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### Citation for published version

Wheeler, Brandon C and Fischer, Julia (2012) Functionally referential signals: a promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews*, 21 (5). pp. 195-205. ISSN 1060-1538.

### DOI

<https://doi.org/10.1002/evan.21319>

### Link to record in KAR

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### Document Version

Author's Accepted Manuscript

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1 **PUBLISHED IN EVOLUTIONARY ANTHROPOLOGY**

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3 **Functionally referential signals: a promising paradigm whose time has passed**

4

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34 Word count (whole manuscript): 9,995

35 References: 92

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37 Note: suggested call out quotes are in <brackets>

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

61

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

64

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

87

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

92 human semantic communication does.<sup>12</sup> 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<sup>13-18</sup> 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<sup>19</sup> 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**.<sup>19</sup> 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.<sup>9-10</sup>

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.<sup>20-21</sup>  
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,<sup>22</sup> 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.<sup>4</sup> This relationship may be obvious or indirectly inferred by the  
132 observer.<sup>21,23</sup>

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.><sup>20</sup> 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).<sup>24-29</sup> 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.<sup>13,30</sup> 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<sup>6,31</sup> 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.”<sup>31:67</sup> 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.<sup>2,4,32</sup>  
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.<sup>2,4,33-35</sup> Notably, a number of recent studies by Kate Arnold and Klaus

154 Zuberbühler<sup>36</sup> 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.<sup>35,37-38</sup> 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.<sup>39-40</sup> 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,<sup>41</sup> although the fact that several avian and nonprimate mammalian taxa also use  
162 functionally referential food and alarm calls<sup>34,43</sup> 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.<sup>24</sup> 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-aqueductal 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.<sup>24,28-29,42</sup>

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,<sup>43</sup> 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.<sup>44</sup> 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.<sup>45</sup> 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,<sup>46</sup> 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.<sup>47-48</sup> This actually shows superficial resemblance to the relationship between human  
208 language families and genetic distance at the global scale.<sup>49</sup> 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.<sup>49</sup>

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.<sup>21,50-51</sup> 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.<sup>52-54</sup> (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.<sup>55</sup> 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.<sup>33</sup> 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.<sup>56</sup> 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

244 inform among chimpanzees and a possible role for learning in the development of particular call  
245 types in orangutans.

246  
247 Crockford and colleagues<sup>54</sup> recently presented evidence that wild chimpanzees are more likely to  
248 give alarm calls upon detecting a snake if other group members present were unlikely to be  
249 aware of the snake's presence. Such an ability to selectively communicate based on the  
250 knowledge state of the audience would clearly set them apart from monkeys.<sup>52</sup> However, such  
251 intentionality also requires a **theory of mind**, that is, an ability to understand that others have  
252 thoughts, knowledge, and beliefs, and the evidence that chimpanzees possess such abilities has  
253 engendered some controversy.<sup>57</sup> Nevertheless, the work by Crockford et al. is suggestive and will  
254 almost certainly inspire additional research into the possibility that communication with the  
255 intent to inform exists in the apes.

256  
257 A second recent study has called into question the contention that the vocal repertoires of apes  
258 are completely innate and unlearned. While a number of previous studies have shown that  
259 learning may play some role in the development of "accents" (that is relatively modest variation  
260 in the acoustic structure of otherwise innate call types) among apes, such variation is also fairly  
261 well-documented in a number of species of monkeys.<sup>58</sup> More recently, Wich and colleagues<sup>58</sup>  
262 compared the vocal behavior of orangutans from five different populations and noted differences  
263 between populations in terms of whether or not individuals vocalized in the contexts of nest-  
264 building and infant-retrieval, as well as in the specific call types they give in those contexts.  
265 While such "dialectic" differences could potentially be underpinned by genetic differences  
266 between the populations, the authors found that variation between populations was not explained  
267 by the genetic distance between them, and suggested that the differences may evidence a role of  
268 learning in the development of particular call types. Stronger evidence for the imitation of novel,  
269 non-innate sounds among orangutans comes from a captive individual that learned to imitate the  
270 sound of human whistling.<sup>59</sup> Notably, though, whistles are not vocalizations because their  
271 production does not involve use of the vocal folds. Still, these findings may have implications for  
272 the neurobiology of vocal communication in the apes. While a degree of vocal learning and  
273 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.<sup>13,30</sup> 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.<sup>60</sup> 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.<sup>30</sup> More specific responses to these  
288 alarm signals, however, appear to be strongly affected by prior experience.<sup>61</sup> 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.<sup>62</sup>

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.<sup>43</sup> 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.<sup>43</sup> 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.<sup>39,61,63-64</sup> 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.<sup>65</sup> 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.<sup>62,66-67</sup> Some of the strongest evidence for such mental representations comes from  
309 habituation-dishabituation experiments<sup>68</sup>, especially those conducted by Zuberbühler and  
310 colleagues,<sup>66</sup> 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.<sup>4,30,62,69-70</sup>

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.<sup>13,30,71-72</sup> 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.<sup>71</sup> 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.<sup>73</sup>

336

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

348

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

362

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

365

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.<sup>13</sup> 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.<sup>18,62</sup> 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,<sup>15</sup> 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.<sup>18</sup> 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.<sup>62</sup> 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.<sup>74</sup>

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.<sup>52</sup>  
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.<sup>75-77</sup> While these  
391 kinds of associated factors have been explicitly excluded in discussions of call "referents,"<sup>6,78</sup>  
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.<sup>6,34-35,79-80</sup> However, in contrast to what 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,<sup>81</sup> likely to elicit a stress  
404 response.<sup>34-35,82</sup> 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.<sup>83</sup> 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.<sup>34-35,84</sup> 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.<sup>85</sup> 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.<sup>84</sup> 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.<sup>69</sup> 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,<sup>30</sup> screams can further benefit the caller by attracting allies to come to its  
437 aid.<sup>86-87</sup> 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<sup>86</sup> 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,<sup>62</sup> <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),<sup>12,31</sup>  
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 its 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.<sup>10</sup> 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.<sup>18</sup>  
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,<sup>70</sup> 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.<sup>85</sup> 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,”<sup>69</sup> 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,<sup>88</sup> 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.<sup>52</sup> 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.<sup>20</sup> 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.<sup>52</sup> But by now this is so well understood and widely  
580 acknowledged, even getting the occasional nod from critics of the informational-perspective,<sup>30</sup>  
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.<sup>4,21,89-90</sup> With a few notable exceptions, including playback experiments by Klaus  
592 Zuberbühler<sup>91</sup> and Drew Rendall,<sup>92</sup> 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.<sup>70</sup> 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<sup>6</sup> 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.<sup>36</sup> 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.<sup>33</sup> 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

623 We thank John Fleagle, James Higham, Drew Rendall, Robert Seyfarth, and an anonymous  
624 reviewer for constructive and thoughtful comments on the manuscript. JF would like to express  
625 her gratitude to Dorothy Cheney, Robert Seyfarth and Catherine Crockford for the joint  
626 excursions into the swamps of the meaning of meaning. BW offers thanks to Sue Boinski and  
627 Barbara Tiddi for insightful and skeptical conversation, and his dogs Indigo and Aku for  
628 unintentionally solidifying a number of opinions presented in this paper. BW was supported by  
629 an NSF International Research Fellowship during the writing of this manuscript.

630

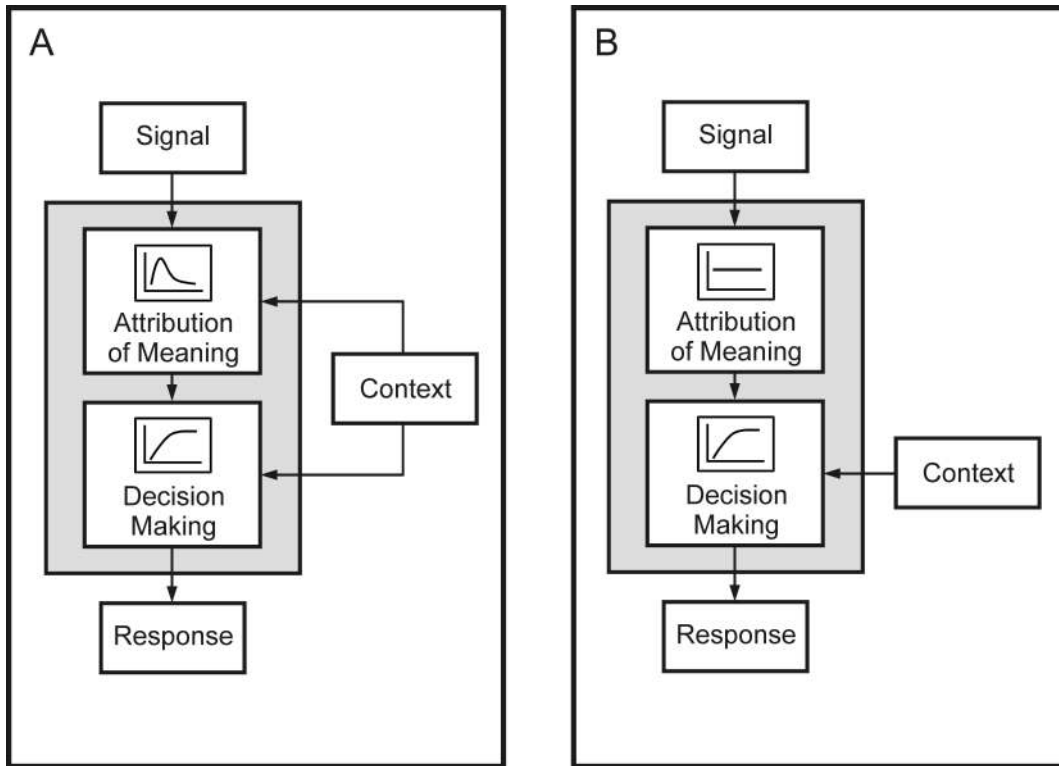
631 **Figure 1.** Schematic diagram illustrating the importance of contextual cues for signal receivers  
632 to attribute meaning to the signal and to make a decision regarding how to respond to the signal,  
633 two related but distinct aspects of signal perception. A) When the production of a given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

646

647

648 **Figure 1**

649



650

651



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