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Report

Spatial Reference in a Bonobo Gesture

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Summary

Great apes frequently produce gestures during social interactions to communicate in flexible, goal-directed ways [1–3], a feature with considerable relevance for the ongoing debate over the evolutionary origins of human language [1, 4]. But despite this shared feature with language, there has been a lack of evidence for semantic content in ape gestures. According to one authoritative view, ape gestures thus do not have any specific referential, iconic, or deictic content, a fundamental difference versus human gestures and spoken language [1, 5] that suggests these features have a more recent origin in human evolution, perhaps caused by a fundamental transition from ape-like individual intentionality to human-like shared intentionality [6]. Here, we revisit this human uniqueness claim with a study of a previously undescribed human-like beckoning gesture in bonobos that has potentially both deictic and iconic character. We analyzed beckoning in two groups of bonobos, kept under near natural environmental and social conditions at the Lola Ya Bonobo sanctuary near Kinshasa, Democratic Republic of Congo, in terms of its linguistic content and underlying communicative intention.

Results and Discussion

Iconic gestures represent a physical object or an event by recreating an aspect of the referent's shape or movement [7]. Deictic gestures, such as pointing, are used to direct attention toward a particular object, person, or location [7], but their referential meaning is given entirely by the context and not by the form of the gesture [8]. Although there is some evidence for iconic and deictic gesturing in language-trained apes [9–14], there is little evidence for such behavior in the natural communication of wild and captive individuals [15–21].

Owing to the privileged observation conditions at our study site, the Lola Ya Bonobo sanctuary near Kinshasa, Democratic Republic of Congo, we were able to observe 20 cases of a beckoning gesture strikingly similar in form to human beckoning. Although there have been a few reports of beckoning in apes [3, 9, 22–29], or equivalent gestures such as "arm-swing-under" in gorillas [2, 15], the behavior is considered extremely rare [27–29], and we are not aware of any systematic analysis of this gesture in apes. It is possible that the rarity of such records, especially for wild populations, is due to the poor observation conditions in forest habitats and the discrete nature of the signals. Finally and most importantly, we are not aware of any evidence that recipients understand and respond to beckoning gestures in any significant way.

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Sample Size and Definition

Over 222 hr of observation time, we collected a total of 471 video clips from two social groups of bonobos that contained n = 1,080 sexual solicitations, initiated by n = 18 males and n = 17 females. Within this large data set, we found that the default way to initiate sexual interactions was for the signaler to actively approach the recipient at a mean distance of 1.0 m (±1.2 m; n = 1,080) in order to produce a sexual initiation posture (typically a "concave back present"; see Table S1 available online), which typically led to an in situ sexual interaction. In some instances, however, the initiator was unable or unwilling to approach, for example because of social competition, spatial inconvenience, or personality, and in such circumstances we found several attempts to signal to a distant partner (mean distance 5.5 ± 4.3 m; n = 20) with the apparent goal of persuading the recipient to approach and jointly retreat to a different location for sex. We identified 40 such attempts, initiated by ten males and four females in different partner combinations (range 1–7 per individual, mean 2.9 ± 2.1; n = 32 male-female, n = 3 female-male, n = 4 female-female, n = 1 male-male). 31 attempts (77.5%) were directed at higher-ranking individuals, mainly two adult females (n = 22; 55.0%), one in each group, that were particularly popular recipients of sexual solicitations. Of these 40 attempts, n = 20 (50.0%) contained a beckoning gesture performed by n = 9 males and n = 2 females (range 1–5 attempts with beckoning; Table 1).

We defined the bonobo beckoning gesture as stretching the arm toward a recipient (Figure 1B) followed by a sideways sweeping movement of the arm toward the self (Figures 1C–1E) and ending with a twirl of the wrist from palm upward to downward (Figure 1F). The beckoning gesture was usually preceded by a sexual initiation posture (Figure 1A) and followed by a pivot of the body in the direction of the forthcoming travel (Figures 1G and 1H). The signaler then walked away in that direction while regularly gazing back (Figure 1I), presumably to ensure the recipient was following. The potential deictic component of the gesture consists in pointing to the desired destination (self), while the potential iconic component describes the desired path geometrically.

Of the 40 total attempts, we excluded 20 because (1) the beginning of the interaction, before the recipient's follow, was not recorded on video (n = 7 total, 35.0%; n = 5 successes); (2) the interaction did not contain a beckoning gesture (initiation posture followed by body pivot and walk-away sequence: n = 7 total, 35.0%; n = 4 successes); or (3) the signaler walked over to the recipient to produce an initiation posture followed by a tactile gesture "touch" (n = 6 total, 30.0%; n = 6 successes). The remaining 20 cases all contained at least one beckoning gesture. Males produced the gesture at significantly higher rates than females (n_{males} = 18, $n_{females}$ = 17; W = 208.5, p = 0.025, Mann-Whitney U test). In 16 of 20 cases (80.0%) beckoning contained a sideways arm sweep movement toward the self (Figures 1C–1E and 2; Movies S1, S2, S3, and S4), and in 11 of these 16 cases (55.0% of the original 20) there was an additional downward twirl of the wrist (Figures 1F and 2; Movies S1, S2, and S4). In the remaining four cases (20.0%) there was no arm sweep but only an upward-to-downward wrist twirl (n = 2) or a downward twirl only (n = 2; Movie S5). In 17 of 20 cases (85.0%) beckoning was preceded by

Table 1. List and Description of Individuals that Performed the Beckoning Gesture, with Frequency of Production and Rank of Recipients

Signaler	Group	Sex	Age Class	Rank	Frequency (n) of Sexual Solicitations	Frequency (n) of Beckoning	Rank of Recipient
Bandundu	1	female	adult	high	31	1	high
Dilolo	1	male	subadult	intermediate	61	1	high
Eleke	2	male	subadult	low	58	1	low
Ilebo	2	male	subadult	intermediate	123	2	low, high
Kasongo	1	male	subadult	low	19	1	high
Keza	2	male	adult	high	51	2	intermediate, high
Likasi	2	female	subadult	intermediate	4	1	low
Lomami	1	male	subadult	intermediate	51	2	high
Mabali	1	male	subadult	low	31	1	high
Matadi	1	male	subadult	intermediate	37	5	high
Max	2	male	adult	high	36	3	high

a sexual initiation posture (Figures 1A and 2; Table S1). In two cases (10.0%) beckoning preceded the sexual invitation posture, and in one case (5.0%) it was produced without the sexual initiation posture.

In 15 of 20 cases (75.0%) beckoning was followed by a pivot of the body (Figures 1G, 1H, and 2) in the direction of the forthcoming travel. In 13 of these 15 cases (88.6%) the body pivots were in the direction opposite to the hand used to perform the gesture (i.e., turned left after using the right hand and vice versa). The signaler then walked to the desired location, while regularly gazing back, and waited there for the recipient to approach (Figure 2). While waiting, the signaler then usually performed a sexual initiation posture (Figure 2; Table S1). In the remaining five cases (25.0%) there was no body pivot, and the signaler waited for the recipient to approach without moving away (Figure 2).

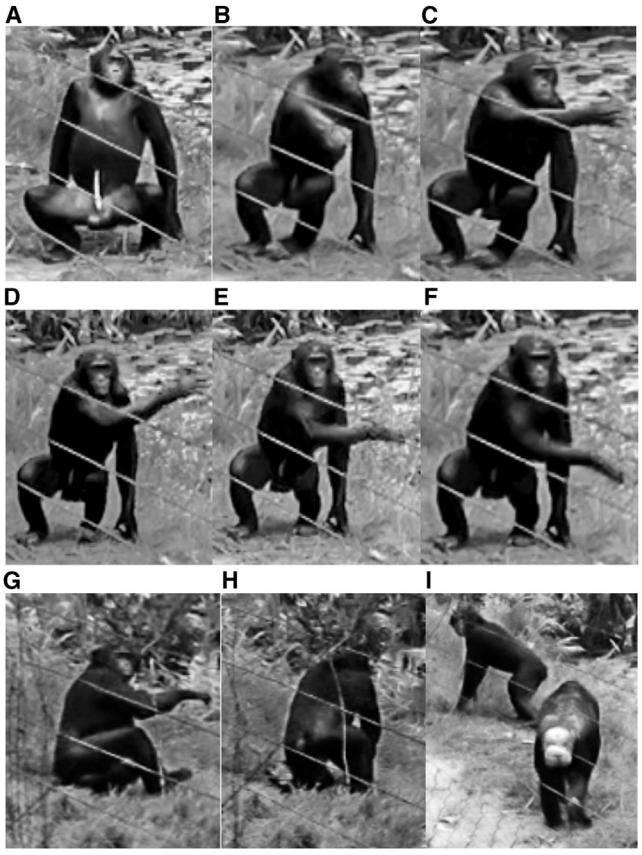

Figure 1. Illustration of the Most Frequent Beckoning Sequence to Persuade a Distant Partner to Approach and Jointly Move to a Different Location

Illustrations depict the sexual initiation posture (A) followed by a beckoning gesture: arm stretch toward recipient (B), sideways arm sweep toward self (C–E), wrist twirl (F), and then a body pivot (G and H) before walking away and regularly gazing back to check whether recipient is following (I).

Intentionality of Production and Recipient Response

An important problem in the iconic-gesturing literature on great apes is that there are very little systematic data on recipient reactions [15, 18]. One exception was provided by a study of wild chimpanzees [18], but there it remains unclear whether or not the gesture was produced intentionally, as there was no evidence for the standard criteria of intentional signaling, i.e., that the signal was directed to a specific recipient, whose attention was taken into account, and no evidence for persistence when communication failed.

Social Directedness and Audience Checking

To be communicatively effective and to qualify as an intentional signal, a gesture must be directed at a specific recipient who is also attending [1–3]. In 15 of 20 cases (75.0%) recipients were fully attending, with the head facing the signaler when the gesture was performed. In the remaining five cases (25.0%) head orientation was between 45 and 90° from signaler, still within its perceptual range. In their natural communication, great apes regularly combine gestures and vocalizations (e.g., [30]) and are capable of inhibiting vocalizations depending on the composition of the nearby audience [31, 32]. Here, we found that beckoning was always completely silent and was never accompanied by any vocalizations or other audible signals. This might be the result of the special environmental conditions at the sanctuary (access to large open areas that promote the production of silent signals) or specific social circumstances (presence of competitors and an associated desire to avoid being "overheard," similar to what has been observed in chimpanzee consortship [33]). Our small sample size, combined with the fact that the whole group was present during observations, prevented us from drawing strong conclusions about why signalers remained discrete during beckoning.

Persistence

Another criterion for intentional communication is whether signalers persist after failed communicative attempts [1–3]. We considered a communication attempt to be successful if the recipient responded appropriately (i.e., by approaching and following the signaler to a different location for sexual intercourse) and found that 13 of 20 cases of beckoning (65.0%) were successful (Figures 2 and 3). In ten cases (50.0%) approach was observed immediately after the first

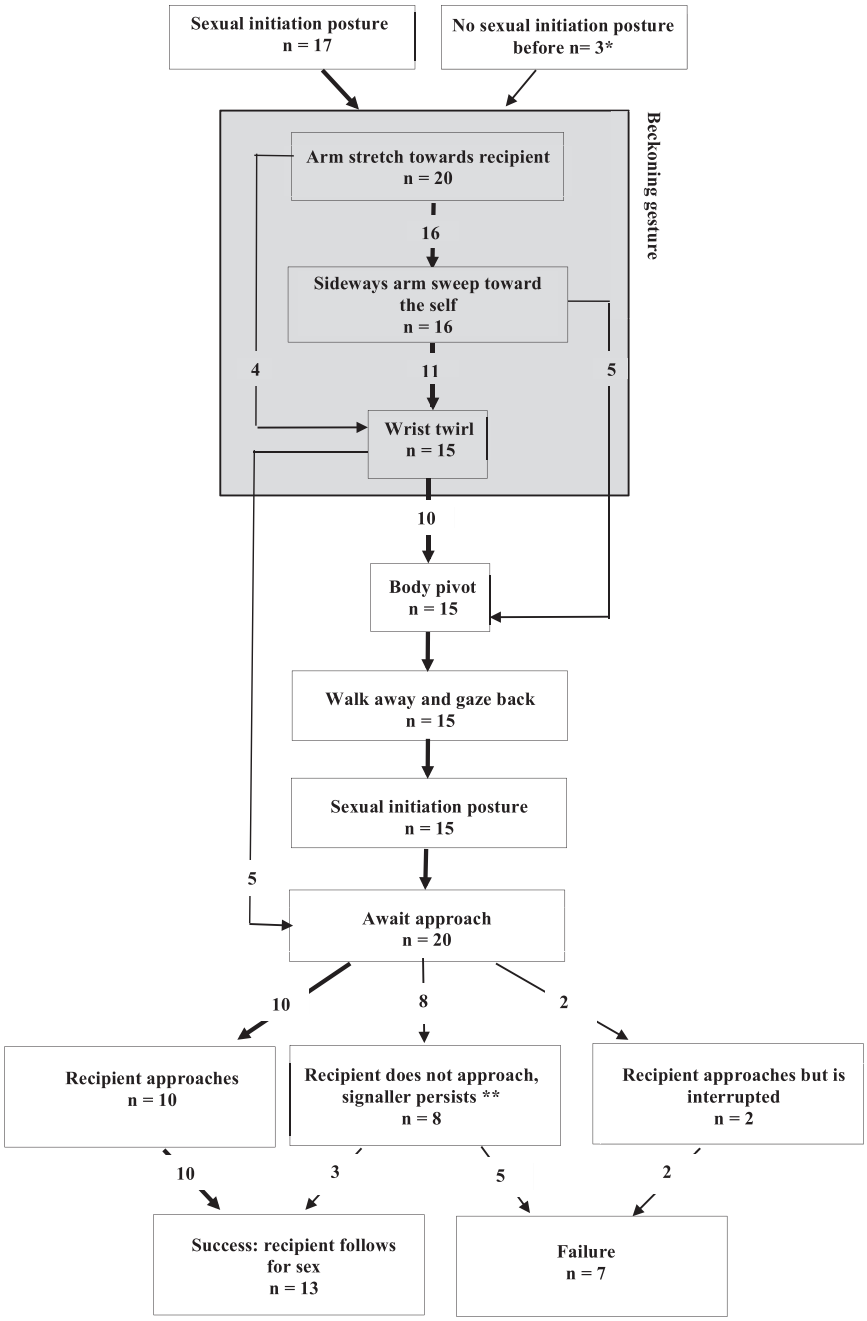

Figure 2. Sequential Organization of the Sexual Initiation Posture, Beckoning Gesture, and Associated Behaviors to Persuade a Partner to Approach and Jointly Move to a Different Location

Numbers in boxes indicates frequency of behavior. Numbers on arrows indicate frequencies of transitions between behaviors. Thick arrows indicate the most frequent sequences. *In n = 1 case there was no sexual initiation posture, and in n = 2 cases the sexual initiation posture occurred after the gesture. **In n = 8 cases the signaler persisted in signaling by repeating the sexual initiation posture, the beckoning gesture, and the body pivot and walk-away sequence and/or elaborated by using new gestures). See also Movies S1, S2, S3, S4, and S5.

signaling bout, but in three cases (15.0%) the signaler initially failed and was successful only after persistence (Figures 2 and 3). Persistence consisted of (1) repeating or using new sexual initiation postures (Table S1), (2) repeating the beckoning gesture, (3) elaborating with gestures other than beckoning (Table S1), or (4) performing other behaviors such as approaching or repeating the body pivot and walk-away sequence until the goal was achieved (Table S2).

In the remaining seven cases, the signaler was partially successful in two cases (10.0%; Figures 2 and 3), in that the recipient initially began to follow but was later interrupted by a third party. In the other five cases (25.0%), however, the signaler failed to elicit an approach despite persistence (Figures 2 and 3). In these failed attempts, the signaler persisted with strings of behaviors and signals (Table S2), including initiation postures, and the production of new gestures but never repeated the beckoning gesture (Tables S1 and S2). Interestingly, some of the new gestures had an audible component (e.g., "object shake," a common consortship signal in chimpanzees [33]; Table S1). In none of these cases did the recipient visibly react, and the signaler eventually abandoned all signaling efforts.

Gesture Acquisition

A current debate in gesture research is whether ape gestures are ontogenetically learned [1, 34] or part of a species-specific repertoire [2, 3]. Despite our relatively small sample size, beckoning gestures were produced by several individuals in both groups (Table 1). Crucially, we found a significant positive correlation between the number of observed sexual initiations and the frequency of beckoning across individuals (Spearman's rank correlation test: $\rho = 4{,}122$, n individuals = 35, $p = 0.011$), suggesting that with more observations, the behavior would probably be observed in most or all mature individuals and could therefore be considered species characteristic of bonobos. Ontogenetic ritualization [1, 34], therefore, can probably be discounted as an acquisition method.

However, because the bonobos at our study site have a history of close interactions with humans, especially during infancy, an alternative hypothesis is that subjects acquired the beckoning gesture from observing and imitating human caretakers. In humans, beckoning is relatively common and is characterized by a standard universal morphology, with some cultural variants [35, 36], suggesting that our subjects may have witnessed and learned from such instances. However, we find this an unlikely explanation, because (1) the observed beckoning behavior was distributed across several individuals of two groups and used in a very specific

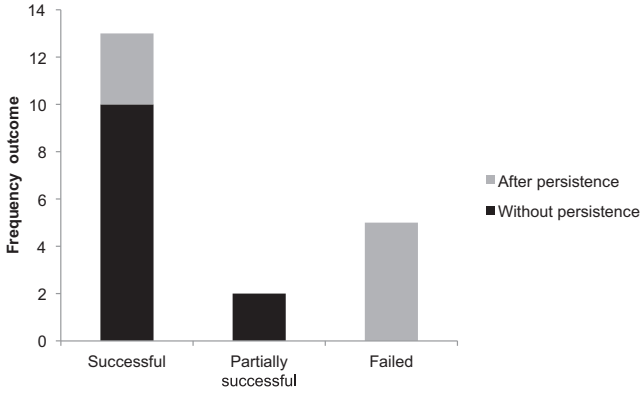

Figure 3. Frequency of Success in Attempts to Lead a Partner Away after Beckoning

Columns represent successful (n = 13, with n = 3 after persistence), partially successful (n = 2), and failed (n = 5) attempts with (gray) and without (black) persistence. See also Tables S1 and S2.

context of high biological relevance, and (2) the ability to imitate novel communication signals has not been demonstrated in apes (e.g., [37, 38]).

Conclusions

Human children use gestures to communicate before they produce their first words [39]. Their earliest gestures are deictic and typically emerge around 10 months of age. Arbitrary and iconic signals are produced around 12 months [40, 41], although the ability to recognize the iconicity of symbols does not usually appear before 26 months, following the acquisition of the corresponding spoken words [8, 42, 43]. Iconic gestures therefore seem to be cognitively more demanding than deictic gestures or other conventionalized signals [6, 8]. In great apes, there is good evidence that language-trained individuals are capable of acquiring and understanding both deictic and iconic signals [9–14], but this is far less clear in their natural communication. Although we cannot claim with confidence that the beckoning gesture is produced with an understanding of its iconic nature, our findings are relevant in that they provide evidence that great apes can naturally use spatial reference as part of a communicative intention, with recipients responding to such signals appropriately. The ability to produce gestures that depict some spatial features of a desired action was therefore probably already present in the common ancestor of humans and apes.

Experimental Procedures

All experiments were performed in accordance with the ethical ASAB/ABS Guidelines for the Use of Animals in Research and were conducted in compliance with animal care regulations and applicable national laws (Democratic Republic of Congo research permit MIN.RS/SG/004/2009). We received ethical approval from the scientific coordinator and scientific committee of Les Amis des Bonobos (http://www.friendsofbonobos.org/) for this study.

Data Collection and Analysis

Observations took place over 68 days and included 222 hr of observation time, split equally between two study groups (see Supplemental Experimental Procedures). Observations usually started around 8:30 a.m. and continued through midafternoon. Data collection usually took place around feeding times when all members of the group were visible or close at the edge of the forest. Behavioral data were collected using all-occurrence sampling [44] with a focus on sexual solicitations. All interactions were recorded with a Panasonic HDC-SD900 HD digital camcorder equipped with a Sennheiser MKE 400 directional microphone.

Any attempt to lead a sexual partner away from the group or to a different location for the purpose of sexual intercourse was considered for further analysis, for which we coded (1) the identity, sex, age class, and social status of signaler and recipient; (2) the recipient's attentional state (fully attending with head facing signaler, head direction 45° to 90° from signaler, or not attending); (3) the distance between signaler and recipient (m); (4) the type of gestures and body postures used to initiate sexual interaction (Table S1); (5) the hand used; (6) the form of gesture (with or without sideways arm sweep and/or wrist twirl; orientation of palm); (7) the direction of locomotion taken by signaler; (8) the recipient's reaction following signaling; (9) whether or not the attempt was successful; and (10) whether or not the signaler persisted in signaling if unsuccessful.

Statistical analyses were carried out with R v3.02 exactRankTests package 0.8-27 [45, 46]. All tests were two-tailed with α level = 0.05.

Supplemental Information

Supplemental Information includes two tables, Supplemental Experimental Procedures, and five movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.05.065.

Author Contributions

E.G. collected and analyzed the data. E.G. and K.Z. wrote the manuscript.

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