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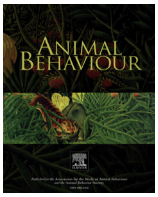

Forum

Contextually variable signals can be functionally referential

Andrea Scarantino [a], [*], Zanna Clay [b], [c], [1]

[a] Department of Philosophy, Neuroscience Institute, Georgia State University, Atlanta, GA, U.S.A.
[b] Living Links Center, Emory University, Yerkes Primate National Research Center, Lawrenceville, GA, U.S.A.
[c] Institute of Biology, Department of Comparative Cognition, University of Neuchâtel, Switzerland

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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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[*] Correspondence: A. Scarantino, Department of Philosophy, Neuroscience Institute, Georgia State University, Georgia State University, 34 Peachtree Street NW, Suite 1100, Atlanta, GA 30303, U.S.A.
E-mail address: ascarantino@gsu.edu (A. Scarantino).
[1] *E-mail address*: zannaclay@gmail.com (Z. Clay).

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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).

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Studies of putty-nosed monkey alarm calls (Arnold, Pohlner, & Zuberbühler, 2008, 2011; Arnold & Zuberbühler, 2006a, 2006b, 2013) further highlight the role of context in call perception. Putty-nosed monkeys typically produce a 'hack' series in response to eagles and a 'pyow' series in response to leopards, although both series are also produced in nonpredatory circumstances. Arnold and Zuberbühler (2013) demonstrated that subjects spent more time looking at the sky when hacks were played alone and more time looking at the source of the call when pyows were played alone than when either call series was preceded by contextual cues that could disambiguate the likely cause of the call.

This study shows exactly the sort of work on the relevance of context that we want to encourage. However, while the authors suggest that listeners integrate contextual information in order to distinguish among possible causes of calls, we argue that such a case demonstrates how calls change their referent depending on contextual cues. Determining how context contributes to the derivation of meaning is integral to understanding what signals functionally refer to.

SHOULD WE REPLACE FUNCTIONAL REFERENCE WITH MEANING?

A good way to set the stage for our positive proposal is to consider Wheeler and Fischer's (2012) (henceforth, WF) recent critique of functional reference (see also Rendall, Owren, & Ryan, 2009; Townsend & Manser, 2013). Although there is considerable overlap between our positions, there also are terminological and substantive differences concerning how to move forward.

The Meaning-based Model

WF proposed replacing the idea that animal signals functionally refer with the idea that receivers ascribe meaning to signals. They recommended dropping the term 'functional reference' altogether from the animal communication literature, and relabelling 'functionally referential signals' as 'context-specific signals'.

WF proposed that, in some cases, receivers attribute meaning to signals without relying on contextual cues, while in other cases, contextual cues are crucial for meaning attribution. Once meaning has been attributed, receivers make decisions about what to do, which are also influenced by contextual cues.

We agree with many aspects of this proposal. First, the authors rightly emphasize that the same general semantic phenomenon of meaning attribution can be instantiated by context-specific signals and by non-context-specific signals. Second, we support their assertion that the heavy influence of the functional reference framework has resulted in the pragmatic dimension of communication being neglected. Third, we agree that, from the receiver's perspective, there may be no 'inherent difference' between external referents like the presence of an eagle and internal features such as a signaller's 'body size, sex, dominance status, or subsequent behavior' (page 200).

Our differences concern the proposal of replacing functional reference with meaning attribution. We find the notion of meaning, as it is commonly used in the animal communication literature, to be ambiguous, and we argue that WF have not provided a clear and explicit empirical test for meaning attribution.

Meaning as Correlation versus Meaning as Reference

WF stated that the sense of meaning they relied on was 'essentially equivalent to what linguist Paul Grice termed "natural meaning", which contrasts specifically with the symbolic meaning characteristic of human words' (page 200). 'Natural meaning' is the sort of meaning that red spots carry about measles and that smoke carries about fire. Grice (1957) contrasted it with 'non-natural meaning', which is the sort of meaning that words like 'fire' and other symbolic representations have by virtue of arbitrary conventions.

Although we agree that animal signals have meaning in a different sense than words and other conventional symbols, Gricean natural meaning is inadequate for explicating the sense in which animal signals have meaning. This is because Grice (1957) asserted that, when it comes to natural meaning, 'x means that p entail[s] p', whereas with respect to non-natural meaning, 'x means that p…do[es] not entail p' (pp. 377–378). On this view, smoke can naturally mean that a fire is present only if a fire is present, whereas the words 'there is a fire' can mean that a fire is present even when it is not.

By the same token, a snake alarm call broadcast in a playback experiment in the absence of a snake cannot naturally mean (sensu Grice) that a snake is present, because by experimental design the snake is not present. But this is clearly not what we want from a notion of natural meaning: snake alarm calls should be able to mean that a snake is present whether it is or not.

The way WF unpack the notion of natural meaning suggests that, unlike Grice, they do not assume that natural meaning entails truth. They state that a signal naturally means Y in the sense that it 'indicate(s) the likelihood of the occurrence of [Y] because of a natural spatial or temporal association with [Y]' (page 200). In this case, the fact that Y does not occur does not interfere with the indication of the likelihood of its occurrence.

We label this notion of natural meaning 'meaning as correlation' (meaning_C), to emphasize that the existence of a meaning_C relation between signal X and state of affairs Y is essentially tied to the existence of a correlation between them. To say that a signal X means_C a state of affairs Y is to say that $p(Y \text{ given } X) \neq p(Y)$, namely that there exists a positive correlation ($p(Y \text{ given } X) > p(Y)$) or a negative correlation ($p(Y \text{ given } X) < p(Y)$) between X and Y (see Scarantino, 2013a, b, for discussion).

A correlation between signal X and state of affairs Y affords receivers with an opportunity to have their uncertainty about Y reduced by the reception of X. To emphasize that correlations offer opportunities for uncertainty reduction, Fischer described signals as being 'potentially informative' (Fischer, 2011, 2013; see also Wheeler & Fischer, 2012). We prefer to speak of a signal X as carrying 'correlational information' about Y whenever $p(Y \text{ given } X) \neq p(Y)$, because we identify carrying correlational information with carrying an opportunity to learn about the likelihood of Y from signal X.

This notion of meaning_C, however, does not capture the sense in which, say, a snake alarm call means that a snake is present. This is because there are innumerable states of affairs about which an animal signal carries correlational information. For example, snake alarm calls produced by vervets correlate not only with the presence of snakes but also with the fear of signallers, with the escape movement of other vervets and so on. If so, a snake alarm call means_C snakes, but it also means_C several things other than snakes, many of which, incidentally, will be more strongly correlated with snake calls than snakes themselves (e.g. the fear of signallers).

To capture the sense in which snake alarm calls mean that a snake is present rather than something else, we need to transition from this correlational notion of natural meaning to what we call 'meaning as reference' (meaning_R). This type of meaning is instantiated when a signal X has an 'effect' on a signal receiver that indicates that the receiver takes X to stand for Y (Morris, 1946; Peirce, 1935). When this condition is satisfied, X is a sign of, or represents, Y. To determine the meaning as reference of a snake alarm signal, it is not enough to know what the signal correlates with: we must also know how the receiver is affected by the signal.

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It is frequently a source of confusion in the animal communication literature that several researchers use the term ‘information’ to designate both meaning as correlation and meaning as reference (e.g. Carazo & Font, 2010; Seyfarth et al., 2010; see Scarantino & Piccinini, 2010, for further discussion). To keep things clear, we will say that when a recipient takes signal X to stand for state of affairs Y, namely when X means$_C$ Y, the recipient acquires ‘referential information’ about Y. ‘Correlational information’ is instead the sort of information X carries about Y just by virtue of the fact that X and Y are correlated, whether or not any effect is produced in a signal receiver.

We will take a case study to illustrate the contrast between WF's correlational notion of meaning and the notion of meaning as reference. Palombit, Seyfarth, and Cheney (1997) showed that the responses of male baboons to the screams of female baboons depend on whether the males and females have an established affiliative relationship and on the presence of other contextual cues, most importantly, the threat calls of a potentially infanticidal male.

In a playback study, male affiliates paid more attention and were more likely than unaffiliated control males to approach screams of female affiliates, especially when their screams were paired with threat calls of a potentially infanticidal male (Palombit et al., 1997). Intervention behaviour is adaptive in this case, because male affiliates have a significant probability of paternity, and so coming to the aid of screaming females may potentially help to protect their own putative offspring.

How are we to interpret how affiliated and unaffiliated males ascribe meaning to female screams paired with contextual cues? WF proposed that both kinds of males ascribe the same meaning to the signal, as they both ‘infer the likelihood of an infanticidal event’, but they make different decisions about it. The unaffiliated males decide to ignore such event, whereas the affiliate males decide to intervene to protect their likely offspring.

We consider this interpretation unwarranted by the empirical data. If we interpret meaning in the correlational sense, female screams in their context of production mean$_C$ infanticide in the sense that they correlate with it. But this notion of meaning fails to distinguish among correlates, and would not allow us to conclude that the female screams mean infanticide any more than they mean, say, that the female is afraid. When we speak of ‘ascription of a specific meaning’ by a recipient, it is meaning as reference that matters.

Responsive males take female screams to stand for an imminent infanticide, as revealed by their protective responses. Two options are possible for the unresponsive males; either they also take the signal to stand for infanticide, but do not act upon it, or they do not take the signal to stand for infanticide. Based on the data available from the study, we cannot accurately determine which of the two options applies. The fact that responsive males take the signal to stand for infanticide is not a reason to lean one way or the other with respect to unresponsive males, contrary to what WF appear to presuppose.

What we need is specific evidence that the unresponsive males also take the call to stand for infanticide despite their lack of overt responses indicating that they do. But it is far from clear what such evidence could amount to. So, although we acknowledge that female screams are potentially informative about an infanticide with respect to every recipient, we can, at best, suspend judgment on whether every recipient gains this referential information from the signal.

To avoid situations in which the empirical data are insufficient for deciding whether meaning is ascribed, we will not follow WF in drawing a distinction between the receiver's attribution of meaning and how the receiver responds to the signal. An inevitable consequence of tying meaning attribution to strict response-based criteria is that we run the risk of underestimating the amount of meaning attribution that may be occurring. We are aware of this danger, but consider our approach to be less misleading than allowing for meaning ascription in the absence of hard evidence about how meaning affects responses. On the account we offer in the next section, recipient's responses are the only evidence that counts towards establishing that meaning as reference has been ascribed.

A NEW DEFINITION OF FUNCTIONAL REFERENCE

The Information Criterion and the Response Criterion

We propose the following new operational definition of functional reference (Scarantino, 2013b): a signal of type X in context C functionally refers to, or means$_R$, a state of affairs of type Y if (1) Xs in context C correlate with Ys (i.e. Xs carry correlation information about/mean$_C$ Ys (information criterion)), and (2) presentations of Xs in context C and in the absence of Ys reliably elicit contextually adaptive responses in receivers specific to Ys (response criterion).

This definition clarifies that the ‘unit of functional reference’ is a combination of what we call the ‘signal-vehicle’ X and of the context C, understood as a set of ‘vehicle- cues’, namely features of the context of production that contribute to determining the referent Y. The standard definition of functional reference is a special case of this definition, instantiated when signals have a referent independently of contextual cues.

In rare cases (e.g. in aerial predator calls and food-specific calls of select number of species; Casar, Zuberbühler, Young, & Byrne, 2013; Kirchhof & Hammerschmidt, 2006; Manser, Bell, & Fletcher, 2001; Slocombe & Zuberbühler, 2005; Wheeler, 2010b; Zuberbühler, Noë, & Seyfarth, 1997), there is a ‘signal-vehicle’ but no ‘vehicle-cues’. A much more common form of functional reference is instantiated by a combination of ‘signal-vehicle + vehicle-cues’. This is what the traditional definition misses out on entirely, gravely underestimating how widespread functional reference is in the natural world.

We emphasize that the state of affairs Y being referred to may both be external (e.g. the presence of a predator) and internal (e.g. the identity of the caller). What matters is not whether the referent is external or internal, but whether receivers respond adaptively to the signal in its context of production as if they directly detected the referent in the absence of the signal.

Let us now consider the two new criteria. The information criterion demands that the signal carries some correlational information about the referent. This requirement replaces the production criterion, whose core flaw was ignoring that there often are different selective pressures acting on the two possible mistakes made by signal receivers (Godfrey-Smith, 1991): (1) false positives: taking Xs to stand for Ys in the absence of Ys and (2) false negatives: not taking Xs to stand for Ys in the presence of Ys. Receivers with an adaptive interest in avoiding false negatives more than false positives have an incentive in taking Xs to stand for Ys even if Xs and Ys are weakly correlated.

Consider vervet alarm calls. Whereas responding to an eagle alarm call with behaviours adaptive to eagles when an eagle is absent involves a minor energy cost (false positives are cheap), failing to respond appropriately to an eagle alarm call when an eagle is present is potentially deadly (false negatives are expensive). Thus, alarm call systems evolve to produce signals that occur at appreciable rates in the absence of their referents, because this minimizes false negatives (but see Beauchamp & Ruxton, 2007; Cheney & Seyfarth, 1988; Hare & Atkins, 2001; Wheeler & Hammerschmidt, 2013, for an analysis of adaptive pressures on receivers to discount unreliable signals).

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In other circumstances, the payoff structure will be different, and functionally referential signals will be more strongly correlated with their referents (e.g. Fichtel & Kappeler, 2002; Kirchhof & Hammerschmidt, 2006; Kiriazis and Slobodchikoff, 2006; Manser et al., 2001). Future research should address the evolutionary forces that lead referential signalling systems to converge on, respectively, high or low production specificity (see Godfrey-Smith, 2013). The point is that the amount of correlational information carried by a signal about its referent can vary significantly in different signalling systems without threatening the referential status of the signal, as long as enough correlational information is carried about the referent to make it evolutionarily advantageous for the receiver to respond as if the referent were present.

Let us now turn to the response criterion, which states that, out of the innumerable correlates of a signal, the referent is the one to which receivers' responses are contextually adaptive. Testing for the response criterion requires stimulus-absent contextual experiments in which signal-vehicle and vehicle-cues are jointly presented to receivers in the absence of the putative referent. For acoustic modalities, this will involve playback studies with a contextual dimension (see Arnold & Zuberbühler, 2013; Price & Fischer, 2013). Stimulus-absent experiments will have to take other forms for nonacoustic modalities, such as visual, olfactory and tactile modalities. If receivers reliably produce contextually adaptive responses to Y when the putative referent is absent but contextual cues are present, the signal X in context C satisfies the response criterion. In some cases (i.e. those traditionally considered functionally referential), the context C will have no referential impact, and so the presentation of contextual cues is unnecessary.

Contextually Adaptive Receiver Responses

A key feature of the response criterion is that it demands that responses are ‘contextually adaptive’, namely adaptive to the referent in the specific spatiotemporal context in which the receiver is placed. We will call ‘response-cues’ those contextual cues that affect which responses are adaptive to a given referent in order to distinguish them from contextual cues that contribute to establishing the referent in conjunction with the signal (‘vehicle-cues’).

Our distinction between vehicle-cues and response-cues is inspired by a similar distinction drawn by Wheeler and Fischer (2012, page 202) between ‘contextual cues for signal receivers to attribute meaning to the signal’ and contextual cues ‘to make a decision regarding how to respond to it’. The key difference is that, in our view, the only evidence that meaning has been attributed to a signal are the responses that the receivers ‘decide’ to produce to it, so referential meaning cannot be attributed prior to observing the outcome of such decisions. What underlies our distinction between vehicle-cues and response-cues is the fact that for each signal there are multiple adaptive responses that receivers may decide to produce (e.g. climbing on a tree if on the ground, climbing higher on the tree if already on it) that count as evidence that the signal has the ‘same’ referent (e.g. a leopard is present).

Whereas vehicle-cues may or may not be involved in settling what the signal functionally refers to, our view is that receivers of functionally referential signals ‘always’ need to rely on response-cues in order to respond adaptively to a signal. Evidence of the pervasive role of response-cues appeared to have concerned Seyfarth and Cheney in the period leading up to their seminal paper on vervet alarm calls (see Radick, 2007, for a historical reconstruction). Their data showed that vervets on the ground select different adaptive responses to alarm calls than vervets already on trees, which is exactly what should be expected if the same referent requires different adaptive responses in different circumstances.

The conclusion that vervet alarm calls are functionally referential was preserved by breaking down receivers' responses in two components: responses that are independent of response-cues and shared across contexts, and responses that depend on response-cues. The main example applies to eagle calls: although receivers respond to such calls differently contingently on response-cues, one response feature common across all contexts is ‘looking up’. Since looking up may already be interpreted as evidence that the receiver takes eagle calls to stand for eagles, Seyfarth et al. (1980b, page 1092) concluded that ‘[i]n our experiments, context was not a systematic determinant of the responses of vervets to alarm calls’.

In light of our new definition, the segregation of responses into context-independent and context-dependent components is unnecessary, because all responses need to be adaptive contextually, given the available response-cues. This is good news, because the partitioning solution proposed by Seyfarth et al. (1980b) does not work for all functionally referential animal signals. For example, receivers of leopard alarm calls display different adaptive responses in different contexts: they are more likely to run up a tree or stand bipedally when on the ground, but they are more likely to run higher in a tree or look up and down when already in a tree.

What is robustly shared across contexts is just looking towards the speaker, which alone is insufficient for concluding that receivers have taken the call to stand for anything in particular. We acknowledge that this approach may potentially underestimate cases of functional reference in which orienting is the adaptive response to a suitably broad description of the referent, but we once again suggest that there is greater risk in overestimating the ascription of meaning than in underestimating it.

THE LIMITS OF CONTEXTUAL FUNCTIONAL REFERENCE

The definition of functional reference we have offered restores the referential status of signals traditionally considered to be functionally referential, despite the fact that, strictly speaking, they do not satisfy either the production criterion or the perception criterion. Moreover, it allows for a significant expansion of the domain of signals that are functionally referential in their context of production, including signals that are functionally referential only by courtesy of vehicle-cues.

Future research must establish the limits of the expanded domain of functionally referential signals ‘in a context’. We predict that the following vehicle-cues will emerge as especially important for reference-fixing purposes.

(1) Identity vehicle-cues affect what the signal in its context of production refers to depending on who produced the signal. Identity cues that are likely to matter referentially include caller status, kinship, age, tolerance, reliability, social affiliation and the social history between signaller and receiver. For example, an infant call produced by a dominant female baboon may be taken to stand for willingness to reconcile after a fight with a subordinate, while the same call may be taken to stand for a friendly interaction between the dominant female and an infant in other circumstances (Seyfarth & Cheney, 2003; see also da Cunha & Byrne, 2013).

(2) Behavioural vehicle-cues affect what the signal in its context of production refers to depending on the activity of the signaller during signal production. Gestures, bodily orientation and gaze are three common cues impacting what an alarm call refers to (Bar-On & Green, 2010). For example, a call may stand for, say, ‘hawk in a particular location’, because the acoustic properties of the call are combined with directed gaze.

(3) Environmental vehicle-cues affect what the signal in its context of production refers to depending on what else is occurring in the environment immediately before or after the signal is produced. For instance, putty nosed monkey hacks are taken to stand

for eagles, as revealed by the fact that their receivers look skyward, only if they are not preceded by the sound of a falling tree (Arnold & Zuberbühler, 2013; see also Price & Fischer, 2013).

(4) Sequence placement vehicle-cues affect what the signal in its context of production refers to depending on where the signal is placed within a sequence of other signals. Evidence from a range of species suggests that variation in the way calls are combined into sequences can be meaningful to receivers (e.g. Arnold & Zuberbühler, 2006a, b; Casar et al., 2013; Clay & Zuberbühler, 2011; Ouattara, Lemasson, & Zuberbühler, 2009; Schel, Candiotti, & Zuberbühler, 2010; Stephan & Zuberbühler, 2008). A recent literature review suggests that the meaning of some call sequences may result from the meaning of the components, instantiating a form of rudimentary 'lexical syntax' (Collier, Bickel, van Schaik, Manser, & Townsend, 2014). In Campbells' monkeys, *Cercopithecus campbelli*, for instance, the addition of a vocal suffix to male alarm calls changes the original referent from a specific predator (e.g. eagle) to a more general disturbance of a similar kind (e.g. disturbance in the canopy), indicating that the meaning of the whole is at least in part a function of the meaning of the components (Ouattara et al., 2009; but see Hurford, 2012; Schlenker et al., 2014). The analogy with lexical syntax is less clear for the pyow—hack call sequences of putty-nosed monkeys, which have a different meaning than pyow sequences or hack sequences taken in isolation, but are arguably interpreted by receivers as a merged unit whose meaning does not depend on the meaning of the component parts, as is the case for idiomatic expressions (Arnold & Zuberbühler, 2012). Alternatively, the component pyows and hacks of the pyow—hack call sequence could be interpreted as having no meaning in isolation, which would make the putty-nosed monkey call sequence an example of 'phonological syntax', instantiated when meaningless sounds combine into larger and potentially meaningful sequences (Collier et al., 2014). As these brief remarks suggest, the role of sequence placement vehicle-cues is still poorly understood in nonhuman animals, so we flag this as an especially promising area for future research on contextual functional reference.

Although our definition will expand the scope of functional reference, we emphasize that many signals are not going to qualify as functionally referential even when conjoined with their context of production. First, we predict that, once tested through stimulus-absent contextual experiments, most signals will elicit generic orienting responses that never transition to responses contextually adaptive to a specific referent. As argued, we do not consider generic orienting responses such as looking towards the speaker or scanning the environment to suffice for the ascription of functional reference, because they do not indicate that the receiver has taken the signal to stand for a specific referent.

On the other hand, a signal that initially only produces an orienting response can become functionally referential as soon as vehicle-cues are detected and adaptive responses to a specific referent are produced. It will consequently be important to set the temporal intervals in which receiver behaviours are observed appropriately: a signal may become functionally referential in combination with contextual cues picked up a few seconds after (or before) it is produced.

At the same time, the signal should not just function as an incentive to look for, or as a redundant addition to, contextual cues that refer on their own: signals and cues must both be essential components of the unit of reference for the contextual version of functional reference to be instantiated. An important task will be to develop informed hypotheses about the relevant timescale of when an adaptive response should be expected to occur after the initial orienting responses for contextual functional reference to be reasonably inferred.

Second, some signals will produce adaptive responses through sensory exploitation rather than functional reference, a possibility brought centre stage by Ryan, Fox, Wilcynski, and Rand (1990), Ryan (1997), Owren and Rendall (2001) and others. For example, in both birds (Cheng & Peng, 1997) and frogs (Wilczynski & Chu, 2001), the auditory system is linked to the neuroendocrine processes and, as a result, females that hear courtship calls automatically enter a state of sexual receptivity. In this case, the acoustic properties of the signal itself have direct and proprietary behavioural effects on the receiver that are not mediated by what the receiver takes the signal to stand for.

FUNCTIONAL REFERENCE AND THE EVOLUTION OF LANGUAGE

The new framework we have offered has several implications for the study of the evolutionary roots of language. First, by expanding the presence of functional reference in animal signalling, the new definition bolsters the case that the ability to refer to entities in the environment (or to internal states) does not presuppose language.

Second, the new definition provides an opportunity for studying the cognitive processes underlying the integration of context and signals in receiver ascription of meaning, which, in agreement with Wheeler and Fischer (2012), we expect to be more complex than those involved in traditional functional reference, and potentially closer to the mechanisms of linguistic comprehension.

Third, by bringing context into the framework of functional reference, the new theory complements empirical advances already being made in the study of pragmatics (e.g. Fitch, 2010; Origgi & Sperber, 2000; Scott-Phillips, 2010; Tomasello, 2003), a branch of linguistics that examines how context contributes to the meaning of linguistic utterances. The key difference here is that, under the new approach, pragmatics and functional reference are complementary rather than alternative to one another.

Fourth, the new approach promotes greater compatibility in the gestural versus vocal approaches to the evolution of language. Because of their frequent usage across multiple contexts, most great ape gestures have been assumed to depend on contextual cues to disambiguate meaning and so would be considered to fall outside the purview of the functional reference framework (but see Genty & Zuberbühler, 2014; Hobaiter & Byrne, 2014; Pika & Mitani, 2006; Tanner & Byrne, 1996). Within the new framework, such gestures have the potential to qualify as functionally referential provided that they correlate adequately with their referents in the given context of production and elicit specific adaptive responses when produced jointly with the relevant vehicle-cues.

Moreover, this new approach is compatible with recent research on great ape gestures showing that, contrary to previous assumptions, certain great ape gestures have specific meanings independent of context, whereas other gestures have multiple meanings that only contextual cues can disambiguate (Hobaiter & Byrne, 2014; see also Genty & Zuberbühler, 2014; Pika & Mitani, 2006).

Fifth, the integration of contextual cues with signals may offer an evolutionary precursor to what Hockett (1960) called 'duality of patterning', one of the basic 'design-features' of language. Duality of patterning consists of patterning at the level of meaningful wholes (governed by the rules of lexical syntax) and patterning at the level of meaningless parts (governed by the rules of phonological syntax), which allows meaningful wholes (e.g. morphemes and words) to be built out of meaningless parts (e.g. phonemes such as /r/, /e/).

In context-dependent forms of functional reference, meaningful wholes can be broken down into component parts (signal-vehicle and vehicle-cues), and there is potential for both lexical syntax (instantiated when the meaning of the whole depends on the meaning of the parts) and phonological syntax (instantiated when the meaning of the whole is put together by combining meaningless parts). It remains to be seen to what extent this potential for proto-syntax is instantiated by actual animal communication systems.

CONCLUSION

The traditional definition of functional reference requires that signals and referents are strongly correlated and that contextual cues play no role in determining reference. We have rejected both assumptions, and formulated a new diagnostic test for functional reference that allows signals to functionally refer by virtue of contextual cues and in the absence of a strong correlation with their referents.

Wheeler and Fischer (2012) recently emphasized the importance of context in shaping how receivers respond to signals, but they also recommended 'dropping the term "functionally referential signals" from the animal communication literature' (page 204). We have examined their alternative meaning-based proposal, and concluded that a comparative advantage of the functional reference framework is that it avoids the ambiguities surrounding the notion of meaning and it has empirically verifiable criteria of application that constitutively tie what signals refer to with how receivers respond to them.

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