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A game theoretic approach to multimodal communication

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Abstract Over the last few decades the animal communication community has become increasingly aware that much communication occurs using multiple signals in multiple modalities. The majority of this work has been empirical, with less theoretical work on the advantages conferred by such communication. In the present paper, we ask: *Why* should animals communicate with multiple signals in multiple modalities? To tackle this question we use game theoretic techniques, and highlight developments in the economic signaling literature that might offer insight into biological problems. We start by establishing a signaling game, and investigate signal honesty under two prevailing paradigms of honest communication – costly signaling and cheap talk. In both paradigms, without further constraint, it is simple to show that anything that can be achieved with multiple signals can be achieved with one. We go on to investigate different sets of possible constraints that may make multiple signals and multimodal signals in particular more likely to evolve. We suggest that constraints on cost functions and bandwidths, orthogonal noise across modalities, strategically distinct modes, multiple qualities, multiple signalers, and multiple audiences, all provide biologically plausible scenarios that theoretically favor multiple and multimodal signaling.

Keywords Multimodal communication · Game theory · Communication · Honest signaling

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Introduction

In recent years, the biological signaling literature has come to an increasing realization that much communication takes place using multiple signals, often in multiple modalities (Partan and Marler 1999, 2005). Though a good deal of empirical work has taken place to investigate complex and multimodal signaling systems, there has been much less theoretical work on the advantages conferred by communicating with multiple signals and the selective pressures that are likely to favor it over unimodal alternatives. In the present paper, the question we pose is simple: *Why* should animals communicate with multiple signals in multiple modalities? We take a game theoretic approach to this question. Game theory has provided a fruitful framework through which researchers have approached signaling in a wide variety of contexts. In animal behavior, game theoretic models have been used extensively to understand communication (e.g., Enquist 1985; Maynard Smith 1991; Számadó 1999; Lachmann et al. 2001; Bergstrom et al. 2002) including models of decision making during mate choice (e.g., Johnstone et al. 1996; Getty 1998; Noë et al. 2001),

animal contests (e.g., Smith and Price 1973; Maynard Smith 1974; Enquist 1985; Hurd 1997), and offspring provisioning (e.g., Godfray 1991; Johnstone and Grafen 1992; Godfray and Johnstone 2000; Johnstone 2004; Johnstone and Hinde 2006), while in economics, signaling games include models of education choices (Spence 1973), political announcements (Alesina 1988), and advertising (Milgrom and Roberts 1986). These models have provided important insights into when and how signaling might work, at least some of which have been borne out empirically (e.g., offspring provisioning, Hinde et al. 2010). Part of our aim is to review the ways in which theory developed for economic applications may be able to inform us about multimodal signaling in a biological setting.

We begin by setting up a canonical version of the signaling problem: a sender has some private information about the state of the world (which we will generally frame as something simple, such as their genetic fitness or current physical state) and a set of signals from which the receiver can infer information (for example, a display). The receiver then responds. The primary aim of this paper is to assess: (1) the impact on this model of allowing the signal space to be multimodal; and (2) possible theoretical advantages that a multimodal signal space might provide over a unimodal one. We begin by formally defining the signaling problem, and then by reviewing the two main forms of signaling in a unimodal setting. The first of these is the standard costly signaling model that has been heavily applied in both economics and animal communication (Spence 1973; Grafen 1990). The second is the "cheap talk" model in which there is no cost to sending any signal, and in which information can be transmitted from the sender to the receiver as long as the preferences of sender and receiver are not completely orthogonal (Crawford and Sobel 1982; Bergstrom and Lachmann 1998; Lachmann and Bergstrom 1998; Johnstone 1998; Silk et al. 2000; Brilot and Johnstone 2002, 2003). We then go on to consider multiple signal arguments and how these impact these models.

Preliminaries

In the canonical model of signaling, we have two players, a sender S and a receiver R. The sequence of play is as follows: (1) the sender observes the state of the world/quality of the sender, $q \in \mathcal{Q}$; (2) the sender chooses a signal to send from a set of possible signals, $s \in \mathcal{S}$; and (3) the receiver observes the signal s and (4) gives a response r from some set of possible response, $r \in \mathcal{R}$. The preferences over final outcomes for sender and receiver are represented by the functions $V(q,s,r)$ and $W(q,r)$, respectively. As an example, suppose the sender is a male and the receiver a female,

then the set of states $\mathcal{Q}$ could be the set of attributes that describe the male's attractiveness as a mate. To illustrate, we will assume the types are just *high* or *low*, represented by the state space $\mathcal{Q} = \{q_{\mathrm{L}}, q_{\mathrm{H}}\}$. The set $\mathcal{S}$ is the set of possible mating-related signals that can be sent (pheromones, calls, visual displays, etc.); and $\mathcal{R}$ is the range of possible decisions by the female, such as whether or not to mate with the male. The utility of the male sender, V, depends on the signal he sends and the response of the female, both of which may depend on his quality q. The utility of the female receiver, W, depends on the suitability of the male—his quality q—and her response r.

This setup is often described as an "action response" game in the biology literature (see Hurd and Enquist 2005 for a taxonomy of different types of communication games). Games of this type have been heavily studied within biology (for example, Grafen 1990; Hurd 1995; Lachmann et al. 2001; Bergstrom et al. 2002; Getty 2006) (Table 1). A variant of this game—the "Dual Action State Response" game—allows the receiver to have different types, a possibility that we discuss in section "Multiple messages for multiple qualities". Other variants, which for simplicity we do not cover in this paper, include models in which the welfare of the signaler enters the utility function of the receiver (Godfray 1991; Számadó 1999) and those that allow for multiple rounds of signaling from both sender and receiver (mutual signaling games, discussed in Enquist 1985 and Hurd 1997). However, our model is flexible enough to cope with the various different types of signals laid out in Hurd and Enquist (2005). Following this taxonomy, performance signals (which cannot be sent by some types) can be modeled by setting $V(q, s, r)$ equal to minus infinity for some type/signal pairs. "Handicap" signals, by which different signals have different costs for different types, and conventional signals, by which different responses have different benefits for different types, can also easily be accommodated .

We assume that the outcome of a signaling situation will be described by some equilibrium concept. The standard equilibrium for this type of game is the Perfect Bayesian (or sequential) equilibrium (For more details, see Kreps and Wilson (1982) and Fudenberg and Tirole (1991)). The equilibrium will be defined with the following objects:

- An *ex ante* probability distribution λ, over the set of types/states $\mathcal{Q}$.
- A *signal function* that maps types of senders into provided signals, $\sigma : \mathcal{Q} \rightarrow \mathcal{S}$. This function indicates the signal that each sender type exhibits for each possible quality level.
- A conditional distribution $\tilde{\lambda}_s$ over the set $\mathcal{Q}$, for each signal s. In the economics literature, this is thought

Table 1 Glossary of terms

Item	Meaning
	Primitives:
V	The fitness value of the sender where $V : \mathcal{Q} \times \mathcal{S} \times \mathcal{R} \to \mathbb{R}$
W	The fitness value of the receiver where $W : \mathcal{Q} \times \mathcal{R} \to \mathbb{R}$
H	The sender's fitness gain from the response, where the sender's fitness value V is separable into a gain H and loss C. This is a function $H : \mathcal{Q} \times \mathcal{R} \to \mathbb{R}$.
C	The sender's fitness cost from sending a signal, where the sender's fitness value V is separable into a gain H and loss C. This is a function $C : \mathcal{Q} \times \mathcal{S} \to \mathbb{R}$
λ	The probability distribution over the possible types of sender $\mathcal{Q}$
$\mathcal{Q}, q$	A set of types of sender, with generic element q
$\mathcal{S}, s$	A set of possible signals that the sender can provide, with generic signal s
$\mathcal{R}, r$	A set of responses that the female receiver of the signal can take, with generic element r
$\star, \diamond$	Generic discrete signals, where we will use $\star$ to represent a display and $\diamond$ the absence of a display.
	Equilibrium Objects:
$\tilde{\lambda}_s$	A conditional distribution over the possible types of sender $\mathcal{Q}$, given a received signal s
σ	A signal function, that associates a signal with every possible type of sender, $\sigma : \mathcal{Q} \to \mathcal{S}$
ρ	A response function, that associates a response with every possible signal, $\rho : \mathcal{S} \to \mathcal{R}$
$\mathcal{M}$	The set of vectors $\mathbf{MRS}(\hat{q}, s, r)$, given a specific signal s and response r, for types $\hat{q}$ of lower quality than some stated quality level q. $\mathcal{M}(q)$ is a correspondence $\mathcal{M} : \mathcal{Q} \rightrightarrows \mathbb{R}^n$.
	Economics Terms:
MRS	Marginal Rate of Substitution, this is the ratio between the marginal cost of sending a higher signal, to the marginal gain of getting a better response. This is defined in a signaling dimension/mode i as $\mathrm{MRS}_i(q, \mathbf{s}, r) := \frac{\partial C(q, \mathbf{s})}{\partial s_i} \Big/ \partial H(q, r) \partial r$, where we denote the vector of marginal rates of substitution across all modes as $\mathrm{MRS}(q, \mathbf{s}, r)$.
ICC	Incentive compatibility constraint, this is an equilibrium restriction
PBNE	Perfect Bayesian Nash Equilibrium

of as the beliefs that the receiver will have upon the receipt of each signal (We avoid this interpretation here so that readers do not infer that we are requiring higher mental states in animal decision makers.)

— A *response function* that maps signals to responses of the receiver, $\rho : \mathcal{S} \to \mathcal{R}$. This represents the receiver's response to each possible signal received from the sender.

The equilibrium conditions on these objects are that:

— For every state $q \in \mathcal{Q}$, the signal $\sigma(q)$ solves $\max_{s \in \mathcal{S}}[V(q, s, \rho(s))]$.
— For every signal $s \in \mathcal{S}$, the response $\rho(s)$ solves $\max_{r \in \mathcal{R}}[\mathbb{E}_q W(q, r)]$ where this expectation is taken over the conditional distribution $\tilde{\lambda}_m$.
— The distribution $\tilde{\lambda}_s$ is determined according to Bayes' rule according to λ and σ wherever possible.

The equilibrium conditions require that the receiver has the correct interpretation of the sender's type conditional on the signal sent, and that both sender and receiver are maximizing given the other's response.

How do we define "honest signaling" in this setup? One way would be to equate it to a totally separating equilibrium, in which the sender sends a different signal in every state of the world. Technically, this means that the function σ, the mapping from states of the world to signals used by the sender, is invertible on its co-domain, so that if the receiver gets any signal $s \in \sigma(\mathcal{Q})$, then they know for certain that the state of the world is $\sigma^{-1}(s) \in \mathcal{Q}$, and the distribution $\tilde{\lambda}_m$ puts all its mass at the point $\sigma^{-1}(s)$. This type of equilibrium is fully revealing in that after receipt of the signal, the receiver is as well informed as the sender. The sender sends the signal $s = \sigma(q)$, and after the receiver gets it, they know that $q = \sigma^{-1}(s)$. However, this is perhaps too restrictive. For example, if the recipient has only two possible responses ($\mathcal{R} = \{\text{mate, not}\}$) and there are three types of sender quality (*low*, *medium*, and *high*), then it may well be impossible to perfectly distinguish between all three types. Yet this does not really matter—as the recipient only has two possible actions, they only really need to distinguish between two groups. For example, if females would happily mate with high or medium quality males, then distinguishing between these two types is unnecessary.

An equilibrium in which low-quality males sent one type of signal, and medium and high types sent another would provide all the information that the receiver needs. If instead the female has three options (for example, mate monogamously, mate non-monogamously, or not mate), and the optimal response is different depending on the type of male, then there would be a benefit to the recipient of distinguishing between *medium-* and *high*-quality individuals. Thus, an equilibrium supports honest signaling in our view if the only types of signaler who send the same signal are those that would evoke the same optimal response from a fully informed receiver.

The alternative to a separating equilibrium is a "pooling equilibrium," in which multiple types that the recipient would ideally like to distinguish their response across send the same signal. So for example, *low-* and *medium*-type males send the same signal despite the fact that the female would like to mate with the medium type but not the low type. We can distinguish between a "fully pooling" equilibrium, in which all types send the same signal, and a "semi-separating" (or partially honest) equilibrium, in which some, but not all types are lumped together. Note that in a pooling equilibrium, the receiver is not deceived, but they cannot perfectly identify the state of the world from the signal that they receive: the concept of equilibrium we have defined does not allow for the receiver to be "fooled" in the sense of having an incorrect posterior distribution $\tilde{\lambda}_s$ ("false beliefs").

Costly signaling

Unimodal model

One mechanism that can ensure a separating equilibrium is if different types of sender have different costs for sending different signals. We therefore introduce a cost for signals given by $C : \mathcal{Q} \times \mathcal{S} \rightarrow \mathbb{R}$ and additively separate the preferences for the sender into a fitness value $H(q, r)$ from the response of the receiver, and a cost for the signal $C(q, s)$, so that the sender's preference is given by

$$V(q, s, r) = H(q, r) - C(q, s).$$

For example, suppose it is more costly for a low-quality male (q_L) to present a mating signal (send the color signal ★, as opposed to the no color signal ◇) than it is for a high-quality male (q_H). So $C(q_L, ★) > C(q_H, ★) > C(\cdot, ◇)$. The female receiver's response is to mate only with colorful males on the basis that colorful males are always high quality, so the response is $\rho(★) = $ Mate and $\rho(◇) = $ Not. (A natural assumption for the receiver's utility is that $W(q_H, \text{Mate}) > W(q_H, \text{Not}) = W(q_L, \text{Not}) > W(q_L, \text{Mate})$.) Both types of male would prefer that the

female mates with them, so that $H(q, \text{Mate}) > H(q, \text{Not})$ for all q. The color–signal mechanism is therefore an honest equilibrium whenever honesty has a relative gain for both types. The condition for the high-quality sender is that

$$H(q_H, \rho(★)) - C(q_H, ★) \geq H(q_H, \rho(◇)) - C(q_H, ◇),$$

which we can just rewrite so that the gain from signaling exceeds the extra incurred costs

$$H(q_H, \rho(★)) - H(q_H, \rho(◇)) \geq C(q_H, ★) - C(q_H, ◇).$$

However, the gain cannot be so large that the low-type can profitably mimic the signal and achieve a higher payoff, so we need that

$$H(q_L, \rho(★)) - H(q_L, \rho(◇)) \leq C(q_L, ★) - C(q_L, ◇).$$

In the economics literature, these are referred to as the *incentive compatibility constraints* (ICC) (such conditions have been discussed commonly in the biological signaling literature, see, for example, Grafen ([1990](#)), Hurd ([1995](#)), and Szamado ([1999](#)). More generally, for every type $q \in \mathcal{Q}$, it must be that if (σ, ρ) is an honest signaling equilibrium, then we require that for all signals $s \in \mathcal{S}$

$$U_S(q, \sigma(\theta), \rho(\sigma(q))) \geq U_S(q, s, \rho(s)),$$

or if the preference function U_S is separable as before into a cost function C and a fitness value H, then this condition is equivalent to saying the benefit of being honest outweighs the additional cost for every other signal s:

$$H(q, \rho(\sigma(q))) - H(q, \rho(s)) \geq c(q, \sigma(q)) - c(q, s). \quad (1)$$

Clearly, we can satisfy the ICCs by either having the type q derive more benefits from the response $\rho(\sigma(q))$ than from some alternative response $\rho(s)$ induced through a signal $s \neq \sigma(q)$; or from having additional costs associated with the signal s over and above the signal $\sigma(q)$; or any combination of the two that satisfy ([1](#)). So, costly signaling works either through relative differences in the costs and/or benefits. The signal itself ends up being somewhat flexible in a fully separating equilibrium—as long as the signal has the relevant cost structure required for the ICC, the actual signal used is just a proxy representing the true state/quality. Given a rich enough signal space, without loss of generality, we can relabel the set of sent signals, $\sigma(\mathcal{Q})$, to be equal to the state space $\mathcal{Q}$. A signal is now just a direct declaration of type, and the cost function $C(q, \hat{q})$ is the cost incurred by an actual type q in pretending to be a type $\hat{q} \in Q$. For an equilibrium signal strategy to be honest, we therefore require that $\sigma(q) = q$. The ICCs can be transformed to

$$H(q, \rho(q)) - H(q, \rho(\hat{q})) \geq C(q, q) - C(q, \hat{q}) \quad (2)$$

for all types $q, \hat{q} \in Q$. This is a global condition where no quality type wants to pretend to be any other quality type, but it also implies a local condition in a neighborhood of the

true quality level q (if the quality, response, and preferences are continuous and smooth) so that

$$H(q, \rho(q)) - H(q, \rho(q + \Delta q)), \geq C(q, q) - C(q, q + \Delta q).$$

In the limit, this implies that

$$\left.\frac{\partial C(q, \hat{q})}{\partial \hat{q}}\right|_{\hat{q}=q} \geq \left.\frac{\partial \rho(\hat{q})}{\partial \hat{q}}\right|_{\hat{q}=q} \cdot \left.\frac{\partial H(q, r)}{\partial r}\right|_{r=\rho(\theta)}.$$

So the slope of the cost for every type must be greater than the product of the response function gradient and the slope of the fitness value from a higher response.

The key question is: What properties do these cost functions have to have in order to support honest signaling? One very general condition that guarantees the existence of an honest signaling equilibrium is the "single crossing property" (see Milgrom and Shannon (1994); for reviews, see Edlin and Shannon (1998), Sobel (2009), and Roddie (2011)). Variants of the single crossing property have been used in the economics literature on signaling since (Spence 1973)—one variant is commonly referred to as the Spence-Mirrlees condition. While the exact statement of the condition depends on the nature of the type and signal space, the intuition can be gained by assuming that types, signals, and responses can be represented by numbers, such that higher numbers represent better types, more costly signals, and more favorable responses (from the point of view of the signaler). The single crossing property then states that for any two types such that

$$q_1 < q_2$$

and any two responses such that

$$r_1 \leq r_2,$$

then

$$H(q_1, r_1) - C(q_1, s_1) \leq H(q_1, r_2) - C(q_1, s_2)$$

implies that

$$H(q_2, r_1) - C(q_2, s_1) \leq H(q_2, r_2) - C(q_2, s_2).$$

In words, this condition states that, if type q_1 prefers to send the signal s_2 to get the better response r_2 rather than the signal s_1 in order to get response r_1, *then* any *better* type q_2 must also be prepared to make that trade. Put another way, it must be the case that the rate at which signalers are prepared to trade off more costly signals for better responses is increasing in their type. If the problem is differentiable, then this condition can be restated as requiring that the marginal rate of substitution between signal and response is

decreasing in type, where the marginal rate of substitution (MRS) is defined as

$$\mathrm{MRS}(q, s, r) = \frac{\dfrac{\partial C(q, s)}{\partial s}}{\dfrac{\partial H(q, r)}{\partial r}}.$$

The single crossing property is so called because it ensures that indifference curves in (s, r) space for any two types will cross at most once. Again, these conditions should be relatively familiar to biologists—for example, from Grafen (1990) (while Getty (1998, 2006) extends the result to the case in which the cost and benefit functions are not additively separable).

One important note here is that the single crossing property and other costly signaling paradigms require only that giving higher quality signals is *relatively* more costly for the low-quality signaler than the high-quality signaler, a point made forcefully in Lachmann et al. (2001). It is not necessary for the high-quality signal to be costly to the high-quality signaler, or for the low-quality signal to be costly to the low-quality signaler (contrary to Grafen (1990)). As such there is not necessarily any realized cost to any signaler in equilibrium, and the "handicaps" proposed by Zahavi (1975), in which signalers must pay a cost to give their own signal, are neither a necessary nor a sufficient feature of honest signaling under the costly signaling paradigm. Biological mechanisms that can fulfill the single crossing property and allow honest signaling are varied, and are discussed at length elsewhere (e.g., Számadó 2011).

It is also important to note that when interactions are repeated, the appropriate preferences for modeling are those that describe the player's utility for the full sequence of outcomes from the repeated games, rather than for a single game. This means that there are games that satisfy ICCs with repeated interaction even when they would not for a single interaction. Honest signaling can even be supported in cases where the per-period benefit and signal cost are exactly the same for all sender types, but where the dynamics lead to differential cost/benefits. For example, consider a pair of breeding birds where the rearing of young by the pair is repeated over two breeding seasons. Before the first breeding season, males display, and then the female chooses whether to mate or not. During the first breeding season, if the female chooses to mate with a male, then the male's type is *perfectly* revealed to the female. If the female prefers not to mate with low-quality types, then she will always break off the relationship with such males after the first breeding season. Thus, a low-quality male who is chosen to mate will be able to do so only for one season, while a high-quality mate will do so for further seasons. Even though low- and high-quality males may have exactly the same

cost of signaling and benefit from mating *in each breeding season*, the *high* type is able to spread this cost over a longer relationship.

Multiple signals

What about multiple signals? It turns out that there is a natural generalization of the single crossing property when signals are multidimensional. This condition was introduced by Engers (1987) and applied to the canonical signaling game by Ramey (1996). In biology, conditions under which honest signaling can be supported with multiple signals under the specific case of linear cost functions have been characterized by Johnstone (1995). For simplicity, assume that types and responses can still be represented by a single number, but now a signal consists of an N dimensional vector, mirroring N different displays/signals that have been sent. Obviously, with multiple signals, honest signaling remains possible whenever any one signal dimension satisfies the single crossing property: the receiver could pay attention only to that dimension of signaling. However, separation can also be achieved even when there is no one signal whose MRS is strictly decreasing in type—as long as at any given point in the type space there is some signal that can be used to differentiate between types.

Engers (1987) provides a sufficient condition. To explain it, we need to extend our concept of MRS to take into account that we now have a vector of signals, so that:

$$\text{MRS}(q, s, r) = \begin{pmatrix} \frac{\partial C(q,s)/\partial s_1}{\partial H(q,r)/\partial r} \\ \vdots \\ \frac{\partial C(q,s)/\partial s_N}{\partial H(q,r)/\partial r} \end{pmatrix}.$$

We now write $\text{MRS}(q, s, r) \geq \text{MRS}(\hat{q}, s, r)$ *if and only if*

$$\frac{\partial C(q, s)/\partial s_i}{\partial H(q, r)/\partial r} \geq \frac{\partial C(\hat{q}, s)/\partial s_i}{\partial H(\hat{q}, r)/\partial r}$$

for every dimension i of the signal space.

Consider some type q, and any signal s and response r. For separation to be supported, clearly it cannot be the case that for some type $\hat{q} > q$ that $\text{MRS}(q, s, r) < \text{MRS}(\hat{q}, s, r)$. That is, it cannot be the case that for some type better than q the MRS is higher in every signal dimension. If this were the case, then any signal that $\hat{q}$ would be prepared to send to demonstrate being a higher type would be mimicked by q.

Thus we know that separating definitely can be supported if the MRS of any one signal is decreasing in type, and definitely cannot be supported if the MRS of *all* signals increases in type. It is natural therefore to look for some

condition between these two extremes that allows truthful signaling to be supported. The condition provided by Engers (1987) asks that the MRS vector of a given type cannot lie above any weighted combination of MRS vectors from a lower type—a weak form of monotonicity in the way that the MRS vector changes with type. Formally, define the set

$$\mathcal{M}(q, s, r) := \left\{ \text{MRS}(\underline{q}, s, r) \,\middle|\, \underline{q} \leq q \right\}$$

as the collection of MRS vectors evaluated at (s, r) from types that are *no better* then q. The convex hull of this set is all the MRS vectors that can be formed as weighted averages of MRS vectors in $\mathcal{M}(q, s, r)$. The condition of Engers (1987) states that there must be no type $\hat{q} > q$ such that

$$\text{MRS}(\hat{q}, s, r) \geqq t$$

for any t in the convex hull of $\mathcal{M}(q, s, r)$. This condition is weaker than requiring MRS(q,s,r) to be decreasing in q along some signal dimension i, but stronger than just ruling out the possibility that it increases along all dimensions. It provides the natural extension to the single crossing property for multiple signals. Multiple dimensions of a signal might then allow for honest signaling even where each separate signal dimension does not satisfy the single crossing property.

Cheap talk

Inspecting the ICC constraints in equation (2) where the signal space is simply a statement of type, if we were to make the cost function $C(\cdot, \cdot)$ zero for all signals and types, we can still maintain an honest equilibrium so long as for all types $q_1, q_2 \in \mathcal{Q}$

$$H(q_1, \rho(q_1)) \geq H(q_1, \rho(q_2)).$$

The condition implies that no sender type wants to be dishonest, and the receiver takes the optimal response for each type. However, this is only true if the preferences of the sender and the receiver are completely aligned over all the responses in $\mathcal{R}$. If there exists some sender type q_1 that strictly prefers the action taken in response to another type q_2, then there can be no honest equilibrium.

Still, with partial alignment of preferences between the sender and receiver, then there may be partially "honest" equilibria even with no difference in the costs of signals. (So the utility of the sender does not vary with the signal sent—i.e., $V(q, s, r) = H(q, r)$ for all $s \in \mathcal{S}$.) Referring to the ICC constraint over the signal space $\mathcal{S}$ given in (1), we can have a partially honest equilibrium

(i.e., a signal function σ such that some types send the same signal) when for every type sender q and every signal s

$$H(q, \rho(\sigma(q))) \geq H(q, \rho(s)). \tag{3}$$

This type of model is referred to as cheap talk (for example, Crawford and Sobel 1982; Bergstrom and Lachmann 1998; Lachmann and Bergstrom 1998; Silk et al. 2000; Brilot and Johnstone 2002, 2003). In a partially honest equilibrium, some information about type is transmitted, so that the conditional distribution of types $\tilde{\lambda}_s$ is different from the ex ante distribution λ.

When there is partial alignment in preferences, then different types of sender can send different signals in equilibrium to convey partial information. Communication will be governed by the condition in (3): all sender types q that send the signal $\sigma(q)$, must prefer the induced response $\rho(\sigma(q))$ to that induced by any other signal $s \in \mathcal{S}$. The degree of information transfer depends critically on the alignment between the sender and receiver over the responses taken.

Animal behavior examples with complete alignment may include the giving of predator alarm calls in primate groups. Here, individuals need the collective vigilance and strength of other group members in watching and possibly fighting off the predator, and for female group members living in female philopatric species, most other group members are additionally close relatives. A good example of partial alignment is the signaling of offspring need to provisioning parents (for example, Nöldeke and Samuelson 1999; Johnstone 2004; Johnstone and Hinde 2006; Hinde et al. 2010). Here, the sender (the offspring) is partially aligned with the receiver (the parent), in that both want the sender to survive. However, the genetic relatedness difference between the two mean that interests are not perfectly aligned, as the offspring may want to exaggerate their need to increase their own survival at the expense of the parent and present/future siblings (Trivers 1974).

In the case of cheap talk, without additional constraints, allowing for multiple dimensions of the signal makes no difference to the signaling game. In the costly signaling scenario, we needed to extend our model to demonstrate that costly signaling with multiple signals is the same as with one; here as the cost function is zero, there is no extension required or that can be undertaken. The signal in cheap talk functions purely as a medium for information exchange, and we can arbitrarily relabel signals. Because all signals are without cost, the signal is only useful through its inferred content. Complex multidimensional signals would be required only if the signal set in any single dimension were bandwidth constrained and more information transfer were desired than the signaling dimension could contain, a topic we discuss in the subsection "Constraints on cost functions and bandwidth".

Multisignal and multimodality arguments

The above framework helps identify the circumstances in which honest signaling can be supported with multiple signals. However, it does not provide a compelling reason *why* an organism might want to choose to use multiple signals, or signals that come in different modalities, over a unimodal alternative. If anything it highlights the degree to which, without further assumptions, multiple signal models look very much like their single signal counterparts. In this section, we review a selection of additional assumptions, or constraints on the nature of the signaling game, under which multiple signals or multiple modalities would be strictly preferable. It is worth noting that many of these conditions have been discussed in the biological literature on multimodal communication. Here, we give formal demonstrations of many of these principles, while also discussing some scenarios that have received little direct attention from biologists as mechanisms likely to lead to multiple and multimodal signals. One important point to note is that we can only investigate how these constraints act on multiple signals, rather than on multimodal signals per se. It is up to our understanding of what such biological constraints might look like in practice to determine whether they are likely to lead specifically to multimodal (over multicomponent and multiple unimodal) communication.

Constraints on cost functions and bandwidth

We begin by discussing a setting in which there are constraints on the costs of single signals, or the amount of information that they can convey.

Recall that under the costly signaling framework, there are conditions that the cost function must satisfy in order to support honest signaling. Taking q_L as a low-quality type and q_H as a high-quality type, the ICC condition (2) tells us that the relative cost of imitation ($C(q_L, q_H) - C(q_L, q_L)$) must be larger that the relative fitness benefit, $H(q_L, \rho(q_H)) - H(q_L, \rho(q_L))$, for honest signaling to be an equilibrium. If the optimal response were that the female only wants to mate with high-quality males, so that $\rho(q_H) = $ mate and $\rho(q_L) = $ not, this means that as the benefit of mating becomes large, the effective cost of imitation must also become large. If there is some physical constraint on the cost that can be incurred in sending a particular signal, then this implies an upper limit to the benefit of mating for which honest signaling can be supported. Suppose the function $C(\cdot, \cdot)$ has an upper bound $\bar{c}$ and a lower bound $\underline{c}$, then it is impossible to support honest signaling if $H(q_L, \text{Mate}) - H(q_L, \text{Not}) > \bar{c} - \underline{c}$

This problem could be solved by using a number of costly signals. Imagine that, rather than using a single signal, we have N signals (for simplicity, take simple replications

of the same signal). Furthermore, assume that in equilibrium, the female decides to mate if and only if she receives N repetitions of the high-type signal. The ICC therefore becomes

$$H(q_L, \rho(q_L)) - H(q_L, \rho(q_H)), \geq N \cdot [C(q_L, q_L) - C(q_L, q_H)]$$

Thus, with the same bounds $\overline{c}$ and $\underline{c}$ on the signal cost, honest signaling with N modes can be supported for mating benefits up to $N \cdot (\overline{c} - \underline{c})$. So long as $\overline{c} > \underline{c}$, we can create an arbitrarily costly signal by combining multiple signals.

In the case of $N = 2$, we would simply rewrite the signal space to be

$$\mathcal{S}_2 = \{(q_L, q_L), (q_H, q_L), (q_L, q_H), (q_H, q_H)\}$$

In a separating equilibrium distribution, $\tilde{\lambda}_{(q_H, q_H)}$ has certainty on the sender being the high type, and every other signal yields a distribution with certainty for the sender being the low type. Importantly, if the cost functions are too constrained within a single dimension, then every signal element across these multiple modes must be received, as the inference for only a partial signal in one mode must still be that the sending male is the low type.

A second obvious theoretical reason that would make multiple signals *necessary* is limited bandwidth in a given signal mode. Consider the case in which there are three types of sender, $\mathcal{Q} = \{q_L, q_M, q_H\}$, and that the receiver would like to respond differently to each with a corresponding fully informed response $\mathcal{R} = \{r_L, r_M, r_H\}$. Clearly, in order to support honest signaling, the signal space $\mathcal{S}$ must contain at least three distinct signals. If a unidimensional signal offers the potentially for only a binary distinction (on or off, colorful or not, loud or quiet), then further signal dimensions are required, regardless of the costs. Two binary signals can (subject to the ICCs) distinguish four types in an honest equilibrium, while three signals allows for eight separated types. Even if the signal dimension were non-binary, transmission mistakes might become more likely as an increasing number of types need to be distinguished within a single mode/dimension of signaling. If a receiver needs to categorize a call into one of eight different "loudness" types, then they are more likely to make mistakes than if they need only to distinguish between a binary "loud" and "quiet" signal and two other binary modes. As shown elsewhere, the use of multimodal signals specifically, as opposed to simply multichannel signals in the same modality, may be particularly effective at ensuring that communication occurs reliably without error (Ay et al. 2007).

Finally, signal dimensions may be limited in the type of information that they can reliably convey about differing traits. Assume that the desirability of a male depends on both body size (which can be large or small) and an ability to provision offspring (which can be at high or low levels), giving four types. It may be that there is simply no physical mode in which the signal cost can be made dependent both on the animal's body size and its provisioning ability. With a single signal mode, the best that might be conveyed is simply to differentiate on one dimension or the other, while multiple signals can allow full differentiation.

Orthogonal noise and multisensory environments

One justification for why multimodality specifically may be favored comes from the existence of noise that affects a signals transmission or reception, either in the environment (Hauser 1997) or in receiver perceptual systems (Rowe 1999), and does so independently across different modalities. Examples of such effects are common in the empirical literature on animal communication, and such efficacy-based effects are particularly likely to lead specifically to multimodal signaling. For example, in anuran mating calls, the transmission of male vocalizations is demonstrably disrupted by the background noise of other conspecific signalers (Grafe et al. 2012, Preininger et al. 2013). As the visual cue of the throat sac which inflates and deflates as calls are made is not disrupted in the same way, females have evolved to pay attention to both elements of the signal. As a consequence, the vocal–visual multimodal call is more effective in eliciting female responses than either unimodal element (Taylor et al. 2008, Preininger et al. 2013, Grafe et al. 2012). Similarly, signaling noise in different modalities may change as precise features in the signaling environment changes. Wolf spider males give both visual and seismic signals that females use in mate choice (see Uetz and Roberts 2002 for review). Visual signal transmission may be affected by current light levels, while independent seismic signals are affected by the present substrate, with dry leaves attenuating seismic signals much better than dirt or rocks (Uetz et al. 2013) .

Consider again the simple case of two types, $\{q_L, q_H\}$ and two signals $\{s_L, s_H\}$, such that, in an honest signaling equilibrium, type q_i sends signal s_i. However, due to environmental noise, a signal sent as s_H is received as s_L with probability ϵ. (We can also think of this as s_H being "signal," and s_L "no signal," where ϵ is the probability that the signal is not received.)

In a separating equilibrium, the probability that the sender is type q_L conditional on receiving the low-type signal s_L is given by Bayes' rule as

$$\tilde{\lambda}_{s_L}(q_L) = \frac{\lambda(q_L)}{\lambda(q_L) + \lambda(q_H)\epsilon}$$

where $\lambda(q)$ is the initial proportion of q types in the population. (Note that in this simple example if the receiver

receives the signal s_H, then they know for sure that the sender is of the high type.)

If we assume that the full information outcome is for the receiver to mate with the high type (response r_H) but not with the low type (response r_L), so that $W(r_L, q_L) > W(r_H, r_L)$ and $W(r_H, q_H) > W(r_L, q_H)$, then noise in the process leads to two types of potential inefficiency. First, a separating equilibrium can only be supported if it is optimal for the receiver to give the response r_L upon receipt of s_L. This implies an upper bound on the size of the noise

$$\frac{[W(r_L, q_L) - W(r_H, q_L)]}{[W(r_H, q_H) - W(r_L, q_H)]} \cdot \frac{\lambda(q_L)}{\lambda(q_H)} \geq \epsilon.$$

The higher the probability of transmission errors, ϵ, the harder it is to support a separating equilibrium.

Second, ϵ of the time, the receiver will give the response r_L when the sender's type is actually q_H, because the wrong signal is received. Again, this inefficiency is increasing in ϵ.

Now consider the case in which the sender must choose both whether to send the signal s_H^A or s_L^A in some mode A, but also whether to send the signal s_H^B or s_L^B in a separate mode B. Additionally, assume that, if the high signal s_H^i is sent in either mode i, then with probability ϵ the signal received is s_L^i. However, transmission errors across modes are independent of one another.

We will look for a separating equilibrium such that the low type chooses to send s_L^i in both modes, while the high type sends s_H^i in both modes. Thus, the probability of a sender being of type q_L conditional on receiving (s_L^A, s_L^B) is

$$\tilde{\lambda}_{(s_L^A, s_L^B)}(q_L) = \frac{\lambda(q_L)}{\lambda(q_L) + \lambda(q_H)\epsilon^2},$$

while for every other received signal, the sender is inferred to be the q_H type with probability one. For the receiver to want to give the response r_L upon receipt of $\{s_L^A, s_L^B\}$, it must be the case that

$$\frac{[W(r_L, q_L) - W(r_H, q_L)]}{[W(r_H, q_H) - W(r_L, q_H)]} \cdot \frac{\lambda(q_L)}{\lambda(q_H)} \geq \epsilon^2,$$

and because $\epsilon > \epsilon^2$ the constraint on the receiver is softened, while the same order of ICC condition as the unimodal case is maintained for the low-type sender. (Though it is now the minimum-cost signal within the two modes). Similarly, the probability of the receiver taking response r_L when the sender's type is q_H reduces to ϵ^2 from ϵ.

Note that, unlike the cost-constraint interpretation given in the subsection "Constraints on cost functions and bandwidth" for multiple modes, not all high-type signaling modes need to be received to induce the high response r_H. In this example the partial signals (s_H, s_L) and (s_L, s_H) must also lead to the r_H response. Because only high types send the signals s_H^A and s_H^B, Bayes' rule implies a certain posterior on the q_H type following receipt of any partial signal. (This observation allows differentiation between the "noisy

signal" and "constraints on cost functions" motives for multimodal signaling, through experimental examination of the manner in which animal receivers react to a high–low signal combinations).

Of course, for this to be a separating equilibrium, it has to be the case that sending (s_H^A, s_H^B) is optimal for the high type. Assuming separable signal costs C_A and C_B in each signal mode, the high type's cost/benefit must satisfy the following for both modes i to be used in signaling:

$$\epsilon(1 - \epsilon) \geq \frac{C_i\left(q_H, s_H^i\right) - C_i\left(q_H, s_L^i\right)}{H(q_H, r_H) - H(q_H, r_L)}.$$

If this were not the case the high sender would prefer to send only a unimodal signal in the cheapest mode. This simple example illustrates that, if the designer of a game can freely choose the costs associated with different types of signal, but where noise is an environmental constant, greater efficiency might be achieved with a multimodal signal over a single signal mode. Given that noise within a specific modality is likely to affect the transmission of additional signals in that same mode, but that signals in a different mode are not likely to be affected by that noise to the same extent, these conditions seem particularly likely to lead specifically to multimodal signaling. Further issues arise when the range of environments in which individuals communicate is highly variable (multiple sensory environments, see Hebets and Papaj 2005), or when environments are themselves highly stochastic (see discussion in Bro-Jørgensen 2010).

Strategically distinct modes

The previous explanations for multimodality have focused on possible advantages of using multiple channels that focus on the necessary cost requirements for the signals chosen in honest signaling. We now discuss multimodal signaling where the signaling dimensions differ in a strategic sense. First we will make a distinction between components of the signal that are based on decisions made by the animal on the level of signal expression, and components of the signal which are immutable but noisy signals of type (such as indices), over which the animal has no power to change. Naturally, these different components will manifest themselves as differing modes. Our example will show how a composite signal from both these components can yield *cheaper* honest equilibria. In the subsection "Costly advertising, diret benefits, and repeated interactions," we will examine modes which differ with respect to whether the receiver directly benefits from the signal. That is, the receiver will directly benefit from some sent signals in one channel (for example, where the sender provides them with food or grooming), while there is no direct benefit in the other. Both

signals can be used to provide an indirect benefit though—increasing the perceived quality of the sender. We will show that in equilibrium, it may be necessary for both signals to be used within an honest equilibrium. This is an example of necessity of multiple signals when multiple modes are available, derived through the ICC constraints and optimal response from the receiver.

Costly signals and indices

Multiple components of an informative signal may be distinct in terms of the degree to which each channel is a behavioral choice for the animal, which in turn would naturally manifest itself through differing modes. Mechanical constants such as the size of an animal's chest cavity may limit the frequencies that the animal can achieve, but the decision on whether to undertake a behavioral display may be voluntary (or act through an involuntary evolutionary equilibrium response). However, combinations of signals with behavioral and indexical components can cause interesting, potentially non-monotone effects, allowing for cheaper honest equilibria, where a smaller subset of the typespace $\mathcal{Q}$ sends costly signals. An example of this from the economic literature is Feltovich et al. (2002), which we will briefly illustrate. They demonstrate that alongside an index, the *absence* of a costly signal can be used to signal high quality. In the presence of indices, this example illustrates how ICC constraints are now modified to be conditioned on the index.

We consider again three types q for a male sender: $\{q_L, q_M, q_H\}$. Information can be sent through two channels: a signal s^D that males can choose to display or not, and an index s^I over which the male has no choice. s^D can take two values, either $s^D = \bigstar$, which we will interpret as a display of strength and which has some cost $C(\bigstar, q) > 0$, or the display $s^D = \diamond$ which we will interpret as not displaying and is costless for all types. Red deer are a sufficient working example for the purposes of illustrating the model. Individual males have cost-free indices, as certain aspects of their vocalizations (formants) can indicate their body size (Reby et al. 2005), with females preferring the roars of larger males (Charlton et al. 2007). Alongside the costless index, they can undertake costly "parallel walks" with persistent challengers which may lead to fights (Clutton-Brock and Albon 1979).

Obviously, if the index is perfectly informative, then further signaling is unnecessary, so for the purposes of the model, the vocalization index will be noisy, such that the realized index signal is either $s^I = H_I$ or $s^I = L_I$. (Consistent with this assumption of noise in the indexical cue, it has been shown that red deer males do have the ability to vary their formant frequencies by a small amount in relation to those of a perceived rival by changing the extention of their vocal tract, see (Reby et al. 2005)). When the

male's type is q_H, the index signal s^I is H_I with certainty, and the call always signals a large chest size. When the male's type is q_L, the index s^2 is L_I with certainty, and calls always indicate a small chest size. However, the *middle* type's call can be confused with either *high* or *low* types, and we will assume a 50–50 chance of the animal's calls producing either signal. As such, the index does not perfectly signal the male's fitness—if it did, there would be no need for anything other than the index to signal type. Note, that we will assume that all males vocalize at some point, which we could support by assuming that the absence of a call is synonymous with the L_I index.

There is an honest equilibrium here where the *low*- and *high*-type males both send the non-costly display signal $s^D = \diamond$, so they do not engage in walks or fights, while the *middle*-type males send the costly display signal $s^D = \bigstar$. The receiver female has three responses, r^H, r^M, and r^L, that she uses if she knows with certainty the type of male she is interacting with. The honest equilibrium responses for the signals are $\rho(\bigstar, H_I) = \rho(\bigstar, L_I) = r^M$, $\rho(\diamond, H_I) = r^H$, and $\rho(\diamond, L_I) = r^L$. That is, the female believes all the males who fight are the *middle* type, regardless of the signal she receives from their vocal index. Those who do not fight (do not send the costly display signal $\bigstar$) are classified according to the vocal index.

The conditions for each sender to go along with the honest equilibrium are then

$$H(\theta_L, r^L) \geq H(\theta_L, r^M) - C(\bigstar, q_L)$$
$$H(q_M, r^M) - C(\bigstar, q_M) \geq \tfrac{1}{2} \cdot H(q_M, r^H) + \tfrac{1}{2} \cdot H(q_M, r^L)$$
$$H(q_H, r^H) \geq H(q_H, r^M) - C(\bigstar, q_H).$$

That is, the *low* type should find the cost of fighting too great to want to pretend to be a *middle* type. The *middle* type must find the cost of fighting is worth it not to be confused either with the *low* or *high* type—if they do not engage in costly signaling there is a 50–50 chance of being confused with a q_L or q_H type. So long as the response r^H is highly desirable, the *high* type's constraint is easily met. For them, *not sending a costly signal* is in fact a signal that they are the *high* type. Refusing to participate in fights or displays of strength can increase the inferred quality, so long as those putting on costly displays are trying to distance themselves from the q_L types. Here, costly signaling is used only by the q_M types, with the other two signaling their relative quality with the vocal index and absence of the display.

The central point of the example is to illustrate that multiple signaling modes in which some are behavioral decisions by the animal and others are fundamental characteristics of their quality (indices) substantially modify the necessary cost constraints. This can lead to results which look strange when set in the previous paradigm (high types send a less costly signal than the medium types), but are rationalized

once we understand the interaction with the index signaling mode.

Costly advertising, direct benefits, and repeated interactions

In many economic situations, particular signal components can have instrumental value: the receiver derives some direct benefit from the provided signal, as well as an indirect benefit through inference of the signaler's type. In economic models, a firm can be thought of as a sender provided with two distinct channels for signaling the quality of their products: burning money (costly advertising) and through a consumer-relevant variable (price competition). The idea is that only a high-quality firm is able to profitably burn money through advertising or offer initial below-cost prices. Consumers learn the quality after purchasing, so only the high-quality firms can derive enough repeat business to incur the costs of signaling. In the context of biological competition, price competition might be seen as signals that involve a transfer to the receiver conditional on the response—that is the receiver directly benefits from the signal. Examples are investment in a nesting environment or territory by a male, transfers of food (Thornhill 1976), or grooming of the receiver (as in male primates initiating friendships with females, with whom they then have improved mating success; Smuts 1985). So long as *low* males cannot easily duplicate these investment, then there is also a signaling component from the transfer.

The classic economics reference is Milgrom and Roberts (1986). Their paper derives conditions under which equilibria will arise in which sender's purposefully burn money through advertisement of quality with costly fights and displays, rather than offering a direct benefit to the receiver, such as providing food or building a nest. Suppose there are two quality levels for a male sender, *high* and *low*. The male provides as a signal a transfer T and chooses some cost for a signal display $c \in \mathbb{R}_+$. The utility to a sender of type q for a signal pair (T, c) is given by $H(q, T, \rho(T, c)) - \alpha_q c$, where α_q is the type-specific cost of the signal. Whenever fully informed of the type of the male, the female will give the responses $\rho_H^\star(T)$ or $\rho_L^\star(T)$, where we allow for a different response depending on the proffered transfer T—so a *low* male might be acceptable given a large enough transfer T. In order to have an honest equilibrium where each type *high* and *low* send different signal pairs such that $(T_H^\star, c_H) \neq (T_L^\star, c_L)$ and the receiver responds with the response $\rho_H^\star(T)$ and $\rho_L^\star(T)$, a necessary condition is that

$$
\begin{aligned}
H\left(q_H, T_H^\star, \rho_H^\star\left(T_H^\star\right)\right) &- H\left(q_H, T_L^\star, \rho_L^\star\left(T_L^\star\right)\right) \\
&\geq \alpha_H \cdot c_H - \alpha_L c_L \geq H\left(q_L, T_H^\star, \rho_H^\star\left(T_H^\star\right)\right) \\
&- H\left(L, T_L^\star, \rho_L^\star\left(T_L^\star\right)\right).
\end{aligned} \tag{4}
$$

Additionally, the *low* type must be best responding with their transfer, so the signal $(T_L^\star, c_L)$ must additionally solve

$$
\max_{T, c} H\left(q_L, T, \rho_L^\star(T)\right) - \alpha_L c.
$$

The *low*-type must choose the lowest-cost signal available in any honest equilibrium, so $c_L = 0$ here, and their transfer T_L is chosen to maximize their outcome with the female, given her response to an identified *low*-type, $\rho_L^\star(T)$. Normalizing the transfer scale so that the optimal *low*-type transfer is $T_L^\star = 0$, the first part of (4) tells us that the costly signal sent by the *high* type *must* cost less than the benefit of being identified as the *high* type:

$$
H\left(q_H, T_H^\star, \rho_H^\star\left(T_H^\star\right)\right) - H\left(q_H, 0, \rho_L^\star(0)\right) \geq \alpha_H c_H.
$$

While the second part tells us that this signal must cost more than the benefit the *low* type would derive from pretending to be *high*:

$$
\alpha_L c_H \geq H\left(q_L, T_H^\star, \rho_H^\star\left(T_H^\star\right)\right) - H\left(q_L, 0, \rho_L^\star(0)\right).
$$

Intuitively, if the *high* types transfer solves

$$
\max_T H\left(q_H, T, \rho_H^\star(T)\right)
$$

and also satisfies the two incentive constraints under $c_H = 0$, then no costly signals are required, the transfer signal alone can be used to sustain an honest equilibrium. However, in general this is a balancing act, and for some types of preferences, both the transfer *and* the costly signal may be required. Were each mode (the transfer and the signal) available separately without the other, honest equilibria might not arise. However, together, they can modify the constraints under separation to enable incentive compatible signaling.

Multiple messages for multiple qualities

The difference between redundant multimodal signals (where the potential information available to receivers from each signal mode is the same) and non-redundant signals (where the potential information available to receivers is different) is a common distinction made in animal communication (Partan and Marler 1999, 2005; Hebets and Papaj 2005) and relates directly to earlier literature distinguishing "backup signals" from "multiple messages" Møller and Pomiankowski 1993; 1996. As has been previously described in the biological signaling literature (Johnstone 1996), where all receivers have the same preference for the sender's types (so receivers rank signalers in the same way) the presence of multiple signaler qualities is not particularly interesting. All qualities can be reconstituted into a single aggregate quality ranking. However, it is often the case that different receivers may differ in their preferences (Jennions and Petrie 1997), and multiple signaler qualities then becomes a lot more interesting (Johnstone 1996). Signalers might now signal their types

along different quality dimensions, rather than just their aggregate quality. If different qualities are naturally signaled with different signal modes, then heterogeneity in preference leads to multimodal signaling.

However, with greater heterogeneity in preference, it is possible to achieve honest signaling outcomes with less costly signals, whenever there are complementarities between senders and receivers of particular types. A well-known biological example of complementarity may be mate choice for MHC types, where one of the major hypotheses is that individuals of a particular MHC type prefer to mate with a complementary type (Setchell and Huchard 2010). Mathematically, the signaling ICCs become less binding as the bilateral gain from specific matches diminishes the costs needed to separate. That is, senders and receivers of particular types share an aligned preference for truthful revelation, diminishing the need for costly signals. Subsequently, with many different sender and receiver types, increasingly rich signal spaces are required to convey all the relevant information.

For example, consider three types q_{AB}, q_A, and q_B for the sender, and similarly three types Q_{AB}, Q_A, and Q_B for the receiver. Suppose that all receivers prefer a q_{AB} sender (and similarly all senders prefer a Q_{AB} receiver) because they possess both qualities. However, q_A receivers have only one quality and prefer senders with the complementary quality, Q_B, over the Q_A receivers with the matched quality. Similarly, q_B senders have the B quality and prefer Q_A receivers with the complementary **A** quality over Q_B receivers. In order for honest signaling to work, we would need a minimum of three costly signals—an appropriate number of signals for the number of types. Where the qualities corresponding to the A and B type are very different, or have evolved independently, we might naturally hypothesize that the modes that evolve for these signals are likely very different. We will therefore assume that there is a binary signal s_A acting through some channel associated with quality A, and another binary signal s_B for signaling quality B. The composite of both qualities will be signaled by the composite signal $s_{AB} = s_A \bigwedge s_B$.

Honest signaling in this environment has senders with only one of the qualities signaling unimodally, while those with both qualities signal multimodally. In order for honest signaling to function, we would require for the q_{AB} type that

$$\mathbb{E}_Q[H(q_{AB}, \rho_Q(s_{AB}), Q) - H(q_{AB}, \rho_Q(s_i), Q)]$$
$$\geq C(q_{AB}, s_{AB}) - C(q_{AB}, s_i),$$

where the expectation is over the type Q of the receiver, and the fitness function H is now over the sender's type, the receiver's response, and the receiver's type. So the expected gain from signaling both qualities must be greater than the cost of the additional signal. For simplicity, assume that all three types are equally likely and that the receivers

preferences are such that all receivers accept q_H-types, but that otherwise only the complementary low-quality types are acceptable (so $\rho_B(s_A)$ and $\rho_A(s_B)$ are accept, $\rho_B(s_B)$ and $\rho_A(s_A)$ are reject); while the Q_{AB} types find all others acceptable. Setting the unmatched fitness value $H(q, \text{Reject}, Q) = 0$ for all sender types q and receiver types Q, the condition for honest signaling of both qualities (not dropping signal $j \neq i$) is therefore

$$\frac{H(q_{AB}, \text{Accept}, Q_j)}{3} \geq C(q_{AB}, s_{AB}) - C(q_{AB}, s_i),$$

and that the costs incurred are worth the benefits of signaling at all

$$\frac{H(q_{AB}, \text{Accept}, Q_A) + H(q_{AB}, \text{Accept}, Q_B)}{3}$$
$$\geq C(q_{AB}, s_{AB}) - C(q_H, \emptyset).$$

Similarly, a type q_i must satisfy the condition

$$C(q_i, s_{AB}) - C(q_i, s_i) \geq \frac{H(q_i, \text{Accept}, Q_i)}{3},$$

in order for it not to be profitable to use both signals. The condition for not mimicking the q_L^j type with the s_j signal on its own is:

$$\frac{H(q_i, \text{Accept}, Q_i) - H(q_i, \text{Accept}, Q_j)}{3}$$
$$\geq C\left(q_L^i, s_j\right) - C\left(q_L^i, s_i\right).$$

Given our assumption that the q_i type prefers to match with the Q_j type, the LHS above is negative, so sending the other signal corresponding to the alternate quality is only problematic if it is cheaper. So, if we assume that qualities that the types possess are costless to signal, but that each type finds it relatively costly to mimic the signal for a quality it does not possess (so that $C(q_i, s_j) > 0 = C(q_i, s_i)$), the q_{AB}-type conditions are automatically satisfied if senders with both qualities derive *any* positive benefit from mating a receiver. Because of the positive costs, and negative benefits, the q_i types never send the false s_j signal. Our single requirement for honest signaling is therefore that

$$C(q_i, s_{AB}) = C(q_i, s_j) \geq \frac{H(q_i, \text{Accept}, Q_i)}{3}.$$

This condition is that the cost of mimicking a quality the sender does not have is greater than the expected match gain to a receiver with the same quality. What we are trying to illustrate here is that with heterogeneity across senders and receivers, the focus for sustaining honest equilibrium is the direction of conflicts. The ICCs appearing between types that derive no gain from imitating each other will be slack.

If there were T different types, and each particular mode for conveying a signal was binary, we would need the number of modes, M, to satisfy $2^M > T$ in order to have honest signaling. If there were some set of attributes/qualities Ξ,

the set of types would be equal to 2^Ξ (to the power set), containing every possible combination of these qualities. The number of distinct signaling modes necessary to convey this type space honestly then is $M = |\Xi|$. So, multimodality may be explicable by heterogeneity in the preferences of each side, and the need to distinguish heterogeneously valued qualities.

Without this richer signal space, the signal must become more directed, and targeted towards a specific receiver of some known type. An interesting example of this scenario can be found in Coles et al. (2013), which examines an assortative labor market with a coarse ascending classification of workers and firms with globally agreed quality, and an additional idiosyncratic preference dimension. Take, for example, a female primate, in which every female prefers a high-ranking male to a middle-ranking male to a low-ranking male. On top of this, there is a separate idiosyncratic element. For example, within a particular class (*high*, *middle*, *low*), one particular female may prefer a high-ranking male with one particular MHC type, while another prefers a high-ranking male with a different MHC type; and similarly for the females over the males within each category. However, each side only knows their own idiosyncratic preferences. Signals in this environment are modeled as constrained resources directed at a specific receiver of known type. Each player has a limited number of signals that they can use, which they direct to an individual on the other side of the market. This limited use induces an *opportunity cost* for the signals; giving them to one receiver comes at the cost of not being able to use the signal on another. In this environment, signaling improves the outcomes for the senders, but there is an indeterminate effect for receivers. In a biological context, we would need one publicly available signal expressing the global quality (e.g., a bright mandrill nose that can be seen by all females; Setchell and Wickings 2005), and a binary private channel for the idiosyncratic element (e.g., a scent only accessible from close distance to mandrill females who are approached by males; Setchell et al. 2010). The fewer opportunities the individual has to give this private signal to their target receiver, the greater the opportunity cost. The sender therefore ends up being more selective over who to approach, and this selection adds to the efficacy of the signal. Signaling models of this type are relatively new to the economics matching literature, but similar models are promising avenues for animal behavior researchers, given their resemblance to biologically plausible scenarios. Differences in signal detection related to sensory systems, environmental noise structures, and signal transmission properties mean that it is much more likely that public and private channels will evolve in different modalities than in the same modality.

The problem of how to match agents when both sides of the market have heterogeneous preferences has been dealt with in the economics literature on two-sided matching. The interested reader should consult (Roth and Sotomayor 1990) for many standard results. Such "matching problems" are now becoming more prevalently discussed within the theoretical biology literature (see Hooper and Miller 2008; Tobias et al. 2011). The economic literature is now beginning to examine unidimensional assortative matching markets with signaling and produce necessary conditions similar to the single crossing property (Hoppe et al. 2009, 2011; Hopkins 2011).

Multiple senders

Another case in which multiple dimensions becomes interesting is one in which there are multiple senders and a single receiver. The basic idea is that competition between two senders that share some common knowledge may increase the information transmitted honestly. By using tensions *between* the senders, the receiver is able to determine more about the true underlying state. When the information process is unidimensional, the two senders' signals s_1 and s_2 end up as a composite signal $s = (s_1, s_2)$, but there is an underlying true state variable $q \in \mathcal{Q}$. The posterior distribution $\tilde{\lambda}_s$ is therefore over the set of states in $\mathcal{Q}$, but each sender's ability to change the receiver's response is conditional on both their own chosen signal, and also the other sender's signal. Because of this, the ICC for a particular sender (conditional on the other being honest) is given by

$$H(q, \rho(\sigma(q), \sigma(q))) - H(q, \rho(s, \sigma(q)))$$
$$\geq C(q, \sigma(q)) - C(q, s),$$

for all possible deviating signals s. It is possible, given harsh reactions to senders that do not agree (so that $s_1 \neq s_2$) to enable honest signaling even with cheap talk. Equilibria of this form rely on heavily constructed posterior distributions, as only a small subset of the signal space is pinned down via Bayes' rule.

Within the cheap talk economics literature where the costs for all signals are zero, two senders with opposed interests who signal sequentially (for instance, two males engaged in a zero-sum game for a female) temper one another's ability to gain from deception, and there are gains to the amount states q where information is honestly transmitted, but there is still not fully revealing honest signaling (see Krishna and Morgan 2001, 2004). When the senders have aligned interests in deceiving the receiver, this type of competition is less useful. For example, consider two carnivorous predators from a single pack trying to signal to a dangerous prey animal that they do not wish to attack. The addition of another sender has no effect on the strategic problem, as both predators would seek send a safe signal even if they were going to attack, and if taking the animal by surprise was profitable.

Interestingly, within the cheap talk setting, multiple dimensions for the underlying state q dramatically increases the scope for information transfer (see Battaglini 2002; for further details and modeling limits, see Levy and Razin 2007; Ambrus and Takahashi 2008). If signal modes are intimately related to the differing dimensions of the signaling problem, then multimodal signaling would again be useful for honest communication without any necessary cost structure for signals. This stands in contrast to the one-dimension, one-sender example, where honest communication was not possible and at best there was partial information revelation. The reason is that each sender's message produces a subset of the state space $\mathcal{Q}$, for which the other sender is conditionally aligned.

In the language of the cheap talk model in the section "Cheap talk" suppose the state is multidimensional and given by $q = (q_1, q_2)$ and the response is similarly multidimensional $r = (r_1, r_2)$. So the information the receiver wishes to understand has two components, 1 and 2. In the simplest case, consider two senders 1 and 2 who are conditionally aligned with the receiver on dimensions 1 and 2, respectively. That is sender i derives the greatest benefit from the receiver's action on issues i being the receiver-optimal response $r_i^\star(q_i)$. However, each sender is misaligned on the other issue, and desires to bias the receiver's choice. Sender 1 would ideally like the response to be $r = (r_1^\star(q_1), H_1(q))$, with decreasing fitness away from this optimal point. Conversely, sender 2 gets the highest utility from the response $r = (H_2(q), r_1^\star(q_2))$ with decreasing fitness the further the response from this point. By selecting and trusting the sender that is conditionally aligned on each issue, the receiver can fully extract the true state. That is, conditional on sender 2 revealing the second element of the state, sender 1's requirement for honest revelation is that

$$H_1(q, (\rho_1^\star(q_1), \rho_2^\star(q_2))) \geq H_1(q, (\rho_1^\star(s), \rho_2^\star(q_2))),$$

for every other signal s. But, given sender 1's preference for responses closer to $(\rho_1^\star(q_1), H_1(q))$, this is satisfied for all signals the sender can make. A similar ICC for sender 2 indicates complete alignment, conditional on the receiver selectively combining the signals, and the other sender being honestly revealing.

The above construction might seem pathological, as in each signal issue we have a completely trustworthy sender. The problem is simply one of trusting the right sender on the conditionally aligned issue, and ignoring senders on the issues where they are misaligned. However, this type of construction can work more generally, where sender i in revealing the state q is trusted to be revealing that the true state lies in some set $\mathcal{Q}_i(q) \subset \mathcal{Q}$. So long as $\mathcal{Q}_1(q) \cap \mathcal{Q}_2(q) = \{q\}$ we will get full revelation, and the ICC condition for sender i will require only that

$$H_i(q, \rho^\star(q)) \geq H_i(q, \rho^\star(\hat{q})), \forall \hat{q} \in \mathcal{Q}_j(q).$$

That is, the sender i is trusted to reveal precisely only within the conditionally aligned set $Q_j(q)$, and their signal is used to construct a set $Q_i(q)$ through which to judge the sender j.

We do not have compelling biological examples that fit the above scenarios, but we believe the theoretical point is worth considering and may prove interesting from biological perspectives. The important point is that even within the cheap talk scenario, tensions between multiple senders can create honest equilibria in which the scope for information transfer is far greater than with just one sender. The signals for this construction are generically multidimensional, but receivers here are also exploiting tensions across senders, combining signals in both dimensions from both senders.

Under the costly signaling paradigm, there has been less work on multiple senders of which we are aware. One natural question in economics is how signaling works in duopolies, i.e., situations in which two signalers are competing for the attentions of a single receiver. This is related to the multiple channels in the section "Costly advertising, direct benefits, and repeated interactions": Do multiple senders mostly compete through transfers (direct benefits), or through costly signaling for indirect benefits? The interested reader may wish to consult Hertzendorf and Overgaard (2001) and Daugherty and Reinganum (2008).

Multiple audiences and eavesdroppers

A final reason why it might be useful to have multimodal signals is that there are many different receivers, and the sender may want different information to be available to different receivers. This is a common scenario in animal communication. Often there may even be multiple audiences of different types, such as both conspecific rivals (e.g., Clark et al. 2012) and heterospecific predators (e.g., Roberts et al. 2007).

For example, consider a female mammalian sender who wishes to mate with the best quality male in her area. The female can be one of two types: ovulating or not. Male receivers want to mate with ovulating females, but not a non-ovulating one. The female is unaware of which males are in her immediate vicinity and willing to mate. In order to attract all available males, she needs to express a public signal to draw males to her and into competition for her. However, once she has attracted male receivers, she wants the highest quality male to mate with her (for simplicity, assume all males' quality is fully observable to the sender). Thus, she may want to send a private signal indicating that she is ovulating only to the highest quality mate in order

to encourage him to mate with her at the appropriate time (see Higham et al. 2009, for baboons).

Such a scenario might be supportable in an equilibrium. However, it must be the case that the public signal, which is used to facilitate search, contains only partial information about the fertility of the female. If the female only makes public calls when she is ovulating, then this search signal is also fully revealing of her state. All males in the vicinity would try to mate with her when she is ovulating, and there would be no additional information contained in the private signal. It must be the case then that females sometimes sends public signals even when not ovulating—and do so often enough to ensure that the likelihood of ovulating conditional on the public signal is high enough to encourage male receivers to approach, but low enough to ensure that they will not mate without an additional private signal. Here, the public signals cannot be fully honest signals of female state.

Similar to the reasoning above for multiple senders, multiple receivers can provide a strategic discipline that allows for honest equilibria, even in cheap talk environments. Public channels for signaling *can* allow for honest revelation where private signals do not. For instance, suppose an alpha male primate is trying to signal dominance to a nearby female through a display, but is in the presence of male bystanders. Where the dominance display is public, the signal can be honest, even if the display is not costly to the male to perform. If the male truly is the dominant male, there will be no realized cost, and the female becomes informed, and the other male receivers do nothing. However, if the male tries to signal dominance falsely, though there might be a small gain from communicating this to the female, there may well be a very large toll exacted by the true dominant individual in the form of physical punishment.

Mathematically, we can change our initial setup to have the sender's utility be $V(q, r_M, r_F)$: a function of the true state q, and the response of two receivers, M and F. In our simple example above, there was a public signal $s \in \{q_H, q_L\} = \mathcal{Q}$. The responses of the two receivers are for the female receiver F to choose to mate with those sending the signal q_H and to *not mate* with those who do not. The response of the *male* receiver M is to challenge the male who sends the dominant q_H signal and to take no action otherwise. Incentive compatibility is maintained so long as the sender prefers

$$V(q_H, \text{Mate}, \text{Challenge}) > V(q_H, \text{NotMate}, \text{NoChallenge}),$$

and

$$V(q_L, \text{NotMate}, \text{NoChallenge}) > V(q_L, \text{Mate}, \text{Challenge}).$$

That is, the true alpha gains more from his increased social status (including more mating opportunities with females) than he incurs from the male receiver challenging, while this is the opposite for the beta male. Effectively, one of the receivers performs the role of the cost function in our costly signaling setup, so long as the signal is public. In economics, the use of private and public channels in this manner are normally illustrated through firms as senders that seek to send positive signals of their prospects to potential investors. The other receiver is normally a competing or incumbent firm, that the signaler would ideally like to keep in the dark as to their financial strength, directly paralleling the mating situation above. In this sense, "multiple receivers" offer an explanation for why many signals (such as a call) that do not seem to incur physical costs might be rationalized through costs imposed through other receivers (punishment of cheaters, e.g., Számadó, 2011). Specific public signaling modes that attract predators or danger, such as bright colors and loud calls, might be more likely to evolve in situations where an honest equilibrium requires higher quality types to incur costs. Modes that are private animal-to-animal signals might be more appropriate where the information communicated represents idiosyncratic preferences, and the ICCs are satisfied without costly signaling. To create both public and private channels, different modes specifically may be sorted because signals are more likely to have very different detectability limits in different modes (vocal vs visual; visual vs olfactory) than multiple signals in the same modality would. Equilibria with public and private signaling are discussed in Farrell and Gibbons (1989), where they examine each signaling mode separately (see also Newman and Sansing, 1993). However, there has been less work examining multimodal communication where both private and public channels are available to senders. The presence of a private channels might undercut the strategic discipline that comes from other receivers being able to observe the public signal. We feel this is an interesting and potentially fruitful area for further research.

Conclusion

In this manuscript, we have asked the question: if nature were designing a signaling game for a sender and receiver to play, are there efficiency or fitness gains to having multiple and multimodal signals over unimodal ones? In both costly signaling and cheap talk paradigms, without further constraints on the problem, the answer is no. It is simple to show that anything that can be achieved with a multimodal signal can be achieved with a single signal. The content of a signal is captured by the inferred information the signal relays to the intended audience, while the incentive compatibility is captured by the effective costs of the signal. Whether the signal is a complex mix of vocal and visual displays in a choreographed dance next to an intricately

prepared nest or a simple audible grunt does not matter theoretically, what matters is that the receiver interprets the signal to infer quality, and that other types will not mimic this signal because the costs of the signal are not worth the benefits of sending it. While the richness of the signal space (that is, the number of different signals that can be sent) is important, without additional constraints, there is no reason for these to signals to be arranged along different dimensions or in different modalities. Having presented this conclusion and set up both single games in both paradigms and extended these to multiple signals, we investigated different sets of possible constraints that may make multiple and multimodal signal more likely to evolve. Constraints on cost functions and bandwidths, orthogonal noise, strategically distinct modes, multiple qualities, multiple signalers, and multiple audiences all provide biologically plausible constraints that favor multiple and multimodal signaling. While some of these do not necessarily favor multimodal signaling per se, a number do seem to specifically favor multimodal signaling, as the biological constraints involved would be more easily solved by additional signals in different modalities than by additional signals in the same modality. These areas are highly promising for future elaboration and investigation. Economic models of signaling have much to offer biology but in turn animal systems may offer unprecedented opportunities for the testing of otherwise abstract economic models that are often difficult to assess within human economies. Combining the theoretical nature of economic models with the empirical nature of biology stands to benefit our understanding of signaling in both fields.

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