

1 **The Meanings of Chimpanzee Gestures**

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3 Catherine Hobaiter and Richard W. Byrne

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17 School of Psychology and Neuroscience, University of St Andrews, St Andrews,

18 KY16 9JP, Scotland

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20 Correspondence: R W Byrne, School of Psychology and Neuroscience, University

21 of St Andrews, St Andrews, Scotland.

22 E-mail: rwb@st-andrews.ac.uk

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25 **HIGHLIGHTS**

- 26 • 66 gestures are used intentionally to communicate 19 meanings by wild
27 chimpanzees
- 28 • We analyzed >4500 cases to extract true (non-play) meanings for 36 gestures
- 29 • Gestures have the same meaning(s) across individual signalers
- 30 • Flexible use of several gestures for same goal is higher during social
31 negotiation
- 32

33 **Summary**

34 Chimpanzees' use of gesture was described in the first detailed field study [1,2], and
35 natural use of specific gestures has been analyzed [3-5]. But it was systematic work
36 with captive groups that revealed compelling evidence that chimpanzees use gestures
37 to communicate in a flexible, goal orientated, and intentional fashion [6-8, replicated
38 across all great ape species in captivity 9-17 and wild chimpanzees 18,19]. All these
39 aspects overlap with human language, but are apparently missing in most animal
40 communication systems: including great ape vocalization, where extensive study has
41 produced meagre evidence for intentional use [20, but see 21,22]. Findings about
42 great ape gestures spurred interest in a potential common ancestral origin with
43 components of human language [23-25]. Of particular interest, given the relevance to
44 language origins, is the question of *what* do chimpanzees intend their gestures to
45 mean; surprisingly, the matter of what the intentional signals are used to achieve has
46 been largely neglected. Here we present the first systematic study of meaning in
47 chimpanzee gestural communication. Individual gestures have specific meanings,
48 independently of signaler identity, and we provide a partial 'lexicon'; flexibility is
49 predominantly in the use of multiple gestures for a specific meaning. We distinguish a
50 range of meanings: from simple requests associated with just a few gestures, to
51 broader social negotiation associated with a wider range of gesture types. Access to a
52 range of alternatives may increase communicative subtlety during important social
53 negotiations.

54

55 **Results**

56 In animal communication, signal meanings have generally been identified with the
57 information exchanged between individuals [26,27]: here, only the characteristic
58 effect of a signal on recipients is assessed. For example, monkey alarm calls function
59 as if they referred to specific predators: recipients act appropriately upon hearing the
60 calls [28-30]. Whether callers intend to influence a specific audience is unknown, and
61 suspected not to be the case [31]. In human communication, however, meaning has
62 been treated quite differently because signals - linguistic utterances - are produced
63 intentionally [32]. Indeed, the signaler's intentions are paramount, and cognitively
64 demanding flexibility is often necessary to interpret meaning [33,34]. Ape gesturing
65 is the only non-human communication system with substantial evidence for
66 intentional use [6-19]; providing a unique opportunity to examine the meanings,
67 analogous to human linguistic meanings, of non-human signals. Ape gestures show at
68 least first order intentionality: they are produced with the purpose of changing the
69 recipient's behavior [35]. We present a systematic analysis of meaning for the
70 gestures employed by a wild chimpanzee community. To date, the widely described
71 flexibility of gestures has been reported in terms of the variety of 'contexts' in which
72 a gesture is observed [8,36]. While this method avoids potential pitfalls of attempting
73 to interpret mental states of another species, it risks exaggerating flexibility where
74 gestures with a single meaning are employed across multiple contexts. One previous
75 study examined the effect on recipients of four hand gestures, concluding that
76 responses were not dependent on situational context and were 'primarily used for
77 directing a recipient's movement or attention' [38]. Here we investigate
78 communication in a natural group across the full range of chimpanzee behavior; and
79 we are able for the first time to distinguish 'real-world usage' from the play-based

80 communication that dominates in captivity. We examine what each gesture is for: if a
81 gesture is used to alter the behavior of a recipient towards a specific goal, what was
82 that goal? To find out, we adopt a holistic approach to the study of meaning that uses
83 the behavior of both signaler and recipient [39], first piloted with captive groups
84 [10,14]. We therefore focus on whether a recipient's reaction *satisfied* the signaler, so
85 indicating their intended meaning. An outcome that resulted in the cessation of
86 communication, and that represented a plausible desire on the part of the signaler (e.g.
87 not an aversive experience), was taken to have satisfied the signaler and termed an
88 Apparently Satisfactory Outcome (ASO; see SI).

89

90 **What do chimpanzees gesture to achieve?**

91 We observed 4531 gestures within 3419 bouts of intentional communication;
92 3175 bouts (4247 gestures) apparently satisfied the signaler (communication ceased
93 following the audience's response; Table S1). We used ASOs to indicate the
94 signalers' intended meanings; recorded ASOs were of 19 different kinds. Most ASOs
95 (17) were requests to encourage interactions to start (e.g. 'groom me') or to develop
96 ('move closer', 'play continue'); however, two that discouraged further social
97 interaction ('stop that' and 'move away') were used broadly across contexts to negate
98 a wide range of behavior.

99 Although we identified 19 ASOs and the chimpanzee has a repertoire of at
100 least 66 gesture types [18], some gestures may have more than one meaning. In fact,
101 only 10 of the 66 gestures were used for just a single ASO, and of these 7 were
102 recorded on ≤ 3 occasions. The majority of the repertoire was used for multiple ASOs
103 (number of ASOs per gesture type: mean=4.6 \pm 3.0, mode=2, range 1-12). The extent
104 of this multiplicity or ambiguity of meaning is likely underestimated, since the

105 number of cases of a gesture type correlated positively with the number of ASOs with
106 which it was associated (gestures with ≥ 3 cases, Pearson's correlation: $r=0.75$, $n=43$,
107 $p<0.0001$). However, some of these ASOs occurred at very low frequencies, raising
108 the possibility that, rather than implying genuine ambiguity, they might stem from
109 observer error, or misunderstandings by the recipient uncorrected in further
110 communication by the signaler. Eliminating those ASOs with less than 3 instances per
111 gesture type across the population as potential errors, the majority of the gestural
112 repertoire was associated with two or three meanings (mean 2.8 ASOs per gesture).
113 Moreover, in most cases (57 of the 66 gestures) at least one ASO was play-related,
114 e.g. 'play start'. The generality with which play-related meanings occurred indicates
115 that there may be something special about play-signals. Play is the most common
116 context for gestural communication [7,10], but in play gestures are not necessarily
117 used with their normal meaning and the outcome may not reliably signal the gesture's
118 meaning in any other context. In subsequent analyses we therefore exclude data from
119 play bouts to avoid masking the 'real-world' meaning of gestures (an analysis
120 including play data is provided in SI).

121

122 **Do gestures have specific meanings?**

123 We examined whether different gestures were associated with a specific
124 pattern of outcomes, differing from the general distribution of ASOs in gestural
125 communication. Fifteen gesture types met the conditions for inclusion in the initial
126 analysis (SI Procedures_d), and 46 individuals contributed data. We found a
127 significant effect of gesture type on distribution of ASOs (gesture: $f=2.30$, $df=14$,
128 $p=0.009$, 2-way ANOVA). Thus, the frequency with which gesture types are used,

129 outside of play, towards particular ASOs varies between gesture types: gestures have
130 specific meanings.

131

132 **Does gesture meaning vary with the identity of the signaler?**

133 The appearance of multiple meanings for a single gesture might be the result
134 of variation among signalers in the ways in which they employ their gestural
135 repertoire. We therefore examined whether meaning varied with signaler identity.
136 Fifteen gesture types met the conditions for inclusion in the detailed analysis (SI
137 Procedures_d), and 46 individuals contributed data. The possible effect of individual
138 identity was examined in two ways, graphical and statistical. For each gesture type,
139 we plotted the deviation from normal distribution of the ASO distribution (as used in
140 the ANOVAs above), per individual signaler. ASOs with similar meanings are plotted
141 adjacent to one another, allowing us to distinguish visually between gestures with
142 multiple meanings that are unambiguously different (e.g. Big Loud Scratch: ‘groom
143 me’ and ‘travel with me’), and those that are more ambiguous, with several similar
144 meanings (e.g. Object shake: ‘sexual attention male’, ‘follow me’, ‘travel with me’,
145 ‘move away’ etc.). These plots gave a graphical indication of whether individual
146 signalers used the same gesture in the same way (Figure S1). An additional 21
147 gestures were regularly used outside of play, but were not recorded with sufficient
148 frequency from enough individuals for parametric analysis; for these gestures, similar
149 plots, indicating whether or not signalers employed these gestures towards the same
150 distribution of ASOs, are provided (Figure S1).

151 In two gestures, Leaf clipping and Present climb on, all usage by all
152 individuals tested was exclusively for their primary ASO (Table S2). In a further three
153 gestures, Big loud scratch, Hand fling and Present groom, the primary ASO was

154 recorded significantly more often than all other (14) ASOs combined, indicating a
155 close association with the primary ASO. In one gesture, Mouth stroke, all usage by all
156 individuals was exclusively for the primary and secondary ASOs combined. In a
157 further three gestures, Directed push, Present sexual and Reach, the primary and
158 secondary ASOs were recorded significantly more often than all other ASOs
159 combined. In three gestures, Embrace, Object move and Object shake, the combined
160 frequency with which the primary, secondary and tertiary ASOs were recorded across
161 individuals was significantly greater than all other ASOs combined. Thus, in 12 cases,
162 of a possible 15, there was statistical evidence of an association across individuals
163 with particular outcomes.

164 We found a statistical effect of individual identity in only two of the 15
165 gesture types: Hand on and Touch other (Table S2), with a borderline effect ($p=0.058$)
166 in Slap object. Both Hand on and Touch other have a clear primary function shared
167 across individuals (respectively: ‘stop that’ and ‘acquire object’); however, their
168 secondary functions varied between individuals, although with common themes of
169 social interaction or negotiation (‘move closer’, ‘move away’, ‘climb on me’, ‘climb
170 on you’). Thus, while some gestures have ambiguous meaning, the majority does not;
171 and gestures used for specific meanings are primarily used in the same way across
172 individuals.

173

174 **What does each gesture mean?**

175 Having shown that gestures are employed for specific outcomes by all
176 individuals, we next examined gesture meaning(s). Thirty-six gestures were suitable
177 for the analysis of their ASO distributions in contexts other than play; the gestures
178 associated with each ASO as both a primary outcome and secondary outcome are

179 listed in Table 1. In 35 of the 36 cases there was a significant association between
180 gesture type and ASO distribution (Table S3: details of analysis in SI).

181 As almost all gestures (32/36) were used towards more than one ASO, we
182 sought a convenient way of describing their level of ambiguity in meaning. Following
183 Cartmill & Byrne [13], we took gestures used towards a single ASO 70% of the time
184 to have 'tight meanings', while gestures used 50-70% of the time towards a single
185 ASO were considered to have 'loose meaning'; all other cases were considered to be
186 'ambiguous'. On this basis, 13 gesture types had tight meaning, 11 loose meaning,
187 and 12 were ambiguous.

188

189 **Which outcomes are associated with the most gesture types?**

190 Thirty-six gestures were associated with 13 non-play ASOs as either a primary
191 or secondary outcome (Tables 2 & S3). We recorded how many times a particular
192 ASO was recorded as being the primary, secondary or tertiary meaning of a gesture
193 type. ASOs varied in the number of gestures for which they were a primary outcome,
194 between 0 and 9 gestures, and for which they were a primary or secondary outcome,
195 between 0 and 16 gestures. In rank ordering, the pattern is the same, whether primary
196 alone or both primary and secondary meanings were assessed (Table 2). The number
197 of gesture types associated with an ASO might be an effect of sample size, i.e. rarely
198 observed outcomes are recorded less often and have fewer gesture types associated
199 with them; however, that was not the case here. Neither the number of gestures
200 associated with an ASO as their primary outcome (Pearson's correlation: $r=0.38$,
201 $n=15$, $p=0.16$), nor primary and secondary outcomes combined (Pearson's correlation:
202 $r=0.34$, $n=15$, $p=0.22$), were correlated to the number of cases of that ASO.

203

204 **Discussion**

205

206 Chimpanzees use their gestures in purposeful communication with other
207 chimpanzees; as such they can be considered meaningful [32]. In the current study of
208 wild chimpanzees, living under conditions that permit the complete expression of
209 their natural behavior, we analyzed the meanings of 36 gestures, finding them used
210 intentionally to achieve 15 purposes, other than in play. There was considerable
211 similarity of use across individuals, indicating that meanings are inherent to gestures,
212 as opposed to idiosyncratic to particular individuals or subgroups of individuals.

213 Similar indications of specific meaning were found in studies of captive
214 orangutan and gorilla gesturing [10,14]. However, in those studies no analysis of
215 individual differences was possible, and gestures used in play were included in
216 analyses (a necessarily consequence of the limited range of behavior expressed in
217 captive groups). Any analysis of meaning from data sets including play should be
218 interpreted with caution. Although playful usage should not be confounded with real-
219 world usage in the analysis of meaning, play may serve as an important learning
220 environment for communication. Play allows younger individuals a safe testing
221 ground for their exploratory use of gesture, towards potentially risky goals such as
222 sexual solicitation or social negotiation. Our method of deciding intended meaning
223 works well in non-play contexts, whereas if data from play are included the
224 overwhelming dominance of play within the overall data set can ‘swamp’ any real
225 statistical association between gesture and (non-play) meaning.

226 Setting aside playful uses greatly reduces the apparent ‘ambiguity’ of gesture
227 meanings: 35 of the 36 gestures have specific individual patterns of meaning used
228 towards 1-3 of the 15 intended outcomes. The degree of ambiguity remaining is not

229 uniform across the repertoire. Some gestures are unambiguous, employed consistently
230 towards a single meaning, for example Leaf Clipping is used only to acquire ‘sexual
231 attention’. Others appear ambiguous: for example Grab is used for ‘stop that’ and
232 ‘climb on me’ and ‘move away’ etc. (Figure S1). Appearance of ambiguity may arise
233 in part from the difficulty for human observers in discerning subtle variations in the
234 nature of the contact. It is evident to a human recipient whether or not a gentle touch
235 is intended to reposition us or to prevent us from moving; however, those distinctions
236 are visually very difficult to distinguish. Finally, gestures can be employed towards
237 two or three outcomes of a very similar nature, for example Push is used for both
238 ‘move away’ and ‘stop that’. This last category is perhaps most similar to the type of
239 broad semantic class of information expressed in primate vocalizations, where an
240 alarm call rarely indicates (say) a leopard, specifically, but is rather used towards a
241 range of similar ground-based threats [28].

242 We found considerable variation in whether an intended meaning was signaled
243 by a single gesture type or several gestures of apparently equivalent meaning.
244 Intriguingly, the degree of this ‘redundancy’ appeared to co-vary with the need for
245 context to fine-tune intended meaning. Our method necessarily restricts analysis to
246 that of imperative demands (declarative communication requires no overt change in
247 recipient behavior to satisfy the signaler). However, amongst these imperative
248 demands we could distinguish different types of meaning, co-varying with the number
249 of gestures used to express it.

250 Where we found that an intended meaning was conveyed by several different
251 gestures, the desired outcome was often apparently one that required some negotiation
252 or persuasion. For example, a request to give affiliative ‘contact’ (Embrace, Rump
253 rub, Shake hands, Bite) does not have a canonical form of response that is always

254 appropriate: exactly what the signaler wants by giving the gesture may often only
255 become clear after some further interaction. In contrast, meanings typically conveyed
256 by a single gesture were often well-defined and unitary: for example, ‘initiate
257 grooming’ (Big Loud Scratch).

258 The subtle regulation of individual social relationships is critical to
259 chimpanzee reproductive strategy, in which strong alliances are formed with related
260 or un-related individuals of both sexes. These relationships can impact on mating
261 success, contributing towards individual fitness. Interpretation will be aided by the
262 integration of contextual cues, some of which may be quite subtle (an individual
263 starting to move in a certain direction, or prior experiences of interacting with a
264 particular signaler). We suggest that in addition the availability of multiple gestures
265 for meanings involved in social negotiation allows for equally subtle distinctions:
266 allowing for room to maneuver in negotiation of outcomes. The majority of non-play
267 use, of the gesture types that are generally employed in play, was in social negotiation
268 meanings, such as ‘follow me’, or ‘move away’. It may be that play is used to explore
269 socially delicate communications: even though gesture meanings are basically
270 species-typical, a young ape may have much to learn about the appropriateness of
271 using gestures in particular social contexts.

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273

274 **Procedures**

275

276 Observations were made on chimpanzees within the Sonso community during three
277 field periods between October 2007 and August 2009. We used focal behavior
278 sampling [40], and filmed all recorded cases of gestural communication using a Sony

279 Handycam. We defined *gestures* as discrete, mechanically ineffective physical
280 movements of the body observed during intentional communication (see [18]).
281 Movements of the whole body, limbs, and head were included; but not facial
282 expressions or static body postures. Following Call and Tomasello [8; see also 18],
283 we restricted analysis to only those gestures for which there was evidence that they
284 were used intentionally, in a goal-directed way.

285 For each individual, for each gesture type, we recorded the frequency of each
286 ASO. To remove any effect of pseudo-replication, these data were converted to
287 proportions for each individual. Thus, we calculated the proportion of the total
288 number of uses, by that individual, of that gesture, that corresponded to each ASO.
289 Then, in order to identify reliable differences in usage between gestures, we
290 calculated the overall proportion of each ASO in the data set, pooled across all other
291 gesture types, for each individual; and this ‘general distribution of ASOs’ served as a
292 null against which the actual distribution for any particular gesture type could be
293 compared. See SI Procedures for full details of all analyses.

294 All research reported was approved by the School of Psychology under the
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299

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308

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400 **Table 1: Gestural Lexicon**

401 Real-world meanings are defined and listed with the gestures to which they are
 402 associated, either a primary or a secondary outcome (Table S3: data from all
 403 individuals, raw scores converted to proportions). Meanings are consistent across
 404 individuals (Figure S1 and Table S2). Meanings are ordered in declining order of the
 405 number of gestures used to effect them: note that negation ('stop that' and 'move
 406 away') can be achieved with the largest variety of gestures, and that more alternatives
 407 are available for social negotiation than for simple requests.

408 **Meaning:** *definition* [primary outcome of these gestures] {secondary outcome of these gestures}

409
410

Stop that: *either cease behavior previously directed towards the signaler or change behavior to direct it towards another* [primary: Grab; Hand on; Jump; Push; Side roulade; Slap other; Somersault; Stomp 2-feet; Tap other] {secondary: Arm swing; Bite; Foot present; Hand fling; Punch other; Shake hands; Slap object}

Move away: *move away from signaler* [primary: Arm swing; Hand fling; Jump; Object shake; Punch object/ground; Punch other; Slap object] {secondary: Arm raise; Object move; Push; Slap other; Stomp; Tap other}

Contact: *physical contact of apparently affiliative nature, e.g. hugging, touching etc.* [primary: Bite; Embrace; Rump rub; Shake hands] {secondary: Present sexual; Reach; Touch other}

Acquire object: *give signaler object* [primary: Arm raise; Mouth stroke; Reach; Touch other] {secondary: Hand on}

Follow me: *mature recipient follows mature signaler, usually in consortship* [primary: Jump; Slap object with object; Throw object] {secondary: Foot present; Rump rub; Stomp 2-feet}

Move closer: *move closer* [primary: Beckon; Grab-pull; Slap object with object] {secondary: Arm swing; Directed push; Mouth stroke}

Sexual attention to male: *♀-responds sexually* [primary: Leaf-clipping; Object move; Stomp] {secondary: Object shake; Punch object/ground}

Climb on me: *climb on signaler's body* [primary: Foot present; Present climb on] {secondary: Grab; Grab-pull}

Initiate grooming: *grooming between signaler and recipient* [primary: Big loud scratch] {secondary: Bite; Present grooming}

Sexual attention to female: *♂-responds sexually* [primary: Present sexual] {secondary: Leaf clipping}

Reposition body: *move (and hold) body into indicated position* [primary: Directed push] {secondary: Beckon}

Attend to specific location: *adjust behavior to focus attention on indicated location* [primary: Present grooming] {secondary: none}

Travel with me (adult): *travel together with adult signaler* [primary: n/a*] {secondary: Big loud scratch; Embrace}

Climb on you: *permits signaler to climb on* [primary: n/a*] {tertiary**: Reach}

Travel with me (infant): *travel together with infant signaler* [primary: n/a*] {other**: Big loud scratch; Grab-pull; Poke}

* only recorded as secondary outcome

** rarely observed outcome; only recorded as tertiary or less frequent

411

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413 **Table 2: Primary or secondary gesture meanings (excluding play)**

414 The ASOs (as defined in Table S1) recorded as the primary, secondary, or tertiary
 415 ASO for each gesture type (Table S3). ASOs are listed in order of the number of
 416 gesture types (N) associated with them as their primary, and then secondary, or
 417 tertiary outcome.

418 *Both these ASOs were recorded only as the tertiary or even less frequent outcome of
 419 a gesture type, as used by the community as a whole. However, their use was
 420 necessarily limited to young infant signalers; evidently they would be more
 421 prominently represented in a study of infant gesturing.
 422

ASO	N ₁ (primary)	N ₁₊₂ (primary or secondary)	N ₁₊₂₊₃ (primary or secondary or tertiary)
Stop that	9	16	20
Move away	7	13	14
Contact	4	7	10
Acquire object	4	5	8
Follow me	3	6	10
Move closer	3	6	8
Sex attention (to male)	3	5	7
Climb on me	2	4	6
Initiate grooming	1	3	4
Sex attention (to female)	1	2	2
Reposition body	1	2	2
Attend to specific location	1	1	1
Travel with me (adult)	0	2	2
Climb on you*	0	0	1
Travel with me (infant)*	0	0	0

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