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2 **Linguistic capacity of non-human animals**

3
4 Klaus Zuberbühler

5
6 Comparative Cognition, University of Neuchatel, Switzerland & School of
7 Psychology & Neuroscience, University of St Andrews, Scotland (UK).

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9 Correspondence: E-mail: klaus.zuberbuehler@unine.ch; Tel +41 32 718 3105

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11
12 **Abstract**

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14 Linguists interested in language evolution tend to focus on combinatorial features and
15 rightly point out the lack of comparable evidence in animal communication. However,
16 human language is based on further uniquely human capacities, such as the motor
17 capacity of sophisticated vocal control and the cognitive ability to act on others'
18 psychological states. These features are only present in rudimentary forms in non-
19 human primates, suggesting they have evolved very recently in the human lineage.
20 Here, I review the evidence from recent fieldwork for precursors of these abilities,
21 notably sequence-based semantic communication, vocal tract control, and complex
22 audience awareness. Overall, the evidence is consistent with the hypothesis that the
23 origin of language is the result of on multiple, gradual transitions from primate-like
24 communication and social cognition, rather than a sudden and fundamental redesign
25 in ancestral human communication and cognition.

26 **Hallmarks of language**

27

28 Humans are unique in a number of ways[1], but perhaps most famously in the
29 capacity of every healthy child to develop language. No other animal species has a
30 communication system that is even remotely comparable, a fact that has puzzled
31 scholars for centuries. How could a complex faculty, such as language, have evolved
32 during the relatively short evolutionary history of our species? A productive way of
33 studying language evolution is to decompose language into its core properties and to
34 investigate them separately [2]. In the following, I will discuss three ways by which
35 humans deviate from what is normally observed in primate communication: 3;
36 compositionality, audience awareness, and vocal control.

37 One empirical approach to study language evolution is to look for transient
38 stages that lead to language, either ontogenetically, by studying infant linguistic
39 development, or comparatively, by studying primate communication. The first
40 approach is based on the premise that ontogeny can recapitulate phylogeny [3],
41 suggesting that the patterns in language acquisition reveal something about language
42 evolution [4]. The second approach is based on the fact that biological adaptations are
43 usually modifications of pre-existing structures rather than truly novel creations. To
44 distinguish precursors from derived structures the approach is to compare closely
45 related species, which can shed light on evolutionary changes of major adaptations,
46 including language [5].

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48

49 **From combinatorial to compositional properties**

50

51 *Call combinations in primate communication*

52 Linguists interested in language evolution tend to focus on the combinatorial
53 property of language ([4,6,7]), and the apparent lack of this feature in animal
54 communication. Great apes that have been taught artificial languages have all but
55 failed to show evidence for generative use of signal combinations [8]. Interestingly,
56 however, there are a number of studies on natural communication in primates that
57 have shown that some species produce various call sequences with distinct meanings,
58 which can be different from the meaning of the component calls (Campbell's
59 monkeys [9,10]; Colobus monkeys [11]; titi monkeys [12]). A particularly relevant
60 example is that of putty-nosed monkeys. In this species, adult males produce different
61 call sequences consisting of two basic call types with distinct meanings (fig. 1,
62 [13,14]).

63

64 -- Figure 1 --

65

66 Importantly, the behaviour appears to have a distinct communicative function,
67 as recipients appear to understand the meaning of the different call combinations.
68 When hearing series of hacks -- an indication predatory eagle presence -- listeners
69 showed appropriate anti-predator responses, which were different from when hearing
70 series of pyows -- an indication of leopard presence [15]. Finally, when hearing
71 combinatorial pyow-hack sequences -- an indication of forthcoming group travel --
72 listeners abandoned their on-going activities and moved in the direction of the
73 presumed caller [16,17]. Although pyow-hack sequences are variable in their
74 composition (1-4 pyows, followed by 1-4 hacks), these numerical differences do not

75 appear to be relevant, suggesting that the sequence is perceived similar to an idiomatic
76 expression [18].

77 For several monkey species, there is also evidence that some of their calls are
78 composed of different, acoustically discrete units that are assembled in context-
79 specific ways [19-21], a topic of on-going investigation [22]. For great apes, the
80 evidence for combinatorial signalling is relatively weak. Yet, fieldwork with
81 chimpanzees has shown that serial calling is the norm, with some call combinations
82 being more common than others, although little is still known about the
83 communicative function of this behaviour [23]. In bonobos, individuals produce
84 different acoustically distinct call types as series during feeding, and the overall call
85 sequence appears to reveal something about the quality of food encountered by the
86 caller (fig. 2; [24]). In gibbons, songs given to predators are composed of the same
87 song units as non-predatory duet songs given without any external disturbance, but
88 the units are arranged differently [25].

89
90 -- Figure 2 --

91 *Multimodal signalling*

92 Communication in great apes is often multi-modal, consisting of vocalisations
93 combined with manual gestures, body postures and facial expressions. In a recent
94 study with male bonobos, males combined one type of vocalisation, the contest hoots,
95 with various gestures [26]. The function of this behaviour is simply to annoy other
96 group members, who typically react with aggravation and chasing. It is likely that the
97 behaviour serves the provocateur to show off his social power to others, suggested by
98 the fact that males only target equal or higher ranking individuals. But contest hoots
99 are sometimes also used in a friendly way, as part of a play bout with another male.
100 The acoustic structure of the contest hoots appears to be identical between the
101 agonistic and the play context, but callers were found to use significantly more soft
102 than rough gestures in the play, compared to the agonistic context. Gestures may help
103 the recipient to recognise the social intentions of the signaller [26].
104
105

106 *The origins of compositional thought*

107 In sum, although there is relatively good evidence that primates and other
108 animals are able to extract meaning from syntactically organised information (e.g.,
109 [10,27,28]), there is practically no evidence that animals make active use of the
110 combinatorial potential that is inherent in their communication systems. Perhaps this
111 is because human cognition is fundamentally more conceptually organised than
112 animal cognition. Although animals have mental concepts for both natural kinds and
113 social function [29,30], the nature of these mental structures and their expression
114 during communication has remained unclear. Compositionality, however, may require
115 a vigorous and opulent system of mental concepts, as it is the case for human
116 thinking.

117 Would an animal equipped with a human-like grammar module be able to
118 develop language? There are at least two further components that are both essential
119 and uniquely human; sophisticated vocal control [31], and the ability to see others as
120 having psychological states [32,33], suggesting that a narrow focus on syntax is
121 unlikely to shed enough light on how language evolved.
122
123
124

125 **Vocal control**

126

127 Language is mainly a vocal behaviour. Of course it is true that rudimentary language-
128 like gestural systems have emerged in deaf populations [34], but this is not the default
129 case for humans. Instead, humans are enormously vocal primates, especially when
130 compared to their nearest primate relatives, the chimpanzees and bonobos. During
131 their first year, human infants begin to play with sounds, they babble [35]. Although
132 babbling has been reported for pygmy marmosets [36] (and one human-raised
133 chimpanzee [37]) the relation to human babbling has remained unclear. More
134 importantly is the fact that wild chimpanzee infants are remain mainly silent during
135 their first few years of life [38], in stark contrast to human infants.

136 More importantly, no published study has succeeded in training primates to
137 produce *new* vocalisations that are not modifications of the existing repertoire. In
138 contrast, from an early age, humans are able to generate a very large range of
139 acoustically distinct sounds by actively changing the vocal tract configurations rapidly
140 and precisely. In non-human primates, this ability is very underdeveloped and poses
141 great difficulties for individuals, even with substantial training [39,40]). For great
142 apes it has been noted that they are simply not interested in spontaneously imitating
143 speech sounds [41], although in other contexts they appear to be very interested in
144 imitating human behaviour. Hayes & Hayes [40] write about their home-raised
145 chimpanzee ‘Viki’: “... and here, again, Viki shows no great difference. Just as the
146 human child copies its parents’ routine chores, so Viki dusts, washes dishes, sharpens
147 pencils, saws, hammers... [...] On the other hand, she is less vocal: while the human
148 child commonly keeps up an almost continual stream of chatter – with or without
149 meaning, Viki is silent.”

150

151 *Explanations*

152 Why are such seemingly trivial vocal imitation tasks near impossible for non-
153 human primates to solve? One popular explanation has been that this is due to
154 anatomical differences in the vocal tract, particularly the permanently low position of
155 the human larynx [42,43]. This view is no longer supported by current research, as the
156 basic layout of the human larynx and vocal tract is not fundamentally different from
157 other mammals (fig. 3; [43-45]). On the matter of vocal control, Hayes & Hayes [40]
158 write about Viki: “...the variety of sounds observed in her babbling, and in her vocal
159 expression of emotion, left no doubt that her vocal mechanisms were adequate for
160 producing satisfactory approximations of most of the elements of human speech”.

161

162 -- Figure 3 --

163

164 Also important is that great apes are able control their supra-laryngeal vocal
165 tracts to a large degree to produce various voiceless calls, such as clicks, smacks,
166 raspberries, kiss-sounds and whistles [46-49]. Furness (1916) writes his home-raised
167 orang-utan: “The orang in one respect does use the lips, to make a sound indicating
168 warning or apprehension; this sound is made with the lips pursed up and the air
169 sucked through them... [...] My oldest orang would make this sound on command (I
170 had merely to say ‘What is the funny sound you make when you are frightened?’)”
171 [39].

172

173 Controlling the vocal folds and the associated sustained airflow, however,
174 appears to be much harder for non-human primates [50]. Hayes & Hayes [40] write:
“The first step was aimed at teaching her merely to vocalize on command, in order to

175 obtain a reward. [...] The task was surprisingly difficult. Although she seemed to
176 learn what was required quickly, she had serious trouble with the motor skill of
177 voluntary vocalization.”

178 Laboratory experiments then showed that it is very challenging to train
179 primates to vocalise on command or to alter the morphology of their calls [51,52],
180 possibly for neuroanatomical reasons. Humans possess direct projection from the
181 lateral motor cortical areas to the laryngeal motor neurons [53], which appears to
182 enable voluntary fine motor control over the laryngeal musculature, something that
183 has not been found in squirrel monkeys. Yet, both all primates appear to have direct
184 premotor cortical connections to the nuclei controlling the jaws, lips and tongue [53],
185 suggesting that control over the supra-laryngeal vocal tract was already present in the
186 common ancestor, while control over the larynx and respiratory muscles may have
187 evolved more recently [54].

188

189 *The origins of vocal control*

190 One hypothesis for why only humans evolve laryngeal control is that it
191 emerged as a bi-product of cooperative breeding. Humans are unusual in the amount
192 of childcare they provide in both in traditional hunter-gatherer and modern societies
193 [55-57]. Often this involves unrelated individuals, which may be especially
194 challenging for infants. Advanced vocal control may have evolved to help infants to
195 secure care from older individuals who often do not have a genetic interest to do so
196 [58]. A relevant finding in this context is that, across primates, there is a relationship
197 between conspicuousness and degree of infant allocare [59]. Babbling may play a
198 special role in this context if it elicits care more efficiently compared to infants with a
199 fixed vocal repertoire. This hypothesis clearly requires further testing, for example by
200 cross-species comparisons between the amount of allocare and the vocal behaviour of
201 infants.

202

203

204 **Social awareness**

205

206 There is good evidence that primates and other animals can make basic inferences
207 about other individuals' vocal behaviour. Vervet monkeys, for instance, produce a
208 range of acoustically distinct vocalisations to different predators, which are
209 meaningful to other group members [60] [61]. Similar findings have been reported
210 from Diana monkeys [62,63], Campbell's monkeys [64], Colobus monkeys [65,66]
211 and many other species. However, what is usually less clear from such studies is the
212 degree to which the signallers are actively trying to inform their recipients. Human
213 communication operates in this Gricean way [67], with signallers pursuing specifiable
214 social goals intending to be understood. For animal communication, a more
215 parsimonious hypothesis suggests that communication is driven by a predisposition to
216 react more or less automatically to biologically relevant events in order to enhance the
217 signaller's fitness.

218 A third hallmark of human language, thus, is in terms of its cooperative use
219 [68,69]. Humans are highly and uniquely cooperative, particularly during foraging
220 and childcare, which requires high degrees of social awareness. Although non-human
221 primates cooperate in various ways, the underlying cognitive mechanisms appear to
222 be simpler and based on behavioural contingency learning rather than an
223 understanding the partner's psychological states. Nevertheless, there is an increasing
224 literature that has demonstrated various degrees of social awareness underlying

225 primate communication. The evidence is particularly compelling for great apes, but a
226 number of monkey studies suggest similar capacities, at least in the context of
227 predation avoidance.

228 In Thomas langurs, for example, it has been found that males continue to
229 produce alarm calls to model predators until every group member has responded with
230 at least one alarm call, suggesting that males keep track of others' awareness [70].
231 Similarly, male blue monkeys produce more alarm calls to a suspected eagle if other
232 group members are close to the danger compared to when they are far, regardless of
233 their own distance [71].

234 In great apes, the evidence for social awareness includes findings that
235 signallers take the visual perspective and attention of their recipients into account
236 when communicating (e.g. orang-utans [72], gorillas [73], chimpanzees [74]). For
237 example, subjects are more likely to use visual signals when the recipient is oriented
238 towards them, and audible signals when facing away. Intention and comprehension
239 also matter. Both chimpanzees and orang-utans adjust their signalling behaviour
240 according to the degree of comprehension manifest in a human partner [75,76].
241 Similarly, chimpanzees behave differently depending on whether a human
242 experimenter is unwilling or unable to give them food [77]. The emerging image from
243 these results is that great ape communication is based on social awareness, in the
244 sense that subjects can take into account basic mental states of their recipients, such as
245 attention, intention and comprehension.

246 A few recent studies on ape vocal behaviour suggest that there is also some
247 cooperative element in communication. One finding in wild chimpanzees has been
248 that, during conflicts, victims are more likely to exaggerate their screams (indicating
249 more violent aggression than actually happened) if high-ranking group members are
250 nearby, who can potentially intervene on behalf of the victim [78]. Similarly,
251 chimpanzee and bonobo females suppress copulation calls when with unfavourable
252 audiences, presumably to avoid negative social consequences [79-82]. Similarly,
253 when encountering higher-ranking group members, female chimpanzees suppress
254 their regular vocal 'greeting' signals if the alpha male is nearby [83]. Recent playback
255 studies have shown that chimpanzees are more likely to produce food calls when with
256 a favourable than an irrelevant audience (e.g., high-ranking group members or
257 'friends'), as if trying to benefit these individuals selectively [84,85]. Other interesting
258 examples are signals used to engage others in a shared activity, notably joint travel.
259 Both chimpanzees and bonobos can produce structurally unique vocal and gestural
260 signals to engage a desirable partner in joint movements ([86], fig. 4).

261
262 -- Figure 4 --

263
264 Finally, when confronted with a potentially dangerous snake, chimpanzees are
265 more likely to produce alarm calls if they are with ignorant group members compared
266 to when with knowledgeable ones, who already know about the snake [87,88].

267
268

269 **Conclusions**

270

271 Much research effort has been devoted to the problem of how human language
272 emerged from a more primate-like communication system. Human language is a vocal
273 behaviour so a natural focus has been the study of non-human primate vocal
274 behaviour. Fieldwork has demonstrated that primate calls are generally perceived as

275 meaningful, in the sense that they allow recipients to make pragmatic inferences about
276 the external event experienced by the caller. Some of these utterances can consist of
277 sequences of acoustically distinct calls, with good evidence that these sequences carry
278 meaning that is different from the component calls. Nonetheless, non-human primates
279 fail to make use of the potential combinatorial power of their communication systems,
280 possibly because their underlying mental concepts are too fuzzy to engender
281 compositionality. In terms of vocal control, the basic vocal tract anatomy is perfectly
282 suited to produce human-like speech signals, and there is evidence that primates can
283 control their supralaryngeal vocal tracts. What appears to be uniquely human is the
284 sophisticated motor control of the larynx to act as a stable acoustic source for speech
285 production. In terms of social cognition, there is some evidence that monkeys make
286 basic assessments of their audiences' psychological states. In great apes, the evidence
287 is generally stronger, both for gestural and vocal signals, with subjects taking into
288 account the social role, intention, attention, comprehension and, to some degree, the
289 knowledge of their recipients. In sum, this evidence reveals a patchwork of
290 continuities but also some clear discontinuities in the evolutionary transition from
291 primate to human communication.

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