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3 **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

92   human semantic communication does.[12] Indeed, the fact each predator-type consistently elicits a

93   distinct call type, regardless of the level of urgency that it presents, is difficult to explain in this

94   framework. Shouldn't a caller's internal state be affected more by the risk the predator presents

95   (high versus low) than the type of predator encountered (aerial versus terrestrial)? The fact that

96   the calls alone were sufficient to elicit predator-specific reactions was interpreted as evidence

97   that listeners were able to obtain very specific **information** (a term which has drawn

98   considerable debate in the animal communication literature in recent years[13-18] and which we will

99   discuss below) from the calls, as if the vocalizations were indeed semantic signals, reinforced the

100 interpretation that these calls shared more in common with human words than with other animal

101 signals.

102

103 The honeybee "waggle dance," which allows hive mates to precisely determine the location of

104 food and far exceeds the specificity of vervet alarm calls, had been known to ethologists since

105 the 1940s[19] but was not considered especially relevant for the evolution of human language. One

106 obvious reason for this is the great evolutionary distance separating the social insects from

107 humans. But the honeybee waggle dance also lacked another key feature of human symbolic

108 communication: **arbitrariness**.[19] That is, rather than lacking any direct association between the

109 signal and its meaning, the number of turns in the honeybee's dance increases with the distance

110 to the food, while the dancer's vertical orientation indicates the direction from the hive relative to

111 the current position of the sun. In contrast, the vervet alarm calls did seem to be arbitrary in that

112 there is no direct association between the acoustic characteristics of each call type and the type of

113 predator that each is associated with, leading to an initial conclusion by Seyfarth and colleagues

114 that the calls are best seen as symbolic and referential.[9-10]

115

116 Vervet alarm calls and other such context-specific signals were thus typically referred to as

117 simply "referential" or "semantic" signals by many ethologists until the early 1990s, although

118 some criticisms arose over the application of such linguistic nomenclature to animal signals.[20-21]

119 To judge whether or not this criticism is warranted, it is necessary to briefly review the core

120 concepts of semiotic theory, which deals with the analysis of signs and signifying practices.

121 **Signs** are meaningful units that stand for something other than themselves. According to

122 Saussure,[22] a sign consists of a signifier and the signified, for instance, the relationship between

123   the spoken word "dog" and the actual animal. There are generally three different forms that the

124   relationship between the signifier and the signified can take: symbolic, iconic, and indexical. In a

125   **symbolic** mode, the relationship between the signifier and the signified is arbitrary and purely

126   conventional. Most words in human languages meet this definition, although onomatopoeic

127   elements in human languages, such as the descriptions of animal sounds ("meow," "woof," "ey-

128   ore"), are considered to be **iconic** because the signifier bears a physical resemblance to the

129   signified. Finally, **indexical** signifiers *indicate* the signified because they are in some way

130   physically or causally linked to it, like smoke is linked to fire, or a vervet's alarm call is linked to

131   the presence of the vervet itself.[4] This relationship may be obvious or indirectly inferred by the

132   observer.[21,23]

133

134   One of the main questions of animal communication researchers interested in the evolution of

135   language was thus whether any communication system attained a symbolic quality. Because the

136   vervet alarm calls were viewed as neither indexical nor iconic, they were considered to be

137   symbolic or proto-symbolic. However, <the core characteristic of symbolic communication is the

138   arbitrary nature of signals and the importance of conventions.>[20] This was at odds with

139   neuroscientists' early reports that the structure of nonhuman primate vocalizations was largely

140   hard-wired, and that no experience was required to develop the species-specific call

141   characteristics (described in the next section).[24-29] Further, the acoustic structure of primate vocal

142   signals is not arbitrary, but rather is shaped by natural selection such that a given vocalization's

143   form is related to its function.[13,30] As it became clear that the similarity between human words

144   and vervet alarms might be less striking than initially assumed, Peter Marler, Chris Evans and

145   colleagues[6,31] suggested the term "functionally referential" to clarify that, although context-

146   specific calls function much in the same way as human words, this conception "remains neutral

147   about the underlying mental processes."[31:67] Nevertheless, the idea that functionally referential

148   signals require greater cognitive complexity and provide a clearer link to human language than

149   do other types of animal signals remains pervasive in the animal communication literature.[2,4,32]

150   Since the initial discovery in vervets, vocal signals that meet one or both of the criteria of

151   functional reference have been described for the social, food, and alarm calls of a range of

152   primate taxa, including New World monkeys, lemurs, apes, and a number of additional Old

153   World monkeys.[2,4,33-35] Notably, a number of recent studies by Kate Arnold and Klaus

154 Zuberbühler[36] have demonstrated that functional reference can be achieved through the

155 production of context-specific call combinations, even if the individual call types are not context-

156 specific. Other studies have similarly shown that the number of times the same call is produced

157 can vary with context.[35,37-38] Finally, studies that combine bioacoustic analysis with playback

158 experiments have shown that acoustic variation within call types can also functionally refer to

159 distinct stimuli.[39-40] These observations of widespread functional reference have been taken as

160 evidence that the phylogenetic roots of human semantic communication likely go deep into the

161 primate lineage,[41] although the fact that several avian and nonprimate mammalian taxa also use

162 functionally referential food and alarm calls[34,43] indicates that context-specific signaling has

163 likely evolved convergently in many taxa.

164

165 **THE INFLEXIBILITY OF SIGNAL PRODUCERS: WHY FUNCTIONALLY**

166 **REFERENTIAL SIGNALS ARE NOT SYMBOLIC**

167 The neural foundations of primate vocal production was greatly illuminated by research by Uwe

168 Jürgens and colleagues beginning in the 1970s.[24] According to their research with squirrel

169 monkeys, the vocal pathway consists of three different subsystems. The first one is responsible

170 for the initiation of vocalizations. The initiation can be triggered by the anterior cingulate cortex

171 or by various limbic brain areas, in response to different external or internal stimuli. The so-

172 called peri-aquaeductal grey (PAG) serves as a relay station for the descending vocalization-

173 controlling pathways. The PAG integrates the incoming information and triggers a specific

174 innate vocal pattern. This system can be found in nonhuman primates and humans alike. The

175 second system is responsible for the voluntary motor control which is necessary to speak or sing,

176 and is apparently restricted to humans, at least among primates. The system is comprised of the

177 motor cortex with its connections to the cerebellum and thalamus as well as the putamen and

178 pyramidal pathway. Importantly, there is a direct connection between the motor cortex and the

179 motoneurons controlling the laryngeal muscles. In addition, there are connection between the

180 limbic cortex and the motor cortex. The third system comprises the formatio reticularis of the

181 lower brain stem and the motoneurons that innervate the respective muscles for vocal fold, lip,

182 jaw and tongue movements. This system receives input from the PAG and, in humans, from the

183 motor cortex. Thus, <the same neurobiological circuits which are responsible for innate

184 vocalizations are existent in both nonhuman primate and human nonverbal vocal production

185 systems (including laughter and reactions to pain in humans), while the more derived parts

186 responsible and necessary for voluntary control of vocalizations seem to be limited to humans>,

187 at least among the primates. This neurobiological evidence accounts for the lack of flexibility in

188 nonhuman primate vocal control.[24,28-29,42]

189 Moreover, no study has ever suggested that – say – vervet monkeys from different populations

190 would use their calls in fundamentally different ways, such as using an alarm call in an affiliative

191 situation, or even an eagle alarm in response to a leopard. Indeed, even though learning appears

192 to be important in the ontogeny of vervet alarm calling, with infants giving alarm calls in

193 inappropriate contexts,[43] their mistakes are not random. Eagle alarms may be given by infants to

194 nonthreatening stimuli in the air, such as vultures or falling leaves, but they are not given to

195 terrestrial animals like leopards or warthogs. The role of learning thus seems to be more related

196 to predator recognition than to learning in what contexts specific vocalizations should be given,

197 as further evinced by the vocal behavior of Diana monkeys in habitats where leopards have been

198 extirpated.[44] The balance of evidence therefore indicates that although nonhuman primates are

199 able to (partly) control the onset of calls, they cannot voluntarily choose which call to produce in

200 which situation.[45] Instead, there is a strong link between specific internal states and the

201 corresponding vocalizations.

202 A number of recent studies have highlighted the genetic underpinnings of this inflexibility in call

203 structure and usage by examining how acoustic variation relates to genetic distance. Early work

204 by Geissmann indicated that acoustic differences in gibbon song mapped onto geographic

205 distance,[46] while more recent studies integrating genetic analyses have revealed that the acoustic

206 structure of gibbon song and leaf monkey loud calls can largely be explained by genetic

207 distance.[47-48] This actually shows superficial resemblance to the relationship between human

208 language families and genetic distance at the global scale.[49] However, this correlation does not

209 apply at the smaller scale and, under specific circumstances, a language within a population can

210 be completely replaced within only 3 or 4 generations.[49]

211 Finally, nonhuman primates also differ from humans in terms of the "common ground" of

212 communication. That is, human communication is seen as fundamentally cooperative, relying on

213 shared knowledge of the world.[21,50-51] While the attribution of mental states and the intent to

214   inform are characteristic of human language, there is only scant evidence that nonhuman

215   primates vocalize with the intent to inform.[52-54] (See Box 1).

216   The proximate mechanisms underpinning the production of context-specific vocal signals in

217   particular have not been well studied, and this is likely a fruitful avenue for future research, but

218   all available evidence indicates that their production is not fundamentally different from less

219   context-specific calls. Indeed, among Belding's ground squirrels, playbacks of trills and whistles,

220   alarm calls associated with terrestrial and aerial predators, respectively, elicit distinct

221   physiological responses in listeners in terms of heart beat and the production of stress

222   hormones.[55] It is thus not at all inconceivable that different predator types also elicit distinct

223   types of aversive reactions in vervets and other primates, or that the discovery of food could

224   elicit a particular degree or type of excitement not elicited by other stimuli, and that there has

225   been selection for the production of specific signals when in such states. Although <all the

226   current evidence indicates that the production of even highly context-specific vocalizations is

227   hardwired in at least most non-human primates>, a better understanding of the specific

228   mechanisms underlying the production of these signals would most certainly be insightful.

229

230   **Box 1. Inflexible signal production: are apes different?**

231

232   Research into the vocal behavior of the living great apes has produced considerably less evidence

233   for functionally referential communication than what has been shown in other primate taxa, due

234   largely to the fact that predator-specific alarm calls are not ecologically-relevant for these large-

235   bodied species. However, studies conducted over the last several years suggest that the food calls

236   of chimpanzees and bonobos may well meet the production and perception requirements of

237   functional reference.[33] At the same time, it seems clear that chimps, like most other primates,

238   have a largely innate vocal repertoire and flexibility in vocal production is highly constrained.

239   Chimps from different populations, for example, give the same basic call type, "rough grunts," in

240   response to food, indicating that the production of a call with these particular acoustic features in

241   response to food is innate in this species.[56] Recent studies have suggested, however, that some

242   apes may differ from monkeys and prosimians in two critical aspects of vocal production that

243   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

274 humans and other animals in these regards, additional research will be needed before firm
275 conclusions can be drawn.

276

277 **THE FLEXIBILITY OF SIGNAL RECEIVERS AND THE QUESTION OF MEANING**
278 **IN ANIMAL COMMUNICATION**

279

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

291

292 Vervets again provide an excellent example for understanding the plasticity demonstrated by
293 signal receivers. Infant vervets, like naïve squirrel monkeys, respond with generalized startle
294 responses to each of the species-specific alarm call types described above, but do not exhibit the
295 predator-specific responses characteristic of adults.[43] Upon hearing an eagle alarm, infant vervets
296 are less likely to run into a bush than are adults or juveniles, and more likely to employ a
297 maladaptive response, such as running into a tree where eagles are adept hunters, or an adaptive
298 but generalized response, like running to their mother. Watching the behavior of adults does,
299 however, increase the likelihood that infant vervets will respond with adaptive, predator-specific
300 behavior, and responses to the different alarm call types become adult-like after several months
301 of locomotor independence.[43] Thus even if innate nervous system reactions to the structure of
302 signals explains general receiver responses to some degree, the specific responses of receivers
303 appear not to be hardwired like the production of those same signals is, but rather are shaped by
304 previous experience.[39,61,63-64] Perhaps the most familiar example of this comes from the behavior

305 of domestic dogs, who in exceptional cases can learn to associate several hundred words with

306 particular objects.[65] Such sophisticated responses have been widely interpreted as evidence that

307 signals elicit mental representations in receivers based on the information extracted from the

308 signals.[62,66-67] Some of the strongest evidence for such mental representations comes from

309 habituation-dishabituation experiments[68], especially those conducted by Zuberbühler and

310 colleagues,[66] which demonstrated that listeners transfer habituation to hearing one call type to a

311 second (distinct) call type, but only if that second call has an identical "referent." The striking

312 asymmetry between inflexible signalers and sophisticated receivers has led to the generally

313 accepted conclusion that any continuities or parallels that exist between the communication

314 systems of humans and our extant primate relatives reside, not in the ability of signal producers

315 to transmit symbolically encoded information, but in the flexible, learned responses of

316 receivers.[4,30,62,69-70]

317

318 But how does the inability of nonhuman primates and other terrestrial mammals to produce

319 symbolically coded vocal signals square with the sophisticated behavior of receivers that

320 indicates that they interpret signal meaning in a referential-like manner? One possible solution to

321 the problem, championed most prominently by Drew Rendall, Michael Owren, and colleagues, is

322 that responses to vocal signals are driven by Pavlovian conditioning working in conjunction with

323 nervous-system responses induced by the acoustic features of the call.[13,30,71-72] Under this "affect-

324 conditioning" model, eagle-specific responses to eagle-specific alarm calls develop because

325 young listeners are first called to attention by the call's jarring structure and are, over time,

326 conditioned by the subsequent events. The response "run into bushes" following the perception

327 of an eagle alarm develops because eagles are repeatedly seen in short order after hearing the

328 calls, and the **affective** response (that is, the emotional or motivational reaction experienced by

329 the listener) triggered by the eagle is eventually transferred to the eagle alarm itself via

330 associative learning. Thus, based on such principles, it is possible that specific responses to

331 signals can develop with experience based on simple classical conditioning and without drawing

332 on the concept of information, the meaning of calls, or mental representations of a signal's

333 purported referent in listeners.[71] Such an explanation is therefore appealing to adherents of

334 Morgan's Canon, which states that psychologically simpler explanations for a given behavior

335 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

366   Although neither conclusively demonstrated nor universally accepted, the idea that animal

367   signals convey information and have meaning, at least in the minds of the receivers, has been

368   prominent in animal communication even prior to the discovery of functionally referential

369   signals.[13] Proponents of this approach generally argue that the information provided by signals

370   comes from their statistical regularities with particular features of the physical and social

371   environment in which they are produced.[18,62] In other words, the uncertainty regarding a given

372   event is reduced for a signal receiver because of the statistical association between the signal and

373   the event, as established through prior experience with the signal. Information is potentially

374   available, in the same way that smoke can potentially inform an observer about the likelihood of

375   a fire,[15] but must be generated by the receiver based on prior experience with the signal and its

376   statistical regularities with other phenomena in the world.[18] Importantly, this is not incompatible

377   with the affect-conditioning model. Indeed, proponents of the informational perspective have

378   invoked classical and operant conditioning to explain how animals learn the association between

379   signals and particular events.[62] A primary distinction between proponents and critics of the

380   informational perspective is that the former allow for prior conditioning to elicit mental

381   representations of the event based on perceiving the signal.[74]

382

383   The strength of the regularities between a signal and the physical and social environment

384   determines the degree to which receivers can obtain precise information from the signal alone.[52]

385   In the case of functionally referential signals, the statistical association between the signal and

386   the eliciting context (that is, the purported referent) is by definition very high, thereby providing

387   receivers with the potential to reduce uncertainty to a very high degree. Strong statistical

388   regularities, however, are not limited to associations with external phenomena such as predators

389   or food. In many cases, the acoustic structure of a given vocal signal will vary with factors such

390   as an individual's body size, sex, dominance status, or subsequent behavior.[75-77] While these

391   kinds of associated factors have been explicitly excluded in discussions of call "referents,"[6,78]

392   there doesn't seem to be any inherent difference for signal perceivers if the relevant statistical

393   association is with an environmental feature external to the caller or is solely a feature internal to

394   the caller itself. Furthermore, responses to signals that are in accordance with uncertainty

395   reduction regarding the occurrence of particular events are also found in cases in which the

396   statistical associations between the signal and those particular events are relatively weak. The

397   generalized alarm calls of many primates and screams of baboons provide two examples.

398

399   Many primates, including lemurs, New World monkeys, and a number of forest-living Old

400   World monkeys, have been shown to give distinct calls in response to aerial and terrestrial

401   predators, respectively.[6,34-35,79-80] However, in contrast to what was has been described for

402   vervets, these calls are not always specific to encounters with potential predators, but are

403   sometimes given in other contexts that are, like predator detections,[81] likely to elicit a stress

404   response.[34-35,82] In most cases, these tend to be aggressive interactions within or between groups,

405   but at least in tufted capuchin monkeys also includes competitive situations without overt

406   aggression.[83] Interestingly, across species it tends to be the call associated with terrestrial

407   predators that is given in other contexts, whereas the call associated with aerial predators tends to

408   be context-specific and meet the criteria of functional reference.[34-35,84] Despite not being context-

409   specific, playbacks of the terrestrial predator-associated alarms of these species still elicit

410   terrestrial predator-specific responses in listeners, although responses to less specific alarm calls

411   may vary more than responses to strictly context-specific ones.[85] For example, the aerial and

412   terrestrial predator-associated alarms of saddleback tamarins cause listeners to look up and

413   down, respectively, where each predator would most likely be spotted.[84] However, whereas

414   production of the aerial predator call seems to be specific to encounters with raptors, terrestrial

415   predator-associated alarms are also given during aggressive intergroup encounters. In turn,

416   listeners most often look up immediately following a playback of an aerial predator alarm call,

417   but are more likely to first look towards the speaker when terrestrial predator alarms are played,

418   with glances downward most often coming afterward. Taking the informational perspective, the

419   responses of listeners are still in line with interpretations that the latter calls elicit mental

420   representations of a terrestrial predator, but suggests that listeners must take into account

421   additional contextual variables (such as the presence or absence of a rival group) before ascribing

422   precise meaning to the call. The primary difference between functionally referential alarm calls

423   and these less specific terrestrial predator alarm calls, then, seems to be not in the potential for

424   listeners to make inferences about the presence of particular predator types, but rather in the

425   degree to which listeners must integrate contextual cues with signal perception in order to do so.

426

427 The screams of baboons provide an even greater demonstration of uncertainty reduction through

428 the integration of signal and context. Like the terrestrial predator alarm calls of most primates,

429 the screams of baboons would not be considered functionally referential because they do not

430 meet the definitional requirement of context-specificity of production. Although such calls are

431 most commonly given in response to aggression from conspecifics, these range from mild

432 aggression over food to potentially infanticidal events, and they can also occur during encounters

433 with predators, parent-offspring conflicts, and other potentially stressful situations.[69] Although

434 one function of screams is likely to create annoyance in the individual that is antagonizing the

435 caller (in these examples the aggressor, predator, or parent) and thereby alter their behavior for

436 the benefit of the caller,[30] screams can further benefit the caller by attracting allies to come to its

437 aid.[86-87] While a scream alone may be insufficient to provide listeners with any more

438 information than that the screamer is in distress, the responses of listeners, in at least some cases,

439 indicates that their uncertainty reduction exceeds this basic information and includes the factors

440 that are likely to be causing the signaler to be distressed. For example, the responses of males to

441 the screams of female "friends" (that is, females with whom the male regularly associates

442 affiliatively, and in almost all cases mated with during the previous conceptive cycle) depends on

443 such additional contextual cues such as whether the calling female currently has a dependent

444 infant and whether the aggressor is likely an infanticidal male. This was demonstrated by Ryne

445 Palombit and colleagues[86] by examining the behavior of males following playbacks of female

446 screams. Males were found to respond more strongly to screams given by female friends than by

447 other females (which they tended to ignore), but only if the female friend had a dependent infant;

448 following the death of an infant, male responses to screams from the same female weakened.

449 Further, the responses of male friends were strongest when the females' screams were coupled

450 with threat calls from a potentially infanticidal male. The responses of males thus varied based

451 on the broader contextual variables associated with the signal, specifically those contextual

452 variables that indicated that the signal was likely to be associated with a potential infanticide

453 event rather than, say, a fight between the female friend and another female over access to a

454 contested resource. In this case, the scream alone provides only limited information to receivers

455 (that the caller is in distress), but the behavior of male listeners indicates that the total

456 information they infer is far richer.

457

458   As these and numerous other examples demonstrate,[62] <even non-functionally referential calls

459   can elicit behaviors in receivers that are equally indicative of attribution of meaning as are

460   responses to context-specific, functionally referential calls>, at least if one accepts the

461   informational perspective. The ability of animals to do so appears to lie in the additional

462   contextual information available to them outside of the signal itself. A tamarin's terrestrial

463   predator alarm is likely to be indicative of the presence of a predator only if a rival group is not

464   present, while the presence of an infant and the aggressive vocalizations of a newly dominant

465   male adds to the information regarding a female's emotional state that baboons are able to get

466   from hearing her scream. The meaning that these relatively ambiguous calls have to perceivers

467   thus depends on the integration of the signal with the broader contextual cues surrounding the

468   signal's production (Fig. 1a). In contrast, because the relevant contextual cues for ascribing

469   meaning to functionally referential signals are held constant (for example, raptors are invariably

470   present when aerial predator alarms are given), it is not necessary for perceivers to integrate such

471   cues to do so (Fig. 1b). Thus if we are to accept that animal signals, even those that are not

472   functionally referential, have meaning to their recipients, and that this meaning is derived from

473   both the signal and the broader context in which it is produced (ideas which have been broadly

474   accepted by adherents of informational perspectives in animal communication for decades),[12,31]

475   then it seems logical to deduce that the attribution of precise meaning is a cognitively simpler

476   process when the calls are context-specific and meaning is invariable. In other words, the

477   meaning of functionally referential signals can be deduced without the need to take current

478   context into account, while the integration of signal and context are crucial to deduce the

479   meaning of calls that are not context-specific.

480

481   This is not to say that the integration of contextual cues plays no role in any part of the process

482   by which receivers respond to functionally referential calls, but it is important to distinguish

483   between a receiver's attribution of meaning to a signal on the one hand, and it's response to the

484   signal, given that meaning, on the other. We argue that for signals that are context-specific,

485   contextual cues need to be taken into account only in the decision-making process, that is, how to

486   respond to the signal (Fig. 1b). In contrast, when the production of signals is not context-specific,

487   receivers must take contextual cues into account both to attribute meaning to a signal *and* to

488   make a decision regarding the best course of action considering that meaning (Fig 1a). If we take

489   again vervet alarm calls as an example, the reactions of listeners may vary based on additional

490   contextual factors, including the location of the listener at the time of the alarm: listeners on the

491   ground react differently to alarm calls than do individuals in trees, presumably because the

492   degree of danger that the different predators pose to individuals when in each location.[10] Thus for

493   functionally referential signals, even though attribution of meaning is by definition independent

494   of context, contextual cues are nevertheless important in determining an appropriate response.

495

496   In contrast, when production of a signal is less context-specific, taking contextual cues into

497   account is important for both the generation of meaning and decision-making in terms of the

498   response. Thus in the case of baboon screams, contextual cues first allow listeners to infer the

499   likelihood of an infanticidal event (attribution of meaning), and then are of further importance in

500   determining the response of individuals (decision-making). This explains why males who are not

501   friends of the screaming female are less likely to respond. Weak responses by such males, we

502   argue, should not be taken to indicate that they get no information from the scream (there's no

503   inherent reason that only friends are able to take advantage of the signal's potential information),

504   but that the meaning has less relevance to them because there's little reason for them to be

505   concerned of a potential infanticide of an infant that they did not sire.

506

507   In this section we have, if only for the sake of argument, assumed that the concept of information

508   explains receiver behavior at the proximate level better than do affect-conditioning models.[18]

509   Although we cannot yet state unequivocally that responses to signals are indeed driven

510   proximately by either conditioning or uncertainty reduction, it is our opinion that the balance of

511   current evidence favors the informational perspective, although receiver behavior in a minority

512   of cases may be better explained by affect-conditioning or pure nervous system reactions than

513   attribution of meaning,[70] and we argue that it is these cases in which receiver responses vary

514   based on broader contextual cues that demonstrates this most strongly. In cases in which call

515   production is context-specific, it's easy to see how seemingly complex behaviors, such as

516   predator-specific responses, can develop based on relatively simple Pavlovian conditioning.

517   There's also no inherent reason why conditioning cannot cause signals to induce multiple

518   affective responses based on additional contextual variables (that is, signal S causes emotional

519   response R in context C, but emotional response R' in context C'), and indeed this may well

520 explain why, for example, capuchin monkeys are more likely to ignore terrestrial predator-

521 related alarm calls in competitive feeding contexts, when the calls are less likely to be associated

522 with a predator and more likely to be related to conflicts with other group members.[85] However,

523 achieving variation in responses based on context via conditioning becomes increasingly

524 complex as variation in the relevant contexts increases. In addition, when specific contextual

525 conditions occur relatively rarely, there may be little possibility to be conditioned to perform

526 specific responses to signals observed to occur under those circumstances. Thus although the

527 affect-conditioning model is more "cognitively parsimonious" than are informational accounts in

528 explaining signal responses, it's not clear that it is an overall more parsimonious explanation,

529 given the many steps that an individual would have to go through to, for example, perform the

530 varied responses to screams like those observed in male baboons. Likewise, it seems most

531 parsimonious to explain the differential reactions that baboons show to playbacks that simulate

532 aggression among other group members, including looking towards the kin of those involved in

533 the "fight,"[69] as an indication that listeners take advantage of the potential information that

534 signals make available. Of course, less parsimonious is not the same as incorrect, and both

535 affect-conditioning and information-based explanations are hypotheses to be tested,[88] although

536 this will be no easy task.

537

538 **FUNCTIONALLY REFERENTIAL SIGNALS ARE NOT INHERENTLY DIFFERENT**

539 **FROM OTHER TYPES OF ANIMAL SIGNALS**

540

541 We agree with proponents of the referential signaling paradigm that signals with a high degree of

542 context-specificity of production have the potential to provide receivers with specific

543 information and allow them to make predictions about their environment without the aid of

544 additional contextual cues.[52] At the same time, it's clear that the vervet leopard alarm does not

545 refer to leopards in the way the English word "leopard" does.[20] Rather, to a listener the call

546 means that a leopard is present in the same way that the leopard's growl does, or even the way

547 that the sound of dry leaves crunching under a leopard's foot step might. By the same token,

548 calls with less context-specificity can have just as much meaning to a listener. Contact notes, for

549 example, which are given in a range of contexts and function to maintain appropriate spacing

550 between individuals, may mean to a listener that "individual x is currently approximately in

551   direction y at distance z," a message which is not inherently more complex than "a leopard is

552   somewhere nearby." Likewise, a subordinate juvenile's scream means something different to a

553   baboon listener than does the same type of call from the alpha female, just as a non-semantic

554   chuckle from James Bond means something different to a human listener than does an

555   acoustically identical laugh from Dr. No. It is also irrelevant, from the receiver's perspective, if

556   the signal has a statistical relationship with some phenomenon external, or only internal, to the

557   signaler – one should not be inherently more complex for an animal to infer than the other.

558

559   Given that there is no apparent difference in the mechanisms that underlie the production of

560   context-specific and non-specific calls in primates and most other animals, and that listeners are

561   able to integrate contextual cues with signal features to respond to calls that are not context-

562   specific *as if* they have some meaning (much as users of language do when processing words

563   whose meaning depends on context), then it follows that neither the production nor the

564   perception of functionally referential signals is anywhere closer to human communication than is

565   that of non-functionally referential signals. In fact, <it is precisely because their production is so

566   closely tied to particular contexts, making the integration of contextual cues less critical for the

567   generation of meaning, that functionally referential signals are likely *less* cognitively demanding

568   for perceivers!> While a knee-jerk reaction may be sufficient for a signal with unambiguous

569   meaning, it takes additional cognitive processing to interpret a signal whose meaning is less clear

570   and context-dependent. In this light, we would argue that functionally referential signals have

571   become a red herring in the search for the cognitive link between primate communication and

572   human language.

573

574   That's not to say that the focus on context-specific calls has in any way been a waste. Indeed, we

575   believe that the concept of functional reference has been insightful in terms of understanding the

576   importance of statistical regularities in driving receiver responses. Perhaps the paradigm's

577   greatest contribution has been the demonstration that, despite great differences in the

578   mechanisms underlying signal production, there are striking similarities between humans and

579   other primates in signal perception.[52] But by now this is so well understood and widely

580   acknowledged, even getting the occasional nod from critics of the informational-perspective,[30]

581   that we should consider if the framework of functional reference is still a useful one. We believe

582   that it is not. It over-emphasizes the importance of signals that have relatively strong statistical

583   associations with events external to the caller, and under-emphasizes the similarities such calls

584   share with less context-specific calls in terms of the mechanisms that underlie both their

585   production and perception.

586

587   For those interested in primate communication for what it can tell us about the evolution of

588   human language, the referential signaling paradigm also tends to draw attention away from what

589   we believe will be a more productive framework as the field moves forward: pragmatics, the

590   field of linguistics that examines the role of context in shaping the meaning of linguistic

591   utterances.[4,21,89-90] With a few notable exceptions, including playback experiments by Klaus

592   Zuberbühler[91] and Drew Rendall,[92] very little research has thus far been conducted with the

593   specific intent of understanding how contextual variation contributes to variation in the

594   attribution of meaning among primates. At this point, it's not at all clear that the integration of

595   contextual information with a signal is particularly cognitively taxing, but this is a hypothesis

596   ripe for testing. Clearly, the ability to do so is not limited to primates, but is also present in at

597   least some avian taxa and probably many other mammals.[70] Identifying the taxa that do and do

598   not have these abilities, as well as the extent of the abilities in various taxa, will be crucial for

599   understanding how cognitively taxing it actually is.

600

601   In conclusion, while context-specific calls may well be *functionally* referential, it seems inherent

602   in the informational perspective that any signal which informs recipients is, whatever it's degree

603   of degree of statistical association with a given phenomenon, internal or external to the signaler,

604   *functionally* referential to one degree or another. But applying the term universally to all signals

605   in which receiver behavior is best explained in terms of information is rather superfluous and

606   unlikely to provide additional insight. We thus recommend dropping the term "functionally

607   referential signals" from the animal communication literature in favor of more accurate, and

608   linguistically neutral, descriptions such as "context-specific signals," "predator-specific alarm

609   calls," or "food-specific calls." Context-specificity is still, of course, an interesting phenomenon,

610   and there are a number of open questions in this regard. We don't yet, for example, fully

611   understand the ecological and social conditions which favor their evolution. While the prediction

612   that the need for distinct reactions in response to different predator types favors the evolution of

613 predator-specific alarm calls[6] has been largely supported, the reason that so many primates have

614 evolved specific alarm calls for raptors but more general alarms for terrestrial predators remains

615 a puzzle.[36] Likewise, recent attempts to understand the factors that favor the evolution of food-

616 specific calls have illuminated how little we know in this regard.[33] Research into such

617 ecologically-based questions is likely to be far more fruitful than would further attempts to find

618 true referentiality in animal signals. The evidence reviewed here strongly indicates that the latter

619 is a lost dream, and further pursuit of that dream is likely to be more distracting than insightful.

620

621 **ACKNOWLEDGMENTS**

622

630

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]

648 **Figure 1**

649

650

651
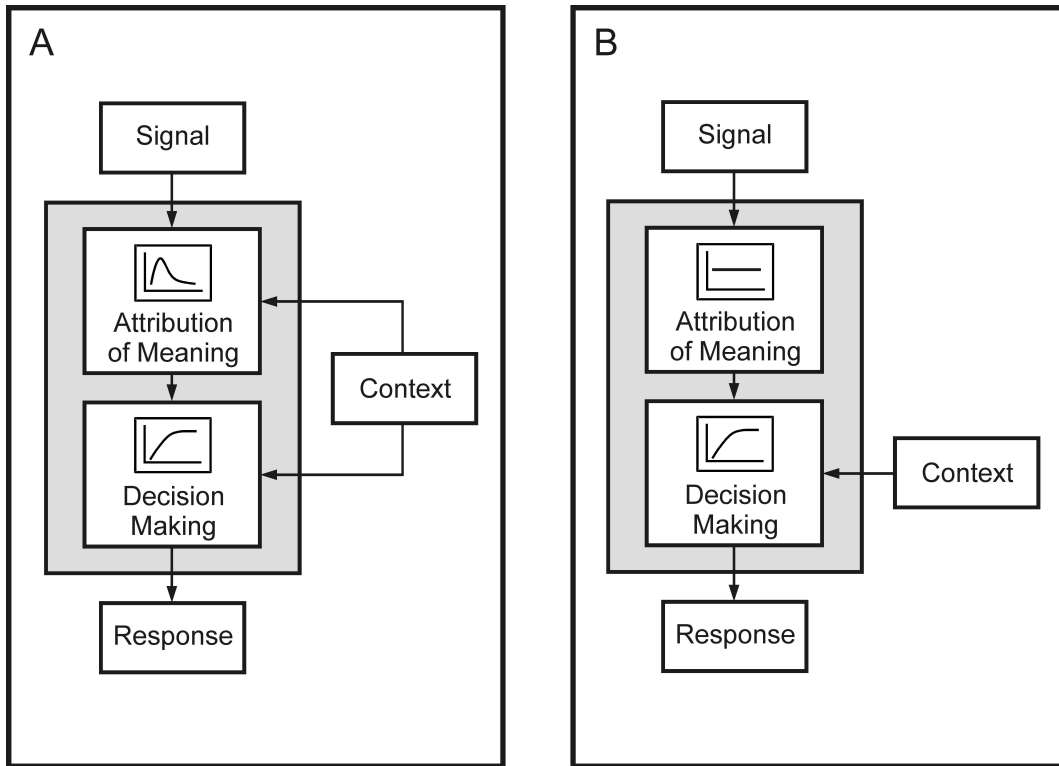
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