Evolutionary Forces Favoring Communicative Flexibility

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Introduction

There is a huge gap between the complexity of communication in humans and nonhumans. In the nonhuman case, signals and functions are few and show limited flexibility in both function and signal characteristics, whereas in humans, signals are of indefinitely large number, signals have a multitude of functions, and mapping from signal to function and vice versa shows massive flexibility. What were the evolutionary conditions that led to such a discrepancy between humans and nonhumans?

To understand these circumstances in general and to shed light on the specific circumstances that were relevant to the explosion of communication in the human case, we turn to observation of other species that show some degree of communicative flexibility. The evidence suggests that specific circumstances and a limited number of selectional pressures favor the evolution of communicative flexibility in animals. In this chapter we assess environmental/social conditions and communication types that appear to favor selection for variability or complexity in communication systems and that may lead to signal and functional flexibility. The goal is to catalogue circumstances or evolutionary scenarios that have led to communicative flexibility in the past and thus might help explain what happened in the remarkable human case.

What Are Signals and How Do They Evolve?

The exposition we plan requires clarity about several concepts and related terms. We begin with an important recent definition of the notion "signal," as an action or feature coevolved between sender and receiver where both benefit on average from the exchange of signals (Maynard Smith and Harper, 2003). The definition is founded on the idea that without benefit to both participants in interaction, signals would not be naturally selected and could not stabilize. For example, a systematically identifiable alarm call produced by a bird fulfills the requirements of a signal. In Hockett's (Hockett, 1960; Hockett and Altmann, 1968) terminology, a signal (as defined by Maynard Smith and Harper) is thus said to be "specialized" for communication.
In contrast to a signal, a “cue,” in the terminology of Maynard Smith and Harper, is a state or action that is perceived by other organisms and used as a guide for action but has not been evolved (has not been specialized) for that purpose. For example, body size can be used as a cue for strength, or substantial concentrations of CO₂ can be used (e.g., by mosquitoes) as a cue to the presence of large animals in the nearby environment. A cue can be interpreted, but the result is not viewed in this terminology as communication—we shall use the term “cue interpretation” in this case.

Signals are believed to evolve from animal traits or actions that begin as cues for certain states of the animal. In the evolution of an alarm call, for example, an animal may at one stage of evolution produce an involuntary vocal cue associated with a bodily reaction when it perceives a predator from afar. Such a vocal cue could result, for example, from a sudden change in breathing pattern in anticipation of flight. If this sound benefits the producer’s kin because they hear the sound, associate it with danger, and develop a retreat response, the sound can be systematically selected to function as an alarm call. In this way, it can become specialized for communication through ritualization (Huxley, 1914; Lorenz, 1951; Tinbergen, 1951), a process through which the signal evolves to be easily recognizable. To be easily recognizable, it must be high in contrast, conspicuous, unambiguous, and stereotyped in form. Such ritualized signals usually also develop a typical intensity, because gradations of a signal can only be understood in the context of a typical intensity.

It has been proposed that some signals may not have started out as cues. Owren and Rendall propose a scenario for the origin of some primate vocal signals (Owren and Rendall, 2001) suggesting manipulative use of vocalizations learned associatively. Such learned vocalizations could capitalize on attention-getting features of certain sounds in situations like predator danger or aggression, and their usage could be enhanced by further associative learning on the part of listeners.

Animal signals such as alarm calls evolve to serve specific functions. For each such signal, the function is fixed, that is, there is a coupling of each signal with a particular function. The function associated with a particular signal cannot be changed within an individual animal. For example, a call evolved as an alarm cannot be reassigned as an aggressive or a courtship signal. Signal and function are thus coupled in the majority of animal signals in a one-to-one mapping (Oller, 2004; Oller and Griebel, 2005) that justifies the classical ethologists’ term “fixed signal” (Lorenz, 1951; Tinbergen, 1951).

Fixed Signals in Animal Communication Systems

The typical repertoire size of fixed signals in social species, such as the primates, appears to include about five to seven function types, not counting gradations of intensity associated with signals for each function type. Much larger numbers can be derived if one categorizes individual gradations as types (Sutton, 1979). The litera-
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ture generally suggests that signal categories can be readily identified and also that the occurrence of each signal can be largely predicted from social context. The functions tend to be mostly drawn from the following social expression types: (1) aggression or threat (with signals often used in intra- as well as interspecific communication), (2) courtship or sexual solicitation, (3) appeasement or submission, (4) distress or complaint, (5) greeting, contact calling, or affiliation (often in the context of parental care), (6) feeding announcement, (7) warning or alarm, (8) comfort or pleasure, and (9) exultation or positive excitement. Of course, not all species have all categories; for example, apparently only gregarious species have alarm and feeding announcement calls. Often one or more of the above categories are served by a single signal type (e.g., exultation and feeding announcement might be served by a single positive arousal signal).

It is important to note that fixed signals are often (perhaps usually) not entirely stereotyped in signal or function (see Snowdon, as well as Hammerschmidt and Fischer, this volume). As mentioned, signals tend to show gradations of intensity, corresponding to gradations of arousal or urgency in the service of the functions that correspond to each signal. In addition, contextual flexibility occurs to a limited extent in the usage of signals, such that, for example, some primates can inhibit the production of an alarm signal in the absence of kin in the vicinity. Further, maturation and learning appear to play important roles such that primate signals become clearer and their functional usage more appropriate with development. Two factors, however, remain fixed: (1) the destiny of each signal type to form a one-to-one mapping with a functional type, broadly defined by a class of contexts appropriate to the function, and (2) the relatively stereotyped form of the signal that serves each function type, making it easily identifiable within the species even with gradations of intensity.

Refinements of the Terms Based on Austinian Distinctions

The distinction between "illocutionary force" and "perlocutionary force" (Austin, 1962) can be adapted usefully here. Illocutionary forces are the functions (aggression, appeasement, greeting, etc.) served by signals (or potential signals) in the act of signaling. Receivers interpret illocutionary forces, but since animal signals tend to be stereotyped, there is relatively little danger of misinterpretation at the illocutionary level. Perlocutionary forces are effects that take place as a result of illocutionary interpretation by the receiver, and these effects are inherently flexible in intelligent creatures such as primates. Thus, in response to an aggressive signal, a receiver may respond in a variety of ways: with counteraggressive signaling, with attack, with retreat, with appeasement, or with indifference, to name a few possibilities that may be dependent on how dangerous the original signaler is believed to be, how seriously the signal is taken, and whether the signal was directed at the receiver or another animal.
Intelligent animals appear to be selected to produce a small number of signal types that transmit illocutionary forces, but they are also selected to interpret these illocutionary forces with considerable flexibility and range.

When we use the terms "function" or "functional flexibility," we intend the terms to apply to the immediate social functions of communication, not subsequent results of the communications. Consequently, the term "function" refers to illocutionary forces specifically, rather than to perlocutionary forces. Illocutionary forces in animal communication and in very early human development are limited to a small class of social interaction types, as indicated above—aggression, appeasement, and so on. We propose that signals can be naturally selected to transmit illocutionary forces because each illocutionary force is a unified type of social interaction. Perlocutionary effects, on the other hand, include everything that can happen as a result of a communication, and as a consequence, perlocutionary effects provide no unified targets for natural selection in communication among intelligent animals. An alarm call does not directly cause an animal to run up a tree but causes an animal to be alarmed (or at least to recognize the alarm call for what it is)—several different reactions can occur (freezing, running up a tree, attacking, merely looking at the caller, etc.). Comprehension of calls usually exceeds production capabilities (e.g., in nonhuman primates see Snowdon, this volume), a fact that corresponds to the observation that individual fixed signals within primate species show perlocutionary flexibility but illocutionary fixedness. In our terminology, then, since fixed signals are illocutionarily fixed, they are not functionally flexible.

In the case of deceptive uses of signals, however, an additional function, not of the illocutionary type, is pursued by the signaler in order to exploit an existing illocutionary function. For example, a warning call can be used to serve an additional function of competition avoidance (e.g., food or mate competition), or a mating signal can be used to function in addition as a lure for prey. Consequently we use the terms "function" and "functional flexibility" to encompass both illocutionary functions and the additional functions that deception may invoke. Deceptive functions are always "parasitic" on an existing communication system including both signals and illocutionary functions (see discussion of deception below).

Illocutionary forces are also distinct from "meanings" following Austin’s terminology. Illocutionary forces are interactive events within a social dyad, a sender and a receiver. Illocutionary forces do not require that the signal make reference to any entity external to the dyad. Meanings, on the other hand, involve a triad in our Austinian scheme, the social dyad plus some entity of reference that can be external to the dyad—"me and you and that thing over there (or me and you and the idea we are talking about)." If one points to a leopard and says "leopard," one not only draws attention to the leopard but also invokes a name for the class of all entities that are
leopards. Naming the leopard is much more specific and includes more information than simply pointing to the leopard and making a sound such as a grunt or a scream, either of which, of course, can also draw attention to the leopard. A meaning invokes a referential entity in this terminology, but an illocutionary force constitutes a social action such as threatening, warning, appeasing, and so forth. When one points to a leopard and names it, one produces both an illocutionary force (e.g., an action of, for example, naming or warning) and a meaning (by invoking the class of leopards).

Importantly, fixed signals cannot have meaning in this Austinian sense because they possess no capacity for free reference, that is, reference independent of the illocutionary force of the signal in question. A predator-specific alarm call (see Snowden, this volume, for a review of such calls) is always an alarm and cannot make reference to a predator independent of the act of alarm calling. The capacity for reference to some external source of alarm such as a predator is bound to the circumstance of alarm and depends on the receiver’s active interpretation of the situation (aided by looking in the direction the alarm caller is looking, by actively seeking to locate a predator, etc.). These facts about alarm calling indicate that their referential effects are circumstantially bound and may be largely or entirely perlocutionary aftereffects of the combination of the receiver’s interpretation of illocutionary force and the context of signal production. In free reference, on the other hand, as occurs in language, we can use a term referring to a predator with or without creating alarm and importantly, we can use the term without the intention of creating alarm. The term for the predator is a word and has a meaning in Austin’s sense but can be used on differing occasions for differing illocutionary effects. In general, it is useful to clarify that animal signals, including primate vocal signals as described in the literature, transmit illocutionary forces, not meanings. Illocutionary forces in these cases constitute social functions coupled with individual signals.

Functional Decoupling in the Human Infant

Humans on the other hand show quite free decoupling of signals and functions, and this pattern of vocal communication begins very early in life. Research from our laboratories (Kwon et al., 2006; Oller et al., 2003; Oller et al., 2007) has shown that even in prespeech sounds of the first six months of life, decoupling of signal and function occurs. For example, a sound identified as pertaining to a “squeal” category can be used to express positive affect (exultation) on one occasion and negative affect (complaint) on another, and on another occasion it can even be used in a neutral state, as in vocal play when the baby vocalizes alone. The same reversal of emotional valence and consequent illocutionary force occurs with other sound categories in the human infant, although some sounds diversify in function more than others. Squealing, growling, and vowel-like sounds show great diversity of function. Crying, on the
other hand, which appears to begin as a fixed signal of physical distress at birth, maintains a negative connotation and cannot acquire a positive one in the infant, even though the range of negative expressions appears to grow as the infant matures; by four months, infants cry instrumentally to get attention as well as to express pain or signal hunger (Green et al., 1987). Only the relatively rare cases of “crying for joy” in adults may present examples of a change to a positive connotation for crying.

Later, when infants start to speak, they not only learn to name a vast number of objects and states but also learn to use these names to serve a wide variety of social functions (or illocutionary forces). For example, humans can use the word “pig” (which always has the effect of invoking the “meaning,” which is to say it invokes a reference to the class of animals that are pigs) with a variety of illocutionary forces: as a simple statement of fact (“this is a pig”), as a warning (“watch out, a pig!”), as a question (“is this a pig?”), as an insult (“you pig!”), as an example (consider the word’s usage throughout this paragraph), or to serve a variety of other illocutionary functions. In language learning, the decoupling of functions and signals multiplies in early infancy like an explosion until, by the end of the second year of life, essentially any word and/or sentence can be used to serve multiple functions, and every function can be served by multiple words and sentences. The signaling system of the human child is essentially open in this sense from a very early stage, surpassing the functional flexibility seen in nonhuman primate vocal systems at any point in life (Oller, 2000).

This functional flexibility of communication in humans extends to other domains beyond the vocal one. Sign languages have the same sort of functional flexibility as vocal language does (Lyons, 1991; Stokoe, 1960). Individual signs serve multiple illocutionary forces by very early in life in sign learners. Further, human “body language” and other natural gestures are not entirely stereotyped to serve fixed functions. Most body language signals can be employed for many functions, just as in the case of vocalization. Information in natural human gesture and body language seems mostly encoded in timing and rhythm of movements, where flexibility of intent is a key feature in the expressive system (Grammer, 1995; Grammer et al., 1999; Grammer et al., 2000; Grammer et al., 1998).

Apes have been taught to use some human sign language, and in that context they have shown limited functional flexibility of learned signs (Fouts, 1987; Gardner and Gardner, 1969; Savage-Rumbaugh, 1988). Further, various animals have learned to understand a considerable number of human words and to use that understanding with some functional flexibility (Pepperberg, 2004; Kaminski et al., 2004). However, this sort of flexibility is clearly limited (Terrace, 1979; Terrace et al., 1979) to a small number of illocutionary functions and has not been shown to extend in any significant way to vocal communications produced by nonhuman primates (Gardner and Gardner, 1969). For this reason it remains a crucial puzzle to determine how humans
came to have such vast vocal flexibility, a capability that seems to have been critical in the evolution of language.

Special Cases Related to Signaling and Communication

This chapter is intended to review forces that have acted to influence communicative flexibility across a variety of species and in a variety of modalities of communication in order to provide perspective on the hominin case. The goal leads us to take into account not only clear cases of evolved communication but also actions such as camouflage and deception, where our notions of signal and communication are pressed to the limit. Developmental patterns also present challenges to the definitions of signal and communication. The following clarifications are in order.

Camouflage is utilized by organisms not to communicate but to prevent any kind of cuing in order to avoid detection by predators or prey. Camouflage also does not obey the Maynard Smith and Harper definition of signals, since it is not evolved to confer benefit on both sender and receiver. Coevolution between sender and receiver can occur nevertheless in an arms race of camouflage and detection. Yet the mechanisms of camouflage in some species include flexible control of actions that could be used to communicative advantage within or across species. Consequently, although camouflage itself is not a signal system, we review certain camouflage phenomena because they may play roles in establishing foundations for flexible signaling.

Deception is a special kind of communication that, as indicated above, is “parasitic” on a primary signaling system or cue interpretation system. Any deceptive signaling act depends upon the existence of a more frequently occurring honest signal or cue against the background of which the deception can be implemented. Like camouflage, deception violates the Maynard Smith and Harper definition of signal because deception does not occur to benefit both sender and receiver. Like camouflage, deceptive systems can coevolve across senders and receivers in an arms race of deception and detection. Consequently, evolutionary pressure on deception can create signaling flexibility since the action of deception must become increasingly adaptive in order to prevent receivers from recognizing deceptions for what they are. Thus, some examples of animal deception research are reviewed below, again because we seek to provide special perspective on the origins of communicative flexibility in general.

Finally, in the very young of some species, flexible actions are often observed that appear to be precursors to the mature signaling system, but where the developmental “signal” events may have different status for senders and receivers from the standpoint of the notion of illocutionary force. In many songbirds and human infants, for example, vocalizations occur that may be purely a form of practice or exploration of sounds (“play”) for the producer, in which case they have no illocutionary function from the standpoint of the producer. On the other hand, these sounds may constitute fitness indicators for caregivers, who may be able to attend to the young more
effectively on the basis of that fitness information. Our interest in the origins of flexible signaling leads us to treat these developmental actions as a type of signaling even though their functions may be different for sender and receiver in the course of development.

**Selection for Variety of Signaling in Hominins and Other Species**

In hominin evolution of an open vocal communicative system, with decoupled vocal signal and function, we propose that a particular change in pressures on selection for vocal capability must have occurred: At some point, there must have existed a selection pressure favoring variable sounds, rather than the stereotyped sounds that are found in fixed vocal signals. At the initial point of selection for variability, we propose that variably produced signals served a specific, single function, presumably fitness indication. In this scenario, the advantages of variability had to outweigh the advantages of stereotypy (speed of production, clarity ...).

We envision two types of enhanced capabilities that could have been selected to produce variability in vocal signaling. The first type of new capability would have constituted an ability to produce sounds more freely and would have enabled an increase in endogenously produced variable sounds, which were presumably very infrequent in an earlier stage of hominin evolution (as they are in modern nonhuman primates). This capability implies spontaneous vocalization and exploration of vocal capability (see Oller and Griebel, this volume). The second new capability would have been based on learning to produce sounds heard in the external environment. The latter mechanism implies mimicry or imitation. These new capabilities, we propose, are foundations required for the emergence of significant functional flexibility.

We do not, for example, find it plausible that an evolutionary process that diversified a particular signal class into a small number of fixed subtypes (e.g., predator-specific alarm calls or alarm calls that encode locations of potential danger; see Struhsaker, 1967) could have blazed the path to an explosion of functional flexibility such as that seen in humans, because diversified subtypes of alarm calls are still stereotyped and fixed in function as alarms; they are not (and presumably cannot be) used to serve other functions, such as greeting, appeasement, or courtship. Human linguistic signals, however, and even prelinguistic infant vocalizations show precisely this sort of flexibility. According to our reasoning, variable production of signals had to evolve first, and these signals had to later be freed from their original functions and applied in variable contexts/functions.

In the comparative enterprise, we seek parallels to the human case: diverse signals that map onto a single function and/or individual signals that map onto several functions. For language, both are required. Our comparative enterprise also seeks to determine the evolutionary conditions for selection for variety. We ask, in what cases does variability or functional flexibility in communicative signaling occur in nature?
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Figure 2.1
Types of contextual flexibility in communication. S, signal; F, function.

Terminological Overview on Flexibility of Communication

Figure 2.1 diagrams the proposed terminology for types of flexibility in communication. Because individual fixed signals in social animals such as primates typically show variation in intensity, maturational change, and inhibitability (e.g., in audience effects), we propose that the term “contextual flexibility” should apply (at least minimally) to all the circumstances of signal mapping that we will be discussing. Fixed signals, however, show limited contextual flexibility and one-to-one mapping. Many-to-one mappings can occur when signals are produced in a variable, nonstereotyped way to serve a single function, or when novel signal categories are developed by individual organisms through motoric exploration and practice or are learned by mimicry or imitation from the environment and then mapped as a group of signal categories to single functions. In many-to-one mappings we will say there is “signal flexibility.” Only when one-to-many or many-to-many mappings occur do we apply the term “functional flexibility.” Camouflage and deception present special cases not directly represented in the figure.
Camouflage itself is, by our definition, not a signal because it does not evolve to benefit both sender and receiver. It is the inverse of communication, an attempt to avoid detection. At the same time, flexibly implemented camouflage can be argued to involve a many-to-one mapping of numerous actions to the single function of detection avoidance. Deception exploits an existing system of communication or cue interpretation, and although deception can influence a communicative system, it is always secondary, being dependent for its function on a primary nondeceptive base of communication or cue interpretation. Deception can involve either signal flexibility or functional flexibility or both, in accord with our definitions, depending on the type of deception involved.

Signal Flexibility as a Prerequisite for Functional Flexibility

As suggested above, we propose that some degree of signal flexibility is a prerequisite for functional flexibility. The proposal is based in part on the logic that communication requires signals to transmit functions—if functions are to become more elaborate or more flexible, signals are required to become more elaborate or more flexible to serve those functions. The reverse, however, is not logically necessary—signal flexibility can be developed, logically speaking, in the absence of functional elaboration.

Empirical evidence is consistent with our proposal. As we shall see below, the animal kingdom displays many cases of signal flexibility—some songbirds, for example, can learn to produce extremely elaborate songs or other sounds from the environment, but these songs usually serve only one or two functions (see the section on sexual selection below). In contrast to the evidence from bird song, we know of no clear examples where functional flexibility is elaborate but signal flexibility is quite limited.

Deceptions may present at least minor exceptions to this general trend. If an animal uses an alarm call for deception, it uses a fixed signal to manipulate communicative effects without changing anything in the signal itself. In essence, the animal uses the regular signal for warning to serve an additional function such as competition avoidance. But as noted above, deceptive actions are by nature infrequent in occurrence and so do not, we think, fundamentally alter the tendency for signal flexibility to have precedence over functional flexibility in evolution.

Consistent with our reasoning, some degree of functional flexibility is typically seen in species where signal flexibility occurs. Importantly, the numbers of illocutionary functions that can be served in animal communication by flexible signals appear to be quite small (five or less as far as the literature indicates—see below for examples). The only case we know of where extremely elaborate functional flexibility occurs is in humans, and in that case signal flexibility is so highly developed that it allows expression of a much larger number of possible specific illocutionary functions than in any other animal as far as we know—humans control, in addition to the repertoire indicated above for nonhumans, functions such as explanation, criticism,
denial, affirmation, acknowledgment, and many others. For a taxonomy of illocutionary functions in humans, see Fraser (1975). Human signal flexibility also allows expression of indefinitely large numbers of words and sentences.

The comparative evidence reviewed here is consistent with our expectation that the evolution of language would have included increases in signal flexibility prior to increases in functional flexibility. This ordering is also consistent with modern human infant development where signal flexibility leads the way in the emergence of communicative skills (see Oller and Griebel, this volume). In what follows we explore the occurrence of the various mapping options for signals and functions in non-humans from invertebrates to primates. The organization of the exposition is based on presumed forces and circumstances of selection that encourage evolution of flexibility in communication or that encourage evolution of flexibility in capabilities that can serve as foundations for flexible communication as suggested by such special cases as camouflage, deception, and developmental patterns.

Selection Factors Favoring Communicative Flexibility

Sexual Selection

It appears that the most effective force yielding signal variety for variety's sake across many species has been sexual selection. Variety of signaling can be used either to impress the opposite sex in courtship, resulting in intersexual selection, or to impress the same sex in competition for territory or mates, resulting in intrasexual selection. Sexual selection is assumed to have produced the well-known mating songs and territorial songs that are found everywhere from invertebrates to mammals (Alexander, 1961; Payne and McVay, 1971; Hausberger, 1997; Kroodsma, 1999; Nooteboom, 1999). Sexually selected signals are usually based on traits that reflect the sender's resource holding potential (RHP; Parker, 1974). Such traits constitute fitness indicators and thus can contribute to both inter- and intrasexual selection at the same time. Nevertheless, it seems that intersexual selection is somewhat more unpredictable in relation to RHP, since factors such as a specific sensory bias of the female can guide selection toward a seemingly random enhancement of specific traits.

Humpback Song and Bird Song as Indicators of Sexual Selection

The most elaborate songs influenced by sexual selection have been reported to occur in many species of songbirds and, interestingly, in a completely different group, which includes a few of the large whales, specifically the humpback (Payne and McVay, 1971; Payne and Payne, 1997; Tyack and Sayigh, 1997). The songs of the humpback are so beautiful to the human ear that they became a commercial best-seller.

If one speeds up humpback songs to match the frequencies of the acoustic elements of bird song, a noteworthy resemblance emerges. If we compare, for example,
the humpback's song to that of the long-billed wren, we find many similarities of structure (Tyack, 1999). Analysis of internal rhythmic structure in both whale songs and bird songs also yields parallels with the rhythm of human vocal communication. Rhythmic groupings of elements are called "songs" in birds and "phrases" in the humpbacks. The minimal rhythmic units within these songs and phrases are sometimes called "notes," but they are also often called "syllables" (Marler and Slabbekorn, 2004). These repeatable minimal units often have comparable durations across many unit types, a pattern that is similar to syllables in speech, which also occur in repeatable units of limited duration. The number of types of these minimal units is one indicator of complexity. Another indicator is the number of transitions between the themes within the songs or phrases, which tend to cycle in a particular order but show some flexibility of cycling. These transitions seem to be more complex in songbirds than in whales; the latter use a smaller number of transitions among fewer than ten themes (Tyack, 1999).

Learning is clearly involved in bird song and humpback song. In many bird species new song elements are acquired by mimicry or imitation. Many species actually show increasing repertoire over the years (Baptista and Petrinovich, 1986; Nottebohm, 1981; Payne and Payne, 1997; West et al., 1997), but in a few species, including the humpback, increase in repertoire size is not seen. Instead all individuals within a population display songs that are very similar at any one time, but the animals slowly change the entire song more or less in synchrony over weeks and months, without increasing repertoire size. New themes appear and old ones disappear many times, so that in a lifetime the total number of elements or themes is essentially open-ended. Some bird song repertoires are known to change seasonally with peaks of repertoire in the mating season.

Clues That Indicate the Operation of Intrasexual and Intersexual Selection
Although mating songs can be used entirely in courtship, they are sometimes shaped by intrasexual and intersexual selection in the same species. In many birds both kinds of shaping seem undeniable. Both selection pressures may also be at work in the humpback whale. Some birds, like the European starling, appear to differentiate their songs into two subtypes, one that they use for male–male competition and the other one for courtship (Hausberger, 1997).

It is complicated to attribute distinct acoustic features to only one of these two selective forces, because the same song elements often appear in both cases. Further, a male sometimes appears to play both roles at once—for example, by singing in a potential mating territory that may attract a female to the territory while simultaneously repelling other males from it. In such cases the general "function" of the variable song may be that of fitness display, serving both courtship and territoriality as subfunctions and thus applying both intra- and intersexually simultaneously. In
lekking circumstances where males display for females, the primary force shaping variable song can often be deemed to be specifically intersexual, while in countersinging between males, for example, specifically intrasexual selection may influence the pattern. Intersexual selection appears to produce signal variety in some cases while favoring convergence of songs in others.

Since inter- and intrasexual selection forces are often both at work in variable song development, encouraging spacing between males and providing a means for males to attract females, it is clear that complex bird song (and perhaps humpback whale song) provides evidence of a several-to-several mapping of signal to function; a multitude of signals correspond to two functions (courtship and male–male competition/territoriality). Thus, sexual selection forces, depending on social circumstances, can favor both variety of nonstereotyped sounds (signal flexibility) and flexibility in vocal usage (functional flexibility). However, it is important to note that very advanced signal flexibility is seen in many songbirds with only two function types being served by that signal flexibility. The very elaborate signal systems of many species of birds (and perhaps the humpback whale) appear not to have resulted from a need for elaborate functional flexibility but to have resulted instead from an arms race in advertisement/fitness signaling and in detection of the characteristics of the elaborated signals by both potential mates and competitors.

A possible third function for the elaborate songs of some birds is based on the “Beau Geste” hypothesis that some birds imitate other species to pretend that the territory is too full for further habitation (Dawkins and Krebs, 1978). If this hypothesis is correct, then these birds may use their elaborate songs in three different ways—in intra- and intersexual selection as well as in deception of other bird species. Birds that imitate are also known to use calls of predators to get rid of food or mate competition—an another deceptive use of the general capability to imitate sound.

Social Cohesion as a Force for Communicative Flexibility

Evolution also sometimes appears to produce variety of signaling in cases where social glue is needed between individuals, either between group members or between parent and offspring. In the first case this social glue is needed to keep a group or two individuals together, to help minimize conflicts, to coordinate activities, and to establish boundaries with other groups. Sounds functioning in this way can be referred to as “social cohesion calls.” Good examples of this type come from cetaceans and other social mammals.

Pod Repertoires of Killer Whales as Social Cohesion Calls

Killer whales (orcas) live in stable groups called pods, which change only by birth and death (Bigg et al., 1987; Miller and Bain, 2000). The whales produce a variety of sounds, echolocation clicks, tonal whistles, and pulsed calls; some of these are
repeated discrete calls, and some are highly variable (Ford, 1991). Discrete calls dominate when killer whales travel or forage. The discrete calls are easy to categorize. Whistles and more variable pulsed calls are common in groups engaged in social interactions; these are difficult to categorize.

Each pod of killer whales has a group-specific repertoire of discrete calls that is stable for many years. Each whale is able to produce the entire repertoire of the pod. Some calls are more common in resting groups, others in more active groups. However, each discrete call in the pod’s repertoire can be heard regardless of what the pod is doing. Different pods may share some discrete calls, but no two have the same entire call repertoire. Different pods also have ranges of overlap and also associate together for hours or days before separating. Individual pods also have clearly defined subpods and matrilineal groups that seldom split up but may separate and converge. These group-specific call repertoires are thought to indicate pod affiliation, maintain pod cohesion, and coordinate activities of pod members. The frequencies of the different types could be indications for certain kinds of moods and activities they are associated with, but more research is needed on this topic.

**Dolphin Societies and Social Cohesion**

At first glance dolphin societies seem similar to killer whale societies. According to McCowan and Reiss (1995, 1997), dolphins also have a group repertoire that varies in composition with context, with presumably similar functions as in orcas. There is also the possibility that these calls can be used by conspecifics to infer the direction of movement of the signaling animal, which would help to coordinate activities in many situations (Lammers and Au, 2003).

Social cohesion could also be supported by a rather unique type of vocalization that has been reported in dolphins. The bottlenose dolphin, for example, has been claimed to show something called a signature whistle unique to each animal, developing within a period of a few months to a few years and remaining stable for a very long time (Caldwell and Caldwell, 1965; Caldwell et al., 1990; Sayigh et al., 1990; Tyack, 1999, Tyack, 2000; Weiß et al., 2006). On the other hand, these so-called signature whistles are also produced by other individuals in the group. Advocates of the signature whistle hypothesis call such occurrences “imitations.” Advocates also claim that these imitations are used to “call” or at least initiate interaction with the signature individual, but experimental evidence for this claim is unavailable. We do not know of a parallel or analog case of a “signature whistle” or “signature vocalization” in other animal groups.

The whole idea of the signature whistle is odd in the context of other signal systems. Possessing a signature whistle seems equivalent to swimming around and calling one’s name out repeatedly. In an overwhelming variety of species, animals that know each other individually recognize each others’ voices whenever they vocalize, so that no special signature sound is required. Therefore, there is reason to question
the interpretation of dolphin whistles as signature whistles on plausibility grounds. However, as advocates argue their case, it could be, of course, that because of the acoustic properties of water where sound is easily distorted, it is hard to recognize individual voices and thus necessary to produce individually specific signature whistles in some marine species.

Dolphin societies differ from those of killer whales in that they are not as stable but are more like the fission–fusion societies of chimpanzees. As in chimpanzees, dolphins bond with certain individuals for long periods of time, mostly in male–male and female–female coalitions, and these coalitions may play a role in the maintenance or establishment of signature whistles. It has been suggested by advocates of the signature whistle idea that the coalition partners may imitate each others' signature whistles to a certain extent in order to call each other when they need to coordinate activities. It has also been argued that the signature whistle could be helpful in locating and recognizing a coalition partner in the murky waters of the inshore environment where vision is limited.

Further Remarks on Cetaceans, Social Cohesion, and a Possible Role for Grooming

Whatever the truth may be about the signature whistle hypothesis, one thing is clear in cetaceans: They use a wide variety of different and acquired whistles, many learned by imitation, and they use these signals to achieve cohesion between the members of matrilinear family groups or between coalition partners.

It is interesting also to consider a social, that is, "vocal grooming" function (Dunbar, 1996; Morris, 1967) for vocalizations in cetacean societies. Bodily grooming is limited in cetaceans, so vocal grooming could have important advantages. There is some rubbing and touching that occurs, but usually it is limited to individuals who are good friends or close kin; since the number of familiar and individually recognizable dolphins is quite large, vocal grooming could help to stabilize relations in the group.

It is particularly difficult to determine function and signal relations in the case of cetacean societies because it is difficult to monitor the vocalizations of individuals in their water environments. From what we do know, it appears the communicative systems consist of a several-to-several mapping of signals and functions. We do not know much about the details yet, but the cetacean circumstance, with its high priority on social cohesion, seems to favor selection for variety of communicative signals and for both signal flexibility and functional flexibility.

Interestingly, the existence in cetaceans of "fixed calls" for specific functions like courtship or aggression has only recently been reported (Blomqvist et al., 2005; Connor and Smolker, 1996; Herzing, 1996; McCowan and Reiss, 1995). Blomqvist et al. (2005) even suggest a signal equivalent in function to human "laughter" in dolphins, which is used in the context of play behavior (see Kuczaj and Makecha, this volume). Nevertheless, it is not quite clear yet to what extent these calls are actually "fixed" in
the sense of being innate and inflexible in usage. It seems possible that the apparent complexity of vocal communication in cetaceans (and especially dolphins, where most cetacean research has been concentrated) makes it difficult to discern functional unity of the many types of whistles and other sounds.

Recent research suggests that social cohesion signals may be found in primates as well—for example, in the Campbell’s monkey where individuals can have variants of a single call type that they share with other individuals in the group and that can change across time (Lemasson et al., 2003; Lemasson and Hausberger, 2004; Lemasson et al., 2005). Also, male chimpanzees, while not producing a group repertoire of different calls, appear to modify a single call category, their pant hoots, through learning, and thereby geographically adjacent groups can be distinguished (see the review in Hammerschmidt and Fischer, this volume).

**Pleasure Sounds as Possible Social Cohesion Devices in Cetaceans and Primates**

One functional category of signals that has been very little studied is comfort and pleasure sounds (see, e.g., Jürgens and Ploog, 1976; Panksepp, 2000). Pleasure sounds may occur vegetatively in solitary species (and thus could only serve as cues rather than signals in such cases). According to the ritualization hypothesis of classical ethology, pleasure sounds may emerge as signals through shaping by natural selection from such vegetative cues in order to reinforce the source of pleasure, for example, a grooming partner. Purring in cats provides an example of a stereotyped fixed signal of pleasure that is even used in interactions with other species (Case, 2003; Morris, 1986). Since purring seems to enhance the cat’s positive state of affect, it may also be used to quell fear, in a way humans sometimes use laughter in circumstances of threat.

In humans, pleasure signaling is very complex, since many elements from the vocal language, vocal nonlanguage, and body language repertoires can be recruited to signal pleasure. For example, sighing is often used to indicate satisfaction with an event but can also be used to indicate weariness. Pleasure sounds in humans can inform the listener of the speaker’s positive reaction and, like the cat’s purring, can encourage continuation of it. In intimate human relationships the importance of such signals may be fundamental. Research on face-to-face interactions between human infants in the first months of life and their caretakers documents the widespread use by parents across cultures and languages of universal intonation types (superimposed on any sentence spoken to the infant regardless of language) including rising intonations as encouragement to the infant to continue vocal interaction and sighing intonations as soothing devices (see Fernald, 1989; Fernald and Simon, 1984; Fernald et al., 1989; Papoušek et al., 1990; Papoušek et al., 1991). The effect of encouragement and soothing on continuing interaction is consistent with our impression that in many social species pleasure sounds have come to reinforce caretaking, grooming, or other pleasant activities and intimate interactions, including copulation.
Even among chimpanzees, who appear to be particularly limited in vocal flexibility within the primates, females produce apparent passion sounds when copulating with the alpha male but appear to show the flexibility to suppress these sounds when copulating with a low-ranking male (de Waal, 1982). Further, the so-called close calls of many primate species seem especially diverse (Becker et al., 2000; Snowdon, 2004). Such sounds are produced primarily in circumstances of social interaction that may reflect comfort and pleasure.

Ford reports that orcas in Johnstone Strait regularly visit a special beach covered with round pebbles where they rub their bodies along these pebbles. While they do this, they produce a wide variety of (presumably) pleasure sounds, which can be either discrete calls from their own pod, discrete calls from other pods, or completely novel calls and whistles that were never recorded before (Ford, 1991; Riesch et al., 2006). In this special case at the pebble beaches, orcas groom themselves—we do not know whether they produce the same kinds of sounds as pleasure indicators during rubbing against each other when at sea or during copulation. This is a topic that deserves study, because the variability of the sounds produced provides further evidence that expression of comfort or pleasure may be particularly conducive to variability.

We also suspect that there may be an audience effect for pleasure sounds in social species. Such an effect clearly occurs in humans—we do not sigh with pleasure to a stranger the way we might to someone with whom we share intimacy. It has already been mentioned above that chimpanzees show audience effects with passion sounds.

Dunbar suggests that increases in group size in primates can make it impossible for bodily grooming to serve the function of maintaining group cohesion, and consequently that a pressure favoring vocal grooming can thus develop (Dunbar, 2004). In particular, he thinks the shift to vocal grooming occurred in the hominin case. Since comfort-inducing sounds are so variable in humans, it would appear that vocal grooming was another circumstance that encouraged variability in vocalization.

We know of relatively little data on this topic, so we are mostly speculating, but it seems that both in signal and in function, pleasure or comfort sounds may be diverse in social species. The pressure for stereotypy seen in other cases (as with alarm or threat calls, e.g.) appears to be weak here, and instead there may be selection for variety; it could be, for example, that the richness of vocal production by the individual being groomed serves as a reinforcer to the grooming individual. Thus, we suspect that a several-to-several mapping of signal and function may be naturally selected in comfort and pleasure sounds. Given the empirical evidence available, it does appear that pleasure sounds are particularly likely to show signal flexibility.

**Parent–Offspring Bonding**

Another case of social cohesion occurs in the context of parental care where there is the necessity to establish a strong bond between parents and offspring. In some
circumstances, signals between parent and offspring can be quite stereotyped—for example, in pinniped rookeries where mother–pup recognition calls are usually stereotyped and need to be recognizable over a distance (Schusterman et al., 1992). Human parents, however, use at least two different intonation types that can be superimposed on any sentence for purposes of soothing and encouragement of vocal interaction with infants (see the citations above).

Further, there are cases where variability in signal production by the offspring seems to pay off. Human infants provide one such example. Variable sounds interpreted by parents and researchers as expressing pleasure have long been recognized as signals to parents of infant well-being and as bonding devices (Locke, 1993; Papoušek, 1994; Stark, 1978; Stark, 1980). Another case of variability in infant vocalization is seen in the socially breeding marmosets where variable “babbling” (production of sequences of sounds that appear to consist primarily of infant versions of several different adult fixed signals in systematic repetition and alternation) seems to elicit attention from parents and other caregivers (Elowson et al., 1998; Snowdon, 2004; Snowdon et al., 1997; and see Snowdon, this volume). These juvenile sounds are interpreted as babbling because during babbling episodes they do not serve the functions that the same sounds serve in mature marmosets. Such babbling appears to occur in some other New World monkeys as well, but observational evidence is less clear in these cases.

Producing variable vocalizations may reinforce the bond between offspring and parent, elicit parental care, and at the same time give the parent clues concerning the offspring’s fitness. Locke (2006) reviews extensive data indicating that human parents use vocalizations of infants as fitness indicators, and both he and Oller and Griebel (2005) argue for parental selection of infants in part based on assessment of infant fitness through vocalization. The evidence is especially suggestive in child abuse and neglect, where infants and children with communication disorders have been shown to be especially vulnerable. In evolution of the hominin line, differential parental (and other caregiver) investment in infants could have played a major role in selection of infants whose vocalizations were particularly indicative of good health and viability. This fitness-indicating “babbling” would present a several-to-one mapping of signal to function and would thus constitute a case of signal flexibility. It could be the case that in some species these babbling sounds are largely drawn from the pleasure and comfort sounds described in the prior section.

Deception

Deceptive Behavior as a Factor in Communicative Flexibility
Another powerful source of selection for variability of signal as well as function in communication is deception. In deceptive behavior, signals that give a false or exag-
gerated portrayal of the environment or of the state or identity of the sender are used. Deceptive signaling is "parasitic" on existing nondeceptive signaling systems or on cue interpretation as indicated above.

Deceptive signaling can occur in several forms (Mitchell and Thompson, 1986) including at least the following: (1) genetically preprogrammed (innate) deception, in, for example, Batesian mimicry, where, for instance, a nonpoisonous species evolves a coloration corresponding to a poisonous species and thus avoids being preyed upon, (2) instinctive behavioral programs for deception, as has been assumed in the case of injury feigning in birds, (3) conditioned behaviors such as learned injury feigning reported anecdotally for dogs and other species, and (4) intentionally planned deceptions, for which real evidence is rare in the animal kingdom (Byrne and Whiten, 1985, 1988, 1990; Gibson, 1990; Mitchell and Thompson, 1986; Whiten and Byrne, 1988) but plentiful in humans. Even though anecdotes of deceptive signaling are numerous in birds and mammals, it is difficult to prove that learned deceptive signaling occurs in animals, and the evidence is not as persuasive as we would wish it to be. The reason for the lack of convincing data in this field is, of course, that in order for deception to work it must be rare, and thus the burden of proof is heavy on those who wish to assert the existence of learned deception in animals.

In most cases of deceptive signaling, it appears that both deceiver and victim are capable of learning, and an arms race of deception and detection ensues. However, in the case of Batesian mimicry only the victim of the deception appears to learn, for example, to avoid the danger of poison in prey with aposematic (warning) coloration, a fact that can be exploited in deception by a nonpoisonous species that evolves the same coloration.

One requirement for deceptive behavior to form foundations for flexibility in communication is that the behavior has to be learned. In genetically preprogrammed deception such as Batesian mimicry the deceptive signal/cue is fixed within each individual of a species and thus cannot form the foundation for either signal or functional flexibility. The same reasoning seems to apply to instinctive behavioral programs for deceptive behavior that do not allow for learning.

However, functional flexibility can result if some learning occurs in the functions for which the signal can be used. For example, an instinctive alarm call could be used to make other animals scatter and thus get rid of food competition or mate competition or to get out of a precarious aggressive interaction with either a conspecific or a predator. When a deceptive behavior is learned, it can form foundations for signal flexibility as well as functional flexibility. The neurological substrate necessary for these learning processes could be capitalized upon in the evolution or development of communication. Of course, as communicative flexibility increases, communicative acts can increasingly be used for deception.
It is noteworthy that in many cases of deceptive signaling, the signaler changes neither the signal (e.g., the alarm call) nor its illocutionary force (alarm) but exploits the intrinsic illocutionary force to achieve a perlocutionary effect (the other animals scatter after perceiving the alarm), eliminating, for example, competition for food. Another example would be a false infant distress call that causes the infant's mother to attack an animal who is not threatening the infant but is in possession of, for example, a food item the infant wants to obtain.

Surprisingly perhaps, there is actually some evidence of learned deception among invertebrates. Since examples for deception in higher vertebrates are relatively well-known, we review some interesting data for an invertebrate species here.

**Fireflies and Communicative Flexibility**

Fireflies are nocturnal insects that manufacture their own visual signals with the aid of biochemical equipment at the tip of their abdomens. The lighting signals would seem conspicuous to predators, but fireflies are protected in part by being poisonous. In different species, unique patterns of light pulses have evolved that vary by species in duration, intensity, frequency of occurrence, and color (Lloyd, 1986). This shows that a selection pressure for distinctiveness and stereotypy is at work in the basic species-specific visual signaling system of fireflies. However, the firefly flashes can be shown to be flexibly mapped to a variety of functions.

Fireflies of the genus *Photuris* seem to have the most complex flashing behavior of any firefly studied to date. Females use the flashes in situations other than mating and courtship. They use their light for illumination as they take off or land, when walking on the ground, when ovipositing (i.e., laying eggs), and when climbing through mazes of Spanish moss. They sometimes flash just at the moment they attack a flying flashing firefly in the air, perhaps as a startling device. Such an aerial attack is used in conjunction with aggressive signal mimicry or sometimes against hesitant suitors.

In aggressive signal mimicry, the females of this genus *Photuris* answer the mating flashes from males of certain other species in the genus *Photuris*. Each species of *Photuris* has its own code with a female's answering her male's distinctive flash pattern by giving a flash pattern of her own after a precise time interval. Some females can respond correctly to male signals of three different *Photuris* species. If a *Photuris* female succeeds in luring a male close enough, she will grab and eat him, and she can absorb the poison and transmit it to her eggs, making her own eggs more poisonous and thus better protected. However, the males have developed a counterstrategy. They do not throw themselves onto the females but land at a safe distance and walk cautiously toward them, ready to escape in case of a trap. This may explain why the females sometimes switch to aerial attacks instead.

What makes the case of the fireflies so interesting is that this mimicry is a learned behavior, because the female fireflies can learn novel human-made flash patterns that
no real firefly uses. Thus, fireflies present a powerful example of a predisposition for learning to reproduce variable patterns that they encounter in their environment.

According to Lloyd, the story is even more complex. Many *Photuris* males produce not only one type of mating pattern but two or more different ones. They imitate mating patterns of males of other firefly species that live in the same area. Lloyd has speculated that they imitate the flash patterns of males that their own females try to lure with false signaling, in order to try to find one of their hunting females to be able to mate with her. Thus, in this case this male mimicry could have evolved as a mate-seeking tactic.

To understand this seemingly odd system, one has to know that competition for females is fierce in fireflies. A mating takes a female out of the game for some time because she will be busy laying eggs; the average ratio of males to females ready for mating is about 100 to 1. One strategy for males to find a rare mating option is to learn to mimic males of other species that the rare females of their own species may be trying to lure into a trap. Another important strategy evolved by the males seeking a mate is a very cautious approach to a female that gives the right answer. The males usually land at some distance and approach carefully. Typically, a small group of males approaches the same female while exchanging flashes. In this group the males sometimes answer the other males with "transvestite flashes" to lead them down the wrong track and to slow them down. They also emit flash patterns of other species as well as other "extraneous" flash patterns that might be used to deter competition or to test the truthfulness of the female.

Another interesting thing *Photuris* males do is to interrupt the courtship pattern of competitive males with an "injected" flash. Females do not usually answer to patterns that have an injected flash. The effect of injected flashes on flying males is that they sometimes land immediately at the location of the injected flash, presumably to join the competition for a female. Needless to say, some *Photuris* females have learned to inject a flash at the right spot to make males of other species land right next to them (Lloyd, 1986).

Even if only half the story is true, communication in fireflies seems to be a very complicated matter. Both male and female *Photuris* are able to use a variety of signals in a variety of contexts, so these species present a case of several-to-several mappings with both signal flexibility and functional flexibility. An interesting aspect of this system is that the variability in communication in this mating system seems to be driven not by sexual selection alone but mainly by advantages that can be achieved through deception and counterdeception. The complexity arises because signal-tracking predators or competitors tend to eliminate simpler, straightforward signalers from the gene pool and thus feed a spiral of more and more complex signaling and signal detection. The firefly data hint at the possibility that complexity may be a universal countermeasure for dealing with deception in communication in
general. This possibility may be relevant to the human case because the extreme elaborateness of human language may also in part be a response to detection and counterdetection pressures (see also Sterelny, this volume).

**Camouflage, Protean Behavior, and Complex Signaling in Cephalopods**

Even though camouflage does not count as a signal by the definition we are using because successful camouflage prevents communication rather than transmitting it and because in many cases the receiver does not have a chance to coevolve with the sender, we will consider it here as a possible source for a signal production mechanism, especially for mechanisms that may yield flexibility. A prime example of this possibility is found in the cephalopods. Usually communication research is heavily biased toward acoustic communication. In the following section we look at a complex visual communication system and its possibilities in some detail.

Cephalopods are the masters of flexible camouflage, being capable of seemingly disappearing instantaneously into a variety of marine backgrounds. Cephalopods have developed a chromatophore system in their skin with which they can match their body surface to the background (Messenger, 2001). Surprisingly, the variety of patterns they need for this behavior is quite limited; two or three different grain types and general brightness matching to the background usually do the trick in the aquatic environment, which does not favor high visual acuity anyway.

**Evolution of Chromatophores as Camouflage and Signaling Devices**

As the theory goes, cephalopods originated as shelled creatures with sluggish swimming capability. In order to compete in the open water with fish, they gave up their outer shells for speed and flexibility and became streamlined, fast, and brainy predators. But at the same time they gave up the protection afforded by their shells. Their vulnerability without shells encouraged the evolution of a camouflage system on their skin that would fool predators (Packard et al., 1980). Many believe that chromatophores evolved for camouflage purposes and were later adapted for social communication (Packard et al., 1980). However, this is just speculation; it could have been the other way around. Consider, for example, chameleons, a group commonly believed to use color change for camouflage. In fact, the primary function of color change in chameleons is social communication, and secondary functions are physiological ones to regulate body temperature (LeBerre et al., 2000).

Pelagic (open water) creatures are best camouflaged either by transparency or by reflective surfaces and countershading. Consequently, chromatophores would be of little use in camouflage for creatures that evolved from a shelled life to that of pelagic predators. Therefore, it is plausible to assume that chromatophores might have developed first for reasons other than camouflage, for example, for communication, and indeed the chromatophore system is used extensively for communication. In
either case the development of the chromatophore system has led to a very flexible system of displays on the skin in cephalopods that can be brought to the service of communication as well as camouflage.

Of course, the cephalopods do rely partly on background matching and countershading strategies, but additionally they have evolved a whole array of efficient strategies in case they are detected anyway. One of them is deimatic or startling behavior, where they use their chromatophores to produce false eyespots, a very popular startling pattern in the animal kingdom. In some cephalopod species deimatic spots can appear in a variety of body locations.

**Protean Behavior in Cephalopods Utilizing the Chromatophore System**

Another strategy cephalopods use to avoid predators is called "protean behavior" (Chance and Russell, 1959; Driver and Humphries, 1988), or highly unpredictable behavior. It is universally used in the animal kingdom to confuse either predators or prey. Consider the zigzag flight paths of many animals pursued by predators or the "crazy dance" in weasels or foxes during hunting. In cephalopods the protean display for escaping a predator includes inking and, most importantly, the production of a wide variety of color patterns that present the predator with an ever-changing target (Hanlon and Messenger, 1996; Holmes, 1940). Thus, what a squid or an octopus does when it is detected is not predictable, and the predator is prevented from developing a search image for these targets because they tend to change in appearance with every encounter.

One species, the Caribbean reef squid, *Sepioteuthis sepioidea*, produces a wide variety of body patterns out of several different background colors, along with several pattern types such as horizontal bars, vertical stripes, a mottle, and roundish units (Moynihan and Rodaniche, 1982). All background colors are used as camouflage patterns either alone or combined with patterns such as stripes, bars, or a combination of stripes and bars called "plaid" or combined with mottles and/or spots. However, the social signals for aggression and courtship are composed of the same patterns; thus, several pattern combinations are used for two different functions. One is social communication; for example, the pattern Stripe can be a courtship signal, and the other function is that of hiding when it is used as a camouflage pattern. The aggressive pattern Zebra (which consists of a type of mottle) is used in both intraspecific and interspecific aggression but is also used as a camouflage pattern when the animal is close to the sea bottom. Pale is used as a default pattern during the night, but it is also used as a startling pattern during the day, for camouflage during rapid flight, and to indicate a state of high arousal during courtship. Essentially all body patterns can be used as protean or "startling" patterns.

**Deception through Chromatophore Signaling in Cephalopods**

We have observed on several occasions that when a male Caribbean reef squid was being chased by another male and challenged for a contest, it sometimes happened
that the chased male produced a Saddle, which is a female courtship pattern (Griebel et al., 2004). The effect was that the chasing male stopped the chase immediately, and, probably confused, sometimes even produced the mating pattern that answers Saddle, which is Stripe. At first it appeared that this behavior might be an appeasement signal, but the rarity of occurrence of such cases argues against its being a consistent appeasement signal. More likely, it appears the female courtship signal is produced by the threatened male as a kind of deception—causing the attacker to cease aggression.

We find another case of deception in a different cephalopod species. The giant cuttlefish uses the female “dress” to sneak into position in order to copulate with the female even under the guarding eyes of a dominant male (Hanlon et al., 2005). So in Sepioteuthis, and some other cephalopod species, we find a several-to-several mapping of signal to function, with both signal flexibility and functional flexibility.

**Multiple Signaling in Sepioteuthis Sepioidea**

Another specialty feature of the Caribbean reef squid communication system is seen in production of two to three different signals at the same time. The squid either uses the dorsal and ventral side of the body or divides the body in half longitudinally, thus sending different signals to the receiver on the left and on the right. In addition, Sepioteuthis sepioidea can combine social signals with startling signals like deimatic spots at the same time if it is advantageous to do so—for example, if a fish plunges into a social interaction among squid (Griebel et al., 2004). We propose that because of the selection pressures for unpredictable or protean behavior, the Caribbean reef squid has evolved a multiple signaling system that allows for combining almost all the signals in the repertoire in a very flexible way. The big question for which we do not have an answer at this point is whether these behaviors are innate or learned in cephalopods. Either way, flexible camouflage capabilities are clearly related to flexible communication capabilities in cephalopods.

**Summary on Factors Favoring Contextual Flexibility**

Consistent with our reasoning above, we propose that there exist two classes of contradictory selection pressures affecting signaling, one favoring stereotyped fixed signals and one favoring variability of signaling for specific purposes. The relative balance of these contradictory forces can be expected to incline the process of evolution either toward a stereotyped system that stays stereotyped or toward evolution from a primarily stereotyped system to one that also includes variability of production and usage.

The conditions that we have observed in this cross-species review that seem to favor the selection of one-to-several, several-to-one, or several-to-several mapping for signals and functions include sexual selection, social cohesion (either between group members or parents and offspring), deception, camouflage, and possibly protean be-
havior. We do not intend to suggest that this list is complete but merely that these circumstances seem to have favored both signal and functional flexibility in cases that have been described sufficiently to justify their inclusion in the list.

Evolutionary Pressures Pertaining to Human Communication in Particular

Comments on the Possible Role of Gesture in the Origins of Language

Our focus with regard to the origins of human language is on the vocal–auditory channel of communication that is the primary one in all human societies other than those composed primarily of deaf individuals. On the other hand, there has been considerable advocacy for the idea that language originated in gestural acts rather than in vocal ones (see the review in Corballis, 2000). The argument takes stock of the tendency of human infants to use gesture importantly in pointing and requesting early in life and of the fact that languages of trade often include an extensive role for gesture. Further, the argument in favor of gestural origins draws on the fact that nonhuman primates show much more gestural flexibility than vocal flexibility (see Call, this volume) and that apes have been capable of learning the rudiments of a sign language system even though they appear incapable of vocal learning to any significant extent.

It is, of course, possible that gesture played a role in early language evolution, just as gesture plays a role in modern language. However, even if gesture did play a particularly important role at some early stage in hominin evolution, it is still required in the search for evolutionary origins of language to determine how vocal flexibility emerged. A gestural theory does not automatically solve that problem. The reasoning regarding the possible origins of vocal flexibility in humans presented in this chapter would apply even if gesture did play a particularly important role in the early evolution of language.

Given what is presently known about language, development of language, and comparative communication systems, we differ from gestural-origin advocates and favor the view that the earliest origins of language were primarily vocal. Here are a few summarial reasons for our preference: (1) Gestural language is never the primary communicative system in human societies composed of hearing individuals, (2) human infants communicate vocally with considerable elaborateness in the first months of life (see Oller and Griebel, this volume), but their gestural communication (as important as it is) begins most importantly with pointing late in the second half year of life, (3) the manual channel is largely nullified when the hands are occupied as with carrying objects or children, and importantly, vocal communication does not interfere with use of the hands for these other purposes, (4) the vocal channel is largely free for communication (it has no other primary uses), while the manual channel is complicated by many hand movements that are intended for other purposes, and consequently a vocalization tends to be interpreted as a potential communication to a
much greater extent than a hand movement, (5) vocalization is effective in darkness, when the potential audience is out of view, or when the potential audience is not looking at the sender, and (6) acknowledging that some sign language can be learned by certain apes, it is important to remember that no sign language has emerged in the wild in a nonhuman primate and that natural gestural communication in apes is very unlike language (see Call, this volume, for examples of natural ape gestures). Thus, the present chapter seeks to explain the flexibility of communication in humans primarily in the vocal domain, even though the review also takes account of flexible communication and foundations for it in other modalities.

Comments on the Vocal Origin of Language

In the human case, natural selection produced explosive flexibility in vocalization and vocal usage. Our hypotheses about the special circumstances that led to this evolutionary pattern include the following: Since human infants are probably the most altricial offspring in the animal kingdom and dependent on their parents for a period of six to eight years (and ancient hominin infants were already more altricial than other primates and dependent on their parents for long periods), we think a likely scenario for the evolution of signal flexibility was based on a special premium in ancient hominins for parent–offspring bonding. We have proposed (Oller and Griebel, 2005) along with Locke (2006) that modern infants use (and ancestral hominin infants used) early vocal behavior and babbling to elicit attention and care, a contention that is also consistent with reasoning of Snowdon (2004). The more variable and elaborate the sounds produced by the infant, the more effectively the sounds could elicit parental care, and thus, according to the reasoning, there was selection for variability, that is, signal flexibility itself. Details regarding how we propose infant vocal behavior to have provided the basis for parental selection on variable vocalization as well as empirical data on parental selection based on vocalization in modern humans are found in Oller and Griebel (2005) and Locke (2006).

Importantly, we reason that the immediate effect of attention-getting through variable vocalization may have been supplemented by even more important effects in terms of long-term commitments of parents to infants (Locke, 2006). The balance of forces appears to have favored variability especially in the hominin case because the hominin infant was in special need, given its altriciality, to prove its fitness, and it was selected to do so, we reason, by exhibiting a complex vocal capability.

Another likely pressure favoring vocal variability in the hominins at a very early stage in differentiation from the primate background could have emerged in the context of social grooming as suggested above (Dunbar, 1996, 2004). Pleasure and comfort sounds may have been evolved in the hominins to reinforce grooming and, in an extended function, to reinforce social relationships directly, especially as group sizes increased across early hominin evolution.
Evolutionary Forces Favoring Communicative Flexibility

Even further, once vocalizations were used to reinforce social relations in the bodily grooming circumstance, they could have begun to function as social pacifiers through vocalization alone. In this latter way, vocalizations may have begun to supplant bodily grooming, taking the form of vocal grooming (Morris, 1967) and making it possible for group sizes to increase further. We also note that hominins whose infancies included variable vocalizations developed to elicit parental investment would have been in a particularly strong position to use the same vocalization capability in the vocal grooming circumstance. Thus, we reason, at an early stage of hominin evolution, the special parental bonding needs of the hominin infant may have tipped the balance in favor of variability as opposed to stereotypy in vocalization, and additional social cohesion forces associated with grooming may have added to the advantages of variable vocalization.

The reasons we do not think it is likely that sexual selection played a particularly major role at the earliest phase of special hominin vocal evolution are based on comparative assessments. We do not know of any elaborate and variable mating songs among the primates. Such sexual displays appear to be rare in mammals in general and only occur in specific circumstances such as those pertaining to lekking systems (consider, e.g., marine mammals such as humpback whales or walruses). Sexual selection may, of course, have played a significant role in the evolution of language at a later point in time; our contention is merely that it seems likely to have played little role at the point when hominins began to evolve away from the general primate pattern of vocalization.

Similarly we do not know of any example where deception or protean behavior created major innovations in vocal variability in primates or other mammals. And so we doubt that these factors played important roles at the very beginning of hominin evolution of vocal variability. At the same time, it is clear that deception and protean behavior (razzle-dazzle 'em, and baffle 'em with yer blarney; see Miller, 2000) are major usages of modern human language, and so we reason that these factors could have come into play once a neurological substrate for vocal contextual flexibility had been established. Thus, our proposal is that human communicative flexibility emerged first under pressures of social cohesion, especially related to parent–infant bonding and the needs of grooming.

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