Evolution of Signaling Systems with Multiple Senders and Receivers

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Abstract: Sender-Receiver games provide simple, tractable models of information transmission. It is possible to study not only the equilibrium structure of these games but also the dynamics of evolution and learning – with sometimes surprising results. Generalizations of the usual binary game to interactions with multiple senders, multiple receivers, or both, provide models of information processing and teamwork.

1. Introduction. To coordinate action, information must be transmitted, processed, and utilized to make decisions. Transmission of information requires the existence of a signaling system in which the signals that are exchanged are coordinated with the appropriate content. Signaling systems in nature range from quorum signaling in bacteria [Schauder and Bassler (2001), Kaiser (2004)], through the dance of the bees [Dyer and Seeley (1991)], birdcalls [Hailman, Ficken, and Ficken (1985), Gyger, Marler and Pickert (1987), Evans, Evans, and Marler (1994), Charrier and Sturdy (2005)], and alarm calls in many species [Seyfarth and Cheney (1990), Green and Maegner (1998) ,Manser, Seyfarth and Cheney (2002)], up to human language. Information processing includes filtering – that is discarding irrelevant information and passing along what is important – and integration of multiple pieces of information. Integration includes logical inference and voting. Finally, the information must be used to make decisions with consequences for payoffs that drive evolution or learning.

From an evolutionary perspective, these three aspects of coordination are best addressed simultaneously. They may sometimes be separable in human affairs, but elsewhere in nature it is more typical that they have coevolved. It is possible to construct simplified models which capture essential aspects of these issues as evolutionary games. These models may also be viewed a modules that, once evolved, may be put together to form more complex interactions. Evolutionary games may be studied from a both a static and a dynamic point of view. Dynamic analysis sometimes reveals complexities that are not immediately apparent from the study of equilibria. Computer simulations are always available as a tool, but in these simple game theoretic models analytic methods are also applicable.

We start with dyadic sender-receiver games – one sender and one receiver – and then generalize the model to multiple senders and multiple receivers. It can be shown that surprisingly sophisticated behavior can emerge from dynamics of evolution. A full analysis, however, is non-trivial in even the simplest dyadic signaling games, and much remains to be done.

2. Classic Two-Agent Sender-Receiver Games: Equilibrium Considerations. In the model introduced by Lewis (1969), there are two players, the sender and the receiver. Nature chooses a state with some probability (each state having non-zero probability of being chosen) and the sender observes the state. The sender then sends a signal to the receiver, who cannot observe the state directly but does observe the signal. The receiver then chooses an act, the outcome of which affects them both, with the payoff depending on the state.. It is assumed that the numbers of states, signals and acts are equal. Where this number is N, we refer to this as an NbyNbyN game.

There is pure common interest between sender and receiver– they get the same payoff. There exactly one "correct" act for each state. In the correct act-state combination they both get a payoff of one; otherwise payoff is zero. We number the states and acts so that in a play of the game, <state, signal, act> = $<s_i, m_j, a_k>$ the payoff is 1 if j=k, 0 otherwise.

A sender's strategy consists of a function from states to signals; a receiver's strategy consists of a function from signals to acts. Expected payoffs are determined by the probability with which nature chooses states, and the probability of sender's and receiver's strategies.

Signals are not endowed with any intrinsic meaning. If they are to acquire meaning, the players must somehow find their way to an equilibrium where information is transmitted. An equilibrium is a combination of strategies such the neither sender nor receiver can increase expected payoff by unilateral change in strategy.

When transmission is perfect, so that the act always matches the state and the payoff is optimal, Lewis calls the equilibrium a *signaling system*. Signals are not endowed with any intrinsic meaning. If they are to acquire meaning, the players must somehow find their way to an equilibrium where information is transmitted. When transmission is perfect, so that the act always matches the state and the payoff is optimal, Lewis calls the equilibrium a *signaling system*. For instance, in a 3by3by3 game the following combination of strategies is a signaling system equilibrium:

SENDER	RECEIVER
State 1 => Signal 3	Signal 3 => Act 1
State 2 => Signal 2	Signal 2 => Act 2
State 3 => Signal 1	Signal 1 => Act 3

as is any combination of strategies that can be gotten from this one by permutation of signals. The "meaning" of the signals is thus purely conventional, depending on the equilibrium into which the agents have settled.

There are also other equilibria in signaling games. There are *pooling equilibria*, in which the sender ignores the state, and the receiver ignores the signal. For example, suppose that in state 3 is the most probable. Then the following is a pooling equilibrium:

SENDER	RECEIVER
State 1 => Signal 1	Signal 3 => Act 3
State 2 => Signal 1	Signal 2 => Act 3
State 3 => Signal 1	Signal 1 => Act 3

Since the sender conveys no information, the receiver can do no better than choose the act that pays off in the most probable state. Since the receiver ignores the signal, the sender can do no better by changing his signaling strategy.

In NbyNbyN games with N>2, there are also *partial pooling equilibria*, for example:

SENDER	RECEIVER
State 1 => Signal 3	Signal 3 => Act 1
State 2 => Signal 1	Signal 2 => Act 3
State 3 => Signal 1	Signal 1 => Act 3

The sender's strategy does not discriminate between states 2 and 3, and leaves signal 2 unused. Upon receiving the "ambiguous" signal, the receiver chooses optimally given the limited information that was transmitted. For larger N, there are more kinds of partial pooling equilibria, depending on which states are "pooled."

Among these equilibria, signaling systems yield optimal payoff, but this is no guarantee that one will arrive at them. They also, however, have the distinction of being *strict*, that is to say that any unilateral deviation results a strictly worse payoff. This has the immediate consequence that in an evolutionary setting a signaling system is an *evolutionarily stable* state of the population. This is true both in a 2-population evolutionary model, with a population of senders and a population of receivers and in a one population model in which an individual is sometimes in a sender role and sometimes in a position of being a receiver.

It is also easy to see that signaling systems are the *only* evolutionarily stable states. [Wärneryd (1993)] In the pooling example above, a mutant sender who always sent signal 2 would do just as well as the native population. Likewise, a mutant receiver whose strategy responded differently to the signal 3 (which is never sent) would not suffer for doing so. In the partial pooling example, a mutant sender who sent signal 2 in states 2 and 3 would elicit the same receiver response, and thus would have the same payoff as the natives.

In each of these cases, the mutants do not better than the natives. The pooling and partial pooling equilibria *are* equilibria. But the mutants do no worse, so they are not

driven out. Pooling and partial pooling are not evolutionarily stable. Equilibrium analysis might then lead one to suspect that evolutionary dynamics would always (or almost always) take us to signaling systems. [(1996)] This was an overly hasty conclusion. [Pawlowitsch (forthcoming), Huttegger(2007a,b), (forthcoming)].

3. Dynamics. The simplest dynamic model of differential reproduction for a large population is the *replicator dynamics*. [Taylor and Jonker (1978), Hofbauer and Sigmund (1998)]. We can consider a single population models where strategies are conditional (if sender do this, if receiver do that), or a two population model with one population of senders and another population of receivers.

For a single population, let the strategies be $\{S_i\}$, let x_i be the population proportion of those who use strategy S_i and let the fitness of strategy S_i played against S_j be denoted $W(S_i|S_j)$. Then, assuming random matching, the average fitness of strategy S_i is:

$$W(S_i) = \sum_j x_j \, W(S_i|S_j)$$

and the average fitness of the population is:

$$W(S) = \sum_i W(S_i) \, x_i$$

The replicator dynamics is the system of differential equations:

$$dx_i/dt = x_i \, [W(S_i)-W(S)]$$

For the two-population case, let x_i be the population proportion of those who use strategy S_i in the population of senders and y_i be the population of those who use strategy R_i in the population of receivers. We again assume random matching of senders and receivers, so that:

$$W(S_i) = \sum_j y_j \, W(S_i|R_j) \text{ and } W(R_j) = \sum_i x_i \, W(R_j|S_i)$$

The average fitnesses of the sender and receiver populations respectively are:

$$W(S) = \sum_i W(S_i) \, x_i \text{ and } W(R) = \sum_j W(R_j) \, y_i$$

We consider the evolution of this two population system using bipartite replicator dynamics [Taylor and Jonker (1978), Hofbauer and Sigmund (1998)]:

$$dx_i/dt = x_i \, [W(S_i)-W(S)]$$

$$dy_j/dt = y_j \, [W(R_j)-W(R)]$$

In both the single population and two-population models of Lewis signaling games, the strong common interest between sender and receiver assures *global convergence* of the replicator dynamics; all trajectories must lead to dynamic equilibria. [Hofbauer and Sigmund (1998), Huttegger (1997a,b)].

In the case of a 2by2by2 Lewis signaling game, with states equiprobable, the "hasty conclusion" from ESS analysis is, in fact, born out by the dynamics. Equilibria other than the signaling systems are all dynamically unstable. In both two population and one-population models, replicator dynamics carries almost all possible population proportions to a signaling system. [Huttegger (2007a,b)(forthcoming), Hofbauer and Huttegger (forthcoming)].

But if states are not equiprobable, this is no longer so. Suppose that state 2 is much more probable that state 1. Then the receiver might just do the act that is best in state 2 and ignore the signal. And since the signal is being ignored, the sender might ignore the state and send the 2 signals with some fixed probabilities that do not depend on the state. We have described a connected component of polymorphic pooling equilibria, varying with the sender's allocation of probability between signals 1 and 2. These equilibria are stable, even they are not ESS and not strongly stable attractors in the dynamics. They are "neutrally stable" in that points near them stay near them under the action of the dynamics. But they do not attract all points near them. Other pooling equilibria near them are not moved at all by the dynamics. The question is whether the component of pooling equilibrium considered as a whole has a basin of attraction. It has been shown analytically that it does [Hofbauer and Huttegger (forthcoming)]. Simulations show that the size of the basin of attraction need not be negligible. The size depends, as would be expected, on the difference in probabilities of the two states. If we were to depart from the assumption that the states have equal payoffs, it would also depend on the magnitudes of the payoffs.

Even if we keep the states equiprobable and the magnitudes of the payoffs equal, almost sure convergence to a signaling system is lost of we move from 2by2by2 to 3by3by3. In this game, total pooling equilibria are dynamically unstable, but there are connected components of neutrally stable partial pooling equilibria like the ones discussed in the last section. It can be shown analytically that the set of these partial pooling equilibria has a positive basin of attraction, and simulation shows that this basin is not negligible. [Huttegger, Skyrms, Smead and Zollman (1996).]

Even with the strong common interest assumptions built into Lewis signaling games, the emergence of signaling is not quite the sure thing that it may initially have seemed on the basis of equilibrium considerations. Perfect signaling systems can evolve, but it is not guaranteed that they will do so. Dynamic analysis has revealed unexpected subtleties.

There are more subtleties to explore, because the connected components of suboptimal equilibria are not *structurally stable* [Guckenheimer and Holmes (1983),

Skyrms (1999)]. Small perturbations of the dynamics can make a big difference. The natural perturbation to pure differential reproduction that needs to be considered is the addition of a little mutation. We can move from the replicator dynamics to the replicator-mutator dynamics [Hadeler (1981), Hofbauer (1985)]. For a two-population model with uniform mutation this is:

$$dx_i/dt = x_i [(1-e)W(S_i)-W(S)] + (e/n)W(S)$$

$$dy_j/dt = y_j [(1-e)W(R_j)-W(R)] + (e/n)W(R)$$

where e is the mutation rate and n is the number of strategies.

If there is no selection pressure within a connected component of equilibria, addition uniform mutation will drive the strategies towards the center of the component that only a single point survived as an equilibrium. That equilibrium can be displaced a little off the component because mutation imports a little proportion of every strategy into the population.

We can illustrate by returning to the 2by2by2 signaling game, two populations, states with unequal probability. Suppose state 2 is more probable than state 1. Then, as we have seen, there is a connected component of pooling equilibria for the replicator dynamics. In the receiver population, the strategy of always doing act 2, no matter what the state, goes to fixation. In the sender population there is a polymorphism between two types of sender. One sends signal 1, no matter what the state; the other sends signal 2, no matter what the state. Since there is no selection pressure between the senders' types, every such sender polymorphism is an equilibrium. Addition of *any* amount of uniform mutation leads set of pooling equilibria to collapse to a single point at which "Always send signal 1" and "Always send signal 2" are represented with equal probability. But all other strategies are also present in small amounts at this population state.

The big question concerns the stability properties of this *perturbed pooling equilibrium.* Is it dynamically stable or unstable. There is no unequivocal answer. It depends on the disparity in probability between the two states. This is analyzed in a forthcoming paper by Hofbauer and Huttegger. A little mutation can help the evolution of signaling systems, but does not always guarantee that they evolve.

4. Costs. Let us return to the case of 2by2by2, states equiprobable, but not assume that *one of the signals costs something to send, while the other is cost-free.* (We could interpret the cost-free signal as just keeping quiet.) Now there are pooling equilibria in which the sender always sends the cost-free signal and there are various proportions of receiver types.

Denoting the sender's strategies as:

Sender 1: State 1 => Signal 1, State 2 => Signal 2

Sender 2: State 1 => Signal 2, State 2 => Signal 1
Sender 3: State 1 => Signal 1, State 2 => Signal 1
Sender 4: State 1 => Signal 2, State 2 => Signal 2

and the receiver's strategies as:

Receiver 1: Signal 1 => Act 1, Signal 2 => Act 2
Receiver 2: Signal 1 => Act 2, Signal 2 => Act 1
Receiver 3: Signal 1 => Act 1, Signal 2 => Act 1
Receiver 4: Signal 1 => Act 2, Signal 2 => Act 2

For cost = 2c, states equiprobable, and a background fitness of 1, we have the payoff matrix (sender's payoff, receiver's payoff):

	Receiver 1	Receiver 2	Receiver 3	Receiver 4
Sender 1	**2-c, 2**	1-c, 1	1.5-c, 1.5	1.5-c, 1.5
Sender 2	1-c, 1	**2-c, 2**	1.5-c , 1.5	1.5-c, 1.5
Sender 3	1.5-2c, 1.5	1.5-2c, 1.5	1.5-2c., 1.5	1.5-2c, 1.5
Sender 4	1.5, 1.5	1.5, 1.5	**1.5, 1.5**	**1.5, 1.5**

Sender's strategy 1 and 2 pay the cost half the time, strategy 3 all the time, and strategy 4 never. Pure Nash equilibria of the game for small c are boldfaced.(If c>.5 it is never worth the cost to send a signal, and the signaling system equilibria disappear.) There is also a large range of mixed strategies (corresponding to receiver polymorphisms) that are equilibria. States when receiver types are approximately equally represented and senders all always send the costless signal, are such pooling equilibria.

It might also *cost the receiver something to listen*. Let us combine this with a costly message and unequal state probabilities. For example, probability of state 1 is 1/3, cost of signal 1 = .3, cost of receiver paying attention to the signals is .1, background fitness is 1. Then the foregoing payoff matrix changes to:

	Receiver 1	Receiver 2	Receiver 3	Receiver 4
Sender 1	**2-.1, 2-.1**	1-.1, 1-.1	1.33-.1, 1.33	1.67-.1, 1.67
Sender 2	1-.2, 1-.1	**2-.2, 2-.1**	1.33-.2, 1.33	1.67-.2, 1.67
Sender 3	1.5-.3, 1.5-.1	1.5-.3, 1.5-.1	1.33-.3, 1.33	1.67-.3, 1.67
Sender 4	1.5, 1.5-.1	1.5, 1.5-.1	1.33, 1.33	**1.67, 1.67**

The *pooling equilibrium*, <sender 4, receiver 4>, where sender always sends signal 2 and receiver always does act 2, is now a *strict* Nash equilibrium of the game. Either sender or receiver who deviates does strictly worse. Thus, in both one and two population evolutionary models, it is *evolutionarily stable* and a strong (attracting) equilibrium in the replicator dynamics.

If costs are state-specific, a rosier picture is possible [Zahavi (1975)]. We alter the previous example so that signal 1 is free in state 1 but costs .3 in state 2 and signal 2 is

free in state 2 but costs .3 in state 1. Sender 1 now pays no penalty, sender 2 always pays .3, sender 3 pays 2/3 of the time (.2) and sender 4 pays .1.

	Receiver 1	Receiver 2	Receiver 3	Receiver 4
Sender 1	**2, 2-.1**	1, 1-.1	1.33, 1.33	1.67, 1.67
Sender 2	1-.3, 1-.1	**2-.3, 2-.1**	1.33-.3, 1.33	1.67-.3, 1.67
Sender 3	1.5-.2, 1.5-.1	1.5-.2, 1.5-.1	1.33-.2, 1.33	1.67-.2, 1.67
Sender 4	1.5-.1, 1.5-.1	1.5-.1, 1.5-.1	1.33-.1, 1.33	1.67-.1, 1.67

The pooling state, <Sender 4, Receiver 4>, is no longer an equilibrium at all. Given that the receiver is ignoring the message, the sender is better off switching to the costless strategy, Sender 1. If so, the receiver is better off switching to Receiver 1, yielding the optimal signaling system <Sender 1, Receiver 1>. Optimality, however, may not evolve. The *suboptimal signaling system* <Sender 2, Receiver 2>, in which the sender uses the "wrong" signals and always pays a signaling cost, is also a strict equilibrium. Both signaling systems are strong (attracting) equilibrium in both one and two population replicator dynamic models.

5. Signaling Networks

There is no reason to limit ourselves to signaling between just two actors, one sender and one receiver. In fact, most signaling systems in nature involve multiple senders, or multiple receivers, or both. If a receiver gets signals carrying different pieces of information from different senders, the signaling system is called upon to solve some problem of information processing. Consider a toy model with two senders and one receiver:

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Signaling Complementary Information. There are four states of nature, each of which occurs with non-zero probability. Two individuals are situated so as to make different incomplete observations of the state. The first sees whether it is in {S1, S2} or in {S3, S4} and the second sees whether it is in {S1, S3} or in {S2, S4}. Together they have enough information to pin down the state of nature, but separately they do not. Each sends one of two signals to a receiver who must choose one of four acts. Let's say the first send chooses "red" or "green" and the second chooses "blue" or "yellow." The payoffs favor cooperation. Exactly one act is "right" for each of the states in that each of the individuals is reinforced just in case the "right" act for the state is chosen.

In this extended Lewis signaling game the observational situation of sender 1 is characterized by a partition of the states, $O_1 = \{\{S1,S2\},\{S3,S4\}\}$. Her signaling strategy is a function from the elements of this partition into her set of signals, {R,G}. Likewise sender 2 in observational situation $O_2 = \{\{S1,S3\},\{S2,S4\}\}$ has a signaling strategy that maps the elements of her partition into her signal set, {B,Y}. The receiver's strategy maps pairs of signals {{R,B},{R,Y},{G,B},{G,Y}} into her set of acts {A1,A2,A3,A4}.

Payoffs are:

	Act 1	Act 2	Act 3	Act 4
State 1	1,1,1	0,0,0	0,0,0	0,0,0
State 2	0,0,0	1,1,1	0,0,0	0,0,0
State 3	0,0,0	0,0,0	1,1,1	0,0,0
State 4	0,0,0	0,0,0	0,0,0	1,1,1

A *signaling system* equilibrium is a combination of sender and receiver strategies such that payoff is equal to one in each state. As before, a signaling system is a *strict equilibrium* of the game, and signaling systems are the *only* strict equilibria. There are lots of pooling and partial pooling equilibria.

In an evolutionary setting, this three-player game gives rise to three-population models, two-population models, and one population models. In a one-population model, an individual's strategy would be of the form: *If sender in observational situation O_1 have this sender's strategy, if sender in observational situation O_2 have that sender's strategy; if receiver have this strategy.* The most natural two population model has a population of senders with different observational roles and a population of receivers. In all three evolutionary settings the signaling system is the unique evolutionarily stable state. It is no longer certain that a signaling system must evolve, but it is certain that a signaling system *can* evolve. In each of these settings a signaling system is a strongly stable (attracting) equilibrium in the replicator dynamics.

Each sender's signal conveys perfect information about her observation – about the partition of states of the world that she can see. The combination of signals has perfect information about the states of the world. Exactly one state corresponds to each combination of signals. And the receiver puts the signals together. The receiver's acts contain perfect information about the state of the world. *The signaling system simultaneously solves problems of transmission and integration of information.*

The basic model admits of interesting variations. Of course there may be more senders. And depending on the act set available to the receiver, he may draw the appropriate logical "conclusion" from the "premises" supplied by the various senders. [Skyrms (2000)(2004)(2008)] The senders' partitions may not be fixed by nature, but may themselves evolve in the presence of information bottlenecks, as in the models of (2006)(2007a,b).

Error: There is another class of multiple sender models, where the question is not one of imprecision but one of error. In the previous example, senders observed different partitions but there was no error in identifying the true element of the partition. Here we suppose that the senders all observe the same states but with some error in correctly identifying them. (An alternative, essentially equivalent, interpretation of the model would locate the errors in the transmission of the signals.)

For the simplest model, suppose that there are only two states and two acts. States are equiprobable. Three senders observe the states with error probability of 10%, with the errors being independent between senders and between trials. Each sender sends a message to the receiver, who must then choose one of the two acts. As before, we assume that act one pays off 1 for everyone involved in state 1 and act 2 pays of 1 for everyone in state 2. Otherwise no one gets anything.

Nature here first flips a coin to pick a state, and then picks *apparent states* to present to the three senders according to the error probabilities. A sender's strategy is a function from apparent state into the set of signals, {S1,S2}. We have a choice about how to set up the receiver's strategies. If we were to assume that the receiver could distinguish between senders, we could take the receiver's strategy to be a function from ordered triples of signals to acts. But here we assume that the receiver cannot distinguish between <S1,S2,S1> , <S1,S1,S2> and <S1,S1,S2>. The receiver here has an observational partition and can only count signals. This might be thought of as discrete approximation to a situation where the receiver perceives an intensity arising from many chemical signals, or the sound intensity arising from many calls. A receiver's strategy is then a function from frequencies of signal received to act.

Optimal signaling in this model consists in what we might call a *Condorcet equilibrium*. There is one signal that the senders all use for apparent state 1 and another that they all use for apparent state 2. The receiver goes with a majority vote. For instance, if the senders all send signal 2 in state 1, the receiver will do act 2 if two or more senders send signal 2 and act 1 otherwise. In our example, individuals at a Condorcet equilibrium reduce their error rate from 10% to under 3% .

Rather that thinking of evolution taking place solely in the context of this game, we might assume that sender's strategies already evolved in the context of single sender-receiver interactions. Then receivers usually get one signal, or multiple agreeing signals according to the evolved signaling system, but occasionally get disagreeing signals. Slow adaptation for mixed signals in such an environment is a simple problem of optimization, well-known analytic results guarantee that replicator dynamics will converge to the optimal receiver strategy.

But suppose we forego this easy route and ask whether Condorcet signaling equilibria can evolve in the context of the original four-person game. Both the sender's signals and the receiver's voting rule must co-evolve. It is still possible for efficient signaling to evolve. Condorcet equilibria are strict. They are stable attractors in evolutionary versions of this game using replicator dynamics. In fact, simulations show frequent evolution of Condorcet equilibria in the foregoing model.

There may be one sender and multiple receivers:

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Teamwork: It is sometimes the case that a well-placed sender knows what needs to be done, and can send messages to receivers who can act, but that no one receiver can do everything that needs to be done. Success for all requires teamwork.

For a simple teamwork problem, suppose that there are two receivers and one sender. The sender observes one of four equiprobable states of the world and sends one of two signals to each receiver. The receivers must each choose between two acts, and the acts must be coordinated in a way determined by the state for all to get a payoff. We take payoffs to be:

	<A1, A1>	<A1, A2>	<A2, A1>	<A2, A2>
State 1	1,1,1	0,0,0	0,0,0	0,0,0
State 2	0,0,0	1,1,1	0,0,0	0,0,0
State 3	0,0,0	0,0,0	1,1,1	0,0,0
State 4	0,0,0	0,0,0	0,0,0	1,1,1

We assume that the sender can distinguish members of the team, so sender's strategy maps states into ordered pairs of signals and a receiver's strategy maps her signal into her space of acts. Here the problem to be solved is a combination of one of communication and one of co-ordination. It is solved in a signaling system equilibrium, in which everyone always gets payoff of one. A signaling system equilibrium is again a strict equilibrium, and the unique strict equilibrium in the game. It is a strongly stable attractor in the replicator dynamics.

The example can be varied in many ways, some more interesting than others. The two receivers can be thought of as playing a rather trivial two-person game, but the game is different in every state of the world. In a signaling system, the sender can be thought of either as conveying information about the game or about the optimal act to be done. In these trivial games, these are equivalent. The example could be varied by changing the four embedded two-person games and their effect on the payoffs to the sender.

Chains: Information can flow further than shown in the models given so far. Signalers can form chains, so that information is passed along until it reaches an endpoint at which it can be used. Consider a little signaling chain.

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There are a sender, an intermediary, and a receiver. Nature chooses one of two states with equal probability. The sender observes the state, chooses one of two signals and sends it to the intermediary, the intermediary observes the sender's signal, chooses one her own two signals, and sends it to the receiver. The receiver observes the intermediary's signal

and chooses one of two acts. If the act matches the state, sender, intermediary and receiver all get a payoff of one, otherwise a payoff of zero.

Suppose that the set of potential signals is available to the sender is {R, B}, and that available to the receiver is {G, Y} A sender's strategy is a function from {S1, S2} into {R, B}, and intermediary's from {R, B} into {G, Y}, and a receiver's from {G, Y} into {A1, A2}. A signaling system here is a triple of strategies such that the composition of sender's strategy, intermediary's strategy, receiver's strategy, maps state 1 to act 1 and state 2 to act 2. Signaling systems are the unique strict equilibria in this game, and the unique evolutionarily stable states in the corresponding one, two and three population signaling games. They are attractors in the replicator dynamics. In principle signaling chains can evolve out of nothing.

However, simulations show that in this case evolution is very slow when compared with the other signaling games discussed so far. The speed with which the chain signaling system can evolve is much improved if the sender and receiver have pre-existing signaling systems. They could be the same signaling system, which would be plausible if sender and receiver were members of the same population, but the signaling systems need not be the same. Sender and receiver can have different "languages" so that the intermediary has to act as a "translator", or signal transducer.

SENDER	RECEIVER
State 1 => R	G => Act 2
State 2 => B	Y =>Act 1

A successful translator must learn to receive one signal and send another, so that the chain leads to a successful outcome.

SENDER	TRANSLATOR	RECEIVER
State 1 => R	see R => send Y	Y => Act 1
State 2 => B	see B => send G	G => Act 2

The translator's learning problem is now really quite simple. The requisite strategy strictly dominates all alternatives, and it follows from known properties of the replicator dynamics [Hofbauer and Sigmund (1998)] that it will evolve.

Dialogue: The chain model showed one way in which simple interactions could be strung together to form more complex signaling systems. Here is another. Suppose that a sender's observational partition is not fixed. The sender can choose which observation to make. That is to say, she can choose which partition of states to observe. Suppose also, that the receiver's decision problem is not fixed. Nature chooses a decision problem to present to the receiver. Different sorts of information are relevant to different decision problems. Knowing the actual element of partition A (the element that contains the actual state) may be relevant to decision problem 1, while knowing the actual element of

partition B may be relevant to decision problem 2. This opens up the possibility of signaling dialogue, where information flows in two directions:

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In the simplest sort of example, nature flips a coin and presents player 2 with one or another decision problem. Player 2 sends one of two signals to player 1. Player 1 selects one of two partitions of the state of nature to observe. Nature flips a coin and presents player 1 with the true state. Player 1 sends one of two signals to player 2. Player 2 chooses one of two acts.

Suppose that there are four states, {S1, S2, S3, S4}, with alternative partitions: P1 = {{S1, S2}, {S3, S4}}, P2 = {{S1, S3}, {S2, S4}}. The two decision problems require choices in different act sets: D1 = {A1, A2}, D2 = {A3, A4}. Payoffs for the two decision problems are:

	Decision 1	Decision 1	Decision 2	Decision 2
	Act 1	Act 2	Act 3	Act 4
State 1	1	0	1	0
State 2	1	0	0	1
State 3	0	1	1	0
State 4	0	1	0	1

Player 2 has a signal set {R, G} and player 1 has a signal set {B, Y}. A strategy for player 2 now consists of three functions, one a sender strategy from {P1, P2} into {R,G}, one a receiver strategy form {B,Y} into {A1, A2}, one a receiver strategy from {B,Y} into {A3,A4}. In a signaling system equilibrium each player gets always gets a payoff of one. The possibility of dialogue introduces a plasticity of signaling that is absent in fixed sender-receiver games. Signaling systems are strict, and evolutionarily stable as before.

Signaling systems can evolve in the dialogue interaction in isolation, but simulations show this process to be very slow. As in the case of chains, evolution of a signaling system is much easier if we assume that some of its components have evolved in less complicated interactions. Player one may already have signaling systems in place for the two different observational partitions as a consequence of evolution in simple sender-receiver interactions. If so, the evolution of dialogue only requires that the second player signal the problem and the first choose what to observe. This is no more difficult than evolution of a signaling system in the original Lewis signaling game.

6. Conclusion. We have investigated the evolution of signaling in some modest extensions of Lewis signaling games with multiple senders and receivers. This discussion has focused on one particular setting – a large (infinite) population or several large populations with random interactions between individuals. Different settings would call

for different relevant dynamics. A small population with random encounters calls for a stochastic model of evolution [Shreiber (2001) ,Benaim, Shreiber and Tarres (2004)]. Individuals might interact with neighbors in some spatial structure [Grim, St. Denis and Kokalis (2002), Zollman (2005)]. Isolated individuals might invent signaling systems by trial and error learning in repeated interactions. [Skyrms (2004)(2008), Barrett(2004)(2007a,b)], which might then spread by a process of cultural evolution [Komarova and Niyogi (2004)]. In fact, urn models of reinforcement learning are very close to urn models of evolution in a small, growing population. It has been recently proved that reinforcement dynamics in the simplest Lewis signaling game - 2by2by2 states equiprobable – converges with probability one to a signaling system [Argiento, Pemantle, Skyrms and Volkov (forthcoming)]. Such an analytic treatment of reinforcement learning does not yet exist for more complicated signaling interactions, but simulations tend to give results parallel to the evolutionary analysis given here. This is not entirely surprising, given the close connections between reinforcement learning and the replicator dynamics [Beggs (2005), Hopkins and Posch (2005)].

The simple models investigated here invite all sorts of variations. For instance, the two sender – one receiver topology might not be a case of teamwork by the receivers, but rather a case where one receiver is an eavesdropper. The sender and primary receiver might be from one species, while the eavesdroppers are from another. There are many instantiations of this pattern in real animal communication [McGregor (1995)]. Looking further, simple modules such as those discussed here can be assembled into more complex and biologically interesting signaling systems.

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