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Anniversary Essay

Semantic communication in vervet monkeys and other animals

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The research field of semantic communication in animals was initiated by the study on alarm calls of vervet monkeys, *Chlorocebus pygerythrus* (then known as *Cercopithecus aethiops*) by Seyfarth, Cheney and Marler (*Animal Behaviour*, 1980, **28**, 1070–1094). Based on observations of alarm call production and playback experiments in the natural habitat of the monkeys, Seyfarth, Cheney and Marler provided evidence that the alarm calls designated predators as external referents and conveyed sufficient information to listeners to make distinct adaptive responses in the absence of the stimulus. Their interpretation that ‘these calls show semantic properties, potentially based on the formation of internal perceptual concepts’ contrasted with the existing consensus of the time, which saw animal signals as ‘affective’, providing information only about the internal motivational state of the signaller and/or the signaller’s likely behaviour. This study, particularly its semantic approach, was hugely influential in revitalizing the discussion of what animal calls ‘mean’, specifically how they are interpreted in the minds of the animals, and ultimately acted as the impetus for the construction of the ‘functionally referential’ framework in animal communication. Although this semantic approach has been criticized in terms of anthropomorphizing animal communication, understanding the underlying cognitive mechanisms is a crucial component of deconstructing animal communication systems and hence we can greatly profit from such a research trajectory. Applying linguistic concepts to animal vocal communication has opened up an enormous research field regarding the continuity between animal vocalizations and human language, integrating different disciplines including animal behaviour, comparative psychology, neurobiology, linguistics and philosophy.

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The discussion on animal vocalizations in the 1980s concerned affective communication (Smith 1977), and Dawkins & Krebs (1978) argued that communication in animals should not be seen as information transfer, but as the process by which senders manipulate receivers. Two years later, in their seminal paper ‘Vervet monkey alarm calls: semantic communication in a free-ranging primate’ published in *Animal Behaviour* in 1980, Robert Seyfarth, Dorothy Cheney and Peter Marler provided evidence that alarm calls to designated predators, as external referents, conveyed sufficient information to listeners to make distinct adaptive responses. With this paper, Seyfarth and his colleagues opened up an entire research area focusing on animal vocalizations as semantic signals with a defined external referent meaningful to the listening animal. At around the same time, researchers such as Donald Griffin highlighted the importance of investigating what animals ‘think’ and noted that vocalizations

can act as windows into the minds of animals (Griffin 1986). These two complementary research areas contributed substantially to the emergence of the field of cognitive ethology. This investigation of vervet monkey alarm calls marked the beginning of an array of elegantly designed experimental field studies, which have, over the last 30 years, attempted to get at how primates perceive their surrounding social and ecological worlds (summarized in their books *How Monkeys See the World* (Cheney & Seyfarth 1992) and *Baboon Metaphysics* (Cheney & Seyfarth 2008)), leading the research on semantic communication and cognition in animals in their natural habitat. Many colleagues, and in particular their students, have taken similar research paths, extending this approach to other primate species, nonprimate mammals and birds. This influential paper has stimulated research not only in animal behaviour but also in a broad array of allied disciplines, including comparative psychology, neurobiology, linguistics and philosophy, emphasizing the importance of animal vocal communication in studying the evolution of language (for a recent review see the book *The Evolution of Language* by Fitch 2010). However, the interpretation of their results has also generated considerable criticism from different sides, with some arguing that notions of information transfer and signal meaning have biased

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the field of animal communication towards a potentially misleading anthropomorphic approach (Smith 1981; Owings & Morton 1997; Owren & Rendall 1997).

The study on vervet monkeys, *Chlorocebus pygerythrus* (then known as *Cercopithecus aethiops*), focused on the issue of semantics and whether 'any species other than man evolved the ability to use signs to refer to objects in the external world' (Seyfarth et al. 1980, page 1070). Since Darwin (1872), animal vocalizations had been assumed to reflect the expression of the emotional state of animals that had no control of the production of these signals (Smith 1977). Based on Struhsaker's (1967) descriptions of vervet monkeys producing acoustically different alarm calls to different types of predators, with each call type eliciting a different response, Seyfarth et al. (1980) aimed in their study to determine whether these calls serve to designate different classes of external objects.

By confirming the observations on alarm call production of Struhsaker and the use of playbacks of prerecorded calls in the absence of contextual cues, that is, the predator, to isolate the context-independent information provided by signals, Seyfarth et al. provided the first evidence of referential communication in animals. Spending many hours in the field following several different groups of vervet monkeys during their daily foraging excursions in their natural habitat, Seyfarth and his colleagues recorded alarm calls produced during natural predator encounters and described in detail receiver responses. They confirmed that vervet monkeys produce distinct alarm calls for leopards, eagles, snakes and baboons. They quantified the unique responses to these predator types, vervets running up into a tree when a leopard appeared, individuals on the ground running into a bush or tree when an eagle appeared, but when already in the tree moving down from the top to the centre of the tree. When a snake was encountered, they all stood up bipedally. Prerecorded alarm calls for each predator category were played back in the absence of the eliciting predators, and were found to elicit distinct responses that were appropriate for the type of predator that had originally prompted the call. Within these different call types some variation in call structure, such as call length, call interval or amplitude, appeared to be arousal-related. Although, for example, an increase in alarm call length increased responsiveness in some cases, these acoustic properties did not affect the qualitative distinctions among responses to the predator-specific call types.

From both the observational and specifically the experimental playback data, it was suggested that vervet monkey alarm calls have semantic properties, potentially based on the formation of internal perceptual concepts. This explanation contrasted with the existing view of animal vocalizations. Traditionally, animal signals were considered as being 'affective', providing information about the internal motivational state of the signaller and/or the behaviour in which the signaller was likely to engage (Smith 1977, 1981). In addition, rather than using a linguistic approach based on a transfer of information and subsequent representation and trying to identify the underlying cognitive mechanisms of vocal communication, behavioural ecologists had defended a more functional approach. With an assessment/management approach (Owings & Morton 1997) or affect-conditioning model (Owren & Rendall 1997) animal communication was instead regarded as manipulation of the receiver by the signaller (Dawkins & Krebs 1978). Identifying the underlying mechanisms, including the cognitive processes (proximate level), and the functions (ultimate level) on the sender and receiver sides are of course not mutually exclusive, but complement each other in understanding the evolution of animal communication (Seyfarth et al. 2010; for a whole volume on this topic, see the edited book *Animal Communication Theory: Information and Influence* by Stegmann 2013). This discussion has prompted more care in the use of linguistic terms, such as what we understand by

semantics and reference (see Wheeler & Fischer 2012). However, it is now important to generate new hypotheses based on the opposing arguments if the field of animal communication is to move ahead. One particularly promising approach would be to bring together biologists, linguists, bioacousticians and phoneticians to ensure the application of the same methods and agreement on the correct terms when attempting to identify homologous traits between specific animal communication systems and human language.

SEMANTICS, FUNCTIONAL REFERENCE AND REPRESENTATIONS

Although in their paper Seyfarth et al. (1980) did not introduce the concept of 'functional reference' (Marler et al. 1992; Macedonia & Evans 1993), their study on semantics in vervet monkey alarm calls contributed to the work by Marler and his students on other primate species (Pereira & Macedonia 1991) and chickens, *Gallus gallus* (Gyger et al. 1987; Evans et al. 1993), which eventually provided the basis for this highly influential theoretical concept of 'reference' in animal communication. Because the underlying cognitive mechanisms driving the production of signals, such as the alarm calls investigated by Seyfarth and his colleagues, were unclear, Macedonia & Evans (1993) drew a distinction between semantics or linguistic reference in human language, for which mechanisms of both production and comprehension were known, and 'functional reference' in animal calls, for which production mechanisms were unknown but the information acquired by listeners could be studied. Only vocalizations that (1) were correlated with the occurrence of objects or events in the external world of the signaller and (2) induced the receiver to respond adaptively in the absence of direct cues from the eliciting stimulus fulfilled the criteria of being functionally referential (Marler et al. 1992; Macedonia & Evans 1993; Evans 1997).

Evidence for functional reference in vocalizations exists not only for alarm calls, but also for food calls (Karakashian et al. 1988; Evans & Evans 2007; but see the recent review by Clay et al. 2012) and calls produced in some social contexts (Gouzoules et al. 1984; Faragó et al. 2010; also see Townsend & Manser 2013). However, only a few call types in a few species have been described as fulfilling the strict definition of functional reference (see the recent review on mammals: Townsend & Manser 2013; on birds: Gill & Bierema 2013). The evolution of functionally referential alarm calls has been described for species in which different escape responses are necessary to survive (Macedonia & Evans 1993). This explanation has recently been extended, as it does not, for example, explain why Cape ground squirrels, *Xerus inauris*, and the sympatric meerkats, *Suricata suricatta*, have not both evolved either urgency based or functionally referential alarm calls (Manser et al. 2002; Furrer & Manser 2009). In these two similar-sized species that live in the same habitat, are exposed to the same predators and use bolt holes for shelter, the difference is not due to the need for a difference in escape response to predators related to the three-dimensional habitat (Macedonia & Evans 1993). The evolution of predator type-specific alarm calls in meerkats seems more likely to be related to the cohesion of the foraging group and the need for individuals to coordinate their escape, while this is not the case for the ground squirrels which typically forage next to their burrow system. In general, the evolution of functionally referential signals, in comparison to less context-dependent signals, appears to relate to situations in which an immediate response is necessary based on unambiguous signals, without the need to take into account any additional information from the surroundings (Meise et al. 2011; Townsend & Manser 2013).

A central issue concerning the semantic properties of referential signals is whether they have their effects by evoking representations of the eliciting objects or events in the mind of the receiver.

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