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Forum

Contextually variable signals can be functionally referential

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A central challenge in the study of human language is to understand how it evolved from earlier forms of animal communication. One long-debated question is whether animal signalling constitutes an evolutionary precursor of linguistic reference. The view defended by Darwin (1872) was that animal signals are essentially read-outs of internal states and, thus, lack the ability to refer to external events. However, over the past 35 years, a number of theorists have argued that animal signals can functionally refer, in the sense that they can 'hook on to' features of the external world in a nonlinguistic way (e.g. Di Bitetti, 2003; Evans & Evans, 1999; Evans & Marler, 1994; Macedonia & Evans, 1993; Seyfarth, Cheney, & Marler, 1980a, 1980b; Zuberbühler, 2003).

Following Macedonia and Evans (1993), two key assumptions have so far shaped empirical research on functional reference. The first is that, to functionally refer, animal signals must be strongly correlated with what they refer to; that is, they should have high stimulus specificity (Macedonia & Evans, 1993). The second is that functionally referential animal signals should not change their referent depending on the context in which they are produced. Nevertheless, a growing body of research has shown that animal signals typically lack high stimulus specificity and that context generally does affect how receivers respond to signals (e.g. Arnold & Zuberbühler, 2013; Fischer & Hammerschmidt, 2001; Meise, Keller, Cowlishaw, & Fischer, 2011; Price & Fischer, 2013; Rendall, Seyfarth, Cheney, & Owren, 1999; Wheeler, 2010a; Zuberbühler, 2000).

These studies have been interpreted as either indicating that the signals in question are not functionally referential (e.g. Arnold & Zuberbühler, 2013), or, more radically, as demanding a broad rejection of the functional reference framework (e.g. Wheeler & Fischer, 2012). Here, we argue that neither interpretation is warranted: what the emerging empirical evidence requires is a modified definition of functional reference, according to which signals can functionally refer by virtue of contextual cues and in the absence of a strong correlation with their referents.

Here, we compare and contrast this proposal, first defended by Scarantino (2013b), with Wheeler and Fischer's (2012) proposal, according to which receivers attribute 'meaning' to signals, either dependently or independently of context. A key comparative advantage of our model is that it avoids the ambiguities surrounding the notion of meaning and it has empirically verifiable criteria of application.

By integrating contextually variable signalling into the framework of functional reference, our model builds on existing studies on the role of context and opens the door to new experimental

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techniques for the study of functional reference, providing a better vantage point for understanding the evolutionary roots of language.

THE STANDARD DEFINITION OF FUNCTIONAL REFERENCE

Empirical studies of functional reference have so far relied on the following operational definition (Macedonia & Evans, 1993; Marler, Evans, & Hauser, 1992; Scarantino, 2013b): a signal of type X functionally refers to a state of affairs of type Y if (1) Xs are reliably produced by Ys and only/mostly produced by Ys (production criterion) and (2) Xs reliably elicit responses in receivers that are adaptive to Ys in the absence of Ys and other contextual cues (perception criterion).

According to Macedonia and Evans (1993, page 179), 'referential signals should exhibit a degree of stimulus specificity' to what they refer to; that is, 'eliciting stimuli must belong to a common category…although the size of this category…could vary considerably'. For instance, the category may be as broad as 'raptors' or as narrow as 'African crowned eagles'. As Macedonia and Evans (1993, page 179) explain, 'one clear correlate of the "production specificity" criterion is that referential signals should not occur at appreciable rates in inappropriate contexts'. Therefore, to be specific to raptors or specific to African crowned eagles, alarm signals must be produced reliably only/mostly by, respectively, raptors or African crowned eagles. Signals satisfying the production criterion, which applies to the signaller side, are said to have 'production specificity'.

Regarding the perception criterion, Macedonia and Evans (1993, page 180) stated that functionally referential signals 'should be sufficient, in the absence of the eliciting stimulus and of other available cues, to allow receivers to select appropriate responses'. The absence of both stimulus and cues ensures that the signal is solely responsible for the adaptive responses of receivers. While they acknowledge that contextual cues play an 'important role' in the wild, their view is that functional reference is only instantiated when they are 'not essential' for eliciting the adaptive response. Signals satisfying the perception criterion, which applies to the receiver's side, are said to be context independent.

LOOMING THREATS TO FUNCTIONAL REFERENCE AS TRADITIONALLY UNDERSTOOD

Threats to Production Specificity

Predator alarm calls represent the best examples of functionally referential signals in the wild (Townsend & Manser, 2013; Wheeler & Fischer, 2012; Zuberbühler, 2009). Nevertheless, evidence of production specificity for alarm calls is mixed. Consider vervet monkey, *Chlorocebus pygerythrus*, alarm calls, the seminal example of functional reference (Seyfarth et al., 1980a, 1980b; Struhsaker, 1967). Vervets produce three acoustically distinct alarm calls for their three main predator classes (snakes, leopards and eagles), and these calls elicit adaptive escape responses in receivers specific to these different predator classes (Seyfarth et al., 1980a, 1980b). Nevertheless, these alarm calls also occur at appreciable rates in the absence of the relevant classes of predators, contrary to what the production criterion requires (Searcy & Nowicki, 2005).

A review of the literature reveals that this phenomenon occurs across many species, whose alarm calls, particularly those given to terrestrial predators, are regularly produced to nonpredatory stimuli, such as falling trees, nonthreatening animals and social encounters (e.g. putty-nosed monkeys, *Cercopithecus nictitans*: Arnold, Pohlner, & Zuberbühler, 2011; Arnold & Zuberbühler, 2013; brown lemurs, *Eulemur fulvus rufus*, Verreaux's sifaka, *Propithecus verreauxi verreauxi*: Fichtel & Kappeler, 2002; tufted capuchin monkeys, *Cebus apella*: Wheeler, 2010b).

Some species even produce 'false alarm calls' deceptively in order to usurp foraging competitors (e.g. Wheeler, 2009). For example, fork-tailed drongos, *Dicrurus adsimilis*, utter drongo-specific false alarm calls but also mimic false alarm calls of other target species (e.g. meerkats, *Suricata suricatta*, and pied babblers, *Turdoides bicolor*) to scare members of such species away from their food source, which they then steal (Flower, 2011; Flower, Gribble, & Ridley, 2014).

Food-associated calls typically show even less stimulus specificity than alarm signals and are often produced in a variety of nonfeeding contexts (e.g. toque macaque, *Macaca sinica*: Dittus, 1984; Geoffroy's spider monkey, *Ateles geoffroyi*: Chapman & Lefebvre, 1990; rhesus macaques, *Macaca mulatta*: Hauser & Marler, 1993; golden lion tamarins, *Leontopithecus roaslia*: Halloy & Kleiman, 1994; cottontop tamarins, *Saguinus oedipus*: Roush & Snowdon, 2000; bonobos, *Pan paniscus*: Clay, Smith, & Blumstein, 2012; Clay & Zuberbühler, 2009). For example, golden lion tamarins and spider monkeys produce food calls during intergroup encounters and predator mobbing (Chapman & Lefebvre, 1990; Halloy & Kleiman, 1994).

The important point is that such calls can still elicit adaptive responses in receivers, despite low production specificity. As we discuss below, the adaptive responses produced by various classes of signals depend essentially on the disambiguating effects of contextual cues, something currently unexplained by the functional reference framework.

Threats to Context Independence

It is becoming increasingly clear that context plays an essential role in signal perception. Even in their original study, Seyfarth et al. (1980a, page 802) acknowledged that receivers 'behaved as if searching for additional cues, both from the source of the alarm and elsewhere'. Price and Fischer (2013, page 278) recently emphasized that, in the original study, a 'relatively high number of [vervets] did not respond appropriately to alarm calls when they were broadcast in the absence of supporting contextual cues'.

There has been a resurgence of interest in recent years in understanding how contextual cues affect receivers' responses (e.g. Arnold & Zuberbühler, 2013; Fischer & Hammerschmidt, 2001; Meise et al., 2011; Price & Fischer, 2013; Rendall et al., 1999; Wheeler, 2010a,b; Zuberbühler, 2000). Stressing the importance of context in signal perception is certainly not new, and was widely advocated before the focus shifted to functional reference (i.e. Leger, 1993; Smith, 1977). Our point is that evidence of the role of contextual cueing is not evidence against functional reference.

In one of the earliest experimental studies on contextual cueing, Rendall et al. (1999) showed that receiver responses to baboon 'move' grunts and 'infant' grunts were shaped in part by the context in which the two types of grunts were produced and by rank differences between signaller and receiver. However, since the acoustic properties of grunts permitted accurate inferences about external events (in the move context), the grunts were considered to be functionally referential.

Zuberbühler (2000) emphasized the integration of signal and context in a study of responses of Diana monkeys, *Cercopithecus diana*, to guinea fowl alarm calls, which are given to leopards and sometimes to human poachers. Upon hearing guinea fowl terrestrial alarm calls, Diana monkeys respond as if a leopard were present; however, if they are primed to the presence of humans, they respond as if humans were present. This suggests that receiver responses are driven by contextual cues relating to the cause of the call rather than by the call alone (Zuberbühler, 2000).