

1 A new window onto animal culture: The case of chimpanzee gesturing

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11 Abstract

12 Scientific interest in the diversity of gestural signalling dates back to the figure of Charles
13 Darwin. More than a hundred years later, there is a considerable body of work describing
14 human gestural diversity across languages and cultures. However, the question of
15 communicative culture in our closest living relatives, the nonhuman primates, is relatively
16 unexplored. Here, we will stir new interest into this topic by (i) briefly summarizing the current
17 knowledge of animal culture, and (ii) presenting the current knowledge on gesture cultures,
18 diversity and usage in the most common model for early hominid behavior, the chimpanzee
19 (*Pan troglodytes*). We will focus particularly on well-established behaviours being customary
20 in some and absent in other chimpanzee communities, and recently discovered social customs
21 that have been suggested to differ in their form, and/or meaning across populations. We also
22 introduce latest findings on chimpanzees' gestural diversity, providing further evidence for
23 the role social negotiation plays in gestural acquisition. We conclude that the field has been
24 hampered by misconstruing great ape gestures as FAP's, a strong research bias on the
25 perspective of signalers only, and a lack of coherent methodology to assess the meaning and
26 context of gestures across sites. We argue for systematic cross-site comparisons by viewing
27 communicative exchanges as negotiations, enabling a unique perspective onto the
28 evolutionary trajectory of culture and communication.

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36 **Special issue: The Anthropology of Gesture**

37 Communicative culture in chimpanzee gesturing

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39 Introduction

40 *Anthropology* derived from the Greek words *ánthrōpos* (ἄνθρωπος, "human") and *lógos*
41 (λόγος, "study") (Murray, 1884). It concerns the scientific study of humans and human
42 behaviour and societies in the past and present, and embodies sub-disciplines such as
43 biological, cultural, linguistic and social anthropology. While linguistic anthropology, for
44 instance, examines how language affects the social life of humans, cultural anthropology
45 focuses on the cultural variation among humans.

46 One of Anthropology's most predominant qualitative methods is ethnography, which
47 centres around close observation and descriptions of social practices and interactions in
48 naturalistic rather than experimental settings. It pays special attention to the sociocultural
49 context in which distinct activities occur. Thus, while Anthropologists build upon knowledge
50 from the natural sciences (such as for instance how the evolutionary past of *Homo sapiens* has
51 influenced its social organization and culture), the anthropological method of ethnography
52 has also deeply influenced the way how ethologists and primatologists collect data on cultural
53 and communicative skills of nonhuman animals (Goodall, 1986; Tinbergen, 1963).

54 Here, we aim to stir new interest in the topic of communicative culture, which dates
55 back to Charles Darwin's notion of human gestural diversity (Darwin, 1872b). Although more
56 than a hundred years later, there is a considerable body of work describing human gestural
57 diversity across languages and cultures (e.g. Haviland, 1993; Kendon, 1981b; Kita, 2003;
58 Morris, 1979; Núñez & Sweetser, 2006), systematic, quantitative ecological work on human
59 gestures has received relatively little research attention (Kendon, 1981a, 1993). Similarly,
60 studies into the evolutionary origins of communicative culture are nearly non-existent. The
61 present paper will draw attention to this promising research domain by providing (i) a brief
62 overview of our current knowledge on animal culture, and (ii) insight into the present evidence
63 of communicative culture in the most common model for early hominid behavior, the
64 chimpanzee (*Pan troglodytes*).

65 We will particularly focus on well-established social behaviours being customary
66 (Whiten et al., 1999) at some but absent at other communities (GROOMING HAND-CLASP, SOCIAL
67 SCRATCH), differing in their form (GROOMING HAND-CLASP, LEAF-CLIPPING), and/or meaning across

68 populations (LEAF-CLIP, DIRECTED-SCRATCH). Furthermore, we will briefly introduce a recent multi-
69 year project enabling the first systematic comparison of gestural complexity and development
70 in two different chimpanzee communities and subspecies (Fröhlich, Müller, Zeiträg, Wittig, &
71 Pika, 2017; Fröhlich, Wittig, & Pika, 2016a, 2016b). The results suggest that viewing gestures
72 of chimpanzees (and other great apes) as fixed action patterns (FAP's, defined as highly
73 stereotyped and species-characteristic behavioral sequence such as for instance the zig-zag
74 dance of a male stickleback; Lorenz, 1950; Tinbergen, 1951) has obscured a very promising
75 window onto animal culture and hence also our own cultural and communicative trajectory.

76 Animal culture

77 One of the main factors underlying humans' remarkable success to populate the planet is our
78 capacity for culture. Although, intuitively, we all know what it is, the term culture has been
79 defined in very different ways in different scientific disciplines with relatively little definitional
80 consensus within the social sciences. A comprehensive review carried out in the middle of the
81 last century by Kroeber and Kluckhohn (1952) even presented 168 different definitions of
82 culture. For instance, evolutionary anthropologists define culture relatively broadly as "the
83 transmission from one generation to the next, via teaching and imitation, of knowledge,
84 values, and other factors that influence behaviour" (Boyd & Richerson, 1988, p 2). In contrast,
85 cultural anthropologists have often relied on an overly linguistic model of culture, although
86 the underlying concepts and mechanisms are principally formed independently of language
87 (Bloch, 1991; see also for a critical account of the definition of culture and use in Psychology
88 Hirschfeld, 2018).

89 Due to the reliance on pre-Darwinian philosophical principles in the study of culture
90 (Count, 1973), the question of whether other animal species have culture is not only still highly
91 debated in the field of Anthropology but also across disciplines. Laland and Hoppitt (2003)
92 suggested that nonhuman animals are being judged according to stricter criteria than humans.
93 Interestingly, the field of animal behaviour has recently witnessed unprecedented attention
94 to animal social learning and purported animal culture (Galef, 1992; Heyes & Galef, 1996;
95 McGrew, 1992; Munding, 1980; Zentall & Galef, 1988). Although first struggling with the red
96 herring of near-synonymity (McGrew & Tutin, 1978) in terminology (e.g. using culture in
97 quotation marks, Kummer, 1971; and terms such as protoculture, Menzel, 1972; or sub-
98 culture, Kawamura, 1959), earliest notions of animal culture refer to behaviours characterized
99 by a strong learning component. For instance, Yerkes (1943) mentioned that chimpanzees

100 have to learn nest building and maternal care from others, while King (1955) saw the
101 knowledge of territorial boundaries in prairie dogs (*Cynomys*) as cultural. Lorenz (1927)
102 suggested that jackdaws (*Corvus monedula*) learn the meaning of alarm calls from conspecifics
103 and provided the first hints that genetic and cultural processes interact over evolutionary time
104 (Boyd & Richerson, 1988; Cavalli-Sforza & Feldman, 1981; Laland, Odling-Smee, & Myles,
105 2010). The first systematic investigations into socially propagated behaviours concerned food-
106 processing techniques of Japanese macaques (*Macaca fuscata*) and vocal cultures of
107 songbirds. Japanese macaques, for instance, wash sweet-potatoes in the sea before eating
108 them (Kawamura, 1959), and throw grains of wheat, scattered at the beach, into nearby water
109 to separate them from the sand (Kawai, 1965). Both behaviours were invented by single
110 individuals and then spread in the population (Kawai, 1965; Kawamura, 1959). Concerning
111 vocal cultures, earliest studies focused on vocal learning and stressed the importance of
112 sensitive phases as well as the lack of flexibility once song had developed (Catchpole & Slater,
113 1995; Marler & Tamura, 1962). Subsequently, two different approaches have been
114 established to validate the existence of animal culture. One approach focuses on the social
115 transmission mechanisms involved that enable the propagation of the behaviour between
116 individuals and across generations (Van Leeuwen, Mundry, Cronin, Bodamer, & Haun, 2017).
117 The other approach, the method of exclusion (Whiten et al., 1999), pays special attention to
118 the geographical distribution of behavioural variants, with traits qualifying as cultural only if
119 differences between populations are largely independent of environmental or genetic factors
120 (Whiten, 2018). Following these two approaches, culture has now been described in a variety
121 of animal taxa ranging from fish (Laland & Hoppitt, 2003), birds (West, King, & White, 2003),
122 to cetaceans (Payne & Payne, 1985; Rendell & Whitehead, 2001), and several nonhuman
123 primate species (Byrne, Hobaiter, & Klailova, 2011; Nakamichi, Kato, Kojima, & Itoigawa, 1998;
124 Pika & Tomasello, 2001; van Schaik et al., 2003). Tennie and Hedwig (2009) however argued
125 that it is premature to view any population specific behavioural patterns in nonhuman
126 primates as cultural. They suggest that these behaviours are bound and restricted by 'zones
127 of latent solutions', which refer to the solution space set by the general physical cognitive
128 abilities of a given species (Tennie, Call, & Tomasello, 2009). Furthermore, and in contrast to
129 cultural variants in humans (e.g. Evans & Levinson, 2009), cultural behaviours of nonhuman
130 animals have mainly been studied in foraging contexts. This is surprising since vocal cultures
131 have provided the largest body of and often also the most compelling evidence for cultural

132 transmission of behavioural traits in the animal kingdom (Laland & Janik, 2006; Payne & Payne,
133 1985). Vocal learning is however seen by some scholar as a special adaptation only (Galef,
134 1988; Whiten & Ham, 1992), and has not yet been fully integrated into discussions of animal
135 culture (Laland & Janik, 2006). Furthermore, comparative research into gestural cultures has
136 also been widely neglected, possibly due to the still widespread assumption that learning does
137 not play an important role in the production of communicative displays and gestures (Byrne
138 et al., 2017; de Waal, 2003; Fröhlich & Hobaiter, 2018; but see Pika & Fröhlich, 2019;
139 Tomasello & Call, 2018).

140 Chimpanzee culture

141 The by far most extensive species studied with regards to cultural variation, beside our own,
142 is one of human's closest living relative, the chimpanzee. This bias is due to an anthropocentric
143 or primate centric brainist (Laland & Hoppitt, 2003) perspective onto cognitive abilities but
144 most possibly also to the prevailing need of researchers of the last century to demonstrate
145 continuity of mental abilities (Darwin, 1872a; Kamil, 1987). Nevertheless, this research bias
146 has led to the establishment of an unprecedented number of long-term research stations
147 covering the very diverse habitats of chimpanzees (ranging from coastal forest, coastal
148 lagoons, mangrove swamps, coastal forest, secondary and primary forest to open savannah)
149 in the forests and savannahs of West and Central Africa (McGrew, Marchant, & Nishida, 1996).
150 Systematic syntheses of information from the main communities that have been the subject
151 of long-term fieldwork (Assirik, Senegal; Budongo and Kibale, Uganda; Bossou, Guinea; Gombe
152 and Mahale, Tanzania; Lopé, Gabon; and Taï, Côte d'Ivoire) showed that 39 behaviour patterns
153 — based on the method of exclusion — qualify as cultural variants (Whiten et al., 1999; Whiten
154 et al., 2001). They are sufficiently frequent at one or more communities to be consistent with
155 social transmission, but absent at one or more others where environmental explanations
156 could be rejected (Whiten et al., 1999; Whiten et al., 2001).



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Figure 1. Adolescent chimpanzee male of the South community, Tai National Park, Côte D'Ivoire using cultural variant type CV3, cracking a Coula nut on a stone with a wooden hammer. ©Tobias Deschner

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These cultural variants can be clustered in different relationship types:

- Cv.1: purely behavioural patterns of single individuals (e.g. RAIN-DANCE);
- Cv.2: dyadic relationships between an individual and an inanimate object to protect (e.g. SEAT VEGETATION), clean body parts (e.g. LEAF-NAPKIN), or to please (e.g. SELF-TICKLE);
- Cv.3: triadic relationships involving an individual, (i) an inanimate object and a prey species (e.g. ANT-DIB-SINGLE, TERMITE-FISH using non-leaf material), or (ii) two inanimate objects (e.g. NUT HAMMER, FOOD-POUND ONTO WOOD, see figure 1); and
- CV.4: triadic relationships involving an individual, an inanimate object and a conspecific (e.g. CLUB) (Whiten et al., 1999; Whiten et al., 2001).

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Communicative culture

The majority of cultural variants so far observed in chimpanzees concern relationships between an individual and an inanimate object to gain access to food. Surprisingly little is known, however, about the transmission of social behavioural patterns involving communicative signalling (Nakamura, McGrew, Marchant, & Nishida, 2000; Nishida, Matsusaka, & McGrew, 2009). One reason is that the earliest studies on communicative signalling were highly influenced by Darwin's conception of human facial expressions (Darwin, 1872b). He suggested that they (a) constitute a shared heritage of our species, and (b) show similarities to the expressions of other animals (e.g. cats, dogs and nonhuman primates).

179 Darwin provided here another argument—a behavioural one—to strengthen his hypothesis
180 of evolutionary continuity (de Waal, 2003). In parallel, he coined a powerful example of what
181 ethologist would later call an *Erbkoordination*. The central idea behind the *Erbkoordination* or
182 FAP (see for change of meaning and loss of the 'Erb' part i.e., “inherited”, Pika, 2016) is that
183 complex movement patterns share certain aspects: They (a) are characterized by a relatively
184 high degree of rigidity, (b) are not learned from conspecifics, (c) continue to completion
185 without further stimulation once elicited, (d) can occur spontaneously in *vacuo*, and (e) are
186 species-specific (for an overview see, Pika, 2016)). The insight of ethologists was that each
187 species can not only be characterized by structural features (e.g. eyes, ears, digestive system),
188 but also by stereotypical motor patterns that must have been subject to the same laws of
189 natural selection as any other trait (Lorenz, 1950; Tinbergen, 1951). While Darwin had picked
190 the one feature of human behaviour that indeed seems to fit most or all of the above aspects
191 of an FAP, the strong research emphasis of ethologists on FAPs resulted in studying
192 communicative signals for a long time as inherited and fixed displays (sensu Huxley, 1914).

193 In parallel, comparative psychologists had started to investigate whether great apes
194 are capable to comprehend and produce human language (Hayes, 1951; Hoyt, 1941; Kellog &
195 Kellog, 1933). Since attempts to teach human spoken language to chimpanzees had failed,
196 researchers tried to bypass great apes’ difficulties in speech production by focusing on the
197 gestural modality (for an overview see Pika, 2015). One of the most successful studies showed
198 that a chimpanzee female, Washoe, was able to produce and comprehend over a hundred of
199 manual signs (ASL), invented new ones and modulated taught signs for new goals (Gardner &
200 Gardner, 1969). This work suggested that great ape gestural signalling shows more flexibility
201 and deliberance than their vocal communication and had a strong influence on researchers’
202 approaches to studying spontaneous, natural communicative interactions of nonhuman
203 primates (Liebal, Waller, Burrows, & Slocombe, 2013). In the past two decades, a number of
204 researchers and research labs have begun to investigate great ape gestural communication,
205 including importantly their usage and function in individuals living in their natural
206 environments (Byrne et al., 2017; Call & Tomasello, 2007; Fröhlich, Kuchenbuch, et al., 2016;
207 Fröhlich et al., 2017).

208 Concerning culture, the two best-known communicative cultural variants are the
209 GROOMING HAND-CLASP and LEAF-CLIPPING (Whiten et al., 2001). Recently, three other social
210 customs, the SOCIAL SCRATCH (Nakamura et al., 2000), the DIRECTED-SCRATCH (Pika & Mitani, 2006),

211 and the RAINDANCE (Whiten et al., 1999) were reported, and there is evidence for the influence
212 of interactional and social exposure on gestural diversity (Fröhlich et al., 2017; Fröhlich, Wittig,
213 et al., 2016a). In the following, we will introduce these behaviors and related findings in detail
214 and discuss current limitations hampering research into communicative culture.

215 *The grooming-hand-clasp*

216 In the GROOMING HAND-CLASP “each of the participants simultaneously extends an arm
217 overhead and then either one clasps the other's wrist or hand, or both clasp each other's hand.
218 Meanwhile, the other hand engages in social grooming of the other individual's underarm
219 area revealed by the upraised limb, using typical finger movements. In doing this, the two
220 chimpanzees sit facing each other on the ground in a symmetrical configuration. Either both
221 raise their right arms and groom with their left, or vice-versa” (McGrew & Tutin, 1978, p 238).

222 The GROOMING HAND-CLASP occurs at the beginning of, or during, a bout of social
223 grooming and results in interactants engaging in dyadic and mutual (as opposed to polyadic
224 or reciprocal) grooming each other (McGrew & Tutin, 1978). This behavior was discovered by
225 McGrew and Tutin (1978) in the second half of the last century, when most of the published
226 knowledge of the natural behaviors of individual chimpanzees came from two long-term field
227 projects: the Gombe field station, Gombe Stream Reserve and the Kasoge field station, Mahali
228 Mountains in Tanzania (Nishida, 1968, 1970; Van Lawick-Goodall, 1968, 1973). Both projects
229 started in the 1960's (Gombe: 1960; Kasoge: 1965) and focused on investigations of single
230 well-known groups (Kasakela at Gombe and Kajabala [K-group] at Mahale) in which all
231 members are individually recognizable. The two sites are approximately 170 km apart and
232 represent ideal candidates for comparative and cross-cultural studies applying the method of
233 exclusion (Whiten et al., 1999): The chimpanzees belong to the same subspecies, *Pan*
234 *troglodytes schweinfurthii*, but significant genetic drift seems very unlikely. Furthermore, they
235 inhabit similar ecological habitats and show considerable overlaps in their diet (Nishida, 1974;
236 Wrangham, 1975, 1986). Hence, differences between populations due to environmental or
237 genetic factors can be largely ruled out.

238 The GROOMING HAND-CLASP is one of the best examples for environmental constraints
239 being so broad that they can be ruled out as determining factors. Since grooming is a universal
240 behavior in chimpanzees, and the behavior itself is independent of vegetation, the GROOMING
241 HAND-CLASP could in principle be performed in any given environment. Upon first discovery, it
242 was frequently used by individuals of the K-group at Kasoge, but had never been documented

243 in thousands of hours of observation at Gombe (McGrew & Tutin, 1978). In the mean time, it
244 has also been found to be a customary behavior (i.e. is regularly deployed by all members of
245 a certain age or sex class, Whiten et al., 1999) in the Kanyawara and Ngogo communities
246 (Whiten et al., 2001; Pika unpublished) of the Kibale National Park, while being absent at the
247 other long-term field site Budongo in Uganda (Whiten et al., 2001). Furthermore, details of
248 the behavioural patterns seem to differ between groups at Kasoge: While individuals of the K-
249 group clasp palm-to-palm with both wrists being extended, individuals of the Mimikile group
250 (M-group) prefer to clasp onto the wrist or forearm of conspecifics involving flexed wrists
251 (McGrew, Marchant, Scott, & Tutin, 2001; see figure 2 for the same pattern performed at the
252 Rekambo community, Loango Chimpanzee Project, Loango National Park (Gabon)).
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255 **Figure 2.** Adult chimpanzee males (left and middle) of the Rekambo community, Loango National Park (Gabon)
256 engaging in the GROOMING HAND-CLASP with their left hands. With their right hands they are
257 grooming the exposed underarms. Contact is limited to wrist-to-wrist. ©Lara Southern
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259 At Kanyawara, the behavioural patterns deployed seem to be explained by matrilineal
260 relationship rather than conformity on the group level (Wrangham et al., 2016). The GROOMING
261 HAND-CLASP also represents one of the best-studied cultural variants in chimpanzees living in
262 captive environments (de Waal & Seres, 1997; van Leeuwen, Cronin, Haun, Mundry, &
263 Bodamer, 2012). For instance, at the Yerkes Primate Center Field Station (USA) it originated
264 from one female chimpanzee and took about one decade to spread to all adult chimpanzees

265 in the colony. Furthermore, at the Chimfunshi Wildlife Orphanage Trust (Zambia) it seems to
266 represent a group-level cultural tradition (Van Leeuwen et al., 2017).

267 *Leaf-clipping* —

268 LEAF-CLIPPING has so far only been described in wild individuals. This cultural variant was
269 discovered by Nishida (1980) in individuals of the K-group at Kasoge. It consists of a
270 chimpanzee picking off one to five stiff leaves, grasping the petiole between the thumb and
271 the index finger, repeatedly pulling it from side to side while removing the leaf-blade with the
272 incisors, and thus biting the leaf to pieces. The removing of the leaf-blade results in a
273 conspicuously ripping sound. When only the mid-rib with tiny pieces of the leaf-blade remains
274 (and the mid-rib often resembles a tooth-pick), the chimpanzee drops it and starts another
275 sequence of ripping up a new leaf (Nishida, 1980). In contrast to the GROOMING HAND-CLASP,
276 which occurs in only a single context, the grooming context, LEAF-CLIPPING has been linked to
277 several contexts and behavioral outcomes. For instance at Kasoge it is used to solicit sex, to
278 initiate leaving together on a consortship, to demand food from human observers, during
279 solitary play and as a signal of frustration (Nishida, 1980). At Bossou, it has been observed
280 mainly in the play and frustration context (Sugiyama, 1981), while at Taï, it is used as part of
281 the drumming sequence by adult males and as a signal of frustration (Boesch, 1995).
282 Furthermore, details of the behavioral pattern seem to differ between communities at Kasoge
283 and Taï, with chimpanzees at Taï taking the leaf blades together from both sides of the petiole
284 between their lips and remove them in one movement, instead of repeatedly nipping small
285 pieces (Boesch, 1995).

286 Interestingly, longitudinal observations of LEAF-CLIPPING behavior at Taï strengthen the
287 semantization hypothesis of Wickler (1967; see also Plooi, 1978). This hypothesis postulates
288 that some species evolved a more flexible and diverse communicative tool-kit enabling the
289 attribution of new meaning to signals and dissociation from behavioral domains, ends and
290 contexts (see for a discussion of the use of the term meaning, Liebal & Oña, 2018). For
291 instance, after ten years of studying the behavior of the chimpanzees at Taï, Boesch (1995)
292 noted that in addition to the above mentioned contexts, individuals were employing LEAF-
293 CLIPPING while resting on the ground, thereby interrupting the nap of party members.

294 A recent study in the South group at Taï showed that LEAF-CLIPPING had disappeared for
295 almost two years and re-appeared after an alpha male takeover (Kalan & Boesch, 2018).

296 *The social scratch*

297 In the SOCIAL SCRATCH, one individual rakes the hand back and forth across the body of
298 a conspecific, usually scratching the other with the nails (Nakamura et al., 2000). This behavior
299 has been first observed in individuals of the M-group at Kasoge while being absent at Bossou,
300 Gombe, Kanyawara, and Tai (Nakamura et al., 2000). Although it seems the typical “you
301 scratch my back, I’ll scratch yours” gesture (de Waal, 2003), SOCIAL SCRATCHING does not result
302 in responses and/or changes in behavior by recipients (Nakamura et al., 2000). Recently, a
303 similar behavior has also been observed to be customary in adult males of the Ngogo
304 community (Nishida, Mitani, & Watts, 2004). In contrast to chimpanzees of the M-group,
305 however, who use flexed fingers to stroke the body of their interaction partners, males of the
306 Ngogo community scratch by using their fingers to poke the body of their grooming partner.
307 They also tend to keep their fingers straight (see figure 3). The length covered by a single
308 movement of SOCIAL SCRATCHES among the males at Ngogo is thus much shorter, while
309 movements by M-group males are long. Another difference in the behavioral patterns
310 concerns the targeted body parts, with male chimpanzees of the M-group mostly scratching
311 the back of others, while male chimpanzees of Ngogo do not show such preference.

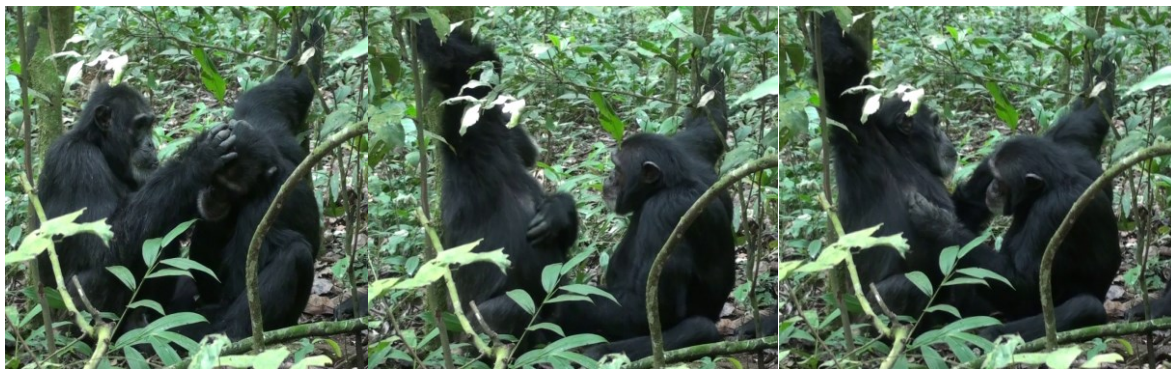


312
313 **Figure 3.** Adult chimpanzee male of the Ngogo community, Kibale National Park (Uganda) poking the neck of
314 his grooming partner with straight fingers of his left hand. ©Simone Pika

315 *The directed scratch*

316 The *directed scratch* was termed by Pika and Mitani (2006) and involves an individual
317 making a relatively loud and exaggerated scratching movement on a part of his own body

318 towards an attending partner. The word ‘directed’ refers to its intentional usage (i.e. directed
319 to a recipient to achieve a desired goal). It was observed in grooming interactions of adult
320 chimpanzees of the Ngogo community, and is a customary behavior (Whiten et al., 1999). The
321 gesture seemed to be used to indicate a precise location on the signaler’s body and to request
322 grooming from the recipient. Especially in dyads of high-ranking and strongly bonded males,
323 recipients immediately groomed the indicated spot and/or used response gestures to
324 negotiate roles during a grooming session and keep the session going (Pika, 2014; Pika &
325 Mitani, 2006; see figure 4). Similarly, Goodall (1968) suggested that deliberate scratching
326 movements during grooming sessions of chimpanzees at Gombe serve as communicative
327 signals since recipients normally responded by grooming the body parts scratched. Plooij
328 (1978, p 125), studying also individuals of the Kasakela group at Gombe, noted: “Two
329 individuals are sitting together and have been engaged in self-grooming for some time.
330 Presently one of them turns her back towards the other, scratches at a certain spot and makes
331 a tonal grunt. At first the other continues his self-grooming. The first individual keeps her hand
332 on the same spot, her back still turned toward the other, and waits. Finally, the other starts
333 grooming her where she has indicated. She then takes her hand away.”



334
335 a) b) c)
336 **Figure 4.** a) Adult chimpanzee male, Hare-lip (left) of the Ngogo community, Kibale National Park (Uganda)
337 grooming another high-ranking male, Basie (right). b) Hare-lip uses a DIRECTED SCRATCH on his right
338 chest. c) Basie subsequently grooms the indicated spot. ©Simone Pika

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340 Furthermore, Goodall (1986, p 133) noted that a chimpanzee mother, “before climbing from
341 a tree, often pauses at a low fork and scratches, looking up at her infant. This serves as a signal;
342 the child usually hurries to the mother and climbs aboard ready for descent”. This observation
343 may suggest that at Gombe DIRECTED SCRATCHES are used to achieve different goals. At Budongo,
344 researchers described BIG LOUD SCRATCHES, which seem to be employed in grooming interactions

345 toward a single outcome only: to initiate grooming (Hobaiter & Byrne, 2014). Although BIG
346 LOUD SCRATCHES also qualify as intentional means, and thus may also be denoted as DIRECTED
347 SCRATCHES, DIRECTED SCRATCHES do not necessarily have to be 'big', but can also involve small,
348 repeated and exaggerated scratches for instance in the facial region. Interestingly, van Hooff
349 (1973) observed in captive chimpanzees the use of a related tactile gesture to solicit grooming:
350 Individuals gently took the hands of conspecifics and brought them into contact with their
351 own bodies. Recipients always responded by grooming the touched location.

352 *The rain-dance*

353 The RAIN-DANCE is performed at the start of heavy rainfall and consists of vigorous,
354 sometimes slow sometimes rapid, charging displays (such as ground slap, buttress-beat,
355 branch drag, but also pant-hoots) of one to several adult males (Goodall, 1971; Whiten et al.,
356 2001; see figure 5). The display sequence tends to return the male/s to his/their starting
357 position, to possibly coordinate or dance in parallel with another male (Goodall, 1971; Whiten
358 et al., 2001). The RAIN-DANCE could, in principle, be performed in any given environment with
359 shakable vegetation. Hence, it is another excellent example for environmental constraints
360 being highly implausible to determine this specific behavioral outcome (Whiten et al., 2001).

361 The RAIN-DANCE has been first observed in males at Gombe. It is also customary at the
362 field sites Lopé, Ngogo, and Taï, but seems to be absent at Bossou and Budongo (Goodall,
363 1971; Whiten et al., 2001; Pika unpublished). Whiten and colleagues (2001) noted that the
364 elements involved in the RAIN-DANCE contrast with normal charging displays in omitting
365 intimidation of other chimpanzees. However, they also describe differences in the behavioral
366 patterns deployed: For instance at Taï, a RAIN-DANCE seems to be totally silent and resembles a
367 slow-motion version of a normal chimpanzee display. In contrast, at all East African sites (with
368 the exception of Ngogo, Pika unpublished; see video 1), the dancing individual/s incorporate
369 their species-typical long-distance vocalization, the pant-hoot. At Kasoge, Nishida (Whiten et
370 al., 2001) distinguished two versions, a 'noisy, vigorous type' involving several adult males and
371 a 'silent, slow type' involving a single male.

372 *Interactional experience and social exposure*

373 As mentioned above, the modality of gesturing has been widely neglected as a window into
374 animal culture due to the mistake to assimilate great ape gestures to the species-typical
375 displays of other mammals (Tomasello & Call, 2018). However, a recent multi-year project by

376 Fröhlich and colleagues (2017; 2016a) systematically compared and quantified gestural
377 diversity and development of subadult chimpanzees living in two different chimpanzee
378 communities (Kanyawara and Tai) and belonging to two different subspecies (*Pan troglodytes*
379 *schweinfurthii*, *Pan troglodytes verus*). The researchers showed that the number of interaction
380 rates with non-maternal conspecifics (e.g. infants of non-related individuals) and the number
381 of previous interaction partners positively impacted upon gesture frequency and, most
382 importantly, gestural diversity (Fröhlich et al., 2017). Hence, infants of social mothers had a
383 richer set of gestural means to maneuver through a world of highly complex social and
384 ecological challenges due to being exposed to a wider social network and multidimensional
385 interaction possibilities. Moreover, the project also provided evidence that chimpanzees
386 flexibly adjust their gestures to social circumstances and individual matrices of interactants
387 (Fröhlich, Wittig, et al., 2016a). These results thus show that gestural interactions are mutually
388 constructed, flexible communicative means on behalf of both, recipients and signalers. They
389 thus have the potential to settle the recent debate on gestural acquisition by strengthening
390 the Social Negotiation Hypothesis (sensu Plooi, 1978; Wittgenstein, 1953). This re-vised
391 hypothesis emphasizes the involvement of underlying social rather than individual learning
392 processes (Tomasello & Call, 2018) or genetic predispositions (Byrne et al., 2017). It proposes
393 that the creation of gestures starts with the shaping and exchange of full-blown behaviors
394 between interactants (including social and non-social behaviours; Fröhlich, Wittig, et al.,
395 2016b; Pika & Fröhlich, 2019). The exchange then results in a shared understanding that
396 certain behaviors

- 397 (a) can be used communicatively;
- 398 (b) carry distinct meaning linked to particular social contexts; and
- 399 (c) are produced to achieve distinct goals.

400 The accumulated knowledge can be generalized across dyads, to enable the most efficient and
401 least costly communication transfer, and is open to subsequent adaptation in terms of form
402 and meaning (e.g. a gesture type might undergo a change in the behavioral pattern, its
403 meaning and/or its diversity of meanings). Hence, each gestural performance by a given
404 signaler represents a highly variable online adjustment (sensu Perlman, Tanner, & King, 2012).

405 *Current limitations and new approaches*

406 The presented findings on communicative customs and gestural diversity in chimpanzees
407 suggest that communicative interactions are useful candidates to gain a better understanding

408 of animal culture. However, the field has been hampered by misconstruing great ape gestures
409 as FAP's, a strong research bias on the perspective of signalers, and a lack of coherent
410 methodology to assess the meaning (see for a recent overview Liebal & Oña, 2018) and
411 context of gestures across sites. For instance, traditionally researchers distinguished between
412 the message of the signaler, the meaning extracted by the recipient, and the context
413 accompanying it (Smith, 1965). This approach conceptualized meaning from the perspective
414 of the recipient only and ignored the communicative interplay between signaler and recipient.
415 In addition, it resulted in using the accompanying context to interpret and assign a distinct
416 meaning to a given signal (Call & Tomasello, 2007). This approach, however, risks to use
417 "context" as a substitute for "meaning" (Liebal & Oña, 2018), and ignores other relevant
418 information crucial for the specific situation including recipient's attention. For instance,
419 rather than being an example for semantization and the ability to create new meaning (Plooij,
420 1978; Wickler, 1967), LEAF-CLIPPING may simply carry a single meaning: to attract the attention
421 of conspecifics. It thus functions as an attention-getter (Tomasello & Call, 1997, 2018),
422 changes the attentional state of recipients and results subsequently in several different
423 behavioural outcomes: sex, going on a consortship, waking up conspecifics, etc.

424 Recently, however, researchers (e.g. Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014)
425 started to employ a more holistic approach to investigate whether great ape gestures carry
426 distinct meaning by integrating both the perspective of signalers and receivers. They
427 investigated whether a recipient's reaction 'satisfied' the signaler (apparent satisfactory
428 outcome: ASO; operationalized by whether or not communication ceased after a response),
429 and whether that outcome represented a plausible desire on behalf of the signaler (e.g. not
430 an aversive experience). However, this approach has not yet been widely accepted (Liebal &
431 Oña, 2018; Roberts, Vick, & Buchanan-Smith, 2012), and should be extended to also take into
432 consideration changes of attentional states as behavioral satisfying outcomes. In line with de
433 Waal (2003, p 7), we thus argue to view communicative exchanges as "a form of negotiation,
434 [with] ... previous classifications hav...[ing] ignored the specifics of what animals ([signalers])
435 try to achieve with their exchanges".

436 Furthermore, the cultural potential of some behaviors (such as for instance the SOCIAL
437 SCRATCH) and hence their usefulness for answering research questions concerning their form,
438 meaning and underlying social transmission processes have been overlooked. We thus
439 propose to concentrate research efforts more efficiently and to form proficient field site

440 collaboration networks to develop and employ shared coding schemes enabling systematic,
441 cross-site and hopefully soon also cross-species comparisons.

442 *Conclusion*

443 Communicative interactions are useful candidates to gain a better understanding of animal
444 culture. Future investigations into communicative cultural variants will thus provide a crucial
445 window into the underlying behavioral plasticity, and aid in tackling the question whether
446 other animals understand and produce *new* meanings (Plooij, 1978). Hence, systematic cross-
447 site (and hopefully also cross-species) investigations into communicative culture in
448 combination with the application of comparable methodology and coding schemes will
449 provide crucial food for thought for any consideration of the role that gestures and
450 communicative interactions may have played in the evolution of human culture and
451 communication (Levinson & Holler, 2014; Pika, Wilkinson, Kendrick, & Vernes, 2018).

452

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459

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