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Functionally referential signals: a promising paradigm whose time has passed

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Finding the evolutionary origins of human language in the communication systems of our closest living relatives has been a major goal of many in the field of animal communication generally and primate communication specifically for the last several decades.[1-4] The so-called "functionally referential" signals have long been considered promising in this regard, with apparent parallels with the semantic communication that characterizes language. Although the once prominent idea that functionally referential signals are word-like, in that they are arbitrary sounds associated with phenomena external to the caller, has largely been abandoned,[5] the idea that these signals offer perhaps the strongest link between primate communication and human language remains widespread, primarily due to the fact the behavior of receivers indicates that such signals enable them to make very specific inferences about their physical or social environment. Here we review the concept of functional reference and discuss modern perspectives that indicate that, although the sophistication of receivers provides some continuity between nonhuman primate and human cognition, this continuity is not unique to functionally referential signals. In fact, because functionally referential signals are, by definition, produced only in specific contexts, receivers are less dependent on the integration of contextual cues with signal features to determine an appropriate response. The processing of functionally referential signals is therefore likely to entail *simpler* cognitive operations than does that of less context-specific signals. While studies of functional reference have been important in highlighting the relatively sophisticated processes that underlie receiver behavior, we believe that the continued focus on context-specific calls detracts from the potentially more complex processes underlying responses to more unspecific calls. In this sense, we argue that the concept of functional reference, while historically important for the field, has outlived its usefulness and become a red herring in the pursuit of the links between primate communication and human language.

WHAT ARE FUNCTIONALLY REFERENTIAL SIGNALS, AND WHY ARE THEY CONSIDERED RELEVANT TO LANGUAGE EVOLUTION?

Functionally referential signals are those signals in which production is **context-specific**, with the relevant contextual feature defining the "referent," and which elicit specific responses in signal perceivers even in the absence of the supposed referent (that is, responses are **stimulus-independent**).[6-7] The textbook example of functional reference is the alarm call system of East African vervet monkeys (now classified as *Chlorocebus pygerythrus*). First noted by Tom Struhsaker in the late 1960s, vervets give distinct alarm calls in response to leopards, eagles, and snakes.[8] A little more than a decade later, Robert Seyfarth, Dorothy Cheney, and Peter Marler conducted playback experiments of each call type in the absence of any predatory stimulus and noted that the calls alone are sufficient to elicit predator-specific responses. According to the textbook version of these results, "leopard alarms" regularly cause listeners to run into the trees, "eagle alarms" cause listeners to look up or run into dense bushes, while the "snake alarms" cause listeners to stand bipedally and scan the ground.[9-10] It should be noted though that the data presented in the original papers[9-10] also indicated substantial variation in responses. This aside, the calls meet both of the criteria of functional reference because the production of the calls is context-specific, linked to particular predator types, and because appropriate responses to the calls are stimulus-independent, deployed even when the contextual cue is absent. This predator-specific alarm call system contrasted with the "urgency-based" systems that had been described for a number of social rodent taxa, wherein distinct alarm call types might be given in high- and low-risk situations, respectively, regardless of the type of predator.[11] Importantly, the type of call given by vervets seemed to be independent of risk, with leopards consistently eliciting one call type regardless if the risk it posed was of high- or low-urgency, and the same being true of the call types given to raptors and snakes.

<The discovery of the vervet alarm call system began a revolution in the field of animal communication because the observations seemed to provide clear evidence against what was then the predominant view in animal communication: animal vocal signals are a reflection of the signaler's internal state and do not refer to phenomena external to the signaler> in the way that

human semantic communication does**.**[12] Indeed, the fact each predator-type consistently elicits a distinct call type, regardless of the level of urgency that it presents, is difficult to explain in this framework. Shouldn't a caller's internal state be affected more by the risk the predator presents (high versus low) than the type of predator encountered (aerial versus terrestrial)? The fact that the calls alone were sufficient to elicit predator-specific reactions was interpreted as evidence that listeners were able to obtain very specific **information** (a term which has drawn considerable debate in the animal communication literature in recent years[13-18] and which we will discuss below) from the calls, as if the vocalizations were indeed semantic signals, reinforced the interpretation that these calls shared more in common with human words than with other animal signals.

The honeybee "waggle dance," which allows hive mates to precisely determine the location of food and far exceeds the specificity of vervet alarm calls, had been known to ethologists since the 1940s[19] but was not considered especially relevant for the evolution of human language. One obvious reason for this is the great evolutionary distance separating the social insects from humans. But the honeybee waggle dance also lacked another key feature of human symbolic communication: **arbitrariness**.[19] That is, rather than lacking any direct association between the signal and its meaning, the number of turns in the honeybee's dance increases with the distance to the food, while the dancer's vertical orientation indicates the direction from the hive relative to the current position of the sun. In contrast, the vervet alarm calls did seem to be arbitrary in that there is no direct association between the acoustic characteristics of each call type and the type of predator that each is associated with, leading to an initial conclusion by Seyfarth and colleagues that the calls are best seen as symbolic and referential.[9-10]

Vervet alarm calls and other such context-specific signals were thus typically referred to as simply "referential" or "semantic" signals by many ethologists until the early 1990s, although some criticisms arose over the application of such linguistic nomenclature to animal signals.[20-21] To judge whether or not this criticism is warranted, it is necessary to briefly review the core concepts of semiotic theory, which deals with the analysis of signs and signifying practices. **Signs** are meaningful units that stand for something other than themselves. According to Saussure,[22] a sign consists of a signifier and the signified, for instance, the relationship between the spoken word “dog” and the actual animal. There are generally three different forms that the relationship between the signifier and the signified can take: symbolic, iconic, and indexical. In a **symbolic** mode, the relationship between the signifier and the signified is arbitrary and purely conventional. Most words in human languages meet this definition, although onomatopoeic elements in human languages, such as the descriptions of animal sounds (“meow,” “woof,” “ey-ore”), are considered to be **iconic** because the signifier bears a physical resemblance to the signified. Finally, **indexical** signifiers *indicate* the signified because they are in some way physically or causally linked to it, like smoke is linked to fire, or a vervet’s alarm call is linked to the presence of the vervet itself.[4] This relationship may be obvious or indirectly inferred by the observer.[21,23]

One of the main questions of animal communication researchers interested in the evolution of language was thus whether any communication system attained a symbolic quality. Because the vervet alarm calls were viewed as neither indexical nor iconic, they were considered to be symbolic or proto-symbolic. However, <the core characteristic of symbolic communication is the arbitrary nature of signals and the importance of conventions.>[20] This was at odds with neuroscientists’ early reports that the structure of nonhuman primate vocalizations was largely hard-wired, and that no experience was required to develop the species-specific call characteristics (described in the next section).[24-29] Further, the acoustic structure of primate vocal signals is not arbitrary, but rather is shaped by natural selection such that a given vocalization’s form is related to its function.[13,30] As it became clear that the similarity between human words and vervet alarms might be less striking than initially assumed, Peter Marler, Chris Evans and colleagues[6,31] suggested the term “functionally referential” to clarify that, although context-specific calls function much in the same way as human words, this conception “remains neutral about the underlying mental processes.”[31:67] Nevertheless, the idea that functionally referential signals require greater cognitive complexity and provide a clearer link to human language than do other types of animal signals remains pervasive in the animal communication literature.[2,4,32] Since the initial discovery in vervets, vocal signals that meet one or both of the criteria of functional reference have been described for the social, food, and alarm calls of a range of primate taxa, including New World monkeys, lemurs, apes, and a number of additional Old World monkeys.[2,4,33-35] Notably, a number of recent studies by Kate Arnold and Klaus

Zuberbühler[36] have demonstrated that functional reference can be achieved through the production of context-specific call combinations, even if the individual call types are not context-specific. Other studies have similarly shown that the number of times the same call is produced can vary with context.[35,37-38] Finally, studies that combine bioacoustic analysis with playback experiments have shown that acoustic variation within call types can also functionally refer to distinct stimuli.[39-40] These observations of widespread functional reference have been taken as evidence that the phylogenetic roots of human semantic communication likely go deep into the primate lineage,[41] although the fact that several avian and nonprimate mammalian taxa also use functionally referential food and alarm calls[34,43] indicates that context-specific signaling has likely evolved convergently in many taxa.

THE INFLEXIBILITY OF SIGNAL PRODUCERS: WHY FUNCTIONALLY REFERENTIAL SIGNALS ARE NOT SYMBOLIC

The neural foundations of primate vocal production was greatly illuminated by research by Uwe Jürgens and colleagues beginning in the 1970s.[24] According to their research with squirrel monkeys, the vocal pathway consists of three different subsystems. The first one is responsible for the initiation of vocalizations. The initiation can be triggered by the anterior cingulate cortex or by various limbic brain areas, in response to different external or internal stimuli. The so-called peri-aquaeductal grey (PAG) serves as a relay station for the descending vocalization-controlling pathways. The PAG integrates the incoming information and triggers a specific innate vocal pattern. This system can be found in nonhuman primates and humans alike. The second system is responsible for the voluntary motor control which is necessary to speak or sing, and is apparently restricted to humans, at least among primates. The system is comprised of the motor cortex with its connections to the cerebellum and thalamus as well as the putamen and pyramidal pathway. Importantly, there is a direct connection between the motor cortex and the motoneurons controlling the laryngeal muscles. In addition, there are connection between the limbic cortex and the motor cortex. The third system comprises the formatio reticularis of the lower brain stem and the motoneurons that innervate the respective muscles for vocal fold, lip, jaw and tongue movements. This system receives input from the PAG and, in humans, from the motor cortex. Thus, <the same neurobiological circuits which are responsible for innate vocalizations are existent in both nonhuman primate and human nonverbal vocal production

systems (including laughter and reactions to pain in humans), while the more derived parts responsible and necessary for voluntary control of vocalizations seem to be limited to humans>, at least among the primates**.** This neurobiological evidence accounts for the lack of flexibility in nonhuman primate vocal control.[24,28-29,42]

Moreover, no study has ever suggested that – say – vervet monkeys from different populations would use their calls in fundamentally different ways, such as using an alarm call in an affiliative situation, or even an eagle alarm in response to a leopard. Indeed, even though learning appears to be important in the ontogeny of vervet alarm calling, with infants giving alarm calls in inappropriate contexts,[43] their mistakes are not random. Eagle alarms may be given by infants to nonthreatening stimuli in the air, such as vultures or falling leaves, but they are not given to terrestrial animals like leopards or warthogs. The role of learning thus seems to be more related to predator recognition than to learning in what contexts specific vocalizations should be given, as further evinced by the vocal behavior of Diana monkeys in habitats where leopards have been extirpated.[44] The balance of evidence therefore indicates that although nonhuman primates are able to (partly) control the onset of calls, they cannot voluntarily choose which call to produce in which situation.[45] Instead, there is a strong link between specific internal states and the corresponding vocalizations.

A number of recent studies have highlighted the genetic underpinnings of this inflexibility in call structure and usage by examining how acoustic variation relates to genetic distance. Early work by Geissmann indicated that acoustic differences in gibbon song mapped onto geographic distance,[46] while more recent studies integrating genetic analyses have revealed that the acoustic structure of gibbon song and leaf monkey loud calls can largely be explained by genetic distance.[47-48] This actually shows superficial resemblance to the relationship between human language families and genetic distance at the global scale.[49] However, this correlation does not apply at the smaller scale and, under specific circumstances, a language within a population can be completely replaced within only 3 or 4 generations.[49]

Finally, nonhuman primates also differ from humans in terms of the “common ground” of communication. That is, human communication is seen as fundamentally cooperative, relying on shared knowledge of the world.[21,50-51] While the attribution of mental states and the intent to inform are characteristic of human language, there is only scant evidence that nonhuman primates vocalize with the intent to inform.[52-54] (See Box 1).

The proximate mechanisms underpinning the production of context-specific vocal signals in particular have not been well studied, and this is likely a fruitful avenue for future research, but all available evidence indicates that their production is not fundamentally different from less context-specific calls. Indeed, among Belding's ground squirrels, playbacks of trills and whistles, alarm calls associated with terrestrial and aerial predators, respectively, elicit distinct physiological responses in listeners in terms of heart beat and the production of stress hormones.[55] It is thus not at all inconceivable that different predator types also elicit distinct types of aversive reactions in vervets and other primates, or that the discovery of food could elicit a particular degree or type of excitement not elicited by other stimuli, and that there has been selection for the production of specific signals when in such states. Although <all the current evidence indicates that the production of even highly context-specific vocalizations is hardwired in at least most non-human primates>**,** a better understanding of the specific mechanisms underlying the production of these signals would most certainly be insightful.

Box 1. Inflexible signal production: are apes different?

Research into the vocal behavior of the living great apes has produced considerably less evidence for functionally referential communication than what has been shown in other primate taxa, due largely to the fact that predator-specific alarm calls are not ecologically-relevant for these large-bodied species. However, studies conducted over the last several years suggest that the food calls of chimpanzees and bonobos may well meet the production and perception requirements of functional reference.[33] At the same time, it seems clear that chimps, like most other primates, have a largely innate vocal repertoire and flexibility in vocal production is highly constrained. Chimps from different populations, for example, give the same basic call type, "rough grunts," in response to food, indicating that the production of a call with these particular acoustic features in response to food is innate in this species.[56] Recent studies have suggested, however, that some apes may differ from monkeys and prosimians in two critical aspects of vocal production that typically distinguish nonhuman primate communication from human language: an intent to inform among chimpanzees and a possible role for learning in the development of particular call types in orangutans.

Crockford and colleagues[54] recently presented evidence that wild chimpanzees are more likely to give alarm calls upon detecting a snake if other group members present were unlikely to be aware of the snake's presence. Such an ability to selectively communicate based on the knowledge state of the audience would clearly set them apart from monkeys.[52] However, such intentionality also requires a **theory of mind**, that is, an ability to understand that others have thoughts, knowledge, and beliefs, and the evidence that chimpanzees possess such abilities has engendered some controversy.[57] Nevertheless, the work by Crockford et al. is suggestive and will almost certainly inspire additional research into the possibility that communication with the intent to inform exists in the apes.

A second recent study has called into question the contention that the vocal repertoires of apes are completely innate and unlearned. While a number of previous studies have shown that learning may play some role in the development of "accents" (that is relatively modest variation in the acoustic structure of otherwise innate call types) among apes, such variation is also fairly well-documented in a number of species of monkeys.[58] More recently, Wich and colleagues[58] compared the vocal behavior of orangutans from five different populations and noted differences between populations in terms of whether or not individuals vocalized in the contexts of nest-building and infant-retrieval, as well as in the specific call types they give in those contexts. While such "dialectic" differences could potentially be underpinned by genetic differences between the populations, the authors found that variation between populations was not explained by the genetic distance between them, and suggested that the differences may evidence a role of learning in the development of particular call types. Stronger evidence for the imitation of novel, non-innate sounds among orangutans comes from a captive individual that learned to imitate the sound of human whistling.[59] Notably, though, whistles are not vocalizations because their production does not involve use of the vocal folds. Still, these findings may have implications for the neurobiology of vocal communication in the apes. While a degree of vocal learning and intent to inform among at least some apes may well turn out to close the gap somewhat between humans and other animals in these regards, additional research will be needed before firm conclusions can be drawn.

THE FLEXIBILITY OF SIGNAL RECEIVERS AND THE QUESTION OF MEANING IN ANIMAL COMMUNICATION

To a certain extent, the responses of primates and other animals to at least some signals appear to be innate and mediated by the unconscious, nervous system-responses to the acoustic features of the calls.[13,30] For example, infant squirrel monkeys raised in social isolation, and without previous exposure to alarm calls, respond to alarm call playbacks with generalized startle and avoid responses, in contrast to control playbacks of other unfamiliar sounds which elicit exploratory behaviors.[60] Such reactions are likely mediated by the acoustic features of alarm calls, often including sharp onsets, which have almost certainly been shaped by natural selection because of the unconscious reactions they cause in receivers.[30] More specific responses to these alarm signals, however, appear to be strongly affected by prior experience.[61] Indeed, in contrast to the marked constraints characterizing vocal signal production among primates, behavioral responses to vocal signals appear to be far more flexible.[62]

Vervets again provide an excellent example for understanding the plasticity demonstrated by signal receivers. Infant vervets, like naïve squirrel monkeys, respond with generalized startle responses to each of the species-specific alarm call types described above, but do not exhibit the predator-specific responses characteristic of adults.[43] Upon hearing an eagle alarm, infant vervets are less likely to run into a bush than are adults or juveniles, and more likely to employ a maladaptive response, such as running into a tree where eagles are adept hunters, or an adaptive but generalized response, like running to their mother. Watching the behavior of adults does, however, increase the likelihood that infant vervets will respond with adaptive, predator-specific behavior, and responses to the different alarm call types become adult-like after several months of locomotor independence.[43] Thus even if innate nervous system reactions to the structure of signals explains general receiver responses to some degree, the specific responses of receivers appear not to be hardwired like the production of those same signals is, but rather are shaped by previous experience.[39,61,63-64] Perhaps the most familiar example of this comes from the behavior of domestic dogs, who in exceptional cases can learn to associate several hundred words with particular objects.[65] Such sophisticated responses have been widely interpreted as evidence that signals elicit mental representations in receivers based on the information extracted from the signals.[62,66-67] Some of the strongest evidence for such mental representations comes from habituation-dishabituation experiments[68], especially those conducted by Zuberbühler and colleagues,[66] which demonstrated that listeners transfer habituation to hearing one call type to a second (distinct) call type, but only if that second call has an identical "referent." The striking asymmetry between inflexible signalers and sophisticated receivers has led to the generally accepted conclusion that any continuities or parallels that exist between the communication systems of humans and our extant primate relatives reside, not in the ability of signal producers to transmit symbolically encoded information, but in the flexible, learned responses of receivers.[4,30,62,69-70]

But how does the inability of nonhuman primates and other terrestrial mammals to produce symbolically coded vocal signals square with the sophisticated behavior of receivers that indicates that they interpret signal meaning in a referential-like manner? One possible solution to the problem, championed most prominently by Drew Rendall, Michael Owren, and colleagues, is that responses to vocal signals are driven by Pavlovian conditioning working in conjunction with nervous-system responses induced by the acoustic features of the call.[13,30,71-72] Under this "affect-conditioning" model, eagle-specific responses to eagle-specific alarm calls develop because young listeners are first called to attention by the call's jarring structure and are, over time, conditioned by the subsequent events. The response "run into bushes" following the perception of an eagle alarm develops because eagles are repeatedly seen in short order after hearing the calls, and the **affective** response (that is, the emotional or motivational reaction experienced by the listener) triggered by the eagle is eventually transferred to the eagle alarm itself via associative learning. Thus, based on such principles, it is possible that specific responses to signals can develop with experience based on simple classical conditioning and without drawing on the concept of information, the meaning of calls, or mental representations of a signal's purported referent in listeners.[71] Such an explanation is therefore appealing to adherents of Morgan's Canon, which states that psychologically simpler explanations for a given behavior should be accepted as more likely than psychologically more complex ones.[73]

Although receiver responses to calls can potentially be explained by conditioning and without evoking information transfer, Owren and Rendall[30] acknowledged that a lack of ability for signalers to encode symbolic information or intentionally inform is not inherently incompatible with an ability of receivers to be informed by signals or attribute some sense of meaning to them. Indeed, we might say, for example, that the sound of footsteps means that someone is coming (or going) or that a sudden burst of laughter means that someone is in a joyous state. We are informed by such nonlinguistic cues and signals in the sense that they have reduced our uncertainty about our environment, including the probability of the presence of another individual and their emotional state, even though these sounds do not have semantic meaning and are not produced with the intent to inform. The term "information" as it relates to animal communication has similarly been defined as a reduction in uncertainty in signal receivers.[14,18,70]

A given primate vocal signal may therefore have meaning *to a receiver*, even if semantic communication on the part of the signaler now seems to now be out of the realm of possibility when it comes to primate calls.[20] But it is important for students of animal communication to keep in mind what this sense of "meaning" really is. It is equivalent to what linguist Paul Grice termed "natural meaning,"[51] which contrasts specifically with the symbolic meaning characteristic of human words. Unlike words, signals with natural meaning mean x only in that they *indicate* the likelihood of the occurrence of x because of a natural spatial or temporal association with x.[15] Based on this logic, Terrence Deacon has argued that functionally referential signals are best seen as indexical signals.[20] Although it's reasonably clear how signals with such indicating functions may well lead to uncertainty reduction in primates and other animals, empirically distinguishing between informational and affect-conditioning accounts is difficult,[4] and there have been no experimental studies which unequivocally support one mechanism over the other.

THE GENERATION OF INFORMATION AND ATTRIBUTION OF MEANING BY RECEIVERS: THE IMPORTANCE OF CONTEXT

Although neither conclusively demonstrated nor universally accepted, the idea that animal signals convey information and have meaning, at least in the minds of the receivers, has been prominent in animal communication even prior to the discovery of functionally referential signals.[13] Proponents of this approach generally argue that the information provided by signals comes from their statistical regularities with particular features of the physical and social environment in which they are produced.[18,62] In other words, the uncertainty regarding a given event is reduced for a signal receiver because of the statistical association between the signal and the event, as established through prior experience with the signal. Information is potentially available, in the same way that smoke can potentially inform an observer about the likelihood of a fire,[15] but must be generated by the receiver based on prior experience with the signal and its statistical regularities with other phenomena in the world.[18] Importantly, this is not incompatible with the affect-conditioning model. Indeed, proponents of the informational perspective have invoked classical and operant conditioning to explain how animals learn the association between signals and particular events.[62] A primary distinction between proponents and critics of the informational perspective is that the former allow for prior conditioning to elicit mental representations of the event based on perceiving the signal.[74]

The strength of the regularities between a signal and the physical and social environment determines the degree to which receivers can obtain precise information from the signal alone.[52] In the case of functionally referential signals, the statistical association between the signal and the eliciting context (that is, the purported referent) is by definition very high, thereby providing receivers with the potential to reduce uncertainty to a very high degree. Strong statistical regularities, however, are not limited to associations with external phenomena such as predators or food. In many cases, the acoustic structure of a given vocal signal will vary with factors such as an individual's body size, sex, dominance status, or subsequent behavior.[75-77] While these kinds of associated factors have been explicitly excluded in discussions of call "referents,"[6,78] there doesn't seem to be any inherent difference for signal perceivers if the relevant statistical association is with an environmental feature external to the caller or is solely a feature internal to the caller itself. Furthermore, responses to signals that are in accordance with uncertainty reduction regarding the occurrence of particular events are also found in cases in which the statistical associations between the signal and those particular events are relatively weak. The generalized alarm calls of many primates and screams of baboons provide two examples.

Many primates, including lemurs, New World monkeys, and a number of forest-living Old World monkeys, have been shown to give distinct calls in response to aerial and terrestrial predators, respectively.[6,34-35,79-80] However, in contrast to what was has been described for vervets, these calls are not always specific to encounters with potential predators, but are sometimes given in other contexts that are, like predator detections,[81] likely to elicit a stress response.[34-35,82] In most cases, these tend to be aggressive interactions within or between groups, but at least in tufted capuchin monkeys also includes competitive situations without overt aggression.[83] Interestingly, across species it tends to be the call associated with terrestrial predators that is given in other contexts, whereas the call associated with aerial predators tends to be context-specific and meet the criteria of functional reference.[34-35,84] Despite not being context-specific, playbacks of the terrestrial predator-associated alarms of these species still elicit terrestrial predator-specific responses in listeners, although responses to less specific alarm calls may vary more than responses to strictly context-specific ones.[85] For example, the aerial and terrestrial predator-associated alarms of saddleback tamarins cause listeners to look up and down, respectively, where each predator would most likely be spotted.[84] However, whereas production of the aerial predator call seems to be specific to encounters with raptors, terrestrial predator-associated alarms are also given during aggressive intergroup encounters. In turn, listeners most often look up immediately following a playback of an aerial predator alarm call, but are more likely to first look towards the speaker when terrestrial predator alarms are played, with glances downward most often coming afterward. Taking the informational perspective, the responses of listeners are still in line with interpretations that the latter calls elicit mental representations of a terrestrial predator, but suggests that listeners must take into account additional contextual variables (such as the presence or absence of a rival group) before ascribing precise meaning to the call. The primary difference between functionally referential alarm calls and these less specific terrestrial predator alarm calls, then, seems to be not in the potential for listeners to make inferences about the presence of particular predator types, but rather in the degree to which listeners must integrate contextual cues with signal perception in order to do so.

The screams of baboons provide an even greater demonstration of uncertainty reduction through the integration of signal and context. Like the terrestrial predator alarm calls of most primates, the screams of baboons would not be considered functionally referential because they do not meet the definitional requirement of context-specificity of production. Although such calls are most commonly given in response to aggression from conspecifics, these range from mild aggression over food to potentially infanticidal events, and they can also occur during encounters with predators, parent-offspring conflicts, and other potentially stressful situations.[69] Although one function of screams is likely to create annoyance in the individual that is antagonizing the caller (in these examples the aggressor, predator, or parent) and thereby alter their behavior for the benefit of the caller,[30] screams can further benefit the caller by attracting allies to come to its aid.[86-87] While a scream alone may be insufficient to provide listeners with any more information than that the screamer is in distress, the responses of listeners, in at least some cases, indicates that their uncertainty reduction exceeds this basic information and includes the factors that are likely to be causing the signaler to be distressed. For example, the responses of males to the screams of female "friends" (that is, females with whom the male regularly associates affiliatively, and in almost all cases mated with during the previous conceptive cycle) depends on such additional contextual cues such as whether the calling female currently has a dependent infant and whether the aggressor is likely an infanticidal male. This was demonstrated by Ryne Palombit and colleagues[86] by examining the behavior of males following playbacks of female screams. Males were found to respond more strongly to screams given by female friends than by other females (which they tended to ignore), but only if the female friend had a dependent infant; following the death of an infant, male responses to screams from the same female weakened. Further, the responses of male friends were strongest when the females' screams were coupled with threat calls from a potentially infanticidal male. The responses of males thus varied based on the broader contextual variables associated with the signal, specifically those contextual variables that indicated that the signal was likely to be associated with a potential infanticide event rather than, say, a fight between the female friend and another female over access to a contested resource. In this case, the scream alone provides only limited information to receivers (that the caller is in distress), but the behavior of male listeners indicates that the total information they infer is far richer.

As these and numerous other examples demonstrate,[62] <even non-functionally referential calls can elicit behaviors in receivers that are equally indicative of attribution of meaning as are responses to context-specific, functionally referential calls>, at least if one accepts the informational perspective. The ability of animals to do so appears to lie in the additional contextual information available to them outside of the signal itself. A tamarin's terrestrial predator alarm is likely to be indicative of the presence of a predator only if a rival group is not present, while the presence of an infant and the aggressive vocalizations of a newly dominant male adds to the information regarding a female's emotional state that baboons are able to get from hearing her scream. The meaning that these relatively ambiguous calls have to perceivers thus depends on the integration of the signal with the broader contextual cues surrounding the signal's production (Fig. 1a). In contrast, because the relevant contextual cues for ascribing meaning to functionally referential signals are held constant (for example, raptors are invariably present when aerial predator alarms are given), it is not necessary for perceivers to integrate such cues to do so (Fig. 1b). Thus if we are to accept that animal signals, even those that are not functionally referential, have meaning to their recipients, and that this meaning is derived from both the signal and the broader context in which it is produced (ideas which have been broadly accepted by adherents of informational perspectives in animal communication for decades),[12,31] then it seems logical to deduce that the attribution of precise meaning is a cognitively simpler process when the calls are context-specific and meaning is invariable. In other words, the meaning of functionally referential signals can be deduced without the need to take current context into account, while the integration of signal and context are crucial to deduce the meaning of calls that are not context-specific.

This is not to say that the integration of contextual cues plays no role in any part of the process by which receivers respond to functionally referential calls, but it is important to distinguish between a receiver's attribution of meaning to a signal on the one hand, and it's response to the signal, given that meaning, on the other. We argue that for signals that are context-specific, contextual cues need to be taken into account only in the decision-making process, that is, how to respond to the signal (Fig. 1b). In contrast, when the production of signals is not context-specific, receivers must take contextual cues into account both to attribute meaning to a signal *and* to make a decision regarding the best course of action considering that meaning (Fig 1a). If we take again vervet alarm calls as an example, the reactions of listeners may vary based on additional contextual factors, including the location of the listener at the time of the alarm: listeners on the ground react differently to alarm calls than do individuals in trees, presumably because the degree of danger that the different predators pose to individuals when in each location.[10] Thus for functionally referential signals, even though attribution of meaning is by definition independent of context, contextual cues are nevertheless important in determining an appropriate response.

In contrast, when production of a signal is less context-specific, taking contextual cues into account is important for both the generation of meaning and decision-making in terms of the response. Thus in the case of baboon screams, contextual cues first allow listeners to infer the likelihood of an infanticidal event (attribution of meaning), and then are of further importance in determining the response of individuals (decision-making). This explains why males who are not friends of the screaming female are less likely to respond. Weak responses by such males, we argue, should not be taken to indicate that they get no information from the scream (there's no inherent reason that only friends are able to take advantage of the signal's potential information), but that the meaning has less relevance to them because there's little reason for them to be concerned of a potential infanticide of an infant that they did not sire.

In this section we have, if only for the sake of argument, assumed that the concept of information explains receiver behavior at the proximate level better than do affect-conditioning models.[18] Although we cannot yet state unequivocally that responses to signals are indeed driven proximately by either conditioning or uncertainty reduction, it is our opinion that the balance of current evidence favors the informational perspective, although receiver behavior in a minority of cases may be better explained by affect-conditioning or pure nervous system reactions than attribution of meaning,[70] and we argue that it is these cases in which receiver responses vary based on broader contextual cues that demonstrates this most strongly. In cases in which call production is context-specific, it's easy to see how seemingly complex behaviors, such as predator-specific responses, can develop based on relatively simple Pavlovian conditioning. There's also no inherent reason why conditioning cannot cause signals to induce multiple affective responses based on additional contextual variables (that is, signal S causes emotional response R in context C, but emotional response R' in context C'), and indeed this may well explain why, for example, capuchin monkeys are more likely to ignore terrestrial predator-related alarm calls in competitive feeding contexts, when the calls are less likely to be associated with a predator and more likely to be related to conflicts with other group members.[85] However, achieving variation in responses based on context via conditioning becomes increasingly complex as variation in the relevant contexts increases. In addition, when specific contextual conditions occur relatively rarely, there may be little possibility to be conditioned to perform specific responses to signals observed to occur under those circumstances. Thus although the affect-conditioning model is more "cognitively parsimonious" than are informational accounts in explaining signal responses, it's not clear that it is an overall more parsimonious explanation, given the many steps that an individual would have to go through to, for example, perform the varied responses to screams like those observed in male baboons. Likewise, it seems most parsimonious to explain the differential reactions that baboons show to playbacks that simulate aggression among other group members, including looking towards the kin of those involved in the "fight,"[69] as an indication that listeners take advantage of the potential information that signals make available. Of course, less parsimonious is not the same as incorrect, and both affect-conditioning and information-based explanations are hypotheses to be tested,[88] although this will be no easy task.

FUNCTIONALLY REFERENTIAL SIGNALS ARE NOT INHERENTLY DIFFERENT FROM OTHER TYPES OF ANIMAL SIGNALS

We agree with proponents of the referential signaling paradigm that signals with a high degree of context-specificity of production have the potential to provide receivers with specific information and allow them to make predictions about their environment without the aid of additional contextual cues.[52] At the same time, it's clear that the vervet leopard alarm does not refer to leopards in the way the English word "leopard" does.[20] Rather, to a listener the call means that a leopard is present in the same way that the leopard's growl does, or even the way that the sound of dry leaves crunching under a leopard's foot step might. By the same token, calls with less context-specificity can have just as much meaning to a listener. Contact notes, for example, which are given in a range of contexts and function to maintain appropriate spacing between individuals, may mean to a listener that "individual *x* is currently approximately in direction *y* at distance *z*," a message which is not inherently more complex than "a leopard is somewhere nearby." Likewise, a subordinate juvenile's scream means something different to a baboon listener than does the same type of call from the alpha female, just as a non-semantic chuckle from James Bond means something different to a human listener than does an acoustically identical laugh from Dr. No. It is also irrelevant, from the receiver's perspective, if the signal has a statistical relationship with some phenomenon external, or only internal, to the signaler – one should not be inherently more complex for an animal to infer than the other.

Given that there is no apparent difference in the mechanisms that underlie the production of context-specific and non-specific calls in primates and most other animals, and that listeners are able to integrate contextual cues with signal features to respond to calls that are not context-specific *as if* they have some meaning (much as users of language do when processing words whose meaning depends on context), then it follows that neither the production nor the perception of functionally referential signals is anywhere closer to human communication than is that of non-functionally referential signals. In fact, <it is precisely because their production is so closely tied to particular contexts, making the integration of contextual cues less critical for the generation of meaning, that functionally referential signals are likely *less* cognitively demanding for perceivers!> While a knee-jerk reaction may be sufficient for a signal with unambiguous meaning, it takes additional cognitive processing to interpret a signal whose meaning is less clear and context-dependent. In this light, we would argue that functionally referential signals have become a red herring in the search for the cognitive link between primate communication and human language.

That's not to say that the focus on context-specific calls has in any way been a waste. Indeed, we believe that the concept of functional reference has been insightful in terms of understanding the importance of statistical regularities in driving receiver responses. Perhaps the paradigm's greatest contribution has been the demonstration that, despite great differences in the mechanisms underlying signal production, there are striking similarities between humans and other primates in signal perception.[52] But by now this is so well understood and widely acknowledged, even getting the occasional nod from critics of the informational-perspective,[30] that we should consider if the framework of functional reference is still a useful one. We believe that it is not. It over-emphasizes the importance of signals that have relatively strong statistical associations with events external to the caller, and under-emphasizes the similarities such calls share with less context-specific calls in terms of the mechanisms that underlie both their production and perception.

For those interested in primate communication for what it can tell us about the evolution of human language, the referential signaling paradigm also tends to draw attention away from what we believe will be a more productive framework as the field moves forward: pragmatics, the field of linguistics that examines the role of context in shaping the meaning of linguistic utterances.[4,21,89-90] With a few notable exceptions, including playback experiments by Klaus Zuberbühler[91] and Drew Rendall,[92] very little research has thus far been conducted with the specific intent of understanding how contextual variation contributes to variation in the attribution of meaning among primates. At this point, it's not at all clear that the integration of contextual information with a signal is particularly cognitively taxing, but this is a hypothesis ripe for testing. Clearly, the ability to do so is not limited to primates, but is also present in at least some avian taxa and probably many other mammals.[70] Identifying the taxa that do and do not have these abilities, as well as the extent of the abilities in various taxa, will be crucial for understanding how cognitively taxing it actually is.

In conclusion, while context-specific calls may well be *functionally* referential, it seems inherent in the informational perspective that any signal which informs recipients is, whatever it's degree of degree of statistical association with a given phenomenon, internal or external to the signaler, *functionally* referential to one degree or another. But applying the term universally to all signals in which receiver behavior is best explained in terms of information is rather superfluous and unlikely to provide additional insight. We thus recommend dropping the term "functionally referential signals" from the animal communication literature in favor of more accurate, and linguistically neutral, descriptions such as "context-specific signals," "predator-specific alarm calls," or "food-specific calls." Context-specificity is still, of course, an interesting phenomenon, and there are a number of open questions in this regard. We don't yet, for example, fully understand the ecological and social conditions which favor their evolution. While the prediction that the need for distinct reactions in response to different predator types favors the evolution of predator-specific alarm calls[6] has been largely supported, the reason that so many primates have evolved specific alarm calls for raptors but more general alarms for terrestrial predators remains a puzzle.[36] Likewise, recent attempts to understand the factors that favor the evolution of food-specific calls have illuminated how little we know in this regard.[33] Research into such ecologically-based questions is likely to be far more fruitful than would further attempts to find true referentiality in animal signals. The evidence reviewed here strongly indicates that the latter is a lost dream, and further pursuit of that dream is likely to be more distracting than insightful.

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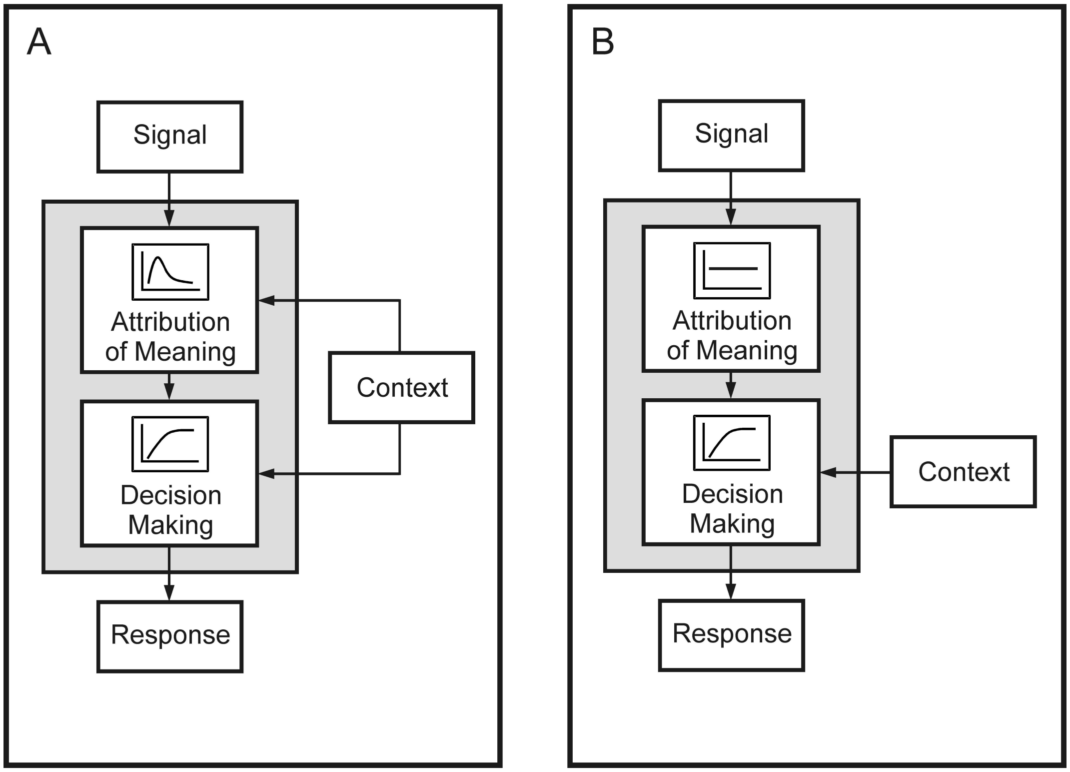
Figure 1. Schematic diagram illustrating the importance of contextual cues for signal receivers to attribute meaning to the signal and to make a decision regarding how to respond to the signal, two related but distinct aspects of signal perception. A) When the production of a given signal is not context-specific, receivers must integrate contextual cues with signal characteristics in order to ascribe precise meaning to the signal. Contextual cues must also be taken into account in deciding which response to the signal would, from the receiver's perspective, be most appropriate. B) When the production of a given signal is context-specific, as is the case for functionally referential signals, receivers do not need to take current contextual features into account to attribute meaning to a signal, because meaning is constant as a direct result of the prior context-specificity. Context becomes important for receivers only in the decision-making process regarding the behavioral response to the signal. The need to integrate contextual information with the characteristics of the signal only for non-functionally referential signals suggests that attributing meaning to these signals may require a greater degree of cognitive sophistication, contrasting with the common implication that functionally referential signals are indicative of greater cognitive sophistication.[32]

Figure 1


A
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