

*Primates, Cephalopods, and  
the Evolution of Communication*

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*1. Introduction*

Recent decades have seen dramatic progress in work on animal communication and its evolution, on both empirical and theoretical fronts. Dorothy Cheney and Robert Seyfarth have long been leaders in this research, especially on the empirical side, with their extraordinarily rich studies of communication and social life in vervet monkeys (1990) and baboons (2007). A range of theoretical models of communication, developed in different fields, have also begun to cohere in recent years. These models illuminate different facets of the central phenomenon: the coevolution of two kinds of behavior seen in sign use. On one side are behaviors of sign *production*; on the other side are behaviors of sign *interpretation*. Communication is comprised of the ways these behaviors fit (or fail to fit) together. When a communication system has become established, the sounds, scents, or other marks that an animal makes have been conditioned, through selection, by the patterns of reception and interpretation waiting downstream. The converse is also true: the evolution of patterns of interpretation is an ongoing response to features of sign production. Production and interpretation coevolve.

My term "coevolve" above is understood in a broad way, referring to the shaping of sender and receiver behaviors within a species as well as between them, often within the same agents. Evolution by natural selection, also, is one of a family of processes that can shape and stabilize sign-using behaviors. Other members of this family include

reinforcement learning, imitation of successful individuals in a population, and deliberate reflection and choice (Skyrms 2010). These selection processes may operate on their own or in tandem, modulating behavior on different timescales. In the first part of this paper I'll describe what I take to be an implicit consensus on the theoretical side, though one that leaves many questions unresolved. Recent work in this area has explored the role played by common and conflicting interests, signal cost, iteration of interactions, and the network structures linking communicators (one-on-one interaction versus broadcast to many receivers).<sup>1</sup> Another theme of recent work is the role of combinatorial or syntactic structure in communication systems. Clearly this is an important feature of human language. How widespread is combinatorial structure in animal sign systems, and what sort of transition is involved in achieving it? From the middle of the chapter onwards, that is the topic I'll focus on, and I'll discuss this topic with particular reference to Seyfarth and Cheney's "The Social Origins of Language." They argue there for significant continuities between human and non-human cases, especially in primates. Human and nonhuman primate communication certainly have substantial differences, especially on the production side, but on some central issues, as Seyfarth and Cheney see things, the main transitions come early and the human/nonhuman similarities are deep. This applies to the social function of communication and also to combinatorial structure: "In baboons – and very likely many other primates – vocalizations and social knowledge combine to form a system of communication that is discrete, combinatorial, rule-governed, and open-ended."

After framing the issue of combinatorial structure as well as I can, I'll argue against some parts of Seyfarth and Cheney's treatment of their own central case, baboons. I'll also make a comparison between baboon communication and a very different signaling system, skin patterning in cephalopods. With respect to some debates about combinatorial structure and complexity in sign use, the two cases are complementary:

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<sup>1</sup> For discussions of signal cost, iteration of interactions, and network structures linking communicators – all topics I don't discuss below – see Maynard Smith and Harper (2003), Silk et al. (2000), and Sterelny (2012) respectively.

baboons have simple production and complex interpretation. Cephalopods have complex production and, most likely, simple interpretation. The two cases are flip sides of each other, and in the evolution of combinatorial communication systems, they are both incomplete cases. This comparison casts light on the special features of genuinely combinatorial systems, those in which combinatorial structure is integrated into both the sender and receiver roles.

## *2. Sender-Receiver Coevolution*

This section sketches a general framework for understanding communication that I take to be supported by a range of models that have been developed, mostly independently, in several different fields.<sup>2</sup> The starting point is the distinction between two roles, which I'll call sometimes "producer and interpreter," and sometimes, more simply, "sender and receiver." These pairs of terms will be used more or less interchangeably. Individuals in an interaction may play one of these roles, or both. The earliest model of the family I have in mind was developed in philosophy, by David Lewis (1969).<sup>3</sup> In the Lewis model, a sender has access to a fact, some information about the world, which might be a feature of the sender itself (such as sex or underlying quality). The sender has access to this fact and sends a message of some kind to a receiver. The receiver acts on the message, in a way that has consequences for both agents. Lewis assumed common interest and common knowledge between sender and receiver, and his model gave a simple account of how rational choice could stabilize the rules of behavior on "each side" of the sign, the rule of production (mapping states of the world to messages) and the rule of interpretation (mapping messages to acts).

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<sup>2</sup> Relevant works in this tradition, beside those discussed in detail in this section, include Millikan (1984), Skyrms (2010), Farrell and Rabin (1996), Zollman et al. (2013), Searcy and Nowicki (2003), Godfrey-Smith (2013).

<sup>3</sup> Lewis's terminology distinguished "communicator" and "audience." C.S. Peirce is sometimes seen as the father of this family of ideas, but within the framework of this paper, his is a receiver-focused view. See Godfrey-Smith (2014) for discussion of the Peirce framework and its influence on some recent scientific work.

Terminologies in this area are diverse. I'm going to use "sign" as a very general term, covering anything that is produced and interpreted in the way covered by the models I'm describing, whether the sign is produced vocally, through gesture, inscription, or in some other way. I'll have to return to some terminological issues below, but for now please read "sign" very broadly.

Not all communication fits the Lewis pattern, and this is true even before we consider relaxing assumptions of common interest and adding other complexities. An essential feature of the Lewis model is an informational asymmetry between sender and receiver – the "private information," as economists call it, available to the sender – along with an asymmetry involving action. The sender can see the world but not act on it; the receiver can act but can only see the sign. The aim of signaling is then to coordinate the receiver's action with the state of the world: *act-to-state* coordination. Not all communication is like this; sometimes the function of communication is to coordinate one agent's acts with another – *act-to-act* coordination – where the difference between "states" and "acts" is the fact that acts are chosen by one of the agents, while states are determined independently of the strategic choices possible in the game. Much communication in actual settings plays both these roles; actions are coordinated, but in a way conditioned by information about variables whose values are externally determined. In these mixed cases, in cases where acts are only coordinated with acts, and also in the original cases modeled by Lewis, the heart of the matter is the mutual shaping of senders' and receivers' behaviors, the rules or policies of sign production and sign interpretation.

The simplest models assume common interest between sender and receiver. This is especially clear in the case of the Lewis model, where the sender's messages guide the receiver by reducing uncertainty about the state of the world (carrying information, in Shannon's 1948 sense). It would seem that if the sender and receiver want different acts performed in any given state of the world, then if the sender makes information about this state available to the receiver, the information will be used to produce actions that the sender does not want performed. In such a situation, the sender would have no incentive to signal informatively and hence the receiver no reason to listen. At equilibrium, silence should reign. If this line of argument is accepted, the next question to ask is what happens when there is *partial* common interest between the two agents. That question is the topic

of a classic model in economics, due to Crawford and Sobel (1982). They modeled a situation where, roughly speaking, the sender wants to *somewhat* exaggerate their quality (or another relevantly similar state of the world), and the receiver wants not to be taken in by the exaggeration. Overlap of interests was measured by quantifying the "somewhat" in my previous sentence – the sender might want to exaggerate hardly at all (more common interest), or a lot (less common interest). If the sender is of quality level  $X$ , he or she wants the receiver to act as if the sender was  $X+d$ , while the receiver prefers to act as if the sender is of quality  $X$ ; so  $d$  then measures the sender's desired exaggeration. Signals that carry some information about the sender's quality can be used in this situation, but Crawford and Sobel showed that as interests diverge, fewer and fewer distinct messages will be used at equilibrium. When interests diverge enough, signaling collapses altogether.

Recent work by Manolo Martínez and myself has filled out this picture and added some surprises.<sup>4</sup> These surprises significantly qualify the intuitive verbal argument about the role of common interest given above. We devised a measure of common interest between sender and receiver, called  $C$ , that requires weaker assumptions than Crawford and Sobel's and other models. Our measure compares the preference orderings that each agent has over actions that might be produced in each state of the world. There is complete common interest ( $C=1$ ) when sender and receiver agree entirely about their rankings of actions for every state; there is complete conflict of interest when they have reversed orderings in every state ( $C=0$ ). That is, there is complete conflict when in every state of the world, the best action for one agent is the worst for the other. We assumed "cheap talk" (no signal costs) and no iteration of play between agents. Across a large sample of three-state games and using two different methodologies (a static "Nash equilibrium" search and a dynamic model), we found that our measure  $C$  is strongly predictive of whether communication can be maintained at all, and of how informative the messages in the system will be. (The "informativeness" of communication is measured as the mutual information between states of the world and the receiver's acts.) We also found surprises; there are cases where informative communication is possible

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<sup>4</sup> See Godfrey-Smith and Martínez (2013), Martínez and Godfrey-Smith (under review).

despite complete reversal of preferences in every state of the world ( $C=0$ ).<sup>5</sup> These results show that some commonly made assumptions about the difficulty of maintaining communication in situations of low common interest (with no iteration, no assortment in the population, and no signal costs) are not reliable. However, common interest does make informative communication much easier to maintain.

These results, which use such a simple setting, establish a baseline. Further factors can then help or hinder communication. In biology, since the work of Amotz Zahavi (1975), there has been much exploration of *differential cost* as an enforcer of honesty in signaling. For example, an advertisement of quality can be relied on by a receiver if it is too costly for a low-quality sender to produce. This effect may not be as general an explainer of signal honesty as was once thought (Huttegger et al. forthcoming), but it is one piece of the picture. The role of signal cost had been modeled in economics by Michael Spence (1973), with a very similar message, a few years before Zahavi (1975) sketched his hypothesis.

The sender-receiver models also make more precise a distinction that had been important in the literature for some time, the distinction between *signals* and *cues*. Maynard Smith and Harper, whose 2003 book is an important part of the multi-disciplinary literature I'm describing here, define a "signal" as "any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (p. 3). A cue, in contrast, is a something an organism can use to guide their action, but which did not evolve *as* a guide of this kind; it is a byproduct of other processes, or a consequence of fixed physical constraints. Maynard Smith and Harper use the example of a mosquito finding a mammal to bite by tracking CO<sub>2</sub>. Carbon dioxide can be used by the mosquito as a cue of the location of a nearby mammal, but it is not a *signal* sent by the mammal. In the terms used here, the production of CO<sub>2</sub> by mammals is not part of a sender's rule that coevolved with the mosquito's use of CO<sub>2</sub> as a "receiver" or "interpreter." The mammal would prefer not to give the mosquito any information about its location, but – as we might say – it can't

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<sup>5</sup> The  $C=0$  criterion for complete conflict of interest is not as strong as the requirement of a "zero sum" relation between sender and receiver payoffs. See Wagner (2012) for a related model in a zero-sum context.

help doing so. CO<sub>2</sub> is an *unsent* sign. It is produced, but not because of a coevolved sending rule.<sup>6</sup>

The vagueness of my phrase above, "can't help doing so," shows another feature of the situation. If avoiding mosquitoes was sufficiently important to mammals, and some sort of sequestering of CO<sub>2</sub> would keep mosquitoes away, we might imagine a situation in which mammals did evolve such sequestering. In a simple sketch of the mosquito case we assume that producing a trackable plume of CO<sub>2</sub> is a fixed constraint, but it is subject to evolution. There are many cases where the "sending" done by an animal *is* evolving, but in a more constrained and slower way than the "receiving" side is evolving. The other relationship is possible too; Owren, Rendall, and Ryan have recently argued, in effect, that this is seen in some important actual cases of animal communication: a sender can successfully exploit a receiver by making use of biases in the receiver's perceptual and neural mechanisms. The situation is not one in which the receiver *cannot* evolve its these mechanisms to counteract the sender's efforts, but, they argue, evolution of these mechanisms on the receiver's side is subject to more constraints.<sup>7</sup>

The cue/signal distinction concerns the role of the sender. In other literatures, "signal" is used to refer to simple signs in which the timing of production is important. The making and use of this book (or its chapters) fits a sender-receiver model, for example, but a book is not a usually "signal." In yet another literature, in microbiology, "signal transduction" includes the use of cues as well as signals in the sense above (Lyon 2015). I don't want terminology to be a distraction here, so I'll keep using "sign" in a broad way and sometimes use other terms that should be clear in the immediate context.

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<sup>6</sup> As Maynard Smith and Harper put it, "the crucial point is that the signal must be able to evolve independently of any quality of the signaler [or other variable] about which it conveys information" (2003, p. 4).

<sup>7</sup> See their (2010). I discuss Owren et al.'s views about exploitation in more detail in Godfrey-Smith (2013). The description of their view given here is what I take to be the most plausible interpretation; sometimes they, like Dawkins and Krebs before them (1978), appear to hold that senders have the upper hand in principle in such interactions. I think there's no reason why this should be the case, and the best way to present their sender-focused view is to do so in the way I have here in the text.

### 3. *Organized Sign Systems and Combinatorial Structure*

This section discusses combinatorial structure in signs and communication media.

Whereas the previous section aimed to describe what I take to be a consensus, even if implicit, in this section I'll set things up differently from some other authors, though I take the ideas here to be a natural extension of those above.

We might start by asking: what distinguishes the simplest cases, sign systems with no combinatorial structure, from those that do have some? I'll approach this question with a distinction I take to be even more basic, between what I'll call *nominal* and *organized* sign systems.<sup>8</sup> Nominal signs are unstructured in a very strong sense. Not only are they not made up of significant parts – words or similar units – but they are part of a sign system where no natural relations between one sign and another play a communicative role. This term "natural relation" is problematic, but it's the best I have for now.<sup>9</sup> The idea can be illustrated with an example. Consider the classic tale of Paul Revere and the sexton of the Old North Church in Boston in the American revolution. The sexton used a lantern code – *one if by land, two if by sea* – to inform Revere of the route of the British attack. This code features a mapping between signs and states of the world, but the difference in magnitude between one and two lanterns does not play any role. One lantern and two lanterns are just distinguishable signals. Compare that case to another. Rather than signaling land versus sea, suppose the sexton only used one lantern, but the brighter the lantern was, the bigger the army he'd seen. Here there is a natural relation between different signs – the *brighter than* relation – that maps to a natural relation between armies – the *larger than* relation. The sexton might instead have used a dimmer lantern for a larger army; that system would work just as well, provided the receiver's rule of interpretation was coordinated with it.

In the case where lantern brightness maps to army size, the sign system is an *organized* one. The actual *one-if-by-land...* rule, in contrast, yielded a purely nominal sign system. But in both those cases there is no internal structure in the signs themselves; there

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<sup>8</sup> This terminology modifies one used by Gallistel and King (2010).

<sup>9</sup> Formally, a relation is often identified with a set of ordered pairs (or *n*-tuples). The term "natural" is supposed to strengthen this. This section owes much to discussions with Ron Planer, though he should not be seen as endorsing the analysis.



is nothing like a syntax. The signs have no internal parts that can be rearranged. An animal alarm call system in which calls are louder (or quieter) when predators are nearer is also a case like this; the sign system is organized even though it has no syntax. Often, though, the way an organized sign system is achieved is by means of syntax and internal structure. The signs in the system are related to each other by the *sharing of constituents*, which can be recombined and rearranged. *Bob arrived* and *Bob left* are related by their shared constituent *Bob*. This shared constituent is a feature of the signs that matters to their interpretation. Both say something about a particular individual, Bob. Sharing a constituent is a natural relation between signs, and it maps to a sharing of constituents between the states of affairs described.

Combinatorial structure is one kind of organization in a sign system, one way that signs can be related to each other by communicatively significant transformations. Having parts is a *means* to organization in my sense. There are other means which don't involve internal structure, as in the case where a louder call maps to a closer threat. The important distinction in this area is not whether or not a sign *has* parts. All physical things have parts (at least at this scale). The question is whether the signs' parts have some role in the sender-receiver system, whether the rules of production and interpretation are sensitive to a particular kind of internal structure in the signs.<sup>10</sup>

Suppose the sexton's rule is: show one lantern per British brigade. That is a feature of the sender's rule, and it may or may not be coordinated with the receiver's rule. Revere might have a receiver's rule that takes this into account, or he might not. He might not realize that each lantern says something definite. Similarly, suppose closer predators lead to an animal alarm caller becoming more excited and making a louder call. This is – so far – a sort of inadvertent or *de facto* organization on the sender's side. It may or may not be picked up in the rule of interpretation used on the receiver's side. We might expect this organization to be quickly made use of by receivers, but it's an open question whether this happens in any particular case. There might be a role for inadvertent or *de*

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<sup>10</sup> Millikan (1984) may hold that *all* sign systems are organized in my sense, as can be seen by looking closely at (for example) the role of time and place of sign production. I think this is probably not true for all cases, but if this view is right, a category of minimal organization might be distinguished from richer forms.

*facto* organization on the receiver side, too. A louder call might make the receiver more agitated, just as a result of general features of their perceptual psychology, and this agitation might be a good – or a bad – thing with respect to their response to the call.

Initially these features might be inadvertent, but they may then come to figure in the coevolution of senders' and receivers' behaviors. They might be amplified, suppressed, or transformed. In principle, there can be useable structure in signs that is unused by the receivers. There can also be a situation where structure is *present* in signs, not because of an evolved sender's rule, but by happenstance. This structure, too, might be used or not used by receivers. Suppose the sexton intends to signal in exactly the same way for any sea invasion, but he does not. His alarm call is inadvertently affected by the details, and Revere may or may not pick up on this.

Now I'll combine this with a point made at the end of previous section. There is another situation where a kind of sign structure arises not by a coevolved sender's rule – not by "design" – but by happenstance. Suppose you hear a lion's roar followed by the bellow of an antelope. You might use this to build a scenario about what's going on.<sup>11</sup> The two pieces, roar and bellow, each play a role. Two roars will be different from one, also (there are two lions to deal with if I go to the waterhole). In cases like this, a structured combination of sounds or other signs makes possible a certain sort of interpretation, but the interpretation is directed at an object whose combinatorial structure is not due to an evolved sender's rule. Instead, there are simpler behaviors of sign production. When they are put together, they yield a structured and interpretable object, but no agent on the sender's side is following a rule of combinatorial sign production. In the lion-antelope case, there is just a useful happenstance combination of simple signs.

These distinctions have grey areas at their boundaries. For example, how do we distinguish a single combinatorially structured sign from a sequence of unstructured, nominal signs from the same sender? Sometimes this is easy, because the parts of the structured sign could not occur on their own. In other cases, the parts might be able to occur on their own, but an argument might be made that their role in a sequence is one

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<sup>11</sup> I don't know whether a lion would actually roar when trying to attack an antelope – my African experience is considerably slimmer than Seyfarth and Cheney's. The point could also be made with other examples of interspecific interactions in which calls are made.

that involves genuine combinatorial structure. There's a connection here to a distinction made by Thom Scott-Phillips in a number of recent articles.<sup>12</sup> He says that there are various cases where two or more animal signals are produced *alongside* one another, and this need not be a "properly combinatorial" system, because in many cases the effect of the sequence is just the sum of the effects of the parts. That is, suppose  $A_1$  is the evolved response to  $M_1$ ,  $A_2$  is the evolved response to  $M_2$ , and if  $M_1$  and  $M_2$  are both sent, the receiver does both  $A_1$  and  $A_2$ . This shows, he says, that the system is not a genuine combinatorial one. I agree that there's an important distinction here, without being so sure about some of his judgments about cases. He says that the honeybee waggle dance is a case where the effect is the sum of the parts, so it's not a genuinely combinatorial system. But if this "sum" talk is to be literally applicable, the parts have to be signs that can be produced, and reacted to, in isolation. In the bee dance, the angle of the dance maps direction and the duration of the runs maps distance. For this to be a sum-of-parts case, it would have to be possible for a bee to dance with a definite direction but no definite duration, and with a definite duration but no direction. At least the latter does make sense, though the former might be doubted. If this separation is not possible, then the angle and duration are more akin to syntactic features of a structured sign. The sentence *Bob arrived* is not the "sum" of *Bob* and *arrived*, in the relevant sense. The word *arrived* cannot achieve anything in isolation, such that we might ask whether this effect is "summed" with the effect of *Bob* when someone interprets *Bob arrived*.

#### 4. Baboons and Cephalopods

With this framework in hand, let's now look at some of the primate behaviors described in Seyfarth and Cheney's "The Social Origins of Language" and elsewhere. The baboons they study live in complex social structures with an important role for ranks. They also make calls. On the production side, there is not a lot of flexibility in what a baboon can do. The repertoire is simple, with about four different calls, and the production rules are stereotypical. But the individuals in a troop can recognize *who* has made a particular call. That means, as Seyfarth and Cheney say, that combinations of signs can carry a lot of

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<sup>12</sup> See Scott-Phillips et al. (2013), (2014).

information – they carry information in Shannon's sense, as they reduce uncertainty about the state of the world. If you hear a threat-grunt from *A* followed closely by a scream from *B*, that is indicative of a particular interaction, one between *A* and *B*, and with particular roles. With Seyfarth and Cheney, consider then this sequence: a threat-grunt from low-ranking individual and scream of submission from higher-ranking one. That is a notable combination, a surprising one. It is very different in what it indicates about social affairs than a threat from a high-ranker and submission from low. The sequence of a threat from low-ranking individual and submission from a higher-ranking one indicates that a social reversal or shift has taken place. The combination is informative in that sense, to a hearer. But no agent has the ability to produce a sign with those features, any more than a lion, which can only roar, can tell you what it has attacked. The combination of baboon calls is informative to a sophisticated interpreter, even though there is no coevolved rule of production whose function is producing such signs and making such information available.

I disagree with Seyfarth and Cheney's own description of these cases in their chapter. They say: "In baboons – and very likely many other primates – vocalizations and social knowledge combine to form a system of communication that is discrete, combinatorial, rule-governed, and open-ended." Their basis for saying this in the case of baboons is the sophistication on the receiver side. I think this is not enough, and baboon behavior does not comprise a "system of communication" with combinatorial features, any more than the lion-prey case does.

This case is interesting in the light of the distinction between signals and cues, discussed above. The baboons who call are both signaling; the calls are not mere cues. But the combinatorial structure (such as it is) in what the receiver hears is cue-like. It is a fortuitous consequence of the social ecology and the rules of nominal sign production being followed by individuals. When I say it is "fortuitous," I don't mean it's an accident. The evolution of call production was shaped by the social ecology of baboon life, and this social ecology includes the fact that pairs of calls, as well as individual calls, can be heard. That fact might have been important. But there is no sender anywhere in this system whose behaviors of sign production have been shaped by selection for making calls with combinatorial structure. The structure in the calls is fortuitous in that sense.

There's a contrast between the way Seyfarth and Cheney present their ideas in "The Social Origins of Language" and in their book *Baboon Metaphysics* (2007). In the book, they use data of this kind to make a case for *internal* sophistication in baboons. They argue for a system of internal representation in these animals, for something like a "language of thought" (p. 251). The hypothesis of a *language* of thought might be too strong given the data, as Elisabeth Camp has argued (2009). But the data do support claims of cognitive sophistication and a kind of internal symbolic structure on the interpreter side. In their new paper, though, these results are described as showing the presence of a system of communication rather than just a system of internal interpretation. In response, Seyfarth and Cheney might say that the first result does indeed establish the second. Once we've shown that the baboons' way of *assessing* calls has a certain kind of complexity, this shows that the communication *system* itself has that sort of complexity. Their chapter contains passages that suggest this interpretation.<sup>13</sup> I am arguing, however, that with respect to combinatorial structure, it takes two to tango.

Am I merely insisting on one particular way of dividing things up? Suppose they reply: "it's a combinatorial system if the receiver treats it that way." What is wrong with that? I agree there will be many reasonable ways to categorize the cases. But considerable progress has resulted from focusing on sender-receiver coevolution, and in the light of that framework, a combinatorial system is one with complementary features on each side. There has to be a combinatorial nature to the making of signs, and to their interpretation. The sender constructs a sign with internal structure and the receiver is sensitive to that structure. Cases with complexity on just one side are important in their own right, but they're important as a different sort of phenomenon.

If we look at things this way, we can identify a complementary case, a flipside, to the baboons' combination of features. This is skin patterning in the coleoid cephalopods (octopuses, cuttlefish, and squid). These animals have the ability to change their skin color and pattern in dramatic ways in less than a second. Larger cuttlefish, such as the Australian Giant Cuttlefish (*Sepia apama*), are probably the most spectacular, especially

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<sup>13</sup> "[D]espite their many well-established differences, language and nonhuman primate communication share a suite of common cognitive operations. Both are discrete, combinatorial systems in which a finite number of signals can generate an infinite number of meanings."

with respect to colorfulness, but each group has its specialties (Hanlon and Messenger 1996, Darmaillacq, Dickel, & Mather 2014). Octopuses can achieve astonishing camouflage, and squid, as discussed below, are perhaps the most communicative. In all these animals, the color and pattern changes are controlled to a considerable extent by the brain. Their skin contains several color-affecting components. Most importantly, *chromatophores* are sacs of pigment which can be expanded and contracted in precise ways with muscles. Other cells, below the chromatophore layer, reflect ambient light. I'll focus on chromatophores, the most precisely controlled elements in the skin.

The skin of one of these animals contains large numbers of chromatophore units. They can be used to make both static and dynamic patterns, with a huge variety possible. A cuttlefish, for example, has three chromatophore colors, and of the order of a million chromatophores across its skin. Control does not seem to be literally chromatophore by chromatophore; they tend to work in clumps. But there is still a large number of independently controllable units, and as a result a vast number of patterns possible at a time. Color and pattern can also change rapidly over time.

So on the production side, there is enormous complexity. What is it for? It is believed that the original function was probably camouflage, and in some species the system has been pressed into a signaling function as well, both intraspecific and interspecific. Some species of cuttlefish have elaborate contests between males, which include displays, and male-female signaling is also common. Octopuses appear to use signaling less than other coleoids (though see Huffard et al. 2008, and Scheel et al. in preparation). In all these cases, though, it is likely that the interpretation side is vastly simpler than the production side. I'll discuss a possible partial exception in a moment, and in some species there is more complex signaling than in others. But a great deal of combinatorial capacity is probably going unused here, especially on the interpretation side.

The species for which the strongest claims about signal complexity have been made is a reef squid, *Sepioteuthis sepioidea*, in the Caribbean. Martin Moynihan and Arcadio Rodaniche (1982), in a very readable monograph that is an underwater analogue of *Baboon Metaphysics*, argued that these squid employ a "language" on their skin. Reef squid are social, forming shifting groups of six to twelve or more. They have fairly

complex courting behaviors, some low-key territoriality, and they also display at predatory fish. Moynihan and Rodaniche charted the combinations of patterns produced and how they were combined with arm positions, and they found quite a rich structure (see figure 1). They then argued that squid have a visual language with a syntax. This claim was based mainly on the structure seen in sequences of basic displays, though they also discussed combinations of patterns present at a time.

Among cephalopod biologists these claims of language and syntax have generally been thought too rich. Moynihan and Rodanich saw too much structure. But what is meant by *too much* here? What determines the "real" amount? In part this is a matter of which patterns are systematically produced, but the other crucial factor is how the patterns are *interpreted* by individuals who see them. Moynihan and Rodaniche were able to chart in some detail the structure of signs produced, but were not able to work out very well their effects on receivers. This is entirely understandable; behavioral observations are difficult with animals of this kind. Squid are skittish and fast-moving, and even a good snorkeler lumbers in comparison.

Moynihan and Rodaniche counted about 31 ritualized patterns. They believed that systematic patterns in the sequence with which these displays were produced must have some meaning:

We cannot, ourselves, in the present state of our knowledge, always and in every case tell the difference in message or meaning between every observed arrangement of particular patterns. We feel, nevertheless, that we must assume that there is a real functional difference of some sort between any two sequences or combinations that can be distinguished from one another. (p. 125)

But the options, by their own lights, seemed limited by the slim range of behaviors seen in intraspecific interactions. They saw occasional territorial defense between groups, many displays directed at predators of other species, and a variety of courtship and sexual behaviors. The variety of displays seems to outrun the variety of responses, and Moynihan and Rodaniche themselves wondered about the possibility of simple explanations for much of what they saw.

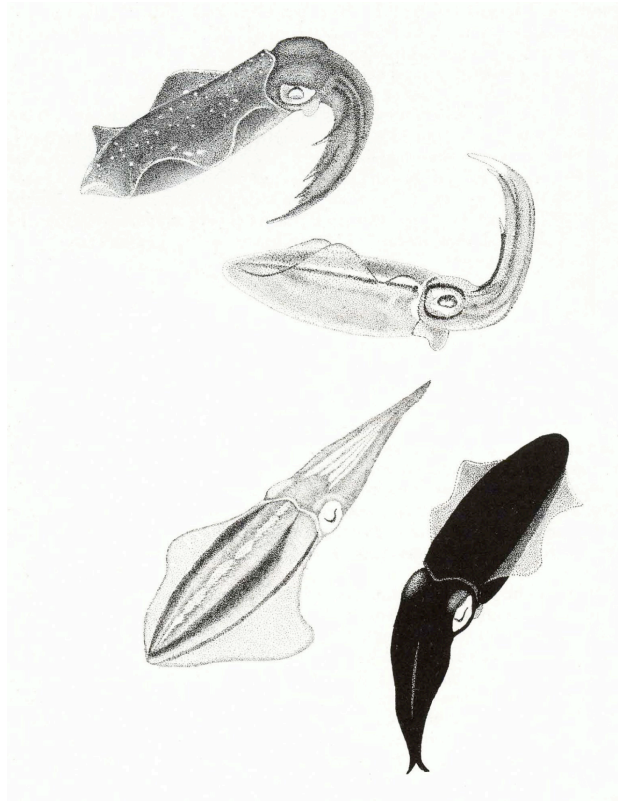


Figure 1: Arcadio Rodaniche's drawings of displays by adult *Sepioteuthis sepioidea*, some of which combine body posture with skin pattern. Originally published in Moynihan and Rodaniche (1982).

The most detailed attempt to follow up Moynihan and Rodaniche's study I know of was done by Jennifer Mather with some collaborators. Mather (2004) discusses a small set of basic communicative displays in *Sepioteuthis*, though some of the displays are graded, the ones discussed aren't claimed to be exhaustive, and the 2004 paper does not consider posture in conjunction with pattern (see also Mather et al. 2010).<sup>14</sup> The more complicated exchanges of signals she described are preludes to mating. Mather also

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<sup>14</sup> I am not sure how to compare the numbers. Mather (2004) discusses four basic communicative body patterns and two concealment ones, but these are not presented as exhaustive. In other work, Mather along with her collaborators distinguishes more basic displays (Mather et al. 2004, Byrne et al. 2003), some of which include body posture as well as skin patterning. I don't know of later studies that recognize the full variety discussed in Moynihan and Rodaniche.



discusses the difficulty of tracking receivers' interpretations of displays.

It may be that in reef squid there is a hidden role for some of the rich combinatorial structure in displays discussed by Moynihan and Rodaniche. This would probably involve subtle and graded modulation of the basic behaviors associated with aggression and sex. It's possible. We could then ask, as Scott-Phillips does, questions about whether a receiver's responses to combinations of signals have an additive relation to their parts, and so on. In other cephalopods this sort of complex signaling is even more unlikely. Reef squid are more social than other coleiod cephalopods. Octopuses, in particular, are not very social at all, though they produce rich combinations of patterns and color changes, many of which do not, apparently, involve camouflage.

How then should we think about complex pattern production in cephalopods? A partial explanation comes just from noting its origins in camouflage. Camouflage, especially in reef environments, involves producing spatially structured patterns, and that is the likely origin of the pattern-producing machinery. Once pressed into service for communication, in a situation where displays are meant to be seen and understood, rather than *not* seen, the result is a lot of combinatorial capacity on the production side. Some displays made by cephalopods to other species are probably designed to startle the other animal, and these "deimatic" displays are very spatially complex, but intended to have simple results. At least in squid, and perhaps in some other cases, there is probably some genuine combinatorial structure to communicative displays between individuals, but there is probably also a great deal of unused capacity and unattended complexity. The interpretation rules in play are probably not tracking much of the combinatorial detail that is inherent to the production mechanisms. In the squid case, Moynihan and Rodaniche probably did enough to show that the production of combinations is not merely random. This is not so clear in other cases. Offering a speculative hypothesis, I suspect (based on informal observations) that some complex cephalopod displays are non-random but also functionless; they are fortuitous reflections of internal processes, byproducts of the close connections between brain and chromatophores, that do not have a comparably complex coevolved interpretation. The complex displays indicate something about the animal, but what is indicated is not being used (much) by normal receivers. Perhaps this is not true, but even if false in all cases, its possibility illustrates how the complexity of sign

production can outrun the complexity of interpretation in a system of animal communication.

The cephalopod case is a complement to the baboons, the flipside. In the baboons there is much complexity on the receiver side, but it is aimed at sign structure that is not put in place by any sender. A communication system that is genuinely complex and combinatorial is one in which rich combinatorial structure figures into the rules on *both* sides of the signs, rather than a system in which simple nominal signs are produced but complex interpretations are possible given the social context, and rather than a system with very complex production but where most of the complexity is insignificant to interpreters. Especially in philosophy, but also in scientific discussions, there is a tendency to "choose sides" when giving a theoretical description of communication. Some people treat communication as a fundamentally expressive phenomenon, and emphasize the sender side (in philosophy, see Grice); other views see communication as a fundamentally interpretive phenomenon, and emphasize the receiver side (in philosophy, see Davidson).<sup>15</sup> The coevolutionary framework shows us that sides should not be chosen.

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<sup>15</sup> See Grice (1969) and Davidson (1984).

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