We comment on a recent behavioral study in which we describe a human-like beckoning gesture in 2 groups of bonobos, used in combination with sexual solicitation postures. The beckoning gesture fulfils key criteria of deixis and iconicity, in that it communicates to a distant recipient the desired travel path in relation to a specific social intention, i.e., to have sex at another location. We discuss this finding in light of the fact that, despite the documented great ape capacity and obvious communicative advantage, referential gestures are still surprisingly rare in their natural communication. We address several possibilities for this peculiar underuse and are most compelled by the notion that non-human primates are generally not very motivated to share their experiences of external objects or events with others, which removes most reasons for referential signaling.

A key problem in science is to understand when and how human language evolved from earlier forms of communication. It is unlikely that this happened without any relevant precursors, that is, that the language faculty emerged ‘de novo’ over the last few million years of hominid evolution. More likely, the capacity for language emerged slowly and gradually from skills already present in the primate lineage. One way to address this hypothesis is to look for homologies and precursors in primate communication and cognition. Ape gestures are particularly relevant in this endeavor because they have shown several key features of human language. Particularly, there is good evidence that apes deploy various gestures during social interactions in flexible and goal-directed ways with novel gestures occasionally incorporated in the repertoire. Surprisingly, however, it has also been very difficult for researchers to identify the semantic content, or ‘meaning’, of ape gestures. The general finding has been that ape gestures are usually given to initiate, maintain or terminate already ongoing social interactions, so it has been difficult to assign specific meaning to most gestures (but see1,2). Moreover, several gestures appear to have several outcomes, suggesting that meaning resides more in the pragmatic context than in the morphological form of the signal. In sum, there has been very little evidence that apes gestures are directed at a specific recipient to refer him or her to an external entity, i.e., that gestures qualify as deictic or iconic signals.3-6

In a recent study6 we revisited this problem with an analysis of a human-like beckoning gesture that we observed in 2 groups of bonobos kept under near-natural environmental and social conditions at the Lola Ya Bonobo sanctuary near Kinshasa, Democratic Republic of Congo. Bonobos beckoning resembled human beckoning in its conspicuous, sideways sweeping movement of one arm toward the self. The behavior was found in 11 individuals of 2 different social groups, and always to invite a sexual partner to approach and jointly retreat to a different location for sex. If successful, the recipient responded by approaching the signaler and following him to the desired location. We interpreted these findings that, in some circumstances, great apes can naturally use spatial reference as part of a communicative intention with recipients responding to such signals appropriately. The meaning of this signal, in other words, is to deictically and iconically describe to a recipient a specific social

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intention and spatial reference – to jointly travel in a specific direction for a specific purpose.\(^6\)

Here, we discuss some of the wider theoretical implications of these results for human language evolution and the potential reasons for why apes do not use referential gestures more often as part of their natural communication.

**Iconic gesturing in great apes**

Humans deploy deictic gestures, such as pointing, to direct a recipient’s attention to a particular object or location, while iconic gestures are deployed to recreate an aspect of the shape or movement of an object or event.\(^7\) Both types of signals are referential, in that they either direct attention to a present referent or generate a mental representation of an absent referent. So far, there has been very little evidence for referential signals of these kinds in great apes.\(^4,5,8,9\) This is surprising because language-trained apes have no difficulties communicating referentially with humans.\(^10–12\) For example, Savage-Rumbaugh et al.\(^13\) reported that Kanzi and Mulika had made hitting motions toward nuts they wanted a human observer to crack open for them. Surprisingly, however, these individuals do not spontaneously use their acquired communication skills to interact with each other. Nevertheless, our study\(^6\) suggests that great apes are capable, in principle, of producing iconic and deictic gestures even when interacting with each other, and a main conundrum is why do not take regular advantage of this capacity.

**Why are iconic gestures rare?**

(1) Motor constraints

Iconic gesturing may be rare because it is mechanically easier for an ape to depict a movement in space (e.g. direction of approach,\(^6\) location of desired grooming\(^8\)), than to pantomime other types of activities. However, a few anecdotes suggest that apes sometimes pantomime actions, although typically when interacting with humans.\(^14,15\) For example, Gruber et al.\(^16\) reported on a bonobo apparently pantomiming ‘drinking from a cup’ to communicate to her caretaker, indicating that great apes are not fundamentally incapable of pantomiming. Also, Byrne and Byrne\(^17\) have shown that gorillas can produce complex, fine-tuned finger movements to process food, suggesting that apes are not fundamentally constrained in terms of their motor control.

(2) Conceptual constraints

Another hypothesis is that great apes may only have limited capacities to mentally represent the world around them. For example, they may be able to mentally represent the notion of ‘movement’ but they may have a concept of ‘fruit tree’ or ‘tool’. Although there is little doubt that primates and other animals can represent their worlds in terms of mental concepts,\(^18,19\) these concepts may be less clearly delineated compared to what is present in humans. Although this is a difficult topic, we interpret the current evidence as consistent with the hypothesis that primates can form mental representations of social categories (such as genetic relatives\(^20–22\)), or physical objects and their functional properties, such as tools (Gruber et al. submitted), suggesting that apes are not fundamentally constrained in terms of cognitive capacities to mentally represent their world in conceptually categories.

(3) Comprehension constraints

Human children use deictic gestures from about 10 months when communicative intentions are well developed, before they produce their first words.\(^7,23\) Iconic gestures emerge somewhat later, around 12 months, an important step toward the ability to use symbols.\(^24,25\) Interestingly, however, the comprehension of iconic symbols appears much later, around 26 months, following the acquisition of basic symbolic speech.\(^26–28\) The comprehension of iconic gestures, in other words, appears to be cognitively more demanding for children than its production or the comprehension of deictic signals, including pointing.\(^28,29\) In our study,\(^6\) however, subjects appeared to understand the intention behind beckoning, but it was unclear whether this was due to general capacity to comprehend iconicity or some simpler process. Here, it would be necessary to explore whether apes can comprehend iconic signals that are novel to them, but depict some natural behavior (e.g., climbing, grooming) or a relevant object (e.g., tool, fruit tree)?

(4) Cooperative constraints

Apes experience personal intentions, and use communication signals to communicate intentions to others, but they appear to be unable to share their intentions with others\(^29\) i.e. they lack a ‘we-intentionality’ as it is typical for humans. Because of this, the argument goes, great apes will only communicate what is beneficial for them and not what is useful for others. Although the hypothesis has intuitive appeal, there are also some contradictory findings, suggesting that, in some conditions, primates communicate intentionally to direct the attention of others to external objects or events relevant to them. This has been found in the contexts of danger,\(^3,30\) foraging,\(^31,32\) and during fights.\(^33\) However, although great apes are not fundamentally incapable of sharing information with others they may only show this behavior in very specific situations where their own reproductive success is directly at stake.

**Conclusions**

Our findings have shown that great apes can naturally use spatial reference as part of a communicative intention with signallers producing gestures that depict the spatial features of a desired action and recipients responding to such signals appropriately. Although this suggests that iconic signaling is part of natural communication in great apes, and as such present in the common ancestor of humans and apes, it is equally puzzling how rare such behavior is in great apes, despite its obvious advantages. We address 4 possible hypotheses on potential shortcomings underlying this human-ape difference: motor control, conceptual organization, comprehension abilities and shared intentional capacities, and find some support for the last one. However, it is also clear that more research is needed to decide what cognitive or psychological shortcomings really are responsible for the apparent underuse of a truly human capacity, the
ability to use communication to iconically refer to an absent entity.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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