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Chimpanzee food calls are directed at specific individuals

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If primates were capable of vocalizing to inform a receiver about an external entity, it would represent an important element of continuity with human language. We tested experimentally whether chimpanzee rough grunts, which function to refer to food, are produced selectively, indicating voluntary control, and whether they are directed at specific individuals. These are prerequisites for a system capable of actively informing others about external events. We conducted a field playback experiment in which we presented silently feeding male chimpanzees, *Pan troglodytes*, with arrival pant hoots of a familiar group member. We found that subjects were significantly more likely to respond with food calls to the simulated arrival of an individual with whom the caller had a high rather than low level of friendship and where there was a large rather than small positive dominance rank difference between the individuals (i.e. caller was lower ranking). We concluded that chimpanzee food calls are not simply reflexive responses to food, but can be selectively directed at socially important individuals. Our findings are thus inconsistent with traditional views of primate vocalizations as inflexibly and indiscriminately produced. Instead, our results indicate that great apes can produce semantically meaningful calls in a highly selective, recipient-directed manner. Further research is needed to test whether chimpanzees use this flexible system to inform ignorant individuals about food, but the prerequisites to support this type of communication seem to be present.

One powerful way to try to understand the evolution of human language is by searching for homologous traits or ‘precursors’ to our linguistic abilities in closely related species (Hauser et al. 2002). While dyadic communication between a signaller and receiver is common in the animal kingdom (Hurford 2007), triadic communication that involves a signaller, receiver and an external referent is relatively rare in animal communication systems, yet abundant in human language. Historically, much attention has been paid to context-specific primate vocalizations that appear to refer to external referents, as they have traditionally been regarded as providing evidence for continuity between primate vocal signals and human language (reviewed in Wheeler & Fischer 2012). Although initially primate predator-specific alarm calls (e.g. Seyfarth et al. 1980) were interpreted as referential in a directly analogous way to human words, uncertainty over the nature of the cognitive mechanisms underlying the production and perception of these calls led to them being termed ‘functionally referential’ (Marler et al. 1992; Macedonia & Evans 1993) or ‘indexical’ (Deacon 1997) calls. For a call to be termed functionally referential it has to be produced reliably in response to a specific external event (production criterion) and receivers must react to the call alone in a similar manner to the external event itself (perception criterion; Marler et al. 1992; Macedonia & Evans 1993). However, no assumptions are made about the underlying cognitive processes when applying these criteria (Macedonia & Evans 1993). It is therefore possible that signallers may not be calling deliberately to manipulate the attention of others (Hurford 2007) or with the intent to inform others about an external entity (Wheeler & Fischer 2012). Instead, they could be reflexively producing an innate response to an external event (e.g. leopard, *Panthera pardus*) and other individuals who hear these calls may simply learn through experience that the call is an effective ‘index’ or predictor for the presence of a leopard and respond accordingly. Thus, receivers might extract information from a call given to an external entity, without the signaller ever having intended to provide this information (Cheney & Seyfarth 2005). Although fundamental, this

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problem has not attracted much empirical attention and because of the lack of data, some researchers have proposed that functionally referential calls are irrelevant for understanding the evolution of human referential abilities (Owren & Rendall 2001; Rendall et al. 2009; Wheeler & Fischer 2012).

To produce a call with the intent to inform a receiver about an external event, at least three different behavioural or cognitive elements are required: (1) production of a functionally referential call (context specific and indexical for receivers); (2) voluntary control over call initiation; and (3) direction of calls at specific receivers, together with an ability to understand and manipulate the mental states of these receivers. There is strong evidence for the first necessary element: functionally referential alarm calls are well documented in a number of species (e.g. Seyfarth et al. 1980; Manser 2001; Manser et al. 2001; Zuberbühler 2003; Templeton et al. 2005). There is also growing evidence that food calls, which are widespread in the animal kingdom (Clay et al. 2012), can function to refer to the presence or quality of a food source, for example in domestic chickens, *Gallus gallus* (Evans & Evans 1999), tufted capuchin monkeys, *Cebus apella nigritus* (Di Bitetti 2003), rhesus monkeys, *Macaca mulatta* (Hauser et al. 1993; Hauser 1998), bonobos, *Pan paniscus* (Clay & Zuberbühler 2009, 2011) and chimpanzees, *Pan troglodytes* (Slocombe & Zuberbühler 2005, 2006).

Evidence for the second necessary element, voluntary call production, is more controversial. While it is now widely accepted that primate vocal repertoires are genetically constrained and callers generally lack the flexibility to invent new vocalizations that engage the larynx, there is more debate over the degree of voluntary control primates have over the initiation of vocalizations. Early brain research indicated that production of species-typical vocalizations in squirrel monkeys, *Saimiri sciureus*, was driven at a neurological level by the limbic system and other subcortical structures, with no direct connections between cortical areas and the laryngeal motor neurons (Jürgens 1979). This supported traditional views of primate vocal production being a product of emotional rather than cognitive processes (Smith 1977), and primate vocal production is still commonly characterized as inflexible, reflexive and automatic (Arbib et al. 2008; Tomasello 2008; Sterelny 2012). There is a growing body of evidence, however, that challenges these views. First, more recent brain research has indicated there is cortical involvement in primate vocal production, with homologues to Broca's area in humans being implicated in the generation of vocalizations in both Japanese macaques, *Macaca fuscata*, and chimpanzees (Gemba et al. 1995; Taglialatela et al. 2011). Second, although there have been a few failures, both monkeys and apes have been successfully trained through operant conditioning techniques to produce species-typical vocalizations in response to arbitrary stimuli (reviewed by Pierce 1985). Third, behavioural studies have shown that primate vocal production is mediated by the social environment and initiation of calls is more likely in the presence of an audience or a certain type of audience (e.g. Cheney & Seyfarth 1985; Wilson et al. 2001; Gros-Louis 2004). Similar results have been obtained in a number of different nonprimate species (e.g. Marler et al. 1986; Townsend et al. 2012). Hurford (2007) highlighted, however, that care must be taken when interpreting these audience effects, as social context could be part of a complex stimulus to which an automatic, innate calling mechanism responds. Hurford (2007, page 232) argued that only if 'circumstances under which calls are given are too implausibly complex to be hardwired into the genes' should we infer vocalizations are under nonautomatic control.

Whether primates possess the third set of elements required for informing recipients about external entities (directing their functionally referential calls to specific individuals while taking into account their mental states) is unclear. For example, in early research on macaques, monkeys failed to inform ignorant offspring of the presence of either a danger or a food source (Cheney & Seyfarth 1990), suggesting a lack of 'theory of mind' (Cheney & Seyfarth 2005). More recently, there is evidence showing that chimpanzees understand knowledge/ignorance states of others (Hare et al. 2001; Kaminski et al. 2008), but the extent to which these skills influence vocal production is still unclear. In one recent field study, wild chimpanzees were reported to produce 'alert hoos' in response to a model snake at different rates depending on the presumed knowledge level of receivers (Crockford et al. 2012). However, the signaller's own prior knowledge of the snake and behavioural cues from recipients approaching the snake may also have accounted for the signaller's behaviour, rather than knowledge attribution. Thus, currently it seems premature to reach a firm conclusion as to whether chimpanzee calling behaviour is mediated by an understanding of receiver mental states, but further research may be able to provide this.

The evidence that primate calls can be directed at specific individuals is somewhat clearer. For example, there is ample evidence of primates directing calls to specific individuals during dyadic face-to-face interactions, such as 'greeting' (Laporte & Zuberbühler 2010) or when expressing affiliative or hostile motivation (Cheney et al. 1995; Bergman et al. 2003). Furthermore, receivers are adept at recognizing to whom such calls are directed (Engh et al. 2006). In captivity, chimpanzees also direct novel 'attention getting' raspberry and extended grunt sounds at human experimenters to beg for food (Leavens et al. 2004; Hopkins et al. 2007). In contrast, there is less convincing evidence that calls that function to reference external events, such as species-typical food calls and alarm calls, are directed at specific receivers. In line with this, Tomasello (2008, page 18) argued that such context-specific calls are best characterized as 'individualistic expressions of emotions, not recipient-directed acts'. This characterization is, however, challenged by research identifying correlations between functionally referential call rate and the presence of kin (Cheney & Seyfarth 1985; Pollick et al. 2005), potential mates (Marler et al. 1986), dominant individuals (Gros-Louis 2004) or important social partners (Slocombe et al. 2010). However, these calls are also sometimes produced in the absence of any audience (Marler et al. 1986; Hopkins et al. 2007; Fedurek & Slocombe 2013), indicating the need for more empirical research to examine the extent to which functionally referential calls are directed at individual receivers.

In summary, although there is currently no convincing evidence that primates produce calls to inform ignorant individuals about external events, there is evidence that they may have some of the necessary elements for this behaviour: primates produce functionally referential alarm and food calls, they seem to have a degree of volitional control over call initiation and they may be able to direct these calls at specific individuals. Evidence for these elements currently comes from a variety of species and contexts. However, if these are to act as prerequisites for intentional triadic communication, they need to occur within a single calling system. In this study we explored the degree of control chimpanzees have over the production of functionally referential calls and the extent to which they are recipient-directed acts, by systematically testing whether individuals selectively produce and direct their functionally referential food calls at specific recipients.

Although several context-specific chimpanzee vocalizations have been identified (e.g. Marler & Tenaza 1977; Crockford & Boesch 2003), food calls are the only vocal signal in the chimpanzee repertoire that has so far met both the production and perception criteria for functioning as a referential signal (Slocombe & Zuberbühler 2005). The literature has consistently identified chimpanzee food calls, often termed 'rough grunts' (Marler & Tenaza 1977), as being specific to the feeding context (Marler & Tenaza 1977; Goodall 1986; Hauser & Wrangham 1987) and data