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How noise determines the evolution of communication

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This essay focuses on a dozen predictions from a previous analysis of the evolution of communication in the presence of noise. First of all, (1) noise creates an unavoidable trade-off between two kinds of error by receivers. Furthermore, (2) a receiver's optimal criterion for response depends on the level of signals and (3) a signaller's optimal level of signalling depends on the receiver's criterion. As a result, (4) communication in noise can evolve to a joint optimum. (5) Communication at a joint optimum is honest on average. (6) Joint optima for communication in noise do not eliminate noise. (7) Many parameters of communication in noise remain poorly studied. (8) Noise leads to strong predictions for the evolution of exaggeration and thresholds. (9) Signals for advertising and for warning are contrasts in probable costs of errors. (10) The evolution of new signals and responses encounters a hurdle. (11) New signals and responses can evolve by exploitation. (12) Joint evolution of signallers and receivers has a predictable direction. These predictions will remain untested hypotheses until communication in noise is studied more thoroughly than it has been previously.

Following Darwin's (1972) detailed argument that animals' displays, or ‘expressions’, served for conspecific communication, almost half a century elapsed before the idea took hold among field biologists (Huxley, 1914). On first investigation, these displays seemed to be whimsical. Although Darwin had suggested his ‘Principle of Antithesis,’ according to which expressions with opposite meanings often had contrasting forms, there was scant suggestion that signals evolved to fit environmental situations. They even seemed to provide direct access to the phylogeny of species, without contamination by environmental adaptations (Heinroth, 1911, pp. 598–702; Lorenz, 1941).

This view was first shaken by Peter Marler's (1955, 1957) studies of the species distinctiveness of birds' vocalizations. He emphasized that although species specificity had advantages in some circumstances, such as territorial advertisement, it had disadvantages in other situations, such as vigilance for predators by flocks of mixed species. Furthermore, he argued that alarm calls in the latter situation had converged on sounds that were especially effective in hindering localization by predators. The time seemed right for reconsidering the importance of adaptations in animal's signals. The crucial advance came when Eugene Morton's (1975) pioneering studies revealed that birds' songs included adaptations to improve transmission through their respective habitats. Since then reports of adaptations in animals' signals have multiplied steadily. Attention has been given especially to adaptations that reduce attenuation, degradation, and effects of background environmental noise. Recently, reports have focused on human activities as widespread sources of environmental noise. Noise is now recognized to have manifold consequences for the evolution of communication.

Nevertheless, the crucial characteristic of noise with deep implications for the evolution of communication is still not generally appreciated. Noise, as Shannon (1948a, 1948b) originally realized, is best measured by receivers' errors. These errors are often thought just to introduce additional variance in responses to signals. As a result, adaptations to noise are assumed to consist of adjustments by signallers to minimize this extra variance. Although noise must often increase the variance of responses, it has even wider significance for the evolution of communication, because noise produces *unavoidable trade-offs for any receiver.* A receiver cannot maximize its performance in the presence of noise; it can only optimize these trade-offs. Furthermore, not only does the optimal behaviour of receivers depend on the behaviour of signallers, but the optimal

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behaviour of signallers also depends on the behaviour of receivers. Neither the evolution of signallers nor the evolution of receivers can be convincingly explained without taking into account the full consequences of noise.

Previous efforts to explain the evolution of signalling include those that emphasize the evolution of honesty (Enquist, Plane, & Röed, 1985; Getty, 1998; Grafen, 1990; Hurd, 1995; Johnstone, 1995; Maynard Smith, 1991; Maynard Smith & Harper, 2003; Számado & Penn, 2015; Zahavi, 1977; Zahavi & Zahavi, 1997), those that focus on the dynamics of mate choice (for instance, Kirkpatrick, 1982; Lande, 1981; Servedio, 2011) and those that focus of the evolution of stable cooperative interactions (for instance, Scott-Phillips, Blythe, Gardner, & West, 2012; Scott-Phillips & Kirby, 2013). Some previous analyses include the effects of noise as additional variance in responses (Johnstone, 1994) and even emphasize the consequences of the receiver's trade-offs in noise (Johnstone, 1998; Wiley, 1994), but none includes these trade-offs in combination with full interdependence of the receiver's and signaller's performances.

A recent effort to understand the interaction of receiver and signaller in noise has produced some unexpected results (Wiley, 2013a, 2013b, 2015). Some long-standing problems, such as conditions for the evolution of honesty and for evolutionarily stable signalling, appear in an entirely new light. The evolution of mate choice takes on a new dimension. Furthermore, it also becomes apparent that some critical features of communication have so far not received much, or any, investigation. The mathematical analysis of the optimal behaviour for receiver and signaller in noise has been described elsewhere (Wiley, 2013a, 2015). This essay instead isolates a dozen principles, or distinctive predictions, of the evolution of communication in noise. They reveal that noise is an essential factor in the evolution of all communication.

NOISE CREATES AN UNAVOIDABLE TRADE-OFF BETWEEN TWO KINDS OF ERROR BY RECEIVERS

In the presence of noise, there are exactly four possible outcomes each time a receiver makes a decision to respond or not: correct detection, correct rejection, false alarm and missed detection. These four possibilities are the logical combinations of two possible external conditions (noise only or noise plus signal) and two possible decisions by a receiver (respond or not). Two of the four are errors: false alarm and missed detection. In an analysis of the evolution of communication, these two would result in lower survival or reproduction. These two kinds of error are conceptually the same as type I and type II errors in analyses of statistical significance, or errors of commission and errors of omission. The probabilities of the four possible outcomes define a receiver's performance in any particular situation, a situation thoroughly analysed by signal detection theory (Green & Swets, 1966; Macmillan, 2002; Macmillan & Creelman, 2005).

These four outcomes are also a direct consequence of the defining feature of communication – responses (changes in behaviour) by one party (a receiver) to signals by another party (a signaller). A signal in this context is any pattern of energy and matter that can evoke a response *without providing all of the power for the response* (Wiley, 1994, 2006, 2013c). As a consequence, a receiver must make the decision to respond. To do so, it must include sensors (to detect impinging energy and matter), gates (switches to determine which inputs elicit a response), and amplifiers (to provide the additional power for the response). A receiver's gate for a particular response might take the form of a threshold (a minimal level of activation of the sensor) or a filter (an optimal level of activation) – or complex combinations of these two to produce a cognitive criterion for response.

The four possible outcomes each time a receiver checks its sensor are an exhaustive and mutually exclusive categorization of possibilities. Whenever a receiver's sensor cannot absolutely eliminate noise, these four possibilities recur. Furthermore, the two kinds of error cannot be simultaneously minimized. Adjusting a threshold or filter to reduce one inevitably augments the other (Wiley, 1994, 2006). False alarms and missed detections are therefore an inevitable trade-off for any receiver in noise. Noise does not just create extra variance in responses; it puts every receiver in a double bind.

A RECEIVER'S OPTIMAL CRITERION FOR RESPONSE DEPENDS ON THE LEVEL OF SIGNALS

Because of the inevitable trade-off between two kinds of errors, a receiver cannot minimize its errors overall; the best it can do is to choose a criterion for response that optimizes the trade-off. The criterion for an evolutionary optimum depends on (1) the probabilities of the four possible outcomes and (2) the consequences of each outcome for the receiver's survival and reproduction (the evolutionary payoff for each outcome). The probability of a correct detection, for instance, is a product of the probability that a signal actually occurs at the moment a receiver checks its sensor and the probability that the receiver responds in this situation. The probability that the receiver responds when a signal occurs depends in turn on its criterion for responses (the location of its threshold, for instance) and on the level of the signal in relation to any noise (the signal/noise ratio). In general, the probability of each of the four possible outcomes depends on (1) the probability that a signal occurs, (2) the receiver's criterion for response and (3) the level of the signal in relation to noise. A linear combination of these probabilities and payoffs for the four possible outcomes specifies the utility of a receiver's criterion for response (Wiley, 1994, 2013a, 2015). This approach is the basis of decision theory (van Neumann & Morgenstern, 1953).

Maximizing this utility depends on the trade-offs between the two possible errors and between the two possible correct responses. It also depends on the level of the signal in relation to the noise (the signal/noise ratio). Consequently, the receiver's optimal criterion for response depends in part on the level of signal produced by the signaller.

A SIGNALLER'S OPTIMAL LEVEL OF SIGNALLING DEPENDS ON THE RECEIVER'S CRITERION

Often, perhaps always, a higher level of signalling (greater intensity, size or saturation, or in general greater ‘exaggeration’) comes with costs, as a result of greater expenditure of energy, commitment of time, opportunities lost, or exposure to inappropriate receivers (such as predators, parasites or competitors). There have previously been two lessons drawn from these costs of signalling: (1) costs are necessary for the evolution of honest signalling (sometimes with a provision that the costs must be ‘wanton’ or ‘excessive’) (Maynard Smith & Harper, 2003; Zahavi & Zahavi, 1997); and (2) increasing costs multiplied by increasing benefits can produce evolutionarily stable signals, which in turn are honest (Getty, 1998; Nur & Hasson, 1984; Wiley, 2000, 2015).

It is easy to show that combinations of benefits and costs can produce equilibrial levels of signalling (including signals for advertisement and for solicitation; see Appendix and Wiley, 2000, 2015). These treatments however ignore the interdependent evolution of the signaller and receiver. The benefit for the signaller comes from responses (correct detections) by appropriate receivers, and the probability of these responses depends on the optimal criterion for response by these receivers.

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