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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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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).

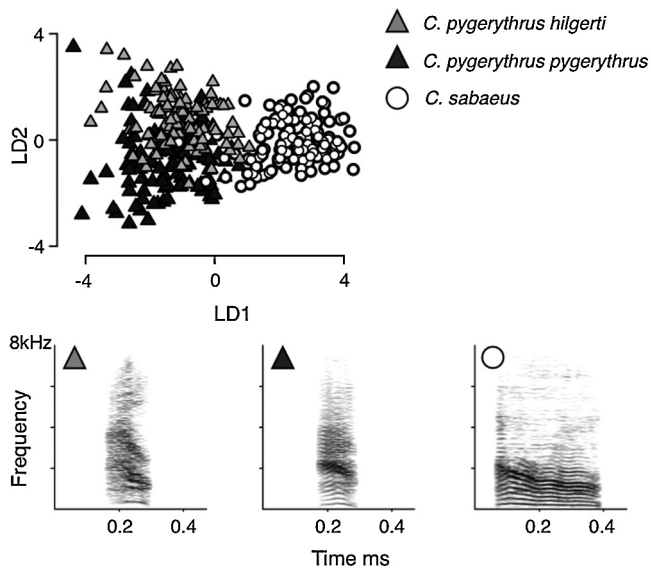


Fig. 1. Scatterplot and spectrograms illustrating population differences in the acoustic structure of *C. sabaesus*, *C. p.hilgerti*, and *C. p.pygerythrus* barks. The scatterplot presents the distribution of the first and second LDA discriminant scores. Spectrograms illustrate a typical call exemplar for each call group, with typical calls defined as those that were most likely to be assigned by LDA to the correct caller/population.

From Price et al. (2014), with permission.

In addition, detailed acoustic analyses revealed that the structure of primate vocalizations may undergo social modification (e.g. Elowson and Snowdon, 1994; Mitani and Gros-Louis, 1998), a process described by Seyfarth and Cheney as “modification within constraints” (1997). Further, baboons systematically altered the length of their contact calls (grunts) in relation to the visibility in the habitat (Ey et al., 2009). The neural mechanisms underlying such vocal accommodation are, however, not well understood (Hammerschmidt and Fischer, 2008). One possibility is that via sensory-motor integration, auditory experience shifts probabilities in pattern generation (Fischer, 2008), but this conjecture requires empirical testing.

In sum, the structure of primate vocalizations is largely hard-wired. There is some evidence for modest vocal accommodation, but it appears that nonhuman primates do not acquire novel learned voiced vocalizations (Fischer, 2002). The core conclusion of this is that the calls of nonhuman primates are neither iconic nor symbolic, but can be best conceived as indexical. The question now is: of what may they be indexical?

4. The case of vervet monkey alarm calls

Initially, primate calls were conceived as expressions of emotions, as Darwin had suggested (Darwin, 1872). This view was widely shared (Premack, 1975; Rowell and Hinde, 1962; Scherer and Kappas, 1988). Yet, some primate calls, notably alarm and food calls given in response to specific stimuli in the environment, raised the intriguing question whether they might have some symbolic or referential quality (Marler, 1977). The paradigmatic case in this discussion is the alarm call system of vervet monkeys (Seyfarth et al., 1980a,b). In response to their three main predator categories (large cats such as leopards, aerial predators such as martial eagles, and snakes, such as pythons), vervet monkeys evolved different adaptive escape strategies and they also utter acoustically distinct calls in these contexts (Seyfarth et al., 1980a,b). Previous studies in captivity had found structural differences between female alarm calls produced to snakes and eagles (Owren and Bernacki, 1988), yet a

detailed quantitative assessment of the acoustic properties of these calls was notably absent from the literature.

To study the properties of the vervet monkey alarm call system in detail, we re-analyzed the original recordings assembled by Tom Struhsaker, Robert Seyfarth and Dorothy Cheney (Price, 2013; Price et al., 2015). We used alarm calls given in response to the different predator categories, but also included calls given during inter- and intra-group aggressive interactions. Because of the substantial differences between male and female vocalizations, we analysed their calls separately (Price et al., 2015). The first goal was to assess whether any objective call types could be identified, without any reference to the context in which the respective calls were given. If the calls given in the different contexts were indeed highly acoustically distinct, one would have predicted the emergence of three alarm call types, as well as one or two call types encompassing calls given in aggressive interactions. The ‘best’ solutions were a 4-cluster solution for the females (Fig. 2a), and a 3-cluster solution for the males. The clusters largely corresponded to previous verbal and spectrographic descriptions of the calls (Seyfarth et al., 1980a; Struhsaker, 1967), but also indicated some overlap between different call types. For females, one cluster corresponded to ‘chirp’ calls, typically given in response to terrestrial predators, one cluster encompassed broadband ‘chutter’ calls typically produced in response to snakes, but also during intergroup encounters (see also Cheney, 1984), while a third cluster corresponded to the low frequency ‘rraup’ calls typically produced in response to raptors, but also during escalated between and within-group aggression (Price et al., 2015). The final cluster fell in between cluster 2 and 3, indicating graded variation between ‘chutter’ and ‘rraup’ calls. For East African male alarm calls, the three clusters largely corresponded to male ‘chutters’ given in response to snakes, ‘barks’ given in response to terrestrial predators, and ‘rraup’ calls given in response to eagles and snakes (Price et al., 2015). No recordings of calls given during aggressive interactions were available.

The corresponding discriminant function analysis revealed that the female alarm calls could be very well assigned to the different contexts, with an average of 98.7% correct classification (Fig. 2b). When we included calls given during aggressive interactions, a higher number of misclassifications occurred. Specifically, calls given during within- and between-group aggression were confused with calls given in eagle and snake contexts. Calls given in response to leopards, however, were clearly distinct. In contrast, ‘chutters’ and ‘rraups’ belonged to one larger category with continuous gradation (Fig. 2c; Price et al., 2015).

The calls that male vervet monkeys gave in response to the different predator categories were also clearly distinguishable, yielding 93.2% correct classification. We added a further analysis of calls recorded from vervet monkey males ranging in South Africa, which had been given in response to leopards and during aggressive interactions between groups. These calls were difficult to distinguish, with a correct classification of 74.9%, which was not significantly different from chance, as evidenced by a permutation analysis (Price et al., 2015). The key conclusion of this analysis was that the alarm calls of East African vervet monkeys are acoustically sufficiently distinct to allow for discrimination of these calls in predator contexts. When calls from aggressive contexts were included into the analysis, then some misclassification could be observed for ‘chutter’ and ‘rraup’ calls from female monkeys, and between barks from South African male vervets.

By now, acoustic variation with different predator types has been found in many animal species, including birds, carnivores and of course other primate species (e.g., Evans et al., 1993; Gill and Sealy, 2004; Kirchhof and Hammerschmidt, 2006; Macedonia, 1990; Manser et al., 2002; Slobodchikoff, 2002; Zuberbühler, 2001). To a lesser extent, variation in calls has been observed between contexts of food discovery (Clay et al., 2012; Kalan and Boesch, 2015)

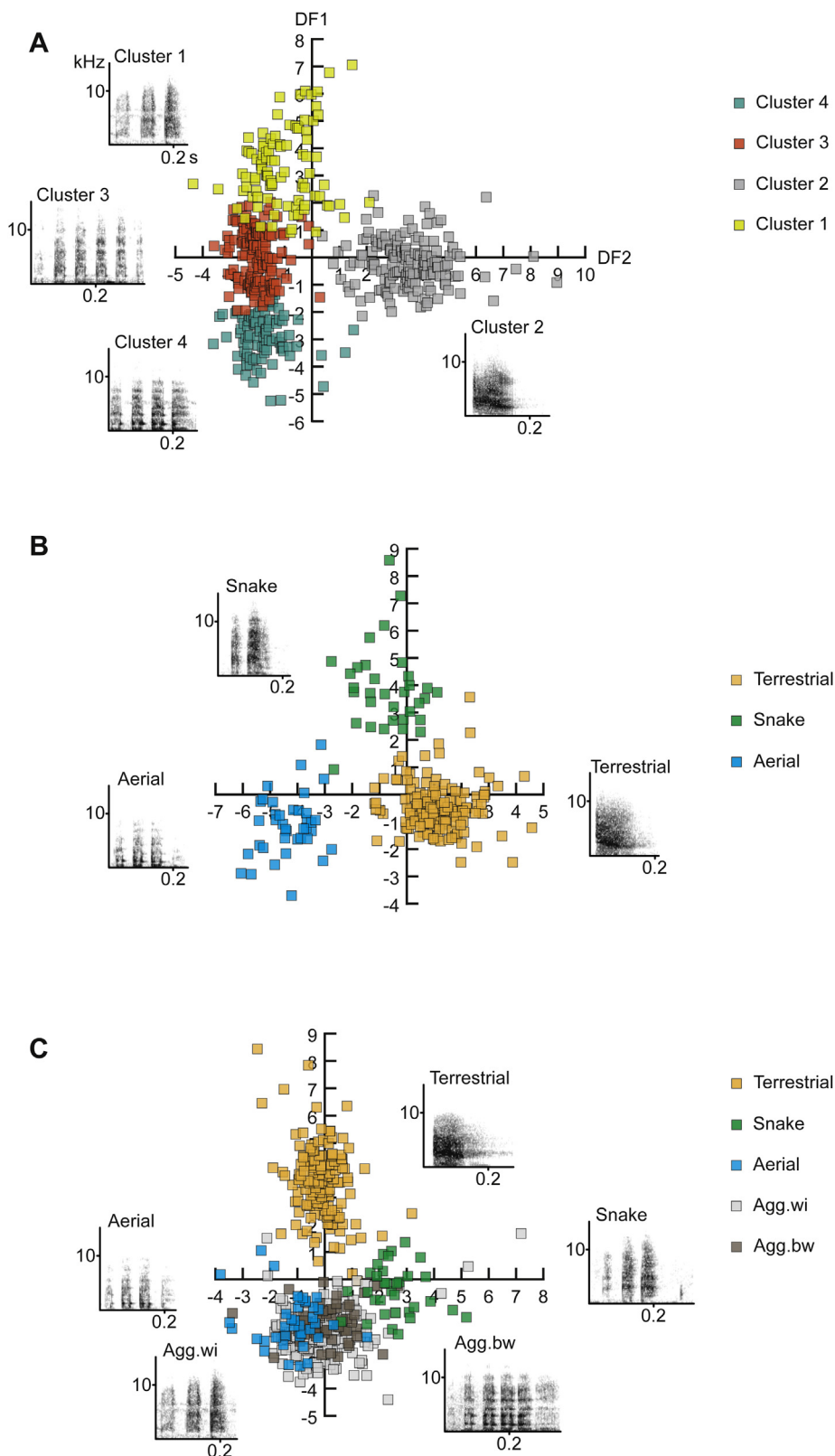


Fig. 2. Structure and discriminability of female vervet vocalizations given in alarm and aggressive contexts. (A) Scatter plot of the four identified clusters based on discriminant function analyses using cluster membership as grouping variable. Spectrograms depict representative call exemplars with a small Euclidean distance to the cluster centre for each cluster. (B) Scatter plot of the discriminant scores with corresponding spectrograms of female alarm calls given in response to leopards, eagles, and snakes. (C) Scatter plot of the discriminant scores with corresponding spectrograms of female alarm calls given in response to leopards, eagles, and snakes, as well as during within- and between-group aggression. All spectrograms were made using the following settings in Avisoft: 256 FFT, frame size of 100% (Hamming window), frequency resolution 172 Hz; 50% window overlap, temporal resolution 2.9 ms. Abbreviations: kHz: Kiloherz, s: seconds, DF1: discriminant function 1, DF2: discriminant function 2.

Figure and figure legend from Price et al. (2015), published under a Creative Commons Attribution 4.0 International License.

and during social interactions (Faragó et al., 2010; Gouzoules et al., 1984; Semple et al., 2002; Struhsaker, 2010). Such context-specific calls have been proposed to be precursors to human words (Fedurek and Slocombe, 2011; Townsend and Manser, 2013; Zuberbühler, 2003).

We argue, however, that context-specificity is not equivalent to flexibility in mapping of sound and referent (here: different predator or food types). In fact, one could conceive a completely hard-wired system where specific releasers invariably give rise to highly specific responses, such as the responses of female bush crickets to male song of the species (Heller and von Helversen, 1986). In other words, context-specificity per se, a key criterion in the identification of so-called referential communication (Macedonia and Evans, 1993; Townsend and Manser, 2013; Wheeler and Fischer, 2012), is a poor diagnostic to establish whether such calls might constitute preadaptations to human speech. The crucial question is what the mechanisms are that mediate the link between the occurrence of a certain event, and the utterance of a specific call.

5. What do primate vocalizations stand for?

In the case of alarm calls, there is a relationship between the occurrence of a specific event, such as the appearance of a predator, and the utterance of certain calls. The available evidence suggests that this relationship is not deterministic (Seyfarth and Cheney, 1997). First of all, the assessment of a given situation may change with experience, altering the link between the event and the calling. For instance, young vervet monkeys spontaneously produce 'aerial alarm calls' to a number of items in the air or falling down, but they subsequently learn to recognize that only specific species pose a danger, such that they restrict the calling to specific raptor species (Seyfarth and Cheney, 1980). Similarly, chacma baboons, *Papio ursinus*, in the Okavango delta, who for the first time spotted elephants, started to alarm call, but rapidly learned that elephants pose no danger to them, and subsequently remained silent (much to the chagrin of the researchers who would have appreciated being alerted to the presence of elephants in the area; D. Cheney, personal communication). These examples indicate that perceptual learning and learning through experience modify the relationship between an event and the production of a given signal. The more fundamental question is how we can best explain the cognitive and emotional processes that lead to calling, once the stimulus in the environment has been evaluated.

Initially, the vervet alarm calls were presumed to refer to the eliciting stimuli because of the presumed patterning of specific calls with specific predators (Seyfarth et al., 1980a; Fig. 3a). What was not fully appreciated was that similar calls could be given in apparently different contexts (Price et al., 2015, Fig. 3b), and that sometimes, different calls could be given in the same situation (Struhsaker, 1967). Presently, it remains unclear whether similar calls are tied to similar or perhaps also different internal states of the animals. In one scenario, different perceptions of the world may elicit similar internal states, which in turn elicit specific calls (Fig. 3c). In an alternative scenario, different perceptions lead to different internal states; these converge onto the same pattern generators and hence calls (Fig. 3d).

By analysing the animals' overt behaviour, it is difficult to distinguish between accounts c and d in Fig. 3 (or yet another model). Yet, it should be noted that internal states may be quite differentiated, and that the structure of vocalizations allow for subtle variations with regards to different aspects of internal states. Todt (1986), for example, proposed that the internal state consisted of an affective component related to the individual's evaluation of the environment, a motivational component related to the individual's action

tendencies, and an arousal component related to the individual's likelihood and urgency to respond. In other words, the emotions reflect whether some event is pleasurable or aversive (associated with positive or negative internal reward), while arousal may be high or low, irrespective of the evaluation of the situation. The motivation is linked to the idea to fulfil certain needs—at the most basic level, to ensure homeostasis. This conception is broadly compatible with appraisal theories of emotion (Arnold, 1960; Lazarus, 1966). Within the framework of appraisal theories, emotional responses encompass the appraisal of the environment (indicated by the mental representation in Fig. 3), the individual's motivational state (readiness to act), peripheral physiology (e.g. hormonal and nervous system changes, likely related to caller arousal), expressive behaviour (e.g. vocalisations), and feeling (subjective experience; for more detail see Moors et al., 2013). Because we are here concerned with emotional states in animals rather than humans, our use of the term emotion does not imply feelings in the sense of subjective and conscious experiences, but rather in the sense of basic emotional urges (Panksepp, 2011). The question is whether these conceptions of internal states are useful for assessing how events are related to vocal output.

A link between specific call types and internal state was established in squirrel monkeys (*Saimiri sciureus*), which were trained to increase or avoid electric stimulation of specific brain areas by switching between different compartments in a cage (Jürgens, 1979). Situations in which the monkeys avoided stimulation (and which were hence deemed to be aversive) were predictably associated with specific call types, namely shriek cackles, shrieks and alarm peeps (Jürgens, 1979). In contrast, in situations that were deemed as pleasurable, the monkeys uttered twitters, groans, and chucks (Jürgens, 1979). These calls are typically given in appetitive situations, such as food contexts. The results support the view that calls are loosely tied to different affective or motivational states.

Unfortunately, the relations between internal state and vocal output are not always clear-cut. For instance, in the self-stimulation study (Jürgens, 1979), the stimulation of the same brain area could evoke different call types. Similarly, Struhsaker had noted that in response to eagles, the animals would sometimes utter a broad array of different calls (Struhsaker, 1967). Thus, the same internal state may ultimately activate different pattern generators, albeit only to a certain degree, because otherwise, the signals would lose their predictive value. The neurological studies by Jürgens (see Jürgens, 2009, 1998 for reviews) suggest that the periaqueductal grey (PAG) functions as an important relay-station. It is conceivable that modulation at the level of the PAG explain the variation in calling within the same context to a certain degree. Nevertheless, we still do not fully understand the link between certain perceptions of the world, associated internal states, and the resulting vocal behaviour. Thus, it is presently not possible to falsify the hypothesis that internal states are driving the variation in animal vocalizations. Perhaps integrated analyses of remote measures of heart rate and vocal behaviour provide first glimpses into this link; yet more detailed analyses of the neural and physiological foundations of vocalizations are certainly needed to achieve a better approximation of the foundations of call production.

There is also ample evidence that variation in arousal (as inferred from the behaviour of the subject, or by variation of stimulus onset or stimulus distance) is related to variation in acoustics structure within call types. With increasing arousal, calls are typically increase in length and rate, and become noisier, higher-pitched, and more variable (Briefer, 2012; Scherer et al., 2003). Correlations such as these have been found in red-fronted lemurs, *Eulemur fulvus* (Fichtel and Hammerschmidt, 2002), squirrel monkeys (Fichtel et al., 2001), common marmosets, *Callithrix jacchus* (Yamaguchi et al., 2010), Barbary macaques, *Macaca sylvanus* (Fischer et al., 1995), chacma baboons (Meise et al., 2011)

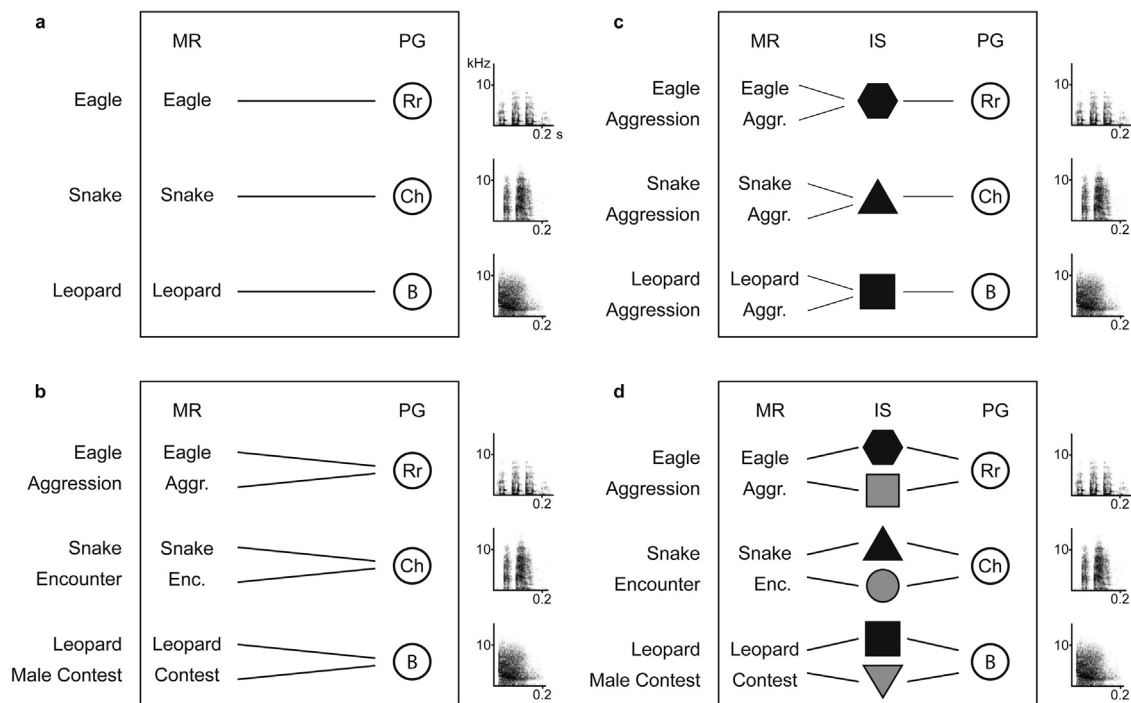


Fig. 3. Different conceptions between the link of external events, putative mental representations and affective evaluations, and specific vocalizations. (a) Earlier ideas about vervet monkey alarm calls implied that specific stimuli (Eagle, Snake, Leopard) in the environment evoked corresponding mental representations, which in turn activated specific pattern generators (PG), resulting in the production of specific call types. (b) Similar calls may be given in different contexts, however. It is conceivable that these different events lead to different mental representations, which activate the same PG. (c) The occurrence of the same calls in different situations could be due to the fact that different situations evoke similar internal states, here represented by different shapes, which in turn activate specific PGs. (d) Finally, different situations may evoke different mental representations, as well as different internal states, which eventually converge onto the same PGs. Abbreviations: MR: mental representation; PG: Pattern generator, IS: internal state; Aggr: Aggressions; Enc: Encounter; Contest: Male Contest; Rr: Rraup, Ch: Chutter; B: Bark.

and chimpanzees (*Pan troglodytes*; Slocombe and Zuberbühler, 2007). Similar results were found in studies of human vocalisations (reviewed in Scherer, 1989) and in a number of species outside of the primate taxon (Esch et al., 2009; Soltis et al., 2005; Taylor et al., 2009; Theis et al., 2007), indicating that comparable effects of caller arousal on call structure are widespread at least in terrestrial mammals.

For the present purposes, that is, what kind of information is available to receivers, we may summarize that some call types broadly correspond to (presumed) internal states, but that there is no one-to-one mapping between events in the environment and specific calls, and perhaps also not between specific presumed internal states and specific calls. Therefore, one may conclude that the code in nonhuman primate communication is underdetermined, and the relationships between event and signal, or state and signal is of statistical nature. This poses specific challenges to the receivers (see Section 7).

6. Intentional signaling

In (adult) human communication, the same utterance can take several different meanings, depending on the constellation between the speaker and the hearer. For instance, if a man tells his partner “you look great”, the meaning of the sentence is not so much that the partner looks great, but rather that he thinks that the partner looks great and that he intends that the partner should know this. Linguistic pragmatics can be described as the study of such intended and/or inferred meaning (Fitch, 2010). A second form of inference, which we will refer to as “contextual pragmatics”, encapsulates that receivers may use contextual cues to disambiguate the meaning (in the loose sense) of signals, both in animal and in human communication (Wheeler et al., 2011). An

example of such inference in human communication is the utterance “the chicken is ready to eat”; whereby the inferred meaning of this phrase would likely be different if the speaker was walking into the garden with a bag of chicken feed in their hand than if they were speaking whilst taking a roast chicken out of the oven (an elaboration of the distinction between speaker’s (or utterer’s) meaning, i.e. what a speaker seeks to communicate, and sentence-meaning, i.e. what a sentence is conventionally used to mean can be found in Grice, 1968). We argue that in terms of linguistic pragmatics, humans differ from other animals both in terms of code and socio-cognitive skills, whilst there is greater continuity in terms of contextual pragmatics.

As discussed above, there is no conventionalized code in primate vocal behaviour, and one hotly debated question is whether such a code could only have arisen if the socio-cognitive abilities required for intentional communication had evolved first. A broad and frequently used definition of intentional signalling (e.g. Tomasello et al., 1997) encompasses the following criteria: (i) ‘means-end dissociation’ (Bruner, 1981), which entails that different signals may be used to achieve the same goal, while the same signal may be used to accomplish different goals; (ii) ‘persistence of the goal’, which means that the sender may either continue to use the same signal or may alter her signalling if the desired result cannot be achieved; (iii) sensitivity to the social context, i.e. consideration of the receiver’s attentional state; and (iv) flexibility in terms of signal combination. Several studies have by now shown that ape gestural communication fulfils these criteria (e.g. Liebal et al., 2004; Pika et al., 2005, 2003). Notably, monkey communication may also meet these criteria, and this may also include the vocal domain. Barbary macaques, for instance, use the same call type in different contexts, while in one context, different call types may be uttered (Hammerschmidt and Fischer, 1998); a subject using a raised-eyebrows threat stare

first waits for a response and when no submissive signal is produced by the target, or the target does not give way, the threat may be escalated in several steps, including round open-mouth threat, head-bob, and ground-slap (Hesler and Fischer, 2007). Furthermore, the monkeys are sensitive to the attentional state of the receiver (N. Hesler, J. Fischer, unpubl. data). Yet, all we can conclude from such form of intentional communication is that it is apparently directed at a specific receiver, and goal-directed in the sense that the animal is sensitive to the outcome, as well as sensitive to the relationship between its action and the outcome. This would amount to first-order intentionality (Dennett, 1971), whilst there is no need to invoke an intention to inform the signaller (i.e., second-order intentionality).

Bar-On (2013) maintains that “expressive signals draw attention to the animal’s psychological state expressed, while at the same time drawing attention to some external object or event at which the state is directed” (p. 356), and argues that these kinds of expressive signals may constitute an important stepping-stone in the evolution of more sophisticated intentional communication. According to Bar-On, a variety of different displays fall under this umbrella term, including “alarm, distress and food calls, but also other vocalizations, such as yelps and growls, screams, pant hoots, barks, and grooming and reconciliation grunts. Furthermore, it encompasses non-vocal behaviors such as teeth-baring, tail-wagging, head tilts, flipper flaps, lip smacks, ground slaps, food-begging gestures, ‘play faces’ and play bows, grimaces, threat gestures, eyebrow flashes, and so on.” (p. 353). But this raises the question where one would draw the line between signals that do serve an expressive function and those that do not. The idea that signals, which are related to some external object or event, provide receivers with a different inferential problem than those that are simply used to broadcast signaller quality, is worthwhile pursuing, however.

Building on Grice (1957), Sperber and Wilson (1986), and Tomasello (2008), Scott-Phillips (2015) argued that the crucial step in language evolution was the development of ‘ostensive’ communication, in which both communicative and informative intent and the recognition of this intent must be fulfilled. One example that is chosen to illustrate ostensive communication is a situation in which the signaller is sitting in a café, and first makes eye contact with the waiter, and then tilts her empty cup “in a particular, *ostensive*, way” (p. 9, italics in the original) to indicate that the cup is empty and that she desires a refill (Scott-Phillips, 2015). Following Scott-Phillips (2015), the expression of an informative intention needs to be accompanied by an expression of communicative intention; otherwise communication would not take place. Thus, humans mark that they are intending to communicate, and provide information with the intent to alter the hearer’s mental state, under the assumption that the hearer understands both the communicative and informative intention. This form of communication requires 4th order mental representation. Scott-Phillips (2015) suggests that only humans possess a specific cognitive module that supports the processing of these levels in a fast and efficient way, but studies that systematically address this assertion in other species are still lacking.

But how do we distinguish between such a rich account that includes informative and communicative intent, as outlined above in the example of the customer tilting his empty cup in a café, and a much simpler one? One might describe the same scene in completely different terms, namely, that the signaller is entirely unaware or ignorant of the mental state of the waiter, and simply has learnt that she gets a refill when she tilts the cup, but only if she previously had made eye contact with the waiter. For infant and animal researchers, reasoning about the role of mental state attribution in communication by way of introspection (“I know that you know that I know. . .” etc.) is prohibitive. Instead, we need

to identify behavioural criteria to decide whether a specific signal was given intentionally (Moore, 2016a), as a result of associative learning, or innate dispositions.

Moore (2016a) argues that some great ape gestures fulfil simpler criteria for ostensive communication. He maintains that chimpanzees deliberately address their signals to a given receiver as a means of indicating their communicative goals (Moore, 2016a). Whether one subscribes to this view depends on which evidence is taken as sufficient. If we accept that making eye contact before gesturing (or vocalizing) as a behavioural criterion for ostensive communication, then one might conclude that signallers indeed mark their communicative intent. Whether or not that makes them Gricean communicators is a different question, however. As noted above, a simpler explanation might be that the signalling behaviour of these animals is goal-oriented, and that the animals have learned that they need to establish eye contact before gesturing, otherwise they would not be able to achieve their goals. Other authors have discussed whether the play-bow of dogs (Fitch, 2015) should be viewed as an ostensive signal. Although intuitively appealing, the more parsimonious explanation is that the play-bow simply signals the motivation to play, and not the motivation to communicate that the animal intends to play. Another interesting display is the ‘head-bob’ that monkeys make when they detect a potentially threatening stimulus. Typically from up in a tree, they stare intently at the predator (or human observer), drawing attention to themselves, but also apparently signalling to the predator that it has been detected (pers. observation). But then again, this signal may simply have evolved because it benefits the signallers to employ it, or because they have learnt that it functions to deter the predator from pursuit (which is now recognized as one important function of alarm calling in many animal species who are faced with stealth predators; Tilson and Norton, 1981; Zuberbühler et al., 1999).

A more complicated case is the class of signals known as “attention-getters”, which signallers use to direct another subject’s attention to herself. One interpretation is that these signals simply function to manipulate the receiver’s attention, without ascribing communicative intent (Scott-Phillips, 2015). An alternative view is that they are indeed expressions of such intent (Bourjade et al., 2014). One example: before hamadryas baboons, *P. hamadryas*, take off from the sleeping site in the morning, males within a subgroup may stalk towards another male in a stylized fashion, then turn around and walk away, while glancing back over the shoulder. This behaviour is known as ‘notifying behaviour’ in the literature (Kummer, 1968). The traditional interpretation is that in this way, the male is aiming to initiate group movement, and is indicating his preferred direction. While it is clear that this behaviour can function to achieve this goal, it is unclear whether the signaller is indicating both his communicative (stalking) as well as informative (choosing a specific direction) intent. A more compelling albeit anecdotal case is from a study in captive olive baboons, *P. anubis*, in which we investigated whether the monkeys would aim to capture the attention of an ignorant observer and point out the location of a hidden food reward (Schmitt et al., 2012). Although the vast majority of monkeys in this study did not appear to comprehend the task, one male baboon approached an ignorant experimenter with the species-typical notifying behaviour, and after successfully drawing her attention, stretched out his hand towards the bucket that contained the food. This could be taken as evidence for Gricean communication, in the sense that the animal is expressing his communicative and his informative intention (note that not all authors use the terms consistently—see Moore, 2016b). Yet, perhaps the stretched-out hand is just a result of the animal’s desire to reach the food, or to coax the experimenter to hand the food, i.e. a directive signal. Similarly, Bourjade and colleagues studied the begging behaviour of captive Olive baboons and found that the animals used more auditory attention-getters when the experimenter was fac-

ing away, before they stretched out their hands to request food (Bourjade et al., 2014). Again, however, one would need to rule out that this behaviour is a result of operant conditioning.

Two studies in chimpanzees explicitly tested whether the subjects altered their signalling behaviour in relation to the knowledge state of their audience (Crockford et al., 2012; Schel et al., 2013). Both studies involved placing a model snake near the traveling path of the animals. Crockford et al. (2012) focused on the question whether a subject that was traveling ahead of the others would produce 'alert hoos' when ignorant party members arrived. Receivers had either seen the snake and heard the initial alarm hoos, or had only heard the alarm hoos, or were entirely ignorant when they approached the scene. While the propensity to alert others was higher when receivers had not seen the snake compared to when they had, this difference might be explained by variation in receiver behaviour. There were only very few cases in the critical third condition where ignorant subjects approached a knowledgeable signaller, however. Schel et al. (2013) found that chimpanzees that had detected a model snake were more likely to produce 'alarm hoos' and 'waa barks' when close allies arrived than when others approached; they also reported gaze alternation between the location of the snake and the newly arrived individual, which the authors took as an indicator of intentional signalling (Schel et al., 2013). Thus, there is some indication that chimpanzees are sensitive to the knowledge state of the receiver, but an alternative view is that the chimpanzees resumed calling, or switched from 'alarm hoos' to 'waa barks' following the arrival of close allies was mediated by a higher arousal in these animals' presence. Similarly, the gaze alternation could be a result of the signaller's motivation to monitor both the snake's movement as well as the behaviour of the newly arrived animals.

7. Primate signals are goal-directed but not intentional

We suggest that primate signals should be best conceived as goal-directed. The signallers' goal is to evoke specific responses in receivers, and they are sensitive to the question whether their actions (the signalling) has the desired effect, such as come hither, or go away. Because primate signals are often directed, human observers may be inclined to assume communicative intent, although this is not strictly necessary. The more parsimonious explanation is that signals provide information about the signaller's motivation to engage in a specific behaviour, such as play, attack, or mate. In other words, signallers communicate, but they do not communicate that they communicate.

What about receivers? As we have seen above, the 'code' in primate vocal (and possibly gestural) communication is under-determined and of probabilistic rather than deterministic nature. Thus, receivers may need to take into account further information to disambiguate situations in which the information that can be gleaned from the signal alone is not sufficient to infer the signaller's intentions, or predict upcoming events. Fischer (2013) suggested to distinguish between the interpretation of the call and the subsequent decision making process. There is now ample evidence that primates take further contextual information into account when responding to signals (Arnold and Zuberbühler, 2013; Price and Fischer, 2014; Rendall et al., 1999; Wheeler and Hammerschmidt, 2013); furthermore, primates consider signaller reliability (Cheney and Seyfarth, 1988), as well as sequential information (Arnold and Zuberbühler, 2008) to infer what the signals predict or stand for. In principle, such additional information may affect both the interpretation of the call as well as the decision-making process, via shifting cost-benefit functions of different behavioural strategies. In contrast, there is little evidence that the attribution of call meaning is influenced by any concept of signaller intentions. Thus,

receivers' responses may be termed inferential (Fitch, 2015), but not 'ostensive-inferential' in the sense that receivers would attend to the communicative or informational intent of the signaller (if it existed). In this sense, we agree with Dorit Bar-On that primate receivers are not 'fulfilling their half of the Gricean equation' (contra Fitch, 2010). In conclusion, a sparse model of primate communication comprises goal-directed signalling with a high sensitivity to receivers' imminent responses, as well as receivers that recognize the sender's signals as such, and that possess a powerful inferential machinery to integrate multiple sources of information.

From an evolutionary point of view, a question is whether there is selective pressure to consider the intended meaning in the first place. As long as signals are reliably associated with specific behaviours, or reliably predict the occurrence of specific events, it is sufficient to attend to the signal and make inferences about what it predicts. This may challenge the view of 'fully blown mental state attribution first', because its presence is not needed to explain the emergence of a functionally adequate system for communication in primates.

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