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## Review article

# Meaning, intention, and inference in primate vocal communication

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### ABSTRACT

Two core questions in the study of speech evolution are whether nonhuman primate signals should be conceived as referential, and what the role of social cognition is in primate communication. Current evidence suggests that the structure of primate vocalizations is largely innate and related to the affective/motivational state of the caller, with a probabilistic and underdetermined relationship between specific events and calls. Moreover, nonhuman primates do not appear to express or comprehend communicative or informative intent, which is in line with a lack of mental state attribution to others. We argue that nonhuman primate vocalizations as well as gestures should be best conceived as goal-directed, where signallers are sensitive to the relation between their signalling and receivers' responses. Receivers in turn use signals to predict signaller behaviour. In combination with their ability to integrate information from multiple sources, this renders the system as a whole relatively powerful, despite the lack of higher-order intentionality on the side of sender or receiver.

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### Contents

1. The evolving language faculty .....	00
2. The question of meaning in primate communication .....	00
3. Flexibility in vocal production .....	00
4. The case of vervet monkey alarm calls .....	00
5. What do primate vocalizations stand for? .....	00
6. Intentional signaling .....	00
7. Primate signals are goal-directed but not intentional .....	00
Acknowledgements .....	00
References .....	00

## 1. The evolving language faculty

According to the evolutionary biologists [John Maynard Smith and Eörs Szathmáry](#), the transition from primate-like calls to speech was “the decisive step in the origin of specifically human society” (1995, p. 12), and the evolving language faculty has been proposed

as the basis from which all other uniquely human accomplishments developed ([Snowdon, 2004](#)). Despite a wide variety of scenarios of how language might have come about, the evidence is scant, and thus the question of language evolution has been suggested to be one of the most difficult problems in science ([Christiansen and Kirby, 2003](#)). This encompasses both the evolution of the representational and socio-cognitive system underpinning the language faculty, as well as specific adaptations that facilitate different modes of externalization, such as speech or sign language ([Hagoort and Poeppel, 2013](#)).

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Although there is still no definitive list of which components make up the language faculty (Hauser et al., 2002), it is clear that it is a complex trait that draws on several subcomponents, including the ability to map external events or objects onto conventionalized signs, a syntactical engine to construct and comprehend the hierarchical structures characterizing language, as well as the ability to attribute intentions and knowledge states to others in communicative interactions (Fitch, 2010; Hauser et al., 2002; Lenneberg, 1967; Scott-Phillips, 2015). Within an evolutionary framework, it seems more likely that the emerging language faculty would have co-opted pre-linguistic components than to evolve entirely novel language-specific modules (Fitch, 2010). These pre-linguistic components can be thought of as pre-adaptations or precursors to language (Hurford, 2003). Over the last decades, much research effort was devoted to identifying such putative pre-adaptations or precursors in closely related species, or to investigating analogue models in more distantly related species (Hauser and Fitch, 2003; Weiss and Newport, 2006). In this contribution, we review the evidence for precursors to semantic communication and pragmatic inference in nonhuman primate (hereafter: 'primate') signals, giving special attention to the auditory-vocal domain. We first discuss concepts of meaning and flexibility in vocal production, with special regard to vervet monkey alarm calls. We then turn to the question whether nonhuman primate vocal communication fulfils criteria for ostensive communication, entailing the expression and understanding of both communicative and informative intent. We conclude with the suggestion that substantial parts of nonhuman primate signalling can best be conceived as goal-directed. In combination with the inferential skills of listeners, this assumption is sufficient to explain much of the sophistication in nonhuman primate communication.

## 2. The question of meaning in primate communication

Words have meaning in that they represent something other than themselves (Deacon, 1997; Fitch, 2010; Hurford, 2007). It was Paul Grice who pointed out that linguistic meaning not only depends on the relationship between a word and what it represents (the key concept of semantics), but also on the fact that both the signaller and the receiver take each other's state of mind into account when communicating (Grice, 1957). This led to the distinction between literal meaning (the code that maps signs onto the signified, i.e. words onto referents), and speaker or intended meaning (Grice, 1957; Moore, 2016a; Scott-Phillips, 2015; Sperber and Wilson, 1986).

Semiotic theory (Chandler, 2007) provides a useful framework for distinguishing different types of relationships between the signifier and the signified. This relationship can take on three different modes, namely arbitrary, i.e. symbolic, iconic, or indexical (de Saussure, 1959). Words have symbolic meaning because the relationship between the word and that to which it refers is mostly arbitrary and based on a set of conventional rules (Peirce, 1958). The creation of such arbitrary relationships between the signifier and the signified, and the resulting symbolic representations have been put forward as a fundamental step in the evolution towards modern human language (Christiansen and Kirby, 2003; Deacon, 1997; Jackendoff, 1999). Iconic relationships in the vocal-auditory domain (speech) often amount to onomatopoeic descriptions, such as 'eeyore' for donkey. There is still some stylization and flexibility between signifier and signified here, and different languages vary in terms of their onomatopoeic renditions of animal sounds – for instance, in German "I-Aah" would be used to refer to the donkey. Indexical relationships, finally, reflect some causal link between the signifier and the signified, such as smoke being indicative of the presence of fire (de Saussure, 1959).

## 3. Flexibility in vocal production

A crucial prerequisite for conventionalized communication in speech is vocal-auditory learning, which gives rise to the open-ended creativity and the different degrees to which speech varies between populations, with regional differences in language type, dialect and accent (Lameira et al., 2010). Flexibility in speech can be attributed to the ability to modify vocal structure as a result of auditory experience, as well as the ability to produce and respond to words in novel contexts (Janik and Slater, 2000). The learnt acquisition of novel sounds has been identified in only a few species within distantly related taxa, including songbirds (Doupe and Kuhl, 1999; Wilbrecht and Nottebohm, 2003), marine mammals (Janik, 1997; Nottebohm, 1972) and elephants (Poole et al., 2005). Primates are notably absent from this group (Egnor and Hauser, 2004), as they acquire species-typical vocalisations even when deprived of normal auditory experience by social isolation (Winter et al., 1973), deafness (Hammerschmidt et al., 2001, 2000), or cross-fostering (Owren et al., 1992). In humans, the ability to exercise voluntary control over the spectral patterning of words and the production of novel sounds depends on a direct connection between the primary motor cortex and the nucleus ambiguus, which in turn controls the laryngeal motoneurons (Kuypers, 1958); a similar direct connection is found between forebrain motor areas and neurones which control syringeal movements in songbirds (Wild, 1993). This connection is missing in primate vocal production (Jürgens, 1976), a difference that likely accounts for nonhuman primates' inability to produce calls outside of the species-typical vocal repertoire (Jürgens, 2009). Interestingly, this direct connection is not involved in the production of human non-verbal sounds, such as laughs, cries and shrieks; thus at the neurological level, animal calls appear more similar to this group of innate vocalisations than to speech (Ackermann et al., 2014; Hage, 2010). A recent study suggests that one route towards higher control of vocal output may be the strengthening of existing weaker projections: while the structural network of the laryngeal motor cortex (LMC) in humans and rhesus monkeys is largely comparable, humans have a much higher connectivity (Kumar et al., 2016). It should be noted at this point that most of the neurobiological evidence comes from a few more distantly related species only (mostly squirrel monkeys and rhesus monkeys, respectively), while comparatively little is known about the functional connectivity in apes, for instance.

Further support for the idea that in terms of their structure, primate vocalizations reveal little flexibility comes from comparative analyses of the call structure of closely related species. For instance, the 'barks' of male members of the genus *Chlorocebus* revealed only minor differences between East African and South African vervets (Fig. 1; Price et al., 2014). These monkeys belong to two different subspecies of *Chlorocebus pygerythrus*, and the split between the two lineages is assumed to have taken place around 1.5 mya (Perelman et al., 2011). Remarkably, males of the West African congener *C. sabaues* also exhibit a highly similar call structure; with a last common ancestor between the two species around 2.1 mya. Such comparative studies strongly suggest that the structure of nonhuman primate vocalizations is not only innate, but also highly conserved (Geissmann, 1984; Meyer et al., 2012; Thinh et al., 2011).

Nonetheless, there are notable changes in the structure of primate vocalizations during ontogeny, but these are most likely the result of maturational development such as growth and the onset of puberty (Ey et al., 2007; Hammerschmidt et al., 2000; Lieblich et al., 1980). It is also clear that there is some flexibility in call usage (Hage et al., 2013). For instance, the presence or identity of other individuals in the vicinity may affect the incidence of call production (Cyger et al., 1986; le Roux et al., 2008; Evans and Marler, 1994; Di Bitetti, 2005), a phenomenon known as an "audience effect" (Seyfarth and Cheney, 2010; Zuberbühler, 2008).

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