiver. The same signal, S, is ‘dishonest’ when action A is in the best interest of the signaller but not in the best interest of the receiver. In the context of our game, an honest signal, when considered together with historical receiver responses, allows receivers to reliably identify the true state. In our experimental signalling games we know the economic payoffs to both players and thus can determine when these definitions are fulfilled.

Subjects, Housing, Experimental Apparatus

We randomly selected adult blue jays from our larger colony of jays. The group of subjects was of mixed sex, age and experimental histories. We kept subjects in individual operant boxes for 23 h/day throughout the duration of training and the experiments. The intervening 1 h provided time for daily health and weight checks, as well as the opportunity to clean and sanitize the operant boxes. We maintained the subjects on a 12:12 h light:dark cycle and provided water ad libitum. We tested the subjects in a closed economy, meaning all food was earned during the experiment.