Title: Context, not sequence order, affects the meaning of bonobo (*Pan paniscus*) gestures

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ABSTRACT

In most languages, individual words can be ambiguous between several different meanings, but through syntax and context the intended meaning of an ambiguous word usually becomes apparent. Many great ape gestures also have ambiguous meanings, which poses the problem of how individuals can interpret the signaller's intended meaning in specific instances. We tested the effects of sequence compositionality and situational context (including behavioural and interpersonal contexts) in wild bonobos (*Pan paniscus*) at Wamba, DRCongo. We found no effect on a gesture's meaning from its presence and position in sequence. However, two aspects of situational context did affect meaning: behaviour of the signaller immediately prior to gesturing, and relative age/sex of signaller and recipient. The intended meaning of ambiguous gestures was almost completely disambiguated by means of these aspects of context. Our findings suggest that the use of contextual information to interpret ambiguous signals predates the uniquely-human lineage and is not specific to language.

KEYWORDS: bonobo, gesture, syntax, context, meaning

Great ape gestures offer an opportunity to reconstruct the evolutionary precursors to human language, since they form an extensive system of mutually-understood intentional signals (Byrne et al., 2017; Corballis, 2002; Fitch, 2010). Intended meanings have been identified by recording the outcomes that satisfy ape signallers (Graham et al., 2018; Hobaiter & Byrne, 2014), and most gestures seem to have several meanings, even when playful uses have been discounted. These ambiguous meanings may arise from gestures having multiple distinct meanings or from having a more general underlying meaning. Such apparent ambiguity seems puzzling, if communication is to be reliable. However, human language frequently shows semantic ambiguity in word meanings, yet is efficiently disambiguated in normal discourse (Rodd, Gaskell, & Marslen-Wilson, 2002). In this paper, we investigate whether two mechanisms that help to disambiguate words may also underlie how great ape gestures are understood.

When a semantically ambiguous word (that is, a word that has multiple meanings either through polysemy (multiple words with related but distinct meanings) or homophony (multiple words that happen to have the same form)) is used in combination with other words, the local semantic-syntactic context of the sentence – which words appear around the semantically ambiguous word and how those words are syntactically arranged – gives the recipient more information than if the ambiguous word were used on its own. When a recipient hears the sentence "let's walk by the bank of the river", it is clear that the word "bank" does not refer to a building where they might withdraw money. Further, the broader situational context – what the signaller and recipient are doing, and who they are – may also help to disambiguate the word's meaning. If two people are walking down the high street and one says "let's walk by the bank", the recipient is unlikely to think that they are heading to the nearest river, unless the speaker is a child obsessed with using their new fishing rod. Both local communicative context (i.e. signal sequences or syntax) and broader situational context might also explain how great apes disambiguate the meanings of gestures.

When considering the local syntactic context of a sequence of signals, there is sparse evidence that non-human animals possess anything like our complicated, recursive, hierarchical syntactic structures (Fitch, 2010). However, there are some indications that animals combine signals, usually in two-slot combinations, and that some combinations alter the meaning of the component signals (chestnut-crowned babbler, *Pomatostomus ruficeps*: Engesser, Crane, Savage, Russell, & Townsend, 2015; southern pied babbler, *Turdoides bicolor*: Engesser, Ridley, & Townsend, 2016; putty-nosed monkey, *Cercopithecus nictitans*: Arnold & Zuberbühler, 2008; titi monkey, *Cercopithecus nictitans*: Cäsar, Zuberbühler, Young, & Byrne, 2013; banded mongoose*, Mungos mungo*: Jansen, Cant, & Manser, 2013). These two-slot combinations, in which two signal types are combined in a fixed order, might be described as "syntax-like". They may be compositional (where the meanings of the signals both contribute to a larger meaning) or combinatorial (where the meanings of the signals individually do not directly relate to the meaning of the signals combined) (Engesser, Ridley, & Townsend, 2016). It has been proposed that a two-slot basic syntax may have been an important step in language evolution for early Hominins, as a potential precursor to complex linguistic syntax (Progovac, 2015). Whether other species' signal combinations represent a homologous or an analogous model, better understanding of the deployment of signal combinations in non-human primates (hereafter "primates") may give insight into the validity of this hypothesis.

Intriguingly, the first evidence that a primate might be able to comprehend syntactic structure came from ape language studies on Kanzi, a bonobo (*Pan paniscus*; Savage-Rumbaugh et al., 1993) (similar abilities have also been found for a language-trained grey parrot, *Psittacus erithacus* (Pepperberg, 1999), and bottlenose dolphins, *Tursiops truncates* (Herman, Kuczaj, & Holder, 1993)). Kanzi showed understanding of signal combinations and argument structure in spoken English but had varying success when word order or word class were altered (Savage-Rumbaugh et al., 1993). In their natural behaviour, bonobos seem to attend to signal sequences in vocal communication, accessing information about the location of desirable food through differing vocal sequences (Clay & Zuberbühler, 2011), although evidence is limited and it remains unclear whether they attend to the order of signals within these sequences. Great ape gesture research has yet to find evidence that sequence order changes the meaning of gestures (Genty & Byrne, 2010; Hobaiter & Byrne, 2011; Liebal, Call, & Tomasello, 2004), but given that bonobos have been shown to comprehend syntax in other domains, it must remain a possibility.

Bonobo gestures have not been studied as extensively as chimpanzee gestures, and most research comes from small, captive groups of bonobos (Halina, Rossano & Tomasello, 2013; Pika, Liebal & Tomasello, 2005; Pollick & de Waal, 2007). While these captive studies regularly report smaller repertoire sizes than those of wild populations, they still show a similar pattern of flexible usage across contexts, i.e. one gesture type may be used in many contexts, and one context may contain many gesture types (Halina, Rossano & Tomasello, 2013; Pika, Liebal & Tomasello, 2005; Pollick & de Waal, 2007). This is often interpreted as "means-end dissociation" (Bruner, 1981), and is considered a hallmark of great ape gestural communication. However, means-end dissociation more accurately describes signals and their "goals" not their contexts, i.e. one signal may have many goals, and one goal may be achieved by many signals (Bruner, 1981). Therefore, to fully examine means-end dissociation in great ape gestures, we must disentangle goals from contexts.

The broader situational context also helps in understanding the intended meaning of semantically ambiguous words and is perhaps a more likely candidate than local, syntactic communicative context for the disambiguation of nonhuman gestures. Situational context is known to affect the meaning of animal signals (Smith, 1965), but its potential to reduce ambiguity in ape signalling is unknown. Plooij and Goodall both recognized that great ape gestures could be used in many different behavioural contexts (Goodall, 1986; Plooij, 1978), and this has been confirmed in captive studies (Call & Tomasello, 2007; Pollick & de Waal, 2007). However, the possibility that gestures might have different *meanings* in different contexts has not yet been examined. Here we investigate two social aspects of situational context: the "behavioural context", the behaviour of the signaller at the time of gesturing; and "interpersonal context", the relationship between signaller and recipient, in terms of the age and sex of each. Both contexts could provide useful information for interpreting the intended meaning of gestures, like what the signaller has been doing or attempting to do, and how they relate (demographically) to their intended audience. Male and female chimpanzees may use different strategies of gestural communication (Scott, 2013), and so it's quite possible that demographic variables also impact on bonobo gestural communication.

In this paper, we begin by examining whether the presence of a gesture in a sequence and the position of that gesture in a sequence alters the gesture's meaning. We then examine whether behavioural and interpersonal context might also affect the meanings of gestures. The aim is that disentangling the role of context may finally help us to understand how an ape recipient is able to correctly interpret the meaning of seemingly ambiguous gestures.

METHODS

Data collection

We conducted fieldwork at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo (00°10'N, 22°30'E), from February to June 2014 and January to June 2015. We followed two neighbouring communities of wild bonobos: E1 group (n = 39) and P group (n = 30). In 2014, there were 63 individuals, with 28 adults (16 females, 12 males), 12 adolescents (7 females, 5 males), 9 juveniles (6 females, 3 males), and 14 infants (8 females, 6 males). In 2015, there were 64 individuals, with 30 adults (18 females, 12 males), 8 adolescents (3 females, 5 males), 10 juveniles (7 females, 3 males), and 16 infants (10 females, 6 males). Age classes for bonobos are taken from Hashimoto, 1997. Habituation for E1 group started in 1974, and for P group in 2010.

We observed bonobos from ~05:50 to ~12:00 on a total of 204 days, totalling 1159 hours of observation time. For filming we used focal behaviour sampling; we started filming whenever two or more individuals came within a 5-metre range of each other, to catch the beginning of social interactions. We recorded video footage using a Panasonic HDC-SD90 video camera with a 3-second pre-record function.

Video coding

Video was sorted into a library and coded using FileMaker Pro (for coding scheme setup see Supplementary Materials 1). We created a separate Filemaker Pro coding sheet for each gesture instance (defined as a single gesture), which included the following information: *signaller, recipient, signaller age/sex, recipient age/sex, bout, sequence, signaller behaviour prior, gesture type, directed, audience checking, persistence, response waiting, recipient response, goal,* and *goal met.* ‘Signaller’ is the individual who produces the gesture, and ‘recipient’ is the target individual. Age is classified as: infant (under 4 years), juvenile (4 to 7 years), adolescent (8 to 14 years), and adult (15 years or older) (Hashimoto, 1997). ‘Bout’ is a single gesture or sequence of gestures separated by >1s, and was coded as a sequential number out of the total number of bouts that occurred in the communication event, e.g. 1-of-1 or 2-of-5. ‘Sequence’ shows the position of single gestures (e.g. 1-of-1, 2-of-3) in a series of gesture instances separated by <1s. ‘Signaller behaviour prior’ determines the behavioural context, defined as the behaviour of an individual immediately prior to gesturing (Supplementary Materials 2). ‘Gesture type’ is the physical form of the gesture as used by bonobos, described (Open Access) in Graham, Furuichi, & Byrne, 2017 (video examples of all gesture types are available online at http://greatapedictionary.ac.uk/video-resources/gesture-videos/).

Directedness, audience checking, response waiting, and persistence are generally accepted markers of intentionality in communication (Bates, 1976; Townsend et al., 2017). If a signal is ‘Directed’, it must be used socially, i.e. in the presence of an audience, with visual monitoring of a target individual. ‘Audience checking’ is when the signaller observes the attention of the recipient before or during gesturing. ‘Response waiting’ is when the signaller pauses for >1s after gesturing. ‘Persistence’ is when the signaller continues to gesture towards the same recipient. All gesture instances were required to be directed and to meet at least one other criterion for intentionality (audience checking, persistence, or response waiting) before being accepted for analysis, giving 4256 intentional gesture instances.

Meaning was defined as the Apparently Satisfactory Outcome (ASO; see Hobaiter & Byrne, 2014)—i.e. a change in behaviour by the recipient that satisfies the signaller, shown by cessation of gesturing. ASOs offer a fine-grained approach to studying meanings (Hobaiter & Byrne, 2014; Graham et al., 2018), in contrast to previous studies that looked at context alone to examine gesture usage (Call & Tomasello, 2007; Pollick & de Waal, 2007). The ASO approach also centres the goal-directedness of gestures, part of Gricean intentionality that allows us to say that gestures have "meaning" in the first place (Moore, 2016). Hereafter, we use the word "meaning" to mean "ASO". For each instance, we coded 'Recipient response' (*No response, ASO, Gesture, Unknown*), 'Goal' (the specific change in behaviour by the recipient, see Supplementary Materials 3), and 'Goal met' (*Yes, No, Unknown*). Context was coded separately from meaning: as described above, behavioural context is taken from 'signaller behaviour prior', and interpersonal context from 'signaller age/sex' and 'recipient age/sex'.

All statistical analyses were performed in R 3.5.3.

Inter-observer reliability

A second experienced coder, Catherine Hobaiter, confirmed our accuracy by coding 100 gesture instances for the following information: gesture type, persistence, and signaller apparently satisfied. CH has experience coding great ape gestures but was not aware of the hypothesis being tested in this study. We calculated inter-observer reliability using Cohen's

Kappa, revealing agreement for all variables (gesture type K = 0.87, persistence K = 0.70, and signaller apparently satisfied K = 0.63).

RESULTS

Do gesture types convey the same meanings when they are used singly as when they are used in sequences?

If the purpose of gesture sequences is to modify the meaning of a gesture type, then one would expect the meaning of gestures in sequences to be different to those used singly. To test this, we looked at gesture types that are used both singly and in sequences (min=2, max=8). To illustrate what these sequences can include, one example of a 2-gesture sequence is *Arm Swing+Directed Push*, and the 8-gesture sequence was *Object Shake+Big Loud Scratch+Object Shake+Big Loud Scratch+Object Shake+Big Loud Scratch+Object Shake+Present (grooming).* We excluded "Play" and "Unknown" meanings in order to examine only properly identified outcomes. Gestures used in play were excluded from analysis, as actions performed in play do not (necessarily) represent those actions' non-playful usage (Hobaiter & Byrne, 2014 in Supplemental Information). We required that a meaning be achieved at least 5 times for a given gesture type.

Fourteen gesture types were suitable for analysis. We first created a proportional stacked histogram to qualitatively examine the data (Figure 1). Most gesture types have a similar profile for single and sequence usage. For 12/14 gesture types, the primary meaning was the same for single gestures and sequences. Only one gesture type, *Grab*, did not share any meanings between single instances and sequences (Table 1).

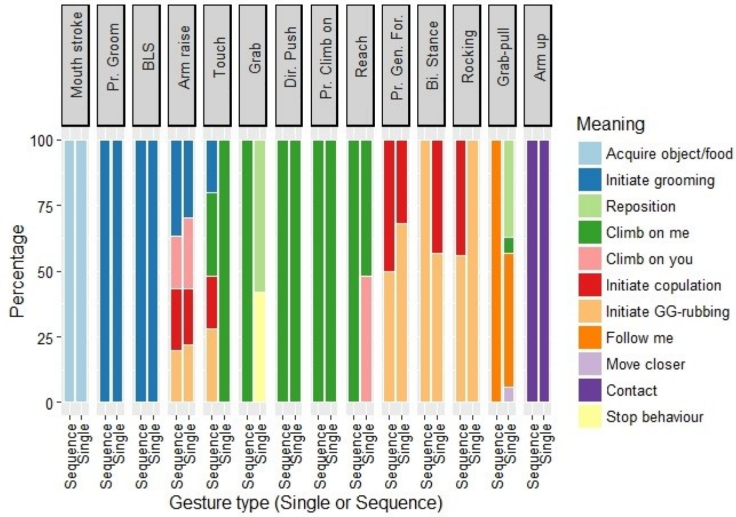

Figure 1. Proportional stacked histogram showing the proportion of total instances that each single instance or sequence for each gesture type achieved each meaning. The chart is arranged so that similar meanings are adjacent, and that gesture types with similar histogram profiles appear in adjacent columns. Abbreviated gesture types are Pr. Groom ("Present (grooming)"), BLS ("Big Loud Scratch"), Dir. Push ("Directed Push"), Pr. Climb on ("Present (climb on)"), Pr. Gen. For. ("Present (genitals forward)"), and Bi. Stance ("Bipedal Stance").

Table 1. Table showing the gesture type (arranged according to similar histogram profile in Figure 1); number of instances in sequences and singly (sequence, single); whether the primary meaning (ASO) is the same; and the number of shared meanings over the number of total meanings.

Gesture Type	# Instances (sequence, single)	Primary meaning (ASO) same?	# Shared meanings/ Total meanings
Mouth stroke	7, 32	Yes	1 / 1
Present (grooming)	90, 975	Yes	1 / 1

Big loud scratch	47, 21	Yes	1 / 1
Arm raise	41, 37	Yes	4 / 4
Grab	8, 12	No	0 / 3
Directed push	18, 28	Yes	1 / 1
Present (climb on)	17, 26	Yes	1 / 1
Reach	7, 21	Yes	1 / 2
Touch other	25, 11	Yes	1 / 4
Present (genitals forward)	107, 373	No	2 / 2
Bipedal stance	7, 15	Yes	1 / 2
Rocking	18, 7	Yes	1 / 2
Grab-pull	16, 81	Yes	1 / 4
Arm up	5, 11	Yes	1 / 1

We then examined whether the distribution of meanings for each gesture type was the same for single gestures and those in sequences. Six gesture types (*Mouth stroke*, *Present (grooming)*, *Big loud scratch*, *Directed push*, *Present (climb on)*, and *Arm up*) had only one meaning and were identical for both single instances and sequences. For the remaining gesture types, where there were enough data (no more than 20% of cells with <5 expected value and no cells with <1 expected value), we performed Chi-square tests on a table of "single" or "sequence" by meaning (Table 2). If there were not adequate data for a Chi-square test and the table was 2x2, we performed Fisher's exact test (Table 2). Fisher's exact test can also be used for m x n contingency tables (Freeman & Halton, 1951; Mehta & Patel, 1983), and when we have used this method, we specify the size of the contingency table in Table 2. Three gesture types (*Arm raise*, *Bipedal stance*, and *Rocking*) had the same distribution for single and sequence (plus the six gesture types of 100% identical meaning), and five gesture types (*Grab, Reach, Touch other, Present (genitals forward)*, and *Grab-pull*) had significantly different distributions.

To answer the question “do gesture types convey the same meanings when they are used singly as when they are used in sequences?”: yes, most gesture types (12/14) had the same primary meaning for single gestures and sequences, and most gesture types (9/14) had the same distribution of meanings for single gestures and sequences. It seems that the simple presence of a gesture type in a sequence is not sufficient for changing the meaning of that gesture type.

Table 2. Gesture type arranged according to similar histogram profile in Figure 1; whether or not the gesture type had the same distribution of meanings for single gestures and sequences; and results for Chi-square and Fisher’s exact tests.

Gesture Type	**Same dist.?**	**Results**
Arm raise	Yes	χ^2=0.86, df=3, p-value =0.84
Grab	No	Fisher's exact test, $p<0.0001$ (2x3 table)
Reach	No	Fisher’s exact test, p=0.03 (2x2 table)
Touch other	No	Fisher's exact test, p=0.002 (2x3 table)
Present (genitals forward)	No	χ^2=12.02, df=1, p-value<0.0001 (Yates’ continuity correction)
Bipedal stance	Yes	Fisher’s exact test, p=0.12 (2x2 table)
Rocking	Yes, but close	Fisher’s exact test, p=0.06 (2x2 table)
Grab-pull	No	Fisher's exact test, p=0.002 (2x4 table)

Are gesture types more likely to appear at a specific position in a sequence?

Before seeing whether the position in a sequence affects the meaning of a gesture, we wanted to see whether gesture types are more likely to occur in certain positions in a sequence. To do this, we first took all gesture instances occurring in sequences for which the position in the full sequence is known (sometimes we observed incomplete sequences, due to filming constraints). We labelled the positions as “First”, “Middle” (occurring in any position in the middle of a sequence), and “Last”. This gave us 291 instances in the “First” position, 291 in the “Last” position, and 101 instances in the “Middle” position (43% First, 15% Middle, 43% Last), with sequences ranging from 2-8 gestures.

We then excluded “Play” and “Unknown” meanings, as in previous analyses, and excluded all gesture types that achieved any one meaning <5 times. Note that for this analysis, there are some additional gesture types – these gesture types achieved a meaning ≥5 times in sequences, so they are included here, but they did not achieve a meaning ≥5 times singly and so were excluded for the previous analysis. This left 415 instances in total: 172 “First” position, 58 “Middle” position, and 185 “Last” position (41% First, 14% Middle, 45% Last), again with sequences ranging from two to eight gestures.

We tested whether the distribution of positions for each gesture type was different from the distribution of positions across all gesture types (Table 3). Where possible, we used a 2x3 Chi-square test, with “gesture type” and “all gesture types” by “First”, “Middle”, and “Last”. If a Chi-square was not appropriate, we used Fisher’s exact test.

Table 3. Gesture type (arranged first by total number of instances, and then alphabetically); the frequency of occurring in the first position in a sequence, anywhere in the middle of a sequence, and at the end of a sequence; the total number of instances observed; and the results for Fisher’s exact test or Chi-square test, including Bonferroni-Holm adjustment.

Gesture	First	Mid	Last	Total	Results
Arm up	4	0	1	5	-
Leg swing*	2	2	1	5	-
Stroking*	3	2	0	5	-
Grab-pull	3	0	3	6	-
Mouth stroke	1	2	3	6	-
Bipedal stance	6	0	1	7	-
Reach	4	1	2	7	-
Grab	5	2	1	8	-
Leg flap*	0	3	5	8	-
Object shake*	4	3	1	8	-
Arm swing*	4	7	6	17	Fisher's exact test, $p=0.016$ (adjusted $p=0.128$)
Present (climb on)	3	2	12	17	Fisher's exact test, $p=0.078$ (adjusted $p=0.546$)
Directed push	5	3	10	18	Fisher's exact test, $p=0.48$ (adjusted $p=1.000$)
Rocking	6	3	9	18	Fisher's exact test, $p=0.76$ (adjusted $p=1.000$)
Touch other	6	5	9	20	Fisher's exact test, $p= 0.29$ (adjusted $p=1.000$)
Arm raise	11	19	6	36	$\chi 2=1.63$, df=2, p-value=0.44 (adjusted $p=1.000$)
Big Loud Scratch	14	9	21	44	$\chi 2=2.14$, df=2, p-value=0.34 (adjusted $p=1.000$)
Present (grooming)	43	0	44	87	$\chi 2=13.80$, df=2, p-value=0.001 (adjusted $p=0.009$)
Present (genitals forward)	48	8	37	93	$\chi 2=3.90$, df=2, p-value=0.14 (adjusted $p=1.000$)
TOTAL	172	58	185		

*Gestures that are included in this analysis, but not in the previous analyses, because they achieve a meaning ≥5 times in a sequence but not singly.

Four gesture types were suitable for Chi-square analysis, comparing the distribution of positions (first, middle, last) for each gesture type to the distribution of positions across all gesture types. Of these, only one gesture type, *Present (grooming)*, had a significantly different distribution, possibly owing to the fact that it never occurred in the middle position. We did not analyse gesture types that were observed <10 times, but did perform Fisher's exact test on those that were observed >10 times but not enough times for a Chi-square test. Of the 5 gesture types analysed with a Fisher's exact test, one (*Arm swing*) was significantly different, and one (*Present (climb on)*) was tending towards significance. Of the nine gesture types that we analysed, only two had a significantly different distribution of positions to the average distribution.

To answer the question "are gesture types more likely to appear at a specific position in a sequence?": no, most gesture types (7/9) appear in a similar distribution across positions to the average distribution of all gestures across all positions. Just as there is no difference of meaning for a gesture type whether used singly or in sequence, there is also no systematic variation in where each gesture type occurs in the sequence. The next question is whether the meaning of each gesture type is affected by the position in which it occurs in a gesture sequence.

Does the position of a gesture in a sequence affect its meaning?

We began with the nine gesture types for which there had been adequate data for Chi-square and Fisher's exact tests in the previous section, and calculated the proportion of instances for which a gesture in each position achieved each meaning. Like in the analysis comparing single gestures and sequences of gestures, we created a proportional stacked histogram to qualitatively examine the data (Figure 2). Most gesture types appear to have a similar profile for all three positions. We then assessed whether the primary meaning was shared for all three positions (first, middle, last): four gesture types (*Big Loud Scratch, Present (grooming), Directed push*, and *Present (climb on)*) shared the primary meaning across all positions; four gesture types (*Touch other, Arm swing, Present (genitals forward)*, and *Rocking*) shared the primary meaning in two positions; and one gesture type (*Arm raise*) did not share a primary meaning in any position (Table 4). All gesture types, except *Rocking*, shared all meanings across positions. *Rocking* shared “Initiate copulation” across all positions, but “Initiate GG-rubbing” was only achieved in the first and last position.

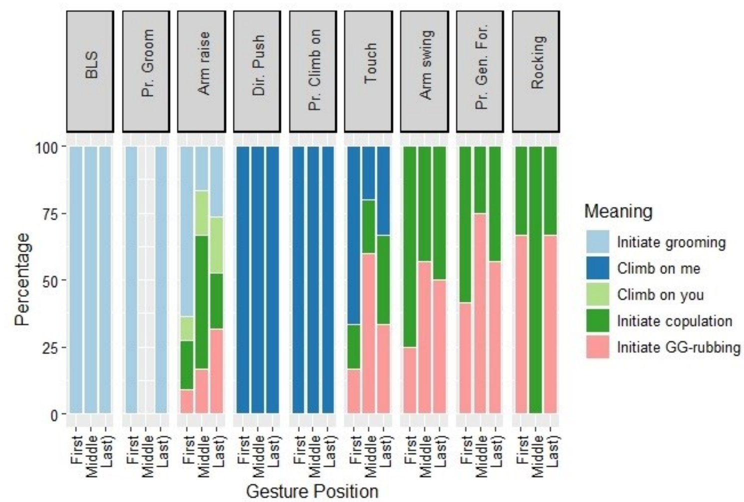

Figure 2. Proportional stacked histogram showing the proportion of total instances that each position (first, middle, last) for each gesture type achieved each meaning. The chart is arranged so that similar meanings are adjacent, and that gesture types with similar histogram profiles appear in adjacent columns. Abbreviated gesture types are expanded in Figure 1.

Table 4. Table showing gesture types (arranged according to similar histogram profile in Figure 2); the primary meaning (ASO) achieved in each position (first, middle, last); whether the primary meaning (ASO) was shared by all gesture types (“Yes” or “No”) or by

2 of the gesture types ("Part"); and the number of total meanings (ASOs) across the gesture types that were shared.

Gesture	Primary meaning - First	Primary meaning - Middle	Primary meaning - Last	Shared Primary	Shared meanings
Big loud scratch	Initiate grooming	Initiate grooming	Initiate grooming	Yes	1/1
Present (grooming)	Initiate grooming	-	Initiate grooming	Yes	1/1
Arm raise	Initiate grooming	Initiate copulation	Initiate GG-rubbing	No	4/4
Directed push	Climb on me	Climb on me	Climb on me	Yes	1/1
Present (climb on)	Climb on me	Climb on me	Climb on me	Yes	1/1
Touch other	Climb on me	Climb on me & Initiate copulation & Initiate GG-rubbing	Initiate GG-rubbing	Part	3/3
Arm swing	Initiate copulation	Initiate GG-rubbing	Initiate copulation & Initiate GG-rubbing	Part	2/2
Present (genitals forward)	Initiate copulation	Initiate GG-rubbing	Initiate GG-rubbing	Part	2/2
Rocking	Initiate GG-rubbing	Initiate copulation	Initiate GG-rubbing	Part	1/2

Big loud scratch, Present (grooming), Directed Push, and *Present (climb on)*, all achieve only one identical meaning for each position, making statistical analysis unnecessary. For the remaining five gesture types, the counts for each cell are too low for Chi-square analysis. We have therefore performed m x n Fisher's exact test (Freeman & Halton, 1951; Mehta & Patel, 1983), but would like to acknowledge that these results should be approached with caution due to low number of observations (Table 5). None of the nine gesture types, those that are 100% identical and those that were tested, had a significantly different distribution of meanings depending on the position in which the gesture occurred. To answer the question "does the position of a gesture in a sequence affect its meaning?": no, all gesture types (9/9) had a similar distribution of meanings in each position.

Table 5. Table showing the gesture type (arranged according to similar histogram profile); whether or not the gesture type had the same distribution of meanings for all positions (first, middle, last); and results for Fisher's exact test.

Gesture Type	Same dist.?	Results
Arm raise	Yes	Fisher's exact test, p=0.34 (3x4 table)
Touch other	Yes	Fisher's exact test, p=0.57 (3x3 table)
Arm swing	Yes	Fisher's exact test, p=0.70 (3x2 table)
Present (genitals forward)	Yes	Fisher's exact test, p=0.14 (3x2 table)
Rocking	Yes	Fisher's exact test, p=0.14 (3x2 table)

Can behavioural context reduce the ambiguity of gesture meanings?

Our evidence supports the hypothesis that bonobo gestural communication is not structured with sequence-order, syntax-like compositionality: gestures used singly versus in sequences do not seem to have different meanings, they do not occur in a distribution of positions different from the average distribution, and their position in the sequence does not seem to affect their meaning. We now examine whether the "behavioural context", defined as the behaviour of an individual immediately prior to gesturing, changes the meaning. To look at behavioural context, we started with all gesture instances (single and in sequences together) that achieved a meaning. Then we limited to meanings that occur ≥5 times for a given gesture type, to maintain consistency with the previous syntax analysis. We calculated the proportion of instances for achieving each meaning by the total number of instances for that gesture type (Table 6). Fifteen gesture types achieved one meaning in 100% of instances. Analysis will continue with the remaining 13 gesture types, which have <1.00 proportion for each meaning.

Table 6. All gesture types that achieve at least one meaning ≥5 times, arranged by decreasing proportion achieved by the primary meaning; Meanings (ASOs) achieved by each gesture type in decreasing proportion; number of instances that each meanings is achieved; and the proportion of instances for each meaning by the total instances of all meanings for that gesture type. Gesture types above the double line achieve one outcome in 100% of instances, and those below the line will be included in context analysis.

Gesture	Meaning (ASO)	# Instances	Proportion
Present (grooming)	Initiate grooming	1065	1.00
Big Loud Scratch	Initiate grooming	68	1.00
Directed push	Climb on me	46	1.00
Present (climb on)	Climb on me	43	1.00
Mouth stroke	Acquire object/food	39	1.00
Dangle	Initiate GG-rubbing	18	1.00
Embrace	Contact	11	1.00
Beckon	Climb on me	8	1.00
Hand fling	Move away	8	1.00
Leg flap	Initiate copulation	8	1.00
Bipedal rocking	Initiate GG-rubbing	7	1.00
Push	Move away	7	1.00
Hip thrust	Initiate copulation	5	1.00
Leg swing	Initiate copulation	5	1.00
Stroking	Initiate GG-rubbing	5	1.00

Arm up	Contact	16	0.76
	Climb on me	5	0.24
Arm swing	Initiate copulation	12	0.68
	Initiate GG-rubbing	12	0.39
	Climb on me	7	0.23
Present (genitals forward)	Initiate GG-rubbing	308	0.64
	Initiate copulation	172	0.36
Bipedal stance	Initiate GG-rubbing	16	0.62
	Initiate copulation	10	0.38
Hand on	Contact	8	0.62
	Initiate grooming	5	0.38
Object shake	Initiate GG-rubbing	9	0.60
	Initiate copulation	6	0.40
Rocking	Initiate GG-rubbing	17	0.59
	Initiate copulation	12	0.41
Present (genitals backward)	Initiate copulation	15	0.58
	Mount me	11	0.42
Grab-pull	Follow me	57	0.55
	Climb on me	8	0.08
	Move closer	6	0.06
Reach	Climb on me	18	0.49
	Climb on you	12	0.32
	Acquire object/food	7	0.19
Grab	Climb on me	10	0.34
	Reposition	8	0.28
	Stop behaviour	6	0.21
	Initiate grooming	5	0.17
Touch other	Climb on - me	19	0.32
	Initiate GG-rubbing	10	0.17
	Initiate grooming	7	0.12
	Move away	7	0.12
	Initiate copulation	6	0.10
	Reposition	5	0.08
	Stop behaviour	5	0.08
Arm raise	Initiate grooming	23	0.31
	Climb on you	18	0.24
	Initiate copulation	18	0.24
	Initiate GG-rubbing	16	0.21

For the 13 gesture types that had more than one meaning, we then cut down the dataset to exclude any meaning seen for a context <5 times. This eliminated *Hand on* and

Arm up from analysis. We then created a proportional stacked histogram of the meanings achieved by the remaining 11 gesture types (Figure 3).

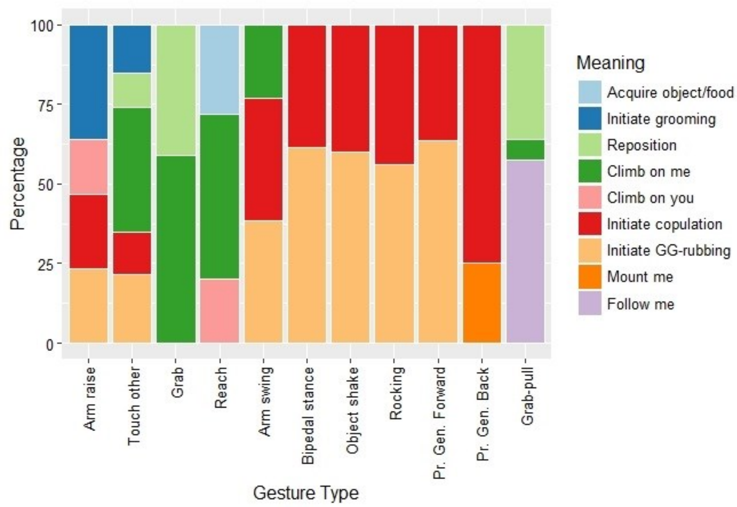

Figure 3. Proportional stacked histogram of meanings achieved by each gesture type. The chart is arranged so that similar meanings are adjacent, and that gesture types with similar histogram profiles appear in adjacent columns. Abbreviated gesture types are expanded in Figure 1.

We then split these 11 gesture types by behavioural context, which is the behaviour of the signaller immediately prior to gesturing (definitions of each behavioural context can be found in Supplementary Materials 1). We created a proportional stacked histogram of meanings achieved in each context by each gesture type (Figure 4). Three gesture types, *Bipedal stance, Object Shake*, and *Rocking,* only occurred in a sexual context and so are not shown on the histogram (see Figure 3 for proportions). The meaning of *Grab* and *Present (genitals backward)* became completely disambiguated when split by context (*Grab* achieved “Reposition” in the Grooming context and “Climb on me” in the Travelling context, *Present (genitals backward)* achieved “Mount me” in the Agonistic context and “Initiate copulation” in the Sexual context); *Arm raise* was disambiguated in 2/3 contexts (achieving “Initiate grooming” in the Grooming context and “Climb on you” in the Vocalisation context); *Reach, Arm swing* and *Grab-pull* in 1/2 contexts (*Reach* achieved “Acquire food” in the Feeding context, and *Arm swing* and Grab-pull achieved “Climb on me” in the Travelling context); and *Touch other* and *Present (genitals forward)* in 1/3 contexts (*Touch other* achieved “Climb on me” in the Travelling context, and *Present (genitals forward)* achieved “Initiate GG-rubbing” in the Agonistic context). One noticeable effect is that in all gesture types occurring in a sexual context (except *Present (genitals backward)*), the gesture can be used to initiate both copulation and GG-rubbing. It is therefore unsurprising that *Present (genitals backward)* is the exception as it is not physically conducive to GG-rubbing.

For all gesture types occurring in multiple contexts, we performed Fisher’s exact tests of Meaning by Context (Table 7). All gesture types had significantly different distributions of meanings compared across contexts.

To answer the question “can behavioural context help to reduce the ambiguity of gesture meanings?”: yes, most gesture types (8/11) became disambiguated in one or more contexts – that is, they achieved only one meaning in that context. The remaining three gesture types only occurred in one context (and so are not displayed in Figure 4). This supports the hypothesis that gestures result in particular meanings because of their specific behavioural contexts; the behaviour of the signaller immediately prior to the gesture provides additional information so that the meaning achieved by the gesture differs depending on the behavioural context.

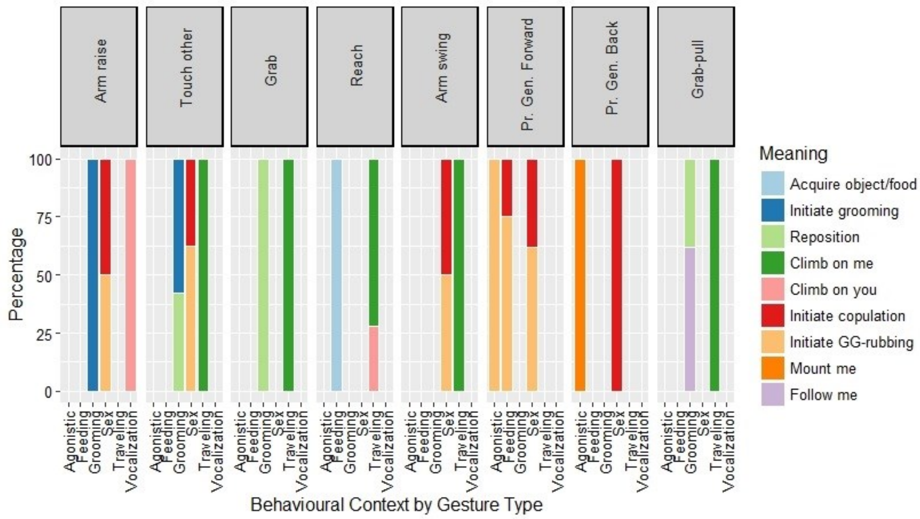

Figure 4. Proportional stacked histogram showing the proportion of instances that each meaning is achieved in each context for each gesture type. The chart is arranged so that similar meanings are adjacent, and that gesture types with similar histogram profiles (from Figure 3) appear in adjacent columns. Abbreviated gesture types are expanded in Figure 1.

Table 7. Gesture types divided by context divided by meaning, giving the proportion of instances for which each meaning is achieved in each context for that gesture type. In the right column, the results of Fisher's exact test comparing the distribution of meanings across contexts for each gesture type.

Gesture	Context	Meaning (ASO)	Proportion	Test Distribution
Arm raise	Grooming	Initiate grooming	1	Fisher's exact test, p<0.0001 (3x4 table)
	Sex	Initiate copulation	0.5	
		Initiate GG-rubbing	0.5	
	Vocalisation	Climb on you	1	
Touch other	Grooming	Reposition	0.42	Fisher's exact test, p<0.0001
		Initiate grooming	0.58	

		Initiate copulation	0.38	(3x5 table)
	Sex	Initiate GG-rubbing	0.63	
	Travelling	Climb on me	1	
Grab	Grooming	Reposition	1	Fisher's exact test, p<0.0001 (2x2 table)
	Travelling	Climb on me	1	
Reach	Feeding	Acquire object/food	1	Fisher's exact test, p<0.0001 (2x3 table)
	Travelling	Climb on you	0.28	
		Climb on me	0.72	
Arm swing	Sex	Initiate copulation	0.5	Fisher's exact test, p<0.0001 (2x3 table)
		Initiate GG-rubbing	0.5	
	Travelling	Climb on me	1	
Bipedal Stance	Sex	Initiate copulation	0.38	-
		Initiate GG-rubbing	0.62	
Object shake	Sex	Initiate copulation	0.4	-
		Initiate GG-rubbing	0.6	
Rocking	Sex	Initiate copulation	0.44	-
		Initiate GG-rubbing	0.56	
Present (genitals forward)	Agonistic	Initiate GG-rubbing	1	Fisher's exact test, p=0.047 (3x2 table)
	Feeding	Initiate copulation	0.25	
		Initiate GG-rubbing	0.75	
	Sex	Initiate copulation	0.38	
		Initiate GG-rubbing	0.62	
Present (genitals backward)	Agonistic	Mount me	1	Fisher's exact test, p<0.0001 (2x2 table)
	Sex	Initiate copulation	1	
Grab-pull	Grooming	Reposition	0.38	Fisher's exact test, p<0.0001 (2x3 table)
		Follow me	0.62	
	Travelling	Climb on me	1	

Does interpersonal context further reduce ambiguity in gesture meaning?

To determine whether interpersonal context, specifically the age and sex of signaller and recipient, affects the gesture meaning, we analysed gestures where the behavioural context failed to disambiguate meaning. Overall, nine gesture types were not fully disambiguated in meaning by behavioural context: in a sexual context, *Arm raise, Arm* *swing, Bipedal Stance, Object Shake, Present (genitals forward), Rocking,* and *Touch other* all achieved both “Initiate copulation” and “Initiate GG-rubbing”; in a travelling context, *Reach* achieved both “Climb on me” and “Climb on you”; in a grooming context. *Grab-pull* achieved both “Reposition” and “Follow me”, and *Touch other* achieved both “Reposition” and “Initiate grooming.” For these cases, we tested whether interpersonal context affected meaning; specifically, the sex and age of interactants.

To address the effect of sex as an interpersonal context, we categorized gestures as *Female-Male*, *Female-Female,* or *Male-Male*, ignoring the direction of the gesture, i.e. male to female or female to male. We required that each category achieve a meaning ≥5 times for inclusion in analysis. Meaning was disambiguated for six gesture types (Figure 5), with an additional gesture type, *Present genitals forward,* almost completely disambiguated. In the Female-Male context, *Present (genitals forward*) achieves “Initiate copulation” 97% of the time and “Initiate GG-rubbing” only 3% of the time. Upon closer examination, all of the female-male GG-rubbing instances are between young individuals and adults not between sexually mature individuals. Even so, the distribution of meanings for *Present (genitals forward)* between sex categories is significantly different (χ^2=443.67, df=1, p-value<0.0001).

Two gesture types, *Grab-pull* and *Reach*, remained ambiguous. For these, we categorized the age and direction of signaller and recipient: *Adult* → *Adult*, *Adult* → *Young*, *Young* → *Adult, or Young* → *Young*. Meaning was disambiguated for one of these gestures, *Reach*, but *Grab-pull* remained ambiguous (Figure 6).

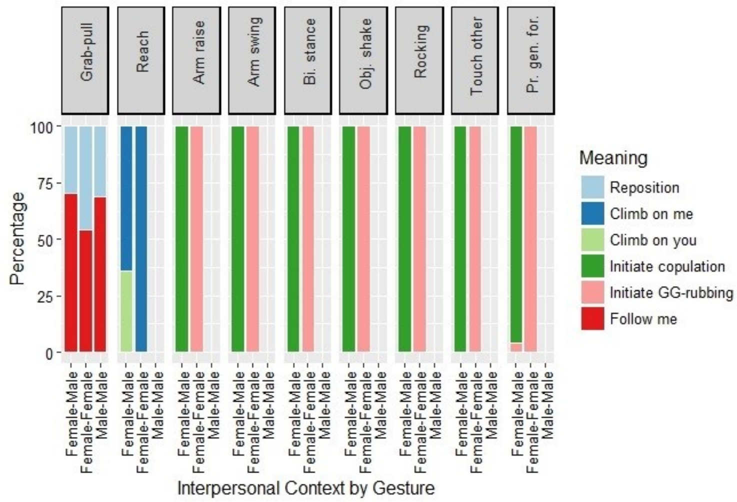

Figure 5. Proportional stacked histogram showing the proportion of instances for which each gesture type in each sex relationship category achieves each meaning. The chart is arranged so that similar meanings are adjacent, and that gesture types with similar histogram profiles appear in adjacent columns. Abbreviated gesture types are expanded in Figure 1.

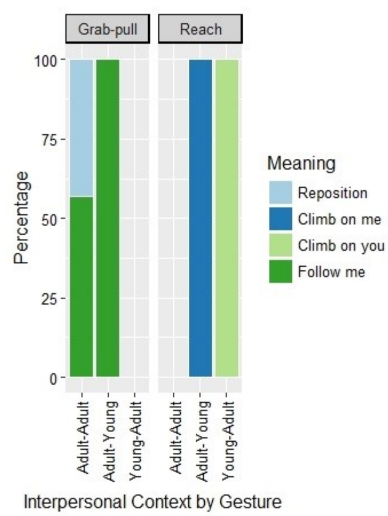

Figure 6. Proportional stacked histogram showing the proportion of instances for which each gesture type in each age relationship category achieves each meaning. The chart is

arranged so that similar meanings are adjacent, and that gesture types with similar histogram profiles appear in adjacent columns.

To answer the question "does interpersonal context further reduce ambiguity in gesture meaning?", yes, interpersonal context (the age and sex of signaller and recipient) entirely disambiguates meaning in 7/9 gesture types. There were two remaining ambiguous gesture types. *Present (genitals forward)*, achieved "Initiate GG-rubbing" in 100% of instances for the Female-Female context and "Initiate copulation" in 97% of instances for the Female-Male context – with the 3% to "Initiate GG-rubbing" involving sub-adult individuals. Grab-pull achieved both "Reposition" and "Climb on me", and illustrates a specific problem of our observational methods, namely that we cannot determine how much force is behind a contact gesture. Overall, behavioural and interpersonal context together largely disambiguate the meanings of bonobo gestures.

Table 8. Gesture type; Relationship is the interpersonal context, split by age or sex relationship of signaller and recipient; Meaning (ASO) achieved by each gesture type given each relationship; Number of instances that the meaning was achieved; and the proportion of instances the meaning was achieved by the total instances that the Relationship used the Gesture Type to achieve that meaning.

Gesture Type	**Relationship**	**Meaning (ASO)**	**# Instances**	**Proportion**
Reach	Young→Adult	Climb on you	7	1.00
	Adult→Young	Climb on me	19	1.00
Arm raise	Female-Male	Initiate copulation	17	1.00

	Female-Female	Initiate GG-rubbing	16	1.00
Arm swing	Female-Male	Initiate copulation	12	1.00
	Female-Female	Initiate GG-rubbing	11	1.00
Rocking	Female-Male	Initiate copulation	12	1.00
	Female-Female	Initiate GG-rubbing	17	1.00
Object shake	Female-Male	Initiate copulation	6	1.00
	Female-Female	Initiate GG-rubbing	9	1.00
Bipedal stance	Female-Male	Initiate copulation	19	1.00
	Female-Female	Initiate GG-rubbing	16	1.00
Touch	Female-Male	Initiate copulation	6	1.00
	Female-Female	Initiate GG-rubbing	9	1.00
Present (genitals forward)	Female-Male	Initiate copulation	168	0.97
		Initiate GG-rubbing	5	0.03
	Female-Female	Initiate GG-rubbing	296	1.00

DISCUSSION

Bonobo gestural communication clearly does not have syntax in the complex, recursive way that human language does. But it now seems that it also lacks syntax-like compositionality. In general, gesture types in sequences are not interpreted differently to the same gestures used singly; gesture types do not occur in specific positions in a sequence; and the position in which a gesture occurs in a sequence does not affect its meaning. Although bonobos may attend to vocal call sequences, it is unclear whether they attend to the order of vocalisations within sequences (Clay & Zuberbühler, 2009, 2011), and we have found here that they do not seem to attend to the composition of gesture sequences.

However, the apparent ambiguity of bonobo gestures is not a matter of vagueness – they mean different things in different contexts. Our classification of behavioural and interpersonal context was a simple one, yet almost entirely resolved the meaning of those bonobo gestures that had appeared ambiguous (Table 8). *Touch other* and *Grab-pull* in the grooming context remained ambiguous, but perhaps important tactile information is missing for these gesture types. How hard is the pressure being applied? Is the pressure being directed? We cannot deduce these things from video and it is possible that this missing information on our part is obvious and important for the bonobos. Minor variations in gesture form, for example "Hand fling" or "Arm fling" where the signaller engages their hand or their full arm in the movement, do not seem to affect the meanings of gestures (Hobaiter & Byrne, 2017). It is therefore unlikely that we are missing subtle differences in the ways that gestures are physically deployed that gives away the differences in meaning. However, it is possible that differences in classifications of gestures, meanings, and contexts in video coding could affect the degree to which gestures appear ambiguous, and it is always important to be mindful of what is meaningful for our study subjects. Overall, bonobos seem able to retrieve sufficient information from behavioural and interpersonal contexts to correctly decipher the intended meaning of ambiguous gestures.

In the past, researchers have examined the context in which gestures occur, and then described a gesture's meaning as flexible because it occurs in multiple contexts – a so-called "means-end dissociation" (Call & Tomasello, 2007; Halina, Rossano & Tomasello, 2013; Pika, Liebal & Tomasello, 2005; Pollick & de Waal, 2007). Here, we build on these previous studies by considering both the flexibility of gestures across context and the flexibility of gestures across meanings (or goals). We found that while most gestures can be used flexibly across contexts, they tend to have a specific meaning in a specific context. This adds an interesting dimension to the interpretation of "means-end dissociation" – gestures can occur in multiple contexts, and gestures can have multiple meanings, but when gesture and context are combined their meanings/goals become more specific.

Moreover, only around half of gestures have multiple meanings. This distinction between gestures that have only one meaning and gestures that have multiple meanings may suggest that great apes have two families of gesture types (unambiguous and ambiguous, respectively). Here we have examined only those gestures that have multiple meanings; whether there is any systematic difference between gestures with single and multiple meanings is a topic for further research.

Neglecting context in inter-species comparisons risks confounding differences in context frequency with real differences in meaning: for instance, many chimpanzee gesture types also appear ambiguous in meaning (Hobaiter & Byrne, 2014), and these too may actually have specific meanings in specific contexts. Moreover, while a large overlap has been found in the meanings of chimpanzee and bonobo gestures (Graham, Hobaiter, Ounsley, Furuichi, & Byrne, 2018), the overlap was not complete. Where gesture meanings apparently differed between the two species, it is possible that the gestures were in fact deployed in different contexts. There are striking differences in social behaviour between the bonobos and chimpanzees, such as the centrality of females to the bonobo group and the high frequency of genito-genital rubbing (Furuichi, 2011). Experiencing behavioural contexts in different proportions may have given rise to different frequencies in intended meanings, even in the absence of differences in underlying gesture meanings. Thus, future comparisons of gestural repertoires among all great ape species must take context into account.

There are two main interpretations for this relationship of meaning and context – an ambiguity account or a general-meaning account. In the ambiguity account, a gesture has multiple meanings and context divides those meanings, allowing the correct meaning to be accessed for each instance. Within the ambiguity account, gestures may be polysemous (one gesture with multiple related but distinct meanings) or homophonic (multiple gestures and associated meanings that happen to have the same form): the two are currently difficult to distinguish in nonhuman communication. In the general-meaning account, a gesture has a more general underlying meaning, for example "I want something", and context adds information, for example what is wanted (food, to travel together, to copulate). The difference between these interpretations is important, but challenging to disentangle through observation, and current methodologies may not yet allow us to differentiate systematically between these accounts. It is possible that both are correct, in different cases. Thus, while there may be a more general meaning for closely related outcomes (e.g. "Climb on me", "Climb on you"), it seems unlikely that a general meaning could underpin others (e.g. the varied outcomes of Arm Raise or Touch gestures).

Our findings reveal that great ape gestures may have greater resemblance to human language than hitherto suspected. Spoken utterances, out of context, are multiply ambiguous; normally, the intended senses are seamlessly resolved using contextual information (Tabossi & Zardon, 1993). In the same way, behavioural and interpersonal context almost entirely disambiguates the meaning of bonobo gestures. We suggest that bonobos use this information in correctly inferring the intended meanings of signallers. Given these results, contextual disambiguation of signals most likely dates to our last common ancestor with the Pan lineage, and there is potential that future comparisons with gorillas and orangutans could trace this back even further. The ability to incorporate context into human communication adds another rich layer of information for signaller and recipient alike, and it now seems that contextual information is also integral to the communication of our closest living relatives.

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