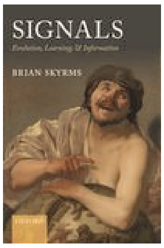

Signals: Evolution, Learning, and Information

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https://doi.org/10.1093/acprof:oso/9780199580828.001.0001

Published: 08 April 2010 **Online ISBN:** 9780191722769 **Print ISBN:** 9780199580828

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CHAPTER

13 13 Networks II: Teamwork

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https://doi.org/10.1093/acprof:oso/9780199580828.003.0014 Pages 149–160

Published: April 2010

Abstract

This chapter shows that for many tasks the use of signals is crucial in establishing the coordination needed for effective teamwork. Teamwork may in some circumstances be achieved by a simple exchange of signals between equals. In other situations a good team may need a leader.

Keywords: signals, signaling systems, teamwork

Subject: Philosophy of Science, Epistemology, Philosophy of Language

Collection: Oxford Scholarship Online

Giant moray eels and groupers are both predators of fish in the Red Sea. Groupers take their prey in open water. Moray eels take theirs in crevices in the reef. Redouin Bshary, Andrea Hohner, Karim Ait-el-Djoudi, and Hans Fricke describe cooperative hunting between eels and groupers.[1] If a prey fish eludes a grouper by entering a crevice, the grouper may approach a moray eel, signal it using special head movements, and lead it to the fish's location. The eel will pursue it in the reef and either catch it or drive it out. If it comes out the grouper gets it. The proportion of times eel and grouper get fed is about equal, and cooperative hunts are more than twice as likely as solitary hunts to bag a prey.

Cooperative hunting within a species has been observed in lions, chimpanzees, dolphins, and hawks. Even the lowly bacterium *Myxococcus xanthus* engages in a kind of cooperative hunting, in which chemical signals are used to coordinate attack.[2] They swarm over prey microorganisms, excrete enzymes to digest them, and absorb the nutrients. Cooperative hunting is one example of teamwork in animals and men. So is cooperative defense, as when wildebeest form a protective circle with young in the center, or birds mob a predator. So are cooperative foraging, rearing of young, or building of communal habitation. Any multicelled organism is a marvel of teamwork.

p. 150 In some teamwork problems, such as mobbing a predator or swarming prey, a uniform action by all members of the team produces the requisite effect. Others call for a more sophisticated teamwork, involving a division of labor and coordination of tasks.[3] Division of labor may involve morphological differentiation. We see this in various ways in the castes of insect societies, in cells and organs of the body, and even in differentiation of soma and spore in reproduction of *Myxococcus xanthus*.

In contrast, division of labor among morphologically similar individuals is central to human economic activity. But it is also found in many other species. Consider, however, group hunts of 3 or 4 lionesses in Etosha National Park, Namibia.[4] Two lionesses, the *wings*, attack a group of prey from either side, panicking them to run forward. They run right into one or two other lionesses, positioned as *centers*, who are waiting for them. This sort of hunting is highly successful. Variations on this kind of cooperative hunting with specialized roles have been observed in many other species.[5]

Bottle-nosed dolphins near Florida engage in group hunts where one individual acts as a *driver* and herds fish into a circle formed by the rest of the dolphins who act as *barrier*, preventing the fish from escaping.[6] Herding into a barrier is implemented in a different way by humpback whales. One whale swims in circles underwater blowing a "curtain" of bubbles. The other whales herd fish into this virtual trap from below and drive them up to the surface where all feed.

For many tasks the use of signals is crucial in establishing the coordination needed for effective teamwork. Teamwork may in some circumstances be achieved by a simple exchange of signals between equals. In other situations a good team may need a leader.

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Quorum-sensing revisited

In quorum-sensing by bacteria there are many senders and receivers, and each individual is both a sender and receiver. Each individual must judge the number (or intensity) of ambient signals, and take the appropriate action when the intensity is high enough. Signaling in the real process is incredibly complex both between cells and within cells, and very far from our toy models of signaling.

At the simplest level, nature chooses the number of individuals. Each individual continually sends out a low level of signal. Individuals can observe the intensity (or number in a discrete model) of ambient "I am here" signals. Thus, everyone signals everyone. Individuals either turn on genes to produce light or not—we don't ask how. The payoff depends on the number of bacteria producing light. If just a few do, the effort is wasted and the squid perhaps is eaten. If a lot do, the effort is rewarded. We assume a threshold of individuals below which the payoff is zero and above which it is one.

Assuming for the moment (and contrary to fact) that the sending strategy is fixed, bacteria need only to evolve a receiver's strategy that switches the lights on if the incoming number of signals is above the *quorum* level, and to switch them off if it is below that level. Pushing ahead with shameless oversimplification, receivers' payoffs are 1 if they all switch the lights on above the quorum and off below the quorum, and zero otherwise. At this level, the problem is related to that of "taking vote" that we considered earlier, but it is even simpler, since there is no alternative sender's strategy. Evolution, learning, or any reasonable adaptive dynamics will have no trouble learning it.

So everything would be easy if signals were discrete, payoffs were step functions, and bacteria could count. The world inside the light organ of the squid is much more complicated. The signal is a small diffusible molecule, and the number of such molecules would be too great for simple organisms to count, even if they could count. The signal input is more like a continuous variable than a discrete number (or rate) of signals received. The
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required ↳ output is binary—light or no light—or close to it. Transient fluctuations due to chance shouldn't cause useless flickering on and off. Nature is faced with designing a robust bi-stable switch which turns the lights on and off in approximate synchrony and at approximately the optimal concentration of bacteria.

A fairly general way to do this, well known in engineering, is to use a positive feedback loop. An input—output function that would otherwise be linear is modified by feedback to produce a "switch" function with some "stickiness" to activation to resist noise. Suppose the optimal point for the light to switch on or off is a concentration x. If the lights are on, a little positive feedback keeps them on for concentrations a little below x. If the lights are off a little positive feedback keeps them off a little above x.

Quorum-sensing bacteria have discovered the positive feedback trick. The signaling molecule is an autoinducer. The more "I am here" messages you get, the more you send. From a game theory point of view, we now have gradations of sender strategies, where number of signals sent depends on number of signals received. The whole story is really much more complicated than this, involving multiple feedback loops.[7] The basic biochemistry implementing this strategy is different in gram-negative and gram-positive bacteria, but the basic idea is the same. The construction of a robust bi-stable switch using feedbacks is not only used in quorum-sensing bacteria, but is one of the basic motifs found throughout biological signaling systems.[8]

Homeostasis

Another ubiquitous example of teamwork is the coupling of sender, receiver, and nature in a negative feedback
p. 153 loop to achieve homeostasis. Here is a maximally simplified model. Nature presents ↳ one of three states to the sender: *too hot*, *too cold*, or *just right*. The sender chooses one of three messages to send. The receiver chooses one of three acts: *turn up the heat*, *turn down the heat*, *don't change it*. The receiver's acts modify the state in the obvious way:

ACT	OLD STATE	NEW STATE
Turn up	*Too Cold =>*	*Just Right*
	Just Right =>	*Too Hot*
	Too Hot =>	*Too Hot*
Don't Change	*Too Cold =>*	*Too Cold*
	Just Right =>	*Just Right*
	Too Hot =>	*Too Hot*
Turn Down	*Too Cold =>*	*Too Cold*
	Just Right =>	*Too Cold*
	Too Hot =>	*Just Right*

Things stay put for a while, but exogenous shocks occasionally perturb the state. The optimal action for a state obviously is one that leaves the state being *just right*. We give this a positive payoff and all others zero payoff.

A signaling-system equilibrium is one which always leads to this optimal action.

It is no more difficult for adaptive dynamics to arrive at such a *homeostatic signaling system* than to learn the three-state, three-signal, three-act signaling systems of earlier chapters.

More complex homeostatic signaling systems occur throughout our bodies, such as the blood glucose regulatory system with the pancreas in the role of sender, the liver in the role of receiver, and the hormones glucagon and insulin in the role of signals. All these systems—regulation of fluid volume, blood ion concentrations, and the rest—require one or more sensors (senders), one or more effectors (receivers), and signals from the former to the latter.

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Dialogue

So far, senders were presented with information and, at most, had to decide what to send.[9] Let us consider a more interactive situation in which receivers can ask for information and senders can seek it out. We can suppose that the 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.[10] 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.

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}}, as shown below:

P1:

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P2: ↳

S1 S2	
	S3 S4

S1 S2	
	S3 S4

The two decision problems require choices in different act sets: {A1, A2} for the first decision problem and {A3, A4} for the second. 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 from {B,Y} into {A1, A2}, one a receiver strategy from {B,Y} into {A3,A4}. In a signaling-system equilibrium each player 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. Evolution of a signaling system is much easier if we assume that some of its components have evolved in less complicated interactions. Player 1 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.

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Team leader I

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. It may also be the case that success requires division of labor. Receivers need to be coordinated in performing different tasks.

Suppose, for instance, 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 for combinations of receivers' acts to be:

	<Act1, Act1>	**<Act1, Act2>**	**<Act2, Act1>**	**<Act2, Act2>**
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 coordination. It is solved in a signaling system equilibrium, in which everyone always gets a 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.

In the foregoing example, 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 state 1 the receivers are playing the game:

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	Act1	**Act2**
Act1	1,1	0,0
Act2	0,0	0,0

They only get paid if they both do act 1.

In state 2:

	Act1	**Act2**
Act1	0,0	1,1
Act2	0,0	0,0

In this state they only get paid if they coordinate on the first receiver doing act 1 and the second doing act 2. Likewise for the other two states. In a signaling system, *the sender tells the receivers what the game is* and the sender gets paid for that information.

Team leader II (correlated equilibrium)

The example can be varied in many ways by changing the embedded two-person games and their effect on the payoffs to the sender. At the other end of the spectrum, we can suppose that the embedded games are all the same. But now we choose a less trivial embedded game, one with multiple equilibria. Consider the Hawk-Dove game a standard model of resource competition.[11]

The game goes by many aliases. In other quarters it is known as "Chicken" or as "Snowdrift game." With the different names go different stories. The story for "Chicken" is that two teenagers drive towards each other at
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high speed, and the first to swerve loses face and is called a "chicken." This usage has migrated from " ↳ Rebel without a Cause" to international relations. The "Snowdrift" story has quite a different flavor.[12] Two drivers approach a snowdrift blocking a road. Doves shovel and Hawks just stand and wait. In the "Hawk-Dove" story of evolutionary game theory, two individuals contest a resource. Hawk beats Dove for the resource but when two Hawks fight there is serious injury or death. If you meet a Hawk it is best to be a Dove; if you meet a Dove it is best to be a Hawk.

Different stories may be appropriate to different versions of the basic kind of payoff matrix. Here are payoffs for one kind of Hawk-Dove game:

	Hawk	**Dove**
Hawk	0,0	7,2.
Dove	2,7	6,6

There are two pure equilibria in this game: player 1 plays Hawk and player 2 Dove and the converse arrangement. But there is also a serious possibility of mis-coordination. If each player aims for his preferred equilibrium, they both play Hawk—each hoping to intimidate the other—and end up fighting.[13]

Conflict could be avoided if a third party could, in an acceptable way, tell them on each occasion who is to play Hawk and who is to play Dove. We add an appropriate sender. The sender observes one of three equiprobable states of the world. Each receiver plays Hawk upon receipt of signal 1 and reacts to signal 2 by playing Dove. In state 1 the sender directs signal 1 to row and signal 2 to column, in state 2 she reverses the signals, and in state
p. 159 3 they both get signal 2. Row and column now end up playing <Hawk, Dove>, <Dove, ↳ Hawk>, and <Dove, Dove>, each ⅓ of the time. They both now have an average payoff of 5.

Is it too convenient to assume that the sender has three equiprobable states to observe? No, the sender can easily create them by rolling a die. Why should the sender do this? The two receivers can each *pay* the sender a commission—say 5% of their payoffs—for performing this service. It is now in the sender′s interest to promote the total payoff of the receivers, and in the receivers′ interests to employ the sender.

The third party is assisting the players in implementing a *correlated equilibrium* of the embedded game—a fundamental solution concept of game theory introduced and analyzed by Robert Aumann.[14] In this example (due to Aumann), the receivers even do better than if they had somehow learned to alternate between the two pure equilibria <Hawk, Dove> and <Dove, Hawk>. And they do much better than if they were just blundering around, getting into fights. This game invites all sorts of interesting variations.

I am sure that you have already thought of some.

How difficult is it for players to learn to correlate in our model situation? They face more challenges than individuals did in the simple situations with which we began the book. We no longer have pure common interest, but rather a complicated web of competing interests. Each of the receivers does best when he is the Hawk while the other is the Dove. The sender would do best if she could get the receivers to both always be Doves, but each would have an incentive to deviate from this arrangement.

Leader-follower

Our two leader-follower examples are bookends for a shelf of models. In the first model the problem is one of
p. 160 coordination. The leader identifies the operative game and sends that information ↳ to the receivers. The receivers then naturally do the best thing. The sender tells the receivers *what the game is*. In the second example the problem is one of partial conflict. The game is fixed, but knowledge of the game does not give unambiguous guidance. The team leader tells receivers *what to do*. In real teams, both considerations may come into play. An effective team leader may transmit some, but not all, of the information at her disposal. She may seek additional information as required, combining dialogue with direction.

Notes

1 Bshary et al. 2006.
2 Berleman et al. 2008.
3 Anderson and Franks 2001 require division of labor in their definition of teamwork.
4 Stander 1992.
5 Dugatkin 1997; Anderson and Franks 2001.
6 Gazada et al. 2005.
7 Goryachev et al. 2006.
8 Alon 2006; Goryachev et al. 2006; Brandman and Meyer 2008.
9 “Decide” being perhaps metaphorical, since our agents may or may not be making conscious decisions.
10 Compare van Rooy 2003, who argues that the pragmatics of decision can be used to disambiguate questions in such conversational contexts.
11 From Maynard Smith and Price 1973.
12 Sugden 2005.
13 They would be better off both playing Dove, but this would fall apart. If one player pays Dove, the other is better off playing Hawk.
14 Aumann 1974, 1987.