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CHAPTER

2   2 Signals in Nature 🔓

Brian Skyrms

Abstract

This chapter surveys some of the signaling systems in nature. Darwin sees some kind of natural salience operating at the origin of language. At that point signals are not conventional, but rather the signal is somehow naturally suited to convey its content. Signaling is then gradually modified by evolution.

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> *"Since monkeys certainly understand much that is said to them by man, and when wild, utter signal-cries of danger to their fellows; and since fowls give distinct warnings for danger on the ground, or in the sky from hawks (both, as well, as third cry, intelligible to dogs), may not some unusually wise ape-like animal have imitated the growl of a beast of prey, and thus told his fellow-monkeys the nature of the expected danger? This would have been the first step in the formation of a language."*
>
> Charles Darwin, *The Descent of Man*

Darwin sees some kind of *natural salience* operating at the origin of language. At that point signals are not conventional, but rather the signal is somehow naturally suited to convey its content. Signaling is then gradually modified by evolution. Darwin is thinking of biological evolution, but for humans (and some other species) there is a version of the account that substitutes cultural evolution or social learning for biological evolution. This view of the origins of language goes back to the late Epicureans.[1] They could not see how language could have originated out of nothing by pure convention, because some pre-existing language seems to be required to set up the convention.

The same objection to a kind of conventionalism comes down through the history of philosophy, through Rousseau[2] to Quine's ↳ "Truth by Convention." It is most trenchantly put by Russell:[3] "We can hardly suppose a parliament of hitherto speechless elders meeting together and agreeing to call a cow a cow and a wolf a wolf."

The conventionalist being refuted is, however, a kind of straw man. That convention need not be explicitly proposed and accepted, but can arise by a gradual evolutionary process, was clearly seen by David Hume:

> Two men, who pull the oars of a boat, do it by an agreement or convention, tho' they have never given promises to each other. Nor is the rule concerning the stability of possession the less derive'd from human conventions, that it arises gradually, and acquires force by a slow progression, and. by our repeated experience of the inconveniences of transgressing it....In like manner are languages gradually establish'd by human conventions without any promise.[4]

Hume did not, however, tell us how this process of cultural evolution started in the first place. The possibility of symmetry-breaking, as discussed in Chapter 1, demonstrates the possibility of an origin of signals without any natural salience whatsoever.

In some cases there may well be natural salience, in which case the amplification of pre-existing inclinations into a full fledged signaling system is that much easier. A dog's baring of teeth as a threat gesture is a particularly plausible example. "Bare teeth to bite" leads to "Conspicuously bare teeth to signal on the verge of biting." (But remember that *we* bare our teeth to smile.)

The Darwin–Lucretius scenario of some small initial natural salience amplified by evolutionary feedback may well be the correct one for many evolutionary histories. It does not require any modification of the signaling games introduced in Chapter 1. It can be represented in signaling games simply by moving the initial probabilities off exact symmetry—in a given state the sender is initially more likely to send one particular signal rather than others, and a ↳ receiver is more likely to react to that signal in the appropriate way. That is to say that signaling game models easily accommodate natural salience but do not require it. Democritus' deep insight is fundamental. Even without natural salience, signaling systems can evolve.

There is more in this remarkable passage from Darwin. He already knows about predator-specific alarm calls. A sentinel of the prey species gives an alarm call that not only signals danger, but also identifies the class of predator present. Classes of predators are grouped according to appropriate escape behavior, and a distinct signal is assigned to each. These have recently become well known through the study of Vervet monkeys in the Amboseli forest by Dorothy Cheney and Richard Seyfarth.[5] Subsequently, species-specific alarm calls have been found in many species of monkeys—Diana Monkeys[6] and Campbell's Monkeys[7] in the old world, and two species of Tamarins[8] in the new—as well as in lemurs,[9] a social mongoose,[10] prairie dogs,[11] and red squirrels.[12] A whole series of careful studies shows that they are used by domestic chickens,[13] [14] just as Darwin says they are.

Cheney and Seyfarth[15] show that vervets have distinct alarm calls for different classes of predator: a "cough" for an eagle, a "bark" for a leopard, and a "chutter" for a snake. For each predator a different evasive action is optimal. For leopards it is usually best to run up a tree and out on a branch where a leopard cannot follow; for snakes one should stand tall and scan the ground to locate the snake and then move away from it; for eagles it is best to exit a tree, take cover ↳ in the underbrush, and look upward to detect the location of the predator. Each alarm call elicits the appropriate behavior—both in the natural setting and in experiments where recorded alarm calls are played back.

Nature has presented vervets with something very close to a classic Lewis signaling game and they have achieved something very close to a signaling-system equilibrium. The states are *eagle present, leopard present, snake present* and the acts are *hide in underbrush, run up tree, scan and move away*. The signaling system consists of a pairing of sender and receiver strategies:

SENDER	RECEIVER
eagle =>cough	*cough=>underbrush*
leopard => bark	*bark=>run up tree*
snake => chutter	*chutter=> scan and move*

that constitutes a Lewis signaling system.

This is, of course a simplification. We could have a state where no predator is present, a null signal consisting of normal sounds, a null action of business as usual, with perhaps some costs to sending a signal other than the null signal. We could include minor predators and minor predator alarm calls, which do really exist. If a leopard is close, a monkey far from a tree might just dive into underbrush. But, for the moment, the idealization is not bad.

The same pattern is repeated in other species with predator-specific alarm calls. Meerkats live in semi-desert areas in South Africa. They are prey to jackals, to eagles and hawks, and to snakes—cape cobra, puff adder, and mole snake. Meerkat alarm calls distinguish these three classes of predator. But they also distinguish the urgency of the threat. This has important implications because of the terrain, and because the meerkats live in burrows and forage within 100–150 feet of a burrow. A high-urgency eagle alarm call will lead meerkats to crouch and freeze. But on hearing ↳ a low-urgency eagle alarm call they will run to the nearest burrow and disappear down it.[16]

Darwin notes in passing that one species may understand the signals of another. Vervet monkeys can learn to understand the alarm calls of a bird, the Superb Starling.[17] These birds also produce different alarm calls for aerial and terrestrial predators. When the Superb Starling alarm calls were played back to captive vervets, they took the appropriate evasive action for the indicated type of predator.[18]

This may not be very surprising. Monkeys are very clever. But some birds reciprocate by using the information in alarm calls of monkeys. Diana monkeys in West Africa are prey to leopards and crowned eagles and have distinct alarm calls for each predator. Crowned eagles also prey upon the yellow-casqued hornbill, a large bird about the same size as a Diana monkey, but leopards do not. Playbacks of recorded Diana monkey alarm calls show hornbills responding to Diana monkey eagle alarms calls just as to recorded eagle shrieks, but not to Diana leopard alarm calls and not to leopard growls.[19]

These cases suggest more complex signaling games. The Diana monkeys play the roles of sender and receiver, as in classic Lewis signaling games, but there is also an eavesdropper—the hornbill—who can utilize and benefit from the information in the signal, but whose correct action benefits neither the sender nor receiver. If so, evolution (or learning) of the signaling system is driven by the interaction between the sender and primary receiver, with the eavesdropper learning to get a free ride.

> *Receiver ← Sender → Eavesdropper*

This case offers no difficulties for the evolution of signaling.

There are further variations worth considering. The hornbill, when alerted to an aerial predator, may take up the cry and utter its own loud alarm, in which case the monkeys may gain some benefit after all—the hornbill acting as an amplifier of the alarm. On the other hand, there is the case where the predator itself is the third

party. The kind of predator who hunts by stealth may be deterred by learning that it has been detected, but a different, swift, predator might be guided to the caller.

The latter case would be an instance of evolution of altruism, and thus strictly speaking not a Lewis signaling game. Such signaling would call for a version of one of the existing evolutionary accounts of evolution of altruism. For instance, altruism may evolve by kin selection. An individual giving the alarm call may expose itself to more danger but nevertheless promote the transmission of the altruistic gene—which is present in kin —by increasing the survival of kin. Where this explanation is correct, one would expect the alarm calls to be given in the presence of kin but neither in solitude, nor in the exclusive presence of strangers. There is evidence that this is often the case.[20] Here, one way of viewing the account is to say that taking account of inclusive fitness, we have a Lewis signaling game after all.[21]

So far, we have dealt with signals that are essentially one-word sentences. That is fine, if there is not much that needs saying. But for a species that needs to communicate a lot of information, this is obviously grossly inefficient. It would be better to be able to construct a variety of complex signals from a small number of simple constituents. We can do it. Can any other species do so?

It is known that non-human primates can be trained to combine symbols to form simple sentences, to p. 26 construct novel sentences, and ↳ to use these sentences to communicate. The most remarkable case is that of Kanzi, a Bonobo, whose (adoptive) mother was being trained to use language. Mom was never very good at it, but Kanzi, who was a bystander—not being trained at all—spontaneously picked it up.[22] The "language" consists of lexograms—geometric symbols. Kanzi's mother, with rigorous training, only managed to learn a few symbols, but Kanzi—as a result of exceptional intelligence, early age, or both—had no trouble acquiring many. He initially tried to convey meaning without any regard to word order, but later learned subject-verb-object order. Other captive animals can be trained to be sensitive to grammatical distinctions, including dolphins[23] and European starlings.[24]

We know rather less about the use of complex signals naturally occurring in the wild. There are intriguing anecdotes, and a few careful studies. Both Campbell's monkeys and Diana monkeys—who often forage together—have predator specific alarm calls for leopards and eagles. The two species have distinct alarm calls. Diana monkeys respond to the alarm calls of male Campbell's by giving their own alarm call for the same predator. However, where the predator is more distant, and not an immediate danger, the male Campbell's monkeys preface their alarm with two low "boom" calls. Alarms calls so modified do not elicit corresponding alarm calls by Diana monkeys. This observation was confirmed in carefully controlled playback experiments using recorded alarm calls.[25] Here we have a natural example that combines sender, receiver, eavesdropper, and a complex signal.

We find a higher level of syntactic complexity in bird calls. The black-capped chickadee has a rich system of signals. In particular, the "chickadee" call from which it takes its name has been known for some time to obey p. 27 rigid syntactic rules. Contrary to the name, there are four—not three—basic acoustic syllables which ↳ are involved in "chickadee," which may be denoted as A, B, C, and D. Playback experiments show that syntactically ill-formed calls are ignored, while well-formed calls evoke a reaction.[26] The rules are (1) any of the basic elements, A, B, C, D may be repeated or omitted, but (2) those that occur must be in the order A, B, C, D. Thus "BCCD" and "ABBCCCD" are well formed, but "ACBBD" and "DCDC" are not.

Two properties of this simple syntax are noteworthy. Given any string whose constituents are only A, B, C, D, it is effectively decidable whether the string is grammatically well formed; you could program a computer to give you the answer. And the class of potential strings that are grammatically well formed is infinite. These properties have sometimes been held up as features unique to human syntax.[27] Chickadee syntax shows us that they are not really so remarkable.

The various chickadee calls appear to convey all kinds of information about group and individual identity, food and predators, but experimental analysis has been slow in coming. In a review article in 1990, Snowdon could comment: "The main limit of this complex grammatical system is that there is no evidence that any of the 362 sequences documented has any functional significance." But more recently it has been shown that information about predator type is encoded in the number of repetitions of D notes in the chickadee call.

Chickadees forage in the brush in small groups. Members of the group often cannot see each other and use calls to keep in contact. They are preyed upon by a large number of different raptors and by a few terrestrial predators, including the domestic cat.

Large raptors, such as the great horned owl, are easier for the small, agile chickadee to evade than small raptors. Raptors in flight can attack rapidly by diving, to which spotted chickadees give a ↳ special "seet" call. Perched raptors and cats evoke a different response. Chickadees give a version of the chickadee call that functions as a recruitment alarm. On hearing the call, birds do not take cover, but rather mob the predator and drive it away. Presentation experiments with 15 species of live predators showed that the number of D′s per call correlates negatively with the size of the predator.[28] There is, no doubt, more to be learned about information content of the full spectrum of chickadee calls.

Alarm calls are about the here and now—or the almost here and now. Honeybees, however, communicate information about how to find distant food sources. That they do so was already known by Aristotle, but he did not know how. Karl von Frisch[29] received a Nobel Prize in 1973 for his analysis of how this information is transmitted through the "waggle dance."

On returning from a new food source close to the hive, a working bee performs a circle dance that motivates others to simply go out and search for the flowers. But if the source is far away, the worker performs a "waggle dance" on a vertical surface. There is a relatively straight run with a zigzag or "waggling" component, followed by circling back and repetition. Bees use the information in the dance to reliably find the vicinity of food sources, and they use scent to home in on them. Although some have found this conclusion hard to accept, is seems now to be well established.[30]

Von Frisch found that the length of the waggling run encodes the distance to the food source and that the angle from the vertical to the main axis of the dance corresponds to the angle from the sun to the food source. To judge this angle accurately the bees must be able to perceive polarization of sunlight, which indeed they can. In fact, it was the analysis of the waggle dance that led to the discovery that bees had this ability to detect polarization.

Here we find—for the first time in the chapter—examples of *natural salience*. Correlation of the run with distance needs no explanation. Equating the angle from the vertical to angle from the sun is more of a stretch. But ancestral bees may have danced on an exposed horizontal surface of the hive with the direction of the run pointing directly towards the food source, as is the case in some dwarf honeybees.[31] Subsequent evolution could then have gradually modified the system to its present, more mysterious state—where dancing is vertical, inside the hive, and requires the bees′ abilities to detect polarization of light to decode the information.

Honeybees have to cooperate to make their living, and cooperation requires the exchange of information. The waggle dance is only one instance of several signaling systems used by bees.[32] Even simpler organisms have evolved ways of exchanging information to coordinate behavior.

Myxococcus xanthus is social bacterium whose groups have been compared to microbial wolf packs. They forage in the soil, and when they detect groups of other bacteria they exude enzymes that digest them, and they absorb the resulting nutrients.[33] When nutrients are exhausted, and they begin to starve, they aggregate by gliding on slime trails, and differentiate to form a fruiting body. In the interior of the fruiting body some cells differentiate to become spores. These lie dormant until favorable environmental conditions allow the life cycle

to repeat. A social group becomes, temporarily, a multicellular organism.[34] All this is accomplished through chemical signals.

Some of these signals are now understood.[35] The first stage of aggregation is triggered by a small molecule produced by starving ↳ bacteria, which diffuses through the cell membrane. Low concentrations of this molecule—call it signal A—have no effect, but at a certain threshold concentration, aggregation is initiated. Later, in the process of fruiting body formation, a different signal plays an essential role. This second signal operates locally. It requires end-to-end contact between individual bacteria.

The fact that the concentration of signal A requires a certain threshold to be effective has important consequences for survival. Fruiting body development kills most of the bacteria involved—most don't become spores. The situation must be dire enough to justify this strategy, and there must be enough starving bacteria to carry it out successfully.

This signaling system is an instance of what is called *quorum-sensing.* The name refers to the fact that a quorum must be present for a particular collective action to be carried out successfully. Quorum-sensing was first discovered in 1977 in a bioluminescent marine bacterium (*Vibrio fisheri*) that lives in the light organs of a squid. The bacterium uses quorum-sensing to activate the genes for bioluminescence. The squid turns the light off or on (for the purpose of camouflage) by controlling the concentration of the signal molecule. The squid increases the concentration by providing nutrients to the bacteria, which multiply rapidly. It decreases the concentration by expelling bacteria into the ocean and taking in seawater. On a sunny day, the squid is visible to predators below it as a shadow. It can disguise itself by activating bioluminescence. At night, it is best to turn off the lights.

Since 1977, it has been discovered that quorum-sensing signaling systems are common among bacteria.[36] Some bacteria have multiple quorum-sensing systems, one specific to the species, but others that enable monitoring the concentrations of other species. Within the family of gram-negative bacteria, different species have small modifications of the basic (AHL) signaling molecule, and put it to different uses: to control biofilm formation (like the plaque on your ↳ teeth), virulence, and spore formation. A different basic signaling circuit is used in gram-positive bacteria to trigger an equally diverse set of behaviors. A third circuit is an interspecies signaling system, shared by both groups. It is sometimes used in infections—for instance in the lungs of those with cystic fibrosis—to help trigger the formation of a mixed species biofilm. Some plants and algae produce molecules that block the quorum-sensing signals used by bacterial infections.[37]

At this level, natural salience almost seems like an understatement. Isn't everything here just chemistry? How could there be any element of conventionality? Well, let's remember that *we* are composed of entities governed by physics and chemistry. Conventionality enters when there is enough plasticity in the signaling interactions to allow alternative signaling systems. For bacteria, biochemistry sets strict rules. But if we look at quorum-sensing over evolutionary time, and reflect on the variety of uses to which the same basic system has been put, we can recover a sense of the plasticity of signaling. Pure convention is gone, but development of the same ancestral signaling system could go one way or another—and in different species of bacteria has done so. Rather than focusing exclusively on pure conventionality, we should also bear in mind cases where there are degrees of conventionality associated with degrees of plasticity in signaling.

Discussions of primate signaling have been dominated by issues imported from human philosophy of mind. What is in the sender's consciousness when she sends the signal and in the hearer's when she receives it? Does the sender have a theory of the receiver's mind, that she uses to predict how the hearer will interpret a signal and respond to it? These are important questions, worthy of careful discussion.

But philosophy of mind will not help us very much in understanding communication in bacteria (or bees, or chickadees), which ↳ nevertheless appear to do it quite successfully. The place to start is not with a self-

conscious mental theory of meaning, intention, or common knowledge, but rather to focus on *information*. Signals transmit information, and it is the flow of information that makes all life possible.

Notes

1   Verlinski 2005.
2   "a unanimous agreement would have to be proposed, which means that speech seems absolutely necessary to establish the use of speech." *Discourse on Inequality* 94.
3   *The Analysis of Mind*, Lecture X, 113.
4   Hume, Bk III, Part I, Sec. 2.
5   Cheney and Seyfarth 1990.
6   Zuberbühler 2000.
7   Zuberbühler 2001.
8   Kirchhof and Hammerschmidt 2006.
9   Macedonia 1990.
10   Manser et al. 2002.
11   Slobodchikoff et al. 1991.
12   Green and Maegner 1998.
13   Gyger et al. 1987.
14   Evans et al. 1994.
15   Following earlier work by Struhsaker 1967.
16   Manser et al. 2002.
17   Hauser 1988.
18   Seyfarth and Cheney 1990.
19   Rainey et al. 2004.
20   Cheney and Seyfarth 1990; Snowdon 1990: 232.
21   Other accounts of the evolution of altruism, such as direct or indirect reciprocity, could also come into play in giving risky alarm calls. All explanations for the evolution of altruism work by establishing some kind of correlation of types. Such correlation allows a unified treatment of altruistic signaling. See the discussion of "Signals for Altruists" in Skyrms 1996: 94–8.
22   Savage-Rumbaugh et al. 1986, and Savage-Rumbaugh and Lewin 1994.
23   Herman et al. 1984.
24   Gentner et al. 2006.
25   Zuberbühler 2002.
26   Hailman et al. 1985.
27   Chomsky 1957 and thereafter. The claim is repeated in Hauser et al. 2002. But compare Pinker and Jackendoff 2005.
28   Tempelton et al. 2005.
29   von Frisch 1967.
30   See, for instance, Gould 1975; Riley et al. 2005.
31   Dyer and Seeley 1991.
32   Maynard-Smith and Harper 2003: 115 compare the known vocabularies of honeybees and Vervet monkeys and find that that of the bees is larger.
33   Berleman, Scott, Chumley, and Kirby 2008.
34   These prokaryotes have discovered the same survival strategy that is well known in the eukaryotes—the cellular slime molds.
35   Kaiser 2004.
36   Taga and Bassler 2003; Schauder and Bassler 2001.
37   Taga and Bassler 2003; Bauer and Mathesius 2004.