Opinion

Linguistic capacity of non-human animals

Klaus Zuberbühler[1,2*]

Linguists interested in language evolution tend to focus on combinatorial features and rightly point out the lack of comparable evidence in animal communication. However, human language is based on various unique capacities, such as a motor capacity of sophisticated vocal control and a cognitive capacity of acting on others' psychological states. These features are only present in very rudimentary forms in non-human primates, suggesting they have evolved more recently in the human lineage. Here, the evidence from recent fieldwork for precursors of these abilities is reviewed, notably sequence-based semantic communication, vocal tract control, and audience awareness. Overall, there is evidence for both continuity and discontinuity when comparing modern primate and human communication, suggesting that the origin of language is the result of multiple gradual transitions from earlier forms of primate-like communication and social cognition, rather than a sudden and fundamental redesign in ancestral human communication and cognition.

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HALLMARKS OF LANGUAGE

Humans are unique in a number of ways,[1] but perhaps most famously in the capacity of every healthy child to develop language. No other animal species has a communication system that is even remotely comparable, a fact that has puzzled scholars for centuries. How could a complex faculty, such as language, have evolved during the relatively short evolutionary history of our species? A productive way of studying language evolution is to decompose language into its core properties and to investigate them separately.[2] Various hallmarks have been proposed that distinguish human language from other forms of communication, e.g., Refs 3, 4 In this study, the focus will be on three ways by which humans deviate from what is normally observed in primate communication: compositionality, audience awareness, and vocal control.

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One major approach to study language evolution empirically is to look for transient stages that lead to language, either ontogenetically by studying infant linguistic development or comparatively by studying primate communication. The developmental approach is based on the premise that ontogeny sometimes recapitulates phylogeny,[5] suggesting that patterns in language acquisition reveal something about language evolution.[6] The second approach is based on the fact that biological adaptations are usually modifications of pre-existing structures rather than truly novel creations. To distinguish precursors from derived structures, the approach here is to compare closely related species, which can shed light on evolutionary changes in major adaptations, including language.[3]

FROM COMBINATORIAL TO COMPOSITIONAL PROPERTIES

Call Combinations in Primate Communication

Linguists interested in language evolution tend to focus on the combinatorial property of language,[6–8] and the apparent lack of this feature in animal communication. A relevant finding here is that great apes that have been taught artificial languages have all but failed to show evidence for generative use of signal combinations.[9] Interestingly, however, there is evidence for several monkey species that some of their natural calls are composed of acoustically discrete subunits that can be assembled in context-specific ways,[10–12] a topic of ongoing investigation.[13] Second, there are a number of other studies showing that some primates produce sequences of calls with distinct meanings, which are different from the meaning of the component calls (Campbell's monkeys;[14,15] colobus monkeys;[16] titi monkeys[17]).

A particularly relevant example is that of putty-nosed monkeys. In this species, adult males produce different call sequences consisting of two basic call types with distinct meanings (Refs 18, 19; Figure 1). Importantly, the behavior appears to have a distinct communicative function, as recipients appear to understand the meaning of the different call combinations. When hearing a series of hacks—an indication of predatory eagle presence—listeners showed appropriate anti-predator responses, which were different from when hearing a series of pyows—an indication of leopard presence.[20] Finally, when hearing combinatorial pyow-hack sequences—an indication of forthcoming group travel—listeners stopped their ongoing activities and moved in the direction of the presumed caller.[18,21] Although pyow-hack sequences varied in their composition (1–4 pyows, followed by 1–4 hacks), playback experiments have demonstrated that these numerical differences do not appear to be relevant, suggesting that the perceived meaning resides in the transition from pyow to hack.[22] Further research will be required to test whether these numerical differences are linked with other variables, such as perceived urgency and the recipients' motivation for travel.

Equally important is research on gibbons, which has shown that songs given to predators are composed of the same song units as non-predatory duet songs given without any external disturbance, although the units are arranged differently.[23] For chimpanzees, it has been shown that serial calling is the norm, with some call combinations being more common than others, although little is still known about the communicative function of this behavior.[24] In bonobos, individuals produce at least four acoustically distinct call types during feeding, with the overall call sequence revealing something about the quality of food encountered by the caller (Ref 25; Figure 2).

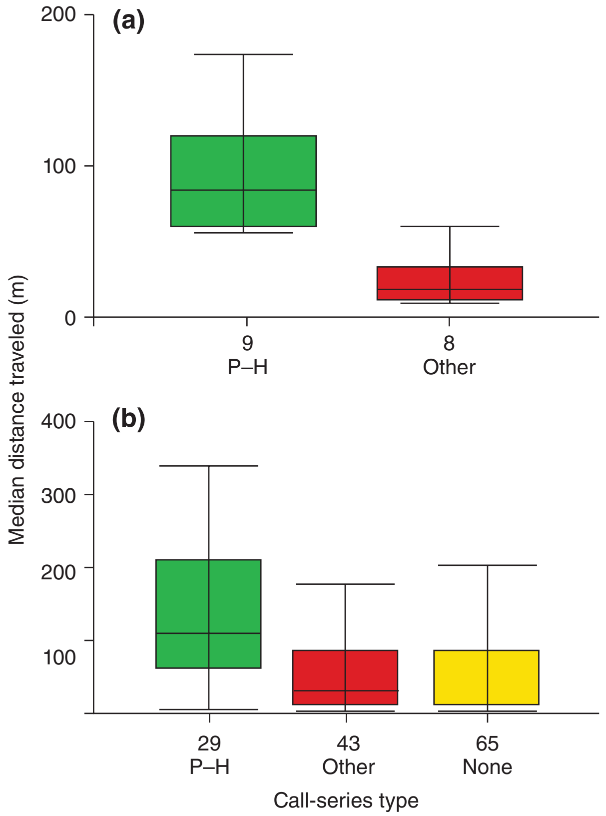

FIGURE 1 | Male putty-nosed monkeys combine two calls, 'pyows' and 'hacks', into different context-specific utterances. A series of pyows are given to general disturbances, including leopards, series of hacks to crowned eagles, and sequences of pyows followed by hacks to indicate forthcoming group movement. (a) Call series experimentally elicited by leopard growling: the group traveled significantly farther after hearing call series that contained at least one pyow–hack (P–H) sequence compared with the distance moved in response to all other sequences. (b) Naturally occurring call series: the habituated study group traveled significantly farther following call series containing at least one P–H sequence (P–H) compared with the distance moved in response to other series that included no P–H sequences (Other) or when there were no calls made by the male (None). Box plots indicate medians, inter-quartiles, and ranges. (Reprinted with permission from Ref 18. Copyright 2008 Nature Publishing Group)

Multimodal Signaling

Communication in great apes is often multimodal, consisting of vocalizations combined with manual gestures, body postures, and facial expressions. In a recent study with male bonobos, males combined one type of vocalization, the contest hoots, with various gestures.[26] The function of this behavior is simply to provoke other group members, who typically react with aggravation, screaming, or chasing. It is likely that the behavior serves the provocateur to show off his social power to others, suggested by the fact that males target only individuals of similar rank. But sometimes contest hoots are also used in a friendly way, as part of a play bout between males. The acoustic structure of the contest hoots appears to be identical between the agonistic and the play context,

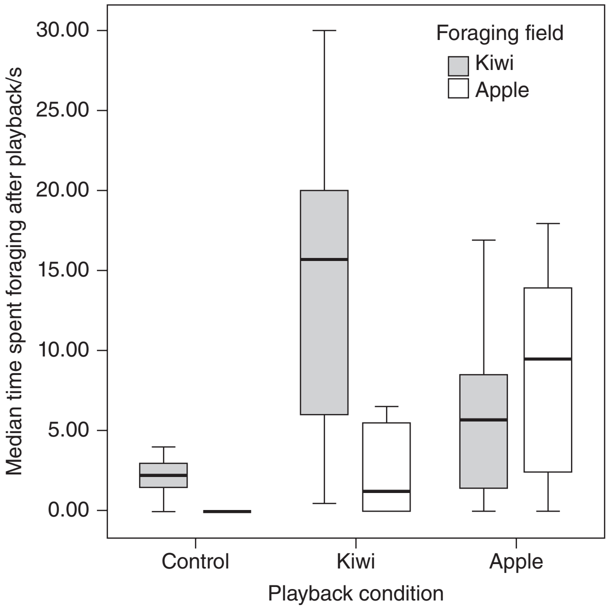

FIGURE 2 | Results of a playback experiment to test whether bonobos can make inferences about the location of food by listening to recordings of other individuals' food call sequences to kiwi (high value) or apples (low value). In the experiment, subjects first learned to find kiwis or apples at two distinct foraging fields within their enclosure. In the subsequent testing phase, subjects then heard recordings of another individual's call sequence given to either kiwi or apple from a concealed speaker. Box plots indicate subjects' foraging responses, at the two foraging fields, in the different playback conditions ('Control', no sound played back; 'Kiwi', playbacks of food call sequences originally given to kiwi; 'Apple', playbacks of food call sequences originally given to apples; medians, inter-quartile ranges, and extreme values). (Reprinted with permission from Ref 24. Copyright 2005 Public Library of Science)

but callers use significantly more soft than rough gestures during play, compared with agonistic interactions. Gestures may help the recipient to recognize the social intentions of the signaller.[26]

The Origins of Compositional Thought

In sum, although there is relatively good evidence that primates and other animals are able to extract meaning from syntactically organized information (e.g., Refs 15, 27, 28), there is practically no evidence that they make active use of the combinatorial potential inherent in their communication systems. Perhaps, this is because compositionality is based on a vigorous and opulent system of mental concepts, as it is the case for human thinking, something that primates may not have access to. Although there is ample evidence that animals have mental concepts for both natural kinds and social function,[29,30] the nature of these mental structures and their expression during communication has remained largely obscure.

Would an animal equipped with human-like conceptual abilities be able to develop language? There are at least two further components that are both essential and uniquely human; sophisticated vocal control[31] and the ability to see others as being governed by psychological states,[32,33] suggesting that a narrow focus on syntax is unlikely to shed sufficient light on how language evolved.

VOCAL CONTROL

Language is mainly a vocal behavior. Of course, it is true that rudimentary language-like gestural systems have emerged in deaf populations,[34] but this is not the default pattern in normally developing humans. Instead, humans are enormously vocal primates, especially when compared with their nearest primate relatives, the chimpanzees and bonobos. During their first year, human infants begin to play with sounds, they babble,[35] something that is not normally observed in non-human primates.[36,37] Instead, wild chimpanzee infants remain mainly silent during their first few years of life, with no evidence for anything akin to human babbling.[38]

Also relevant is that no published study has succeeded in training primates to produce *new* vocalizations that are not modifications of the existing repertoire. In contrast, from early age, humans are able to generate a very wide range of acoustically distinct sounds by actively changing the vocal tract configurations rapidly and precisely. In non-human primates, this ability remains very underdeveloped, even after substantial training.[39,40] For great apes, it has also been noted that they are simply not interested in spontaneously imitating speech sounds,[41] although in other contexts they appear to be very keen to copy human behavior. Hayes and Hayes[40] wrote about their home-raised chimpanzee 'Viki': '… and here, again, Viki shows no great difference. Just as the human child copies its parents' routine chores, so Viki dusts, washes dishes, sharpens pencils, saws, hammers … […] On the other hand, she is less vocal: while the human child commonly keeps up an almost continual stream of chatter—with or without meaning, Viki is silent'.

Explanations

Why are such seemingly trivial vocal imitation tasks near impossible for non-human primates to solve? One popular explanation has been that this is due to anatomical differences in the vocal tract, particularly the permanently low position of the human larynx.[42,43] This view is no longer supported by

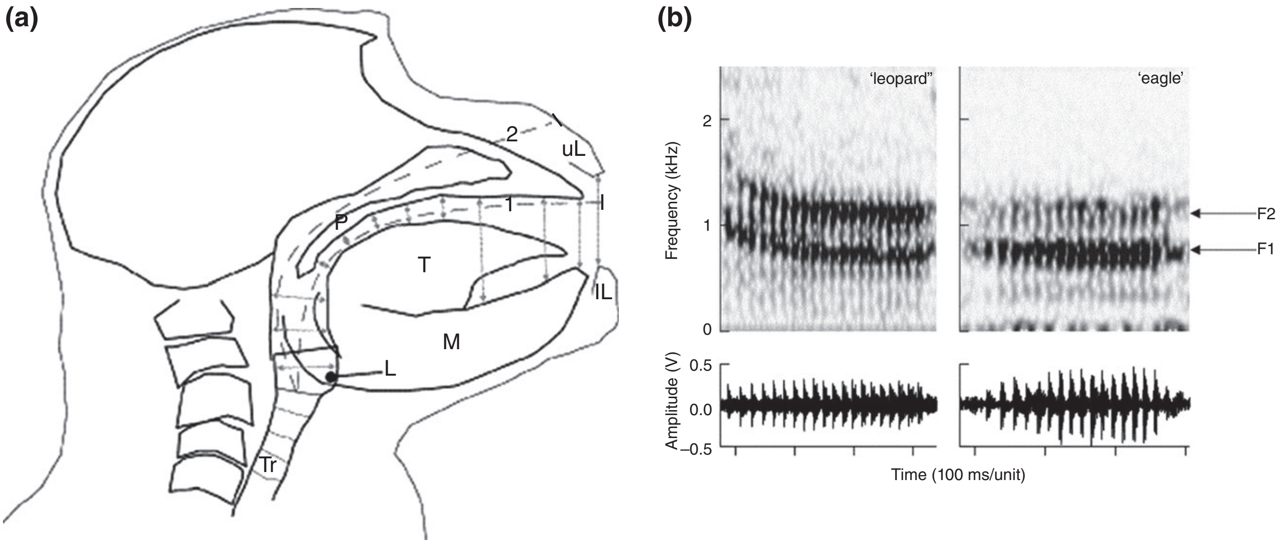

FIGURE 3 | (a)Vocal tracts of non-human primates are homologous to humans in form and function. Illustration of the vocal tract of a Diana monkey with details as seen in dissection and lateral X-ray. T—tongue; Tr—trachea; uL—upper lip; lL—lower lip; L—larynx; P—palate; dashed line 1—oral vocal tract length; dashed line 2—nasal vocal tract length; arrows indicate the dorsoventral distances of the oral vocal tract. (b)Vocal tracts of non-human primates are homologous to humans in form and function. Vowel-like vocal output of male Diana monkeys produced by specific articulatory movements and constrictions of the vocal tract. Spectrograms and time series depict a Diana monkey leopard and eagle alarm call, including the first (F1) and the second (F2) formants with a downward modulation at the beginning of the leopard call but not in the eagle alarm call. (Reprinted with permission from Ref 43. Copyright 2006 Elsevier)

current research, as the basic layout of the human larynx and vocal tract is not fundamentally different from other mammals (Refs 43–45; Figure 3). On the matter of vocal control, Hayes and Hayes[40] wrote about Viki: '… the variety of sounds observed in her babbling, and in her vocal expression of emotion, left no doubt that her vocal mechanisms were adequate for producing satisfactory approximations of most of the elements of human speech'.

Also important is that great apes are quite capable of controlling their supra-laryngeal vocal tracts to produce various voiceless signals, such as clicks, smacks, raspberries, kiss-sounds, and whistles.[39,46–48] Furness wrote of his home-raised orang-utan: 'The orang in one respect does use the lips, to make a sound indicating warning or apprehension; this sound is made with the lips pursed up and the air sucked through them … […] My oldest orang would make this sound on command (I had merely to say "What is the funny sound you make when you are frightened?")'.[39]

Controlling the vocal folds and the associated sustained airflow, however, appears to be much harder for non-human primates.[49] Hayes and Hayes[40] further wrote: 'The first step was aimed at teaching her merely to vocalize on command, in order to obtain a reward. […] The task was surprisingly difficult. Although she seemed to learn what was required quickly, she had serious trouble with the motor skill of voluntary vocalization'.

Laboratory experiments then showed that it is very challenging to train primates to vocalize on command or to alter the morphology of their calls,[50,51] possibly for neuroanatomical reasons. Humans possess a direct projection from the lateral motor cortical areas to the laryngeal motor neurons,[52] which appears to enable voluntary fine motor control over the laryngeal musculature, something that has not been found in squirrel monkeys. Yet, all primates appear to have direct premotor cortical connections to the nuclei controlling the jaws, lips, and tongue,[52] suggesting that control over the supra-laryngeal vocal tract was already present in the common ancestor, while control over the larynx and respiratory muscles may have evolved more recently.[53]

The Origins of Vocal Control

One hypothesis for why only humans evolved laryngeal control is that it emerged as a by-product of cooperative breeding. Humans are unusual in the amount of childcare they provide both in traditional hunter-gatherer and in modern societies.[54–56] Often, this involves unrelated individuals, which may be especially be challenging for infants. Advanced vocal control, the ability to produce vocal utterances beyond a basic primate-like call repertoire, may have evolved to help infants to secure care from older individuals who often do not have a genetic interest to do so.[57] In particular, natural selection may have favored vocal behavior in early human infants that facilitated social bonding between unrelated individuals. Babbling may be particularly important, if it helps human infants to be noted by caregivers and to facilitate social bonding with them. Interestingly, babbling is generally perceived as 'pleasant', suggesting that natural selection may have benefitted from a pre-existing receiver bias. The hypothesis that babbling-like vocalizations elicit infant care more efficiently than other vocal behavior requires further testing, ideally across different primate species.

SOCIAL AWARENESS

There is good evidence that primates and other animals can make basic inferences about other individuals' vocal behavior. Vervet monkeys, for instance, produce a range of acoustically distinct vocalizations to different predators, which are meaningful to other group members.[58,59] Similar findings have been reported from Diana monkeys,[60,61] Campbell's monkeys,[62] colobus monkeys,[16,63] and many other species. However, what is usually less clear from such studies is the degree to which the signalers are actively trying to inform their recipients. Human communication operates in this Gricean way,[64] with signalers pursuing specifiable social goals intending to be understood. For animal communication, a more parsimonious hypothesis suggests that communication is driven by a predisposition to react more or less automatically to biologically relevant events in order to enhance the signaller's fitness.

A third hallmark of human language, thus, is its cooperative use.[65,66] Humans are highly and uniquely cooperative, particularly during foraging and childcare, which require high degrees of social awareness. Although non-human primates cooperate in various ways, the underlying cognitive mechanisms appear to be simpler and based on behavioral contingency learning rather than an understanding the partner's psychological states. Nevertheless, there is an increasing literature that has demonstrated various degrees of social awareness underlying primate communication. The evidence is particularly compelling for great apes, but a number of studies on monkey suggest similar capacities, at least in the context of predation avoidance.

In Thomas langurs, for example, males continue to produce alarm calls to model predators until every group member has responded with at least one alarm call, suggesting that males keep track of others' awareness.[67] Similarly, male blue monkeys produce more alarm calls to a suspected eagle if other group members are close to the danger compared with when they are far, regardless of their own distance.[68] In great apes, signalers take the visual perspective and attention of their recipients into account when communicating, for example, using visual signals when the recipient is oriented toward them and audible signals when facing away (e.g., orang-utans,[69] gorillas,[70] and chimpanzees[71]).

Intention and comprehension also matter. Both chimpanzees and orang-utans adjust their signaling behavior according to the degree of comprehension manifest in a human partner,[72,73] while chimpanzees behave differently depending on whether a human experimenter is unwilling or unable to give them food.[74] The emerging image from these results is that great ape communication is based on some social awareness, in the sense that subjects can take into account basic mental states of their recipients, such as attention, intention, and comprehension.

A few recent studies on ape vocal behavior suggest that there is also some cooperative element in communication. One finding on wild chimpanzees has been that, during conflicts, victims are more likely to exaggerate their screams (indicating more violent aggression than actually happened) if high-ranking group members are nearby, who can potentially intervene on behalf of the victim.[75] Similarly, chimpanzee and bonobo females suppress copulation calls when they are with unfavorable audiences, presumably to avoid negative social consequences,[76–79] while female chimpanzees suppress their regular vocal 'greeting' signals to higher-ranking group members if the alpha male is nearby.[80] Recent playback studies have shown that chimpanzees are more likely to produce food calls when they are with a favorable than an irrelevant audience (e.g., high-ranking group members or 'friends'), as if trying to benefit these individuals selectively.[81,82] Other interesting examples are signals used to engage others in a shared activity, notably joint travel. Both chimpanzees and bonobos can produce structurally unique vocal and gestural signals to engage a desirable partner in joint movements (Ref 83; Figure 4), while chimpanzees are more likely to produce alarm calls to a snake, if they are with ignorant group members compared to when they are with knowledgeable ones, who already know about the snake.[84,85]

Overall, these studies suggest that great apes possess a fairly sophisticated understanding of how their own signals impact on the behavior and psychological states of their recipients, with some preliminary evidence that they can use this capacity to actively inform recipients about events that are relevant to them.

FIGURE 4 | Spatial reference in bonobo gestures. A subadult male produces a beckoning gesture sequence to persuade a distant high-ranking female to approach and jointly move to a different location for sex. Illustrations depict the sexual initiation posture (a) followed by a beckoning gesture: arm stretch toward recipient (b), sideways arm sweep toward self (c–e), wrist twirl (f), and then a body pivot (g and h) before walking away and regularly gazing back to check whether recipient is following (i).

CONCLUSIONS

Much research effort has been devoted to the problem of how human language emerged from a more primate-like communication system. Human language is a vocal behavior so a natural focus has been the study of non-human primate vocal behavior. Fieldwork has demonstrated that primates generally perceived each others' calls as meaningful, in the sense that recipients make pragmatic inferences about the external event experienced by the caller. Some of these utterances consist of sequences of acoustically distinct calls, which sometimes carry meaning that is different from that of the component calls. Nonetheless, non-human primates fail to make use of the potential combinatorial power of their communication systems, possibly because their underlying mental concepts are too fuzzy to engender compositionality.

In terms of vocal control, the basic primate vocal tract anatomy is perfectly suited to produce human-like speech signals, and there is evidence that primates can control their supra-laryngeal vocal tracts. What appears to be uniquely human is the sophisticated motor control of the larynx to act as a stable acoustic source for speech production.

In terms of social cognition, finally, there is some evidence that monkeys make basic assessments of their audiences' psychological states. In great apes, the evidence is generally stronger, both for gestural and for vocal signals, with subjects taking into account the social role, intention, attention, comprehension and, to some degree, the knowledge of their recipients. In sum, this evidence reveals a patchwork of continuities but also some clear discontinuities in the evolutionary transition from primate to human communication.

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FURTHER READING

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