

1 The development of gestural communication in great apes

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12

13 Abstract

14

15 Great apes deploy gestural signals in goal-directed and flexible ways across a wide range of
16 social contexts. Despite growing evidence for profound effects of developmental experience
17 on social cognition, socio-ecological factors shaping gesture use are still poorly understood,
18 particularly in apes living in their natural environment. After discussing current ambiguities
19 in terminology and methods, we review recent work implementing a longitudinal and/or
20 cross-sectional approach in great ape gesture acquisition and development. To understand
21 whether and to what extent the socio-ecological environment influences gestural
22 communication, it is essential to distinguish between the gesture *repertoire* and gesture
23 *usage*, which represent different levels of analysis. While the majority of the apes' gestural
24 repertoire seems to be innate, accumulating evidence shows that the communicative usage of
25 these signals is substantially affected by interactional experiences throughout ontogeny.

26

27 **Keywords**

28 gesture, communication, development, repertoire, usage, great apes

29

30 **Significance statement**

31 Great apes navigate their differentiated social relationships by means of a large and flexible
32 repertoire of gestures. However, gestural ontogeny is still poorly understood, particularly in
33 primates living in their natural environment. We first discuss how the different usages of the
34 term ‘gesture’ have led to a number of apparently disparate views, but highlight that these
35 perspectives each provide their own contribution and may be reconciled by considering them
36 as different levels of explanation. We then review recent studies on the various individual and
37 social factors shaping the gestural use in great apes throughout development. While the
38 majority of the apes’ gestural *repertoire* seems to be innate, the *communicative usage* of
39 these signals is substantially affected by interactional experiences throughout ontogeny.
40 Given that ape gestural signals are inherently multimodal and are then often combined with
41 other communicative signals, a broad multimodal perspective on gesture is important in order
42 to gain a thorough understanding of the developmental processes underlying great ape
43 communication.

44 **Introduction**

45 Gestural communication permeates practically every aspect of great apes' social lives.
46 Broadly defined as socially directed and mechanically ineffective bodily movements (e.g.
47 Cartmill and Byrne 2007; Hobaiter and Byrne 2011a; Pika 2008), gestures occur in everyday
48 communication across the full range of social contexts from meat-sharing and sex to joint
49 travel and grooming and between all possible combinations of age-sex class relationships, for
50 example: same-sex dyads during affiliation, social grooming, or travel (Douglas and
51 Moscovice 2015; Goodall 1986; Pika and Mitani 2006); male-female dyads during
52 consortship and mating (Genty and Zuberbühler 2014; Hobaiter and Byrne 2012) or mother-
53 infant dyads in joint travel, food sharing, and social play (Bard 1992; Fröhlich et al. 2017;
54 Halina et al. 2013; Plooij 1978).

55

56 Early descriptions of gesture use date back to the 1930s (for example: Ladygina-Kohts 1935;
57 Ladygina-Kohts et al. 2002), and were included in the first field studies of chimpanzees
58 (Goodall 1986; Plooij 1978; Plooij 1979; Plooij 1984; Van Lawick-Goodall 1968) and
59 gorillas (Schaller 1963; Schaller 1965). Comparative gestural research was initially focused
60 on great apes living in captive settings (chimpanzees, *Pan troglodytes*: Tomasello et al. 1985;
61 Tomasello et al. 1989; Tomasello et al. 1994; Tomasello et al. 1997; gorillas, *Gorilla gorilla*:
62 Tanner and Byrne 1996; Pika et al. 2003; bonobos, *Pan paniscus*: Pika et al. 2005;
63 orangutans, *Pongo abelii/pygmaeus*: Liebal et al. 2006, Cartmill and Byrne 2007). These
64 studies showed that great apes rely on gestures in their day-to-day intra-specific
65 communication and possess extensive gestural repertoires (for review see: Call and
66 Tomasello 2007). Great ape gestures qualify as *intentional* signals: irrespective of the
67 species, methods, setting (field/captive), or research focus, across studies researchers find
68 abundant evidence that gestures are regularly produced towards individual recipients in goal-

69 oriented ways across a wide range of social contexts (e.g. Bard et al. 2014b; Byrne et al.
70 2017; Call and Tomasello 2007; Fröhlich et al. in press; Perlman et al. 2012; Roberts et al.
71 2014a). For example: gesturing is adjusted to the visual orientation of the target recipient
72 (e.g., Cartmill and Byrne 2007; Leavens et al. 2005b; Liebal et al. 2004); signallers persist in,
73 and sometimes elaborate, their gesturing until their goal is achieved (e.g. Cartmill and Byrne
74 2007; Leavens et al. 2005b; Hobaiter and Byrne., 2011b; Roberts et al. 2014b); and gestures
75 are characterized by a flexible relationship between signal and outcome (means-ends
76 dissociation), implying individual signallers are able to use different signals/gestures to
77 achieve the same outcome/goal, or a single gesture for several outcomes (Graham et al.,
78 2018; Liebal et al. 2006; Pika et al. 2003; Tomasello et al. 1994).

79

80 While the goal-oriented and flexible use of gestural signals by great apes is well established,
81 less attention has been dedicated to the mechanisms underlying gesture acquisition and use
82 during an individual's lifetime. A thorough understanding of development is critical for
83 deciphering to what extent communication depends on input from the social and physical
84 environment (Bard et al. 2014a; Liebal et al. 2013; Pika and Fröhlich 2018). In a pioneering
85 study at the first established chimpanzee field site, Gombe in Tanzania, Frans Plooij (1978)
86 described a sequence of communicative development in chimpanzee infants. Following
87 Plooij's early work (1978; 1979), a number of studies explored gestural acquisition and
88 development in captivity (Bard et al. 2014b; Halina et al. 2013; Savage-Rumbaugh et al.
89 1977; Schneider et al. 2012a; Schneider et al. 2012b; Tomasello et al. 1994; Tomasello et al.
90 1997; Tomasello et al. 1985; Tomasello et al. 1989). However, while captive studies provide
91 opportunities for more fine-grained analyses, apes' behaviour and development may be
92 substantially impacted by the physical and social environment afforded by captive settings
93 (Bard 1992; Boesch 2007; Hobaiter and Byrne 2011a; Seyfarth and Cheney 2017; Tanner and

94 Byrne 1996). To understand to what extent communicative development incorporates input
95 from a range of socio-ecological environments, findings generated in captivity should be
96 complemented by those of populations living in their natural environment (Boesch 2007).
97 Fortunately, the number of studies of gestures and gesturing in wild groups has also grown
98 rapidly in recent years (e.g. Douglas and Moscovice 2015; Fröhlich et al. 2016a; Fröhlich et
99 al. 2017; Fröhlich et al. 2016b; Fröhlich et al. in press; Genty et al. 2009; Graham et al. 2016,
100 2018; Hobaiter and Byrne 2011a; Hobaiter and Byrne 2011b; Hobaiter and Byrne 2012;
101 Hobaiter and Byrne 2014; Pika and Mitani 2006; Roberts et al. 2014a; Roberts et al. 2012).

102

103 This review has two major objectives. First, we discuss how different operationalisations of
104 the term ‘gesture’ have led to substantial variation between lines of gestural research. This
105 variation makes direct comparability between studies challenging, but also highlights the
106 importance of considering different perspectives in building a complete picture of gesture
107 acquisition. Second, we review the breadth of recent research on the mechanisms that shape
108 great ape gestural repertoires and the individual and social factors that impact their use during
109 development.

110

111 **The problem with definitions: what is a ‘gesture’?**

112 Despite decades of research, there remains no strict consensus on to how define a gesture.
113 Many researchers would probably agree that gestures include socially directed, mechanically
114 ineffective movements of the extremities (e.g. Bard et al. 2014b; Cartmill and Byrne 2010;
115 Fröhlich et al. 2016a; Hobaiter and Byrne 2011a; Pika 2008; Tomasello et al. 1997). Given
116 that signals (as opposed to cues) are defined in evolutionary biology as traits that have been
117 under selection specifically for their communicative function (Maynard Smith and Harper
118 2003; Ruxton and Schaefer 2011), this definition has led to many ambiguities. For example,

119 studies including ‘mechanical ineffectiveness’ in their definition seldom specify whether it
120 refers to the form or the outcome of a gesture (Perlman et al. 2012). Moreover, studies vary
121 in terms of whether gesture is restricted only to movements of the hand and fingers (Leavens
122 and Hopkins 1998; Leavens et al. 2010; Pollick and De Waal 2007; Roberts et al. 2014a;
123 Roberts et al. 2012), includes body postures and bodily movements (for example: bobbing,
124 rocking; Genty et al. 2009; Tanner and Byrne 1996), only includes actions qualified by
125 criteria of first-order intentionality, or incorporates different sensory modalities beyond the
126 visual channel.

127

128 The traditional dissociation of animal gesture from signals used in dynamic social displays by
129 the field of comparative psychology is a central concern. In most recent studies on gestural
130 communication, the ‘gestures’ described go beyond movements of the extremities to
131 encompass those of the entire body or even static body postures (e.g. Bard et al. 2014b;
132 Fröhlich et al. 2016a; Genty et al. 2009; Graham et al., 2016; Halina et al. 2013; Hobaiter and
133 Byrne 2011a; although cf. Pollick and de Waal 2007; Roberts et al. 2012). The distinction of
134 a gesture from a ‘display’ is only in the evidence for its intentional use. However, given that
135 the criteria for intentional use are typically not considered or explored in ethological
136 descriptions of displays, comparison across research fields and across taxa becomes
137 problematic. Take, for example, the ‘leaf clip’ gesture used by chimpanzees; outside of
138 gestural research it is typically categorized as a ‘display’ (Matsumoto-Oda and Tomonaga
139 2005; Nishida 1980), but within gestural research as a manual gesture with clear evidence for
140 intentional use (Hobaiter and Byrne 2011a; Hobaiter and Byrne 2012). In the opposite case
141 the ‘hand-clasp’ (a social signal used by chimpanzees in grooming) is often categorised as a
142 gesture in ethology (Arbib et al. 2008; Bard et al. 2014b; Pollick and De Waal 2007; Whiten
143 et al., 1999), but without any evidence for (or at least investigation of) its intentional use.

144 What do we call a mechanically ineffective movement of the extremities that functions as a
145 signal, but without evidence that it is goal-directed? A vocalization researcher would not
146 label a chimpanzee vocal ‘hoo’ signal differently depending on the cognitive state of the
147 signaller, but a gesture researcher might (Liebal et al. 2014).

148

149 The emphasis on intentional use as a key criterion of a gestural signal stems from the
150 excitement generated by the early demonstrations that great ape gestures were the first
151 intentional communicative signals described outside of human language (Hewes 1973;
152 Leavens and Hopkins 1998; Plooiij 1978; Tomasello 2008). Today, most gestural researchers
153 require that every token of signal use, irrespective of its physical similarity to previous cases
154 of gesturing, be accompanied by some evidence of intentional use to be classified as a
155 ‘gesture’. So the distinction between categorising socially directed, goal-directed physical
156 actions that meet the criteria for intentional gesture, and stereotyped and reflexive
157 behavioural signals that do not (such as the mating displays of many birds), depends on our
158 ability to *detect* intentional use. However, the detection and description of intentional signals
159 remains the source of significant debate (Bar-On 2013; Moore 2015; Scott-Phillips 2015;
160 Townsend et al. 2016). We have no access to a signaller’s internal cognitive processes, and
161 instead are reliant on external behavioural indications that together suggest intentional
162 behaviour. These behavioural criteria for establishing intentional use typically refer to the
163 signaller’s and/or recipient’s visual attention – whether that be moving to produce a signal
164 within a recipient’s line of sight, or visual monitoring of the recipient by the signaller during
165 response waiting.

166

167 Here we face another issue in the description of a signal as a ‘gesture’ – modality. Gesture is
168 still frequently considered to be a primarily visual mode of communication, perhaps due to

169 the fact that human gesture is generally investigated as action in visual space (Kendon 2004).
170 However, gestures can be perceived through three sensory channels: vision, hearing, and
171 touch. For those gestures with a salient, or even dominant, audible component (for example:
172 ‘slap object’ or ‘leaf clip’) it can be challenging to establish intentional signal use because
173 they are frequently directed at non *visually*-attending recipients. Gesture is an intrinsically
174 multimodal form of communication (Cartmill and Byrne 2007; Fröhlich 2017; Hobaiter et al.
175 2017; Leavens and Hopkins 2005; Pollick et al. 2008), but at present the bias towards visual
176 attention in the definition of intentional signal use likely impacts both the range of signals
177 described as gestures, and our ability to detect intentional use in vocalizations and other
178 signal types.

179

180 **The problem with definitions: What is ‘a’ gesture?**

181 Comparative psychologists have typically focused on *signal* form in human and non-human
182 primates – particularly great apes – and refer to signal categories such as vocalization,
183 gesture, or facial expression as a ‘modality’ of communication. Multimodal signals are then
184 described as the simultaneous or sequential integration of signals from at least two of the
185 ‘modalities’ (Liebal et al. 2014). However, outside of great ape communication, the term
186 ‘modality’ is typically used to refer to the *sensory* modalities of vision, touch, hearing,
187 olfaction, etc. (Partan and Marler 2005; Rowe 1999). Behavioural ecologists, working across
188 a much wider range of species and taxa, are interested in the ultimate function of complex
189 signals and have typically focused on the senses employed to detect signals (Hebets and
190 Papaj 2005; Partan and Marler 1999b). Here multimodal signals are those that incorporate
191 multiple sensory modalities.

192

193 A single gesture (for example a visual-audible ‘slap object’) thus contains multiple sensory
194 ‘modalities’ from the perspective of a behavioural ecologist, but not from the perspective of a
195 comparative psychologist (Fröhlich and van Schaik 2018). In contrast, a visual-silent gesture
196 such as an ‘arm wave’ combined with a (visual) facial expression would be classified as
197 multimodal by a comparative psychologist, but unimodal (visual) to a behavioural ecologist
198 (Marler 1961; Partan and Marler 1999b; Wilson 1976). It is a mess. The different approaches
199 contribute distinct and important parts of the picture; but the inconsistencies in the
200 terminology makes subsequent comparison of hypotheses and data on ‘multimodal’
201 communication across taxa problematic, limiting our view of the wider whole. Comparative
202 researchers, focused on the phylogeny of language-specific components like intentionality
203 and reference, have justified their emphasis on the combination of multiple signals with the
204 notion that different communicative categories, such as gestures and facial expressions, may
205 have different underlying cognitive processes (Waller et al. 2013). However, comparative
206 psychologists could extend the impact of their findings by realigning their terminology with
207 that of the wider pre-existing literature. Recent studies of chimpanzee communication have
208 started to explore these distinctions. Multimodality in a single signal is ‘fixed’ (a chimpanzee
209 cannot produce the audible components of a pant-hoot vocalization, without also producing
210 the visible facial movements), while multimodality in signal combinations (the addition of a
211 visual-audible vocalization to a visual-silent gesture) is optional, and represents an
212 opportunity for ‘flexible’ communication (Davila-Ross et al. 2015; Fröhlich and van Schaik
213 2018). Signal combinations enable signallers to adapt their signalling to a specific physical or
214 social environment (Hobaiter and Byrne 2017; Wilke et al. 2017). This distinction between
215 fixed and flexible combination of modes of information presents a fascinating new area for
216 testing the function of and cognitive prerequisites for different types of multimodal and
217 multicomponent communication in great apes.

218

219 **Theories of gestural acquisition**

220 The ways in which individuals could acquire gestures during ontogeny (or not) has had
221 important implications for how developmental trajectories in gesture use were investigated.
222 Research on apes' gestural acquisition has been ongoing for several decades (e.g. Arbib et al.
223 2008; Liebal and Call 2012; Pika 2008), with a special issue on the topic published over the
224 past year (Arbib and Gasser, in press; Bard et al. 2017; Byrne et al. 2017; Kersken et al., in
225 press; Leavens et al. 2017; Liebal et al., 2018; Pika and Fröhlich 2018; Schneider et al. 2017;
226 Tomasello and Call 2018), and so here we provide only a brief overview.

227

228 Researchers initially differentiated between individual and social (in particular imitation)
229 learning processes of gesture acquisition (reviewed in Liebal and Call 2012). Building on
230 Plooij's (1978) early descriptions of the 'social negotiation' of a behaviour into a signal
231 (which he termed 'conventionalization'), Tomasello and colleagues developed the first
232 formal hypothesis of gestural acquisition, termed 'Ontogenetic Ritualization' (OR). They
233 adapted the ethological concept of signal evolution over phylogenetic time ('ritualization'); in
234 OR the forms that gestures take derive directly from repeated social interactions in which
235 individuals participate through an individual learning process (Tomasello 1990; Tomasello et
236 al. 1994). A series of studies, all conducted in captivity, found indirect support for this
237 hypothesis by reporting the presence of idiosyncratic gesture types (i.e. gesture types unique
238 to single individuals) and greater levels of similarity within, as opposed to between, groups
239 (Halina et al. 2013; Liebal et al. 2006; Pika et al. 2003; Pika et al. 2005). In contrast, any
240 evidence for the acquisition of gestural signals by imitation, or group-specific socially-
241 learned gesture types remained negligible (Byrne and Tanner 2006; Tanner and Byrne 1996;
242 Tomasello et al. 1997; Tomasello et al. 1989). Research in captive settings has shown that

243 chimpanzee and bonobo infants share a considerably larger portion of their gestural repertoire
244 with individuals of their age group than with their mothers, further indicating that mothers'
245 gestures are most likely not imitated (Schneider et al. 2012b).

246

247 Studies on great ape gestural communication in the wild (Genty et al. 2009; Hobaiter and
248 Byrne 2011a) presented apparently contrasting evidence for the existence of genetically
249 predisposed, species-specific gestural repertoires in great apes (Byrne et al. 2017). Finding an
250 absence of idiosyncratic or group-specific gestures, significant overlap in species-repertoires,
251 and a strong effect of observation time on individual repertoire size, these studies concluded
252 that the repertoire of signals available to great apes was phylogenetically ritualized, in a
253 similar way to the repertoires of signals prevalent across animal and human communication
254 (Hobaiter and Byrne 2011a). In addition to the mechanisms of OR, imitation, and genetic
255 endowment, Perlman and colleagues (2012) proposed that on-line ('real-time') adaptation of
256 action is involved in the acquisition of ape gestures. By studying directive pushes during
257 travel coordination in a captive gorilla mother-infant pair, the authors concluded that these
258 behaviours are 'molded to the physical affordances and social context of the moment of
259 communication'. Bard and colleagues (2014b) examined gestural ontogeny in infant nursery-
260 reared chimpanzees and found partial evidence for both OR and genetic endowment. Their
261 results suggested that there are different modes of acquisition for different gesture types, with
262 the bulk of gestures co-constructed as a result of social interactions. This premise was further
263 explored in the studies of Fröhlich and colleagues (Fröhlich et al. 2017; Fröhlich et al. 2016b;
264 Fröhlich et al. 2016c) on the gestures that infant chimpanzees in two wild communities
265 produce in interactions with their conspecifics. The authors found that social exposure and
266 context play a substantial role for the gestural usage of young apes, and proposed a revised
267 theory of 'social negotiation' (Fröhlich et al. 2016c; Pika and Fröhlich 2018). The hypothesis

268 states that gestures do not originate via shortening of a functional action sequence (contra the
269 Ontogenetic Ritualization Hypothesis), but from the exchange of full-blown social
270 behaviours. This exchange results in a mutual understanding that certain behaviours can carry
271 distinct meaning linked to particular social contexts and are produced to achieve distinct
272 goals (Fröhlich et al. 2016c; Pika and Fröhlich 2018).

273

274 **Different perspectives on gesture and gestural ontogeny**

275 Studies on the onset and development of gestural communications in great apes have been
276 heavily influenced by the diverging definitions of ‘gesture’ as used by the respective
277 researchers. In the past decade, the debate about the acquisition of great ape gestures has
278 pitted hypotheses that incorporate learning mechanisms and genetic predisposition against
279 one another (Hobaiter and Byrne 2011a; Liebal and Call 2012). Here, we argue that the
280 different theories could potentially be reconciled by reconsidering the perspectives taken on
281 gestures and gesturing by the different groups of researchers as representing different levels
282 of explanation (see also Liebal et al. 2018). For example: all groups of gesture researchers
283 describe a gesture type (or category) ‘touch’ – common across all individuals (and indeed all
284 ape species; Call and Tomasello 2007; Hobaiter and Byrne 2011a) – this could be classified
285 as a phylogenetically ritualized gesture. However, at the same time, the specific form of this
286 gesture as produced by any one individual, or in any specific interaction, may vary
287 substantially in the orientation of the signaller’s movement, or the location of contact to the
288 recipient (Bard et al. 2017; Perlman et al. 2012; Tanner and Byrne 1996), showing ‘real time
289 adaptation’ (Perlman et al. 2012) and/or ‘social negotiation’ (Pika and Fröhlich 2018) of the
290 exact form in a specific interaction. Similarly, the gestural ‘repertoires’ of two individuals
291 can be measured at a specific point in time or developmental stage and be found to differ
292 dramatically (e.g. Schneider et al. 2012b); but, over a lifetime, the available ‘repertoire’ of

293 gestures expressed by the two individuals may be identical. We can also distinguish the way
294 in which an ape *produces* the gesture, or the way in which a gesture is *understood* (Hobaiter
295 and Byrne 2017). Hence, depending on the level of explanation investigated, ‘a’ gesture or
296 ‘a’ repertoire might refer to something fundamentally different.

297

298 As a result, the apparent differences in the nature of gesture acquisition may have emerged
299 from a focus on different levels of explanation of the gestural system. Many species have a
300 biologically available repertoire of signals. In human language we could consider this to be
301 phonemes – a set of sounds that all humans can produce or discriminate in very early infancy
302 (Kuhl 2003; Kuhl 2004; Ruben 1997). These are our species-typical repertoire of sounds.
303 Similarly we can ask the question: what are the available species-typical repertoires of ape
304 gestures, the set of gestures that all apes could produce or discriminate (Byrne et al. 2017;
305 Genty et al. 2009; Hobaiter and Byrne 2011a). However, in any one individual, and in any
306 one specific communicative event, the use and expression of this available repertoire will
307 vary. In human language, with its cultural diversity of sounds, words, and structures, our
308 phonemes are rapidly channelled through early experience (Kuhl 2004; Ruben 1997). We are
309 left with an individually- and culturally-specific subset of sounds with which we
310 communicate on a day-to-day basis. Within these, the expression of these sounds in any
311 specific instance of communication may again vary. Any two examples of even a single
312 simple word produced by the same individual likely vary in tone, pitch, and emphasis (e.g.
313 Scherer 1995). Within a species-typical available repertoire of great ape gestures, particular
314 pairs of individuals – such as mothers and infants – may regularly employ a subset of
315 gestures to communicate a goal (Fröhlich et al. 2017; Fröhlich et al. 2016c; Halina et al.
316 2013; Perlman et al. 2012). And, in any one specific instance of gestural communication, the

317 precise deployment of a gesture may vary in its physical form, or where contact may be made
318 with the recipient (e.g. Bard et al. 2017).

319

320 As in any ethological study of behaviour, no individual approach to the study of gesture is
321 ‘correct’ in providing a more accurate explanation than others – a complete understanding of
322 how gestural signals are acquired and deployed is only acquired across the different levels of
323 explanation (Tinbergen 1963). In the study of available gestural repertoires, the focus lies on
324 the study of gesture as a system (i.e. at the level of the ‘tool-set’ available), in the study of
325 gesturing the focus lies on the use of specific cases within the system (i.e. at the level of the
326 ‘tool application’). Moreover, signal production, communicative usage, and comprehension
327 may all show different developmental pathways, which might be in turn suggestive of
328 different cognitive prerequisites (Liebal et al. 2014). Here, interestingly, the variation in the
329 physical and social environment in which captive and wild chimpanzees develop may have
330 contributed to some of the variation in findings between studies. If the available forms of
331 gesture types are vertically transmitted via genetic endowment, the selection of gesture types,
332 and the appropriate *use* and *response* to these gestures may still be learned and affected by
333 development. In other words, although some components of gestures might withstand
334 different rearing environments, others may vary with variation in socio-ecological
335 experiences during development (Fröhlich et al. 2017; Hobaiter and Byrne 2011b; Liebal et
336 al. 2014).

337

338 **Available gestural repertoires: innate and family-typical**

339 In recent studies on the gestural communication of chimpanzees and gorillas, Byrne and
340 colleagues (Genty et al. 2009; Hobaiter and Byrne 2011a) proposed that apes’ available
341 gestural repertoires are biologically ‘hard-wired’ and mainly derived from genetic

342 inheritance. The St Andrews gesture group has identified an array of gesture types commonly
343 found across ape species, providing evidence that large sections of these gestural repertoires
344 are in fact family-typical (Cartmill and Byrne 2010; Genty et al. 2009; Graham et al. 2016;
345 Hobaiter and Byrne 2011a). These species- and family-typical repertoires of gestures are
346 consistent in basic form throughout development (for example ‘arm raise’; Genty et al. 2009;
347 Hobaiter and Byrne 2011a). However, they may be expressed flexibly by specific individuals,
348 or in a specific interaction (for example – in the orientation of the arm and hand). While it
349 remains possible that large species-typical repertoires of gestures could be acquired through
350 social learning, ontogenetic ritualization, or even imitation, biological inheritance provides
351 the most parsimonious explanation – particularly given the prevalence of genetically
352 channelled repertoires of signals across other species, including humans (Kuhl 2003; Kuhl
353 2004; Ruben 1997). Even human communication, with its diversity of sounds, words, and
354 structures, is founded on a shared genetically channelled set of phonemes – available to all
355 individuals at birth, but rapidly channelled through early ontogenetic experience (Kuhl 2003;
356 Kuhl 2004; Ruben 1997).

357

358 One criticism of this approach to the study of gesture has been that, given the natural
359 anatomical constraints of a shared body plan across great apes, gestural repertoires will be
360 inevitably similar in form no matter what the acquisition mechanism. Apes share the same
361 basic body plan, and there are only so many ways you can move a body of this type.
362 However, a recent exploration of chimpanzee gestures showed that only around 12% of the
363 physically possible gesture forms were expressed in the chimpanzee repertoire (Hobaiter and
364 Byrne 2017). Byrne and colleagues thus made a strong case for the notion that the majority of
365 gesture types in the available ape repertoire are biologically inherited and, with an extensive

366 overlap in repertoire across all great ape genera, their phylogenetic origin is thus argued to be
367 relatively old (Byrne et al. 2017).

368

369 One challenging aspect to describing the available repertoire is discriminating different
370 gesture types. For example: the gesture ‘touch’, used as a label across many studies, may or
371 may not include the gesture types: stroke, light touch, etc. (Hobaiter and Byrne 2011a). One
372 recent study distinguished 36 forms of this single ‘gesture’ (Bard et al. 2017). Should we
373 discriminate a ‘hand shake’ from an ‘arm shake’, an ‘arm swing’ from a ‘leg swing’? Again,
374 there is no ‘correct’ approach. The appropriate level of discrimination depends on the
375 question being asked. One approach employed by Hobaiter and Byrne (2017) has been to use
376 ape behaviour to guide the process. If apes employ two ‘types’ of gesture to consistently
377 achieve the same goal, we can make the case that – from the apes’ perspective – they are a
378 single gesture ‘type’. After splitting gesture forms to a highly detailed level (resulting in 1005
379 possible gesture types), gestures were lumped into ‘types’ based on consistencies in the apes’
380 behavioural responses, resulting in a repertoire of 81 gesture types in chimpanzees.

381

382 **Gestural usage: shaped by interactional experiences**

383 Evidence that the available gestural repertoires of great apes are largely innate (Byrne et al.
384 2017) does not prevent considerable modification of and flexibility in gestural usage
385 throughout an individual’s life time (Hobaiter and Byrne 2011b; Pika and Fröhlich 2018).
386 Previous studies in both captive (Bard et al. 2014b; Bard et al. 2017; Schneider et al. 2012a;
387 Schneider et al. 2012b; Tomasello et al. 1994; Tomasello et al. 1997; Tomasello et al. 1989)
388 and wild settings (Fröhlich et al. 2017; Fröhlich et al. 2016b; Fröhlich et al. 2016c; Hobaiter
389 and Byrne 2011b; Plooij 1978; Van Lawick-Goodall 1968) suggested that the development of
390 gesture usage in chimpanzee infants is linked to entering their social world and the

391 opportunities it affords to interact with conspecifics. Given that communication takes place in
392 a wide range of social and physical environments, in many behavioural contexts, and over an
393 individual's lifetime, it is likely that individuals rely on input from their social environment
394 before communicative skills fully manifest (Liebal et al. 2014). Bard and colleagues (2014b)
395 examined gestural ontogeny in nursery-reared chimpanzees and suggested that the majority
396 of gestures used by individuals emerge through co-construction as a result of social
397 interactions. In a study carried out in two communities of wild chimpanzees, Fröhlich et al.
398 (2016c) found evidence for considerable inter-individual variation in the mothers' gestural
399 repertoires used to initiate joint travel with their offspring. Another study focusing on three
400 different communicative contexts—food-sharing, joint travel, and social play—examined the
401 role of social exposure, namely behavioural context, interaction rates, and maternal
402 proximity, for infant gestural production (Fröhlich et al. 2017). Interestingly, the rate of
403 previous interaction with conspecifics, but not with their mothers, had a positive effect on
404 gestural frequency and repertoire. Indeed, the number of gesture types used by infants (aged
405 between 9 and 69 months) increased with the number of interaction partners in the previous
406 month of life. The empirical link between social exposure and gestural performance suggests
407 that learning via repeated social interactions shapes the communicative development of
408 gesturing in young apes (see also Bard et al. 2014b). While the mother-infant relationship is
409 critical for normal social development (Maestriperi 2009), early socialization in the wider
410 social environment seems to be essential to develop social competency later in life (Hamilton
411 2010; Parker and Asher 1987). In sum, accumulating work across studies and sites suggests
412 that communicative development is reliant on the infants' early social environment (e.g.
413 Fröhlich et al. 2017; Hobaiter and Byrne 2011b; Van Lawick-Goodall 1968).

414

415 **The developmental trajectory in gestural communication**

416 In contrast to the mechanisms of acquisition, the age of emergence and developmental
417 trajectory in gesturing appears less controversial. In the first longitudinal study of
418 chimpanzees at Gombe, Goodall (1967; 1986) noted that bodily signals in the first few
419 months of life are limited to variations in body contact for mother-infant coordination. Plooij
420 (1978), later focusing on communicative development in the same community, observed a
421 gradual transition towards goal-oriented and voluntary ('illocutionary') communication in
422 chimpanzees between nine and twelve months, in a similar manner to human infants (Bates et
423 al. 1979; Bates et al. 1975). During this transition, chimpanzee infants gradually began to
424 deploy intentionally communicative gestures to influence the behaviour of conspecifics, and
425 to initiate interactions such as play and grooming.

426

427 In a captive setting, Schneider and colleagues (2012a) investigated gestural onset and the
428 emergence of tactile, visual, and auditory gesturing in all four great ape genera. As seen in
429 wild chimpanzees, infants of the three African ape genera (chimpanzee, bonobo, and gorilla)
430 started gesturing towards the end of their first year. Orang-utan infants showed a later onset,
431 only starting to gesture at around 15 months of age, perhaps reflecting their slower life
432 histories (van Noordwijk and van Schaik 2005; Wich et al. 2004). While tactile and visual
433 gestures emerged at around the same time and were used in similar proportions in the first
434 months of gesturing, auditory gestures emerged significantly later in the African ape genera
435 and were not observed in the orang-utan infants studied (Schneider et al. 2012a). The
436 findings from captive settings are complemented by studies on different chimpanzee
437 communities in the wild, showing that young chimpanzees undergo a developmental shift
438 from actions and tactile gestures to visual communication (Fröhlich et al. 2016c; Plooij
439 1978), and an increase in auditory communication with infant age (Fröhlich et al. 2016b).

440 This incorporation of visual and auditory signals may reflect the infant apes' increasing
441 physical and social independence from their mothers.

442

443 **The effects of context and sex on early gestural communication**

444 Previous research on gesture development suggests that social play is the major context of
445 gesture usage in young African apes (Fröhlich et al. 2017; Genty et al., 2009; Hobaiter and
446 Byrne 2011b; Schneider et al. 2012a; Tomasello et al. 1997). Play interactions with peers
447 and other 'non-mother' individuals may serve as essential platform for experimentation,
448 where great apes can test for the effectiveness of intentional gestures that might gain vital
449 importance in their adult life (Fröhlich et al. 2016b). Early gestural communication also
450 appears to play a substantial role for the solicitation of food transfers by young apes (Fröhlich
451 et al. 2017; Pika et al. 2003; Pika et al. 2005), especially in orang-utans (Bard 1992;
452 Schneider et al. 2012a). Communicative exchanges related to desirable objects (e.g. Hobaiter
453 et al. 2013; Pika and Zuberbühler 2008) may be particularly interesting, as they represent
454 'triadic' interactions, involving a signaller, recipient, and a third entity - prerequisites for the
455 development of referential communication (Leavens et al. 2005a; Pika 2012)

456

457 Recent studies of chimpanzee development have highlighted sex differences in the
458 importance of early socialization in chimpanzees (Murray et al. 2014). In the fission-fusion
459 social structure characteristic of wild chimpanzees (Aureli et al. 2008), the mother can
460 actively influence their offspring's social environment through selective subgrouping
461 (Lonsdorf et al. 2014a). From a very early age, male chimpanzees in particular seem to
462 exploit these social opportunities, with the number of social partners of males increasing with
463 offspring age and distance to the mother (Lonsdorf et al. 2014a; Lonsdorf et al. 2014b).

464 These social differences are reflected in sex differences in infant chimpanzee gesturing. For

465 example: male infants deployed more contact gestures than females to solicit play (Fröhlich
466 et al. 2016b) and request food transfers (Fröhlich et al. in prep); and, after controlling for age,
467 used a larger variety of gesture types (Fröhlich et al. 2017).

468

469 **Towards a multimodal approach to communicative development**

470 In the wider animal communication literature, developmental work has tended to focus on
471 either the vocal or gestural modality independently, with the bulk of work on acquisition
472 carried out on song learning in songbirds (e.g., Beecher and Brenowitz 2005; Brainard and
473 Doupe 2002; Marler 1997). Studies of vocal development in birds and mammals have
474 demonstrated that individual experiences accumulated through social interactions (e.g.
475 responses of conspecifics) can play a substantial role by introducing new sounds and
476 encouraging improvisation (Snowdon and Hausberger 1997). Gros-Louis and colleagues
477 (2006) argued that vocal development in human infants is also shaped by social interactions,
478 but acknowledge that the specific links between social context and pre-linguistic vocal
479 development are understudied (Vihman 1996). Some studies have explored the
480 developmental trajectories of different sensory modalities within ape gesturing (Fröhlich et
481 al. 2016b; Fröhlich et al. 2016c; Schneider et al. 2012a). However, it is crucial to keep in
482 mind that gestures represent part of apes' larger repertoire of communicative signals, which
483 includes vocalisations and facial expressions (Liebal et al. 2014). For a more thorough
484 understanding, it is critical to investigate the impact of socio-ecological factors on
485 communicative development in a holistic fashion, across production modes and sensory
486 modalities (Fröhlich and van Schaik 2018; Hobaiter et al. 2017; Liebal et al. 2014).

487

488 In primates, little is known about whether and how the developmental trajectories of
489 multimodal (or multicomponent) signals (in which two or more components of different
490 sensory modalities must be produced together in order to produce the individual signal) and

491 multimodal signal combinations (in which two distinct signals, which incorporate different
492 sensory modalities, are flexibly coupled) differ from unimodal signalling (Bard et al. 2014b;
493 Gillespie-Lynch et al. 2014; Liebal et al. 2014). Some developmental research on multimodal
494 integration has focused on audio-visual *perception* in human and non-human primates,
495 whereas multimodal *production* remains understudied (reviewed in Partan 2013). Even less is
496 known about the development of multimodal signal combinations (Fröhlich and van Schaik
497 2018). In light of an increasing body of work that demonstrates a substantial impact of social
498 experiences on socio-cognitive and communicative development (Bard et al. 2014b; Fröhlich
499 et al. 2017; Katsu et al. 2017; Laporte and Zuberbühler 2011; Snowdon and Hausberger
500 1997), it is vital to understand the role of learning and social experience in both unimodal and
501 multimodal signal production (see also Higham and Hebets 2013).

502

503 Early explorations of a multimodal or multi-signal approach to chimpanzee communication
504 have found strong effects of age on signal choice (Hobaiter et al. 2017; Wilke et al. 2017),
505 with a bias towards gestural communication in early infancy (e.g. Fröhlich et al. in press;
506 Gillespie-Lynch et al. 2013; Hobaiter et al. 2017). Fröhlich et al. (in press) explored the
507 developmental trajectories of established behavioural markers of intentional communication
508 in apes on a study of infants' gestures, actions, vocalizations and 'bi-modal combinations'
509 (gesture plus vocalization). The authors found that proportions of association with audience
510 checking, goal persistence and sensitivity to the recipient's visual orientation increase with
511 infant age. However, context, interaction partner, and sub-species also impact the selection of
512 signal types, as well as the behavioural markers of intentional communication, strongly
513 suggesting that the social environment urgently needs to be considered in studies of
514 communicative development (Fröhlich et al. in press).

515

516 The ‘backup signal’ hypothesis, initially invoked by behavioural ecologists for multimodal
517 signals, implies that the different components of complex signals are redundant, that is they
518 elicit the same response in the receiver (Møller and Pomiankowski 1993; Partan and Marler
519 1999a). Similarly, multimodal signal combinations might be part of a learning process in
520 communicative development in which the immature ape learns to deploy context-appropriate
521 communicative tactics by first using redundant signals sequentially and/or simultaneously
522 (Fröhlich and van Schaik 2018; Liebal et al. 2014). Some support for this explanation comes
523 from studies on chimpanzees. Hobaiter and Byrne (2011b) found that chimpanzees gradually
524 shift from initially long and largely redundant gestural sequences to selecting more effective
525 single gestures as adults. A recent study on joint travel initiation in mother-infant pairs
526 suggested a developmental shift from multimodal (audible ‘hoo whimper’ vocalizations
527 combined with visual gestures) to unimodal signalling (visual gestures only) in infant
528 chimpanzees (Fröhlich et al. 2016c). There appears to be many more gestures in great ape
529 repertoires than meanings for which they are used (Graham et al. 2018; Hobaiter and Byrne
530 2014); this redundancy may offer signalers the opportunity to select different sensory
531 modalities in which to communicate similar information. However, the restricted range of
532 meanings described might also result from how observers currently classify ‘meaning’ (for
533 example: requiring a visible behavioural change by the recipient) rather than from a naturally
534 constrained set of meanings (Hobaiter and Byrne, 2014; Bard et al. 2017).

535

536 An alternative explanation for the combination of signals and modalities is proposed by the
537 theories of refinement and complementarity (e.g. Fröhlich and van Schaik 2018; Genty et al.,
538 2014; Hobaiter et al., 2017; Jacob et al., 2011; Partan and Marler, 2005). Recent studies of
539 chimpanzee and bonobo communication suggest that vocal and gestural signals are not used
540 interchangeably. Chimpanzee gesture-vocal signal combinations were more likely to elicit a

541 behavioural response than vocal signals, but not as compared to gestural signals (Wilke et al.
542 2017). Similarly, chimpanzees were more likely to switch to gesture-vocal combinations
543 following the failure of a vocal signal but not a gestural one (Hobaiter et al. 2017).

544

545 Apart from the sensory modality in which information is transmitted, the type of information
546 is also a key consideration, for example: bonobos employ gestural signals to differentiate the
547 context in which an ambiguous vocal signal is used (Genty et al. 2014). In chimpanzees,
548 while all vocalizations and some gestures convey information in the auditory modality,
549 vocalizations (and possibly buttress-drumming gestures; Arcadi et al. 1998) also encode the
550 identity of the signaller. This feature may impact their use depending on the potential risk of
551 ‘eavesdroppers’ acquiring the information being transmitted (Hobaiter and Byrne 2012;
552 Hobaiter et al. 2017).

553

554 If the different signal types or signal components of multimodal communication are
555 combined in order to refine or complement a core message, then we would predict that single
556 components and signals precede the use of more complex communication during
557 development. However, substantial comparative work focusing on the ontogeny of
558 multimodal production in nonhuman primates is needed to reveal what role multimodal
559 signal combinations play throughout development, and across social roles that themselves
560 change across ape lifetimes.

561

562

563 **Conclusion**

564 In this review we provide an overview of recent work on gestural ontogeny in great apes. We
565 suggest that apparently disparate views on the fixed or flexible nature of ape repertoires may

566 be reconciled by considering them to be different levels of explanation, and that subtle
567 differences in the use of terminology between studies and fields may be at the root of
568 apparently contradictory findings. A gesture type may be species-typical, but its specific
569 expression in day-to-day gesturing may be highly flexible. The ‘repertoire’ of two individuals
570 may differ dramatically when measured over a month, or even a year, but may match when
571 measured over a lifetime. While available repertoires appear largely innate and species-
572 typical, inter-individual differences in gesture usage suggest an important role for learning,
573 mirroring the current state of knowledge on primate vocalizations (Cheney and Seyfarth
574 2018). For any particular instance of gesturing, individual and social variables including at
575 least: partner identity, age, sex, rank, physical location, visual attention, social and biological
576 relationship, as well as the wider behavioural context determine which gestures are selected
577 from the communicative tool set and how they are deployed. The increasing evidence for the
578 impact of the social environment on gesturing represents both a challenge and an opportunity
579 for comparative studies of behaviour and cognition.

580

581 To develop a more thorough understanding of the socio-ecological factors shaping the
582 communicative use of gesture, we can make use of an explicitly multimodal multicomponent
583 approach. Short-range communication in great apes is inherently multimodal; ‘visual’
584 gestures frequently have salient tactile and audible components, just as vocalisations have
585 visual components (Liebal et al. 2014). More comparative work focusing on the ontogeny of
586 multimodal production in nonhuman primates is needed to reveal what role multimodal
587 signal combinations plays in developmental. In turn, this might shed new light on the
588 cognitive processes underlying ape communication, allowing us to develop our understanding
589 of the evolutionary continuity between non-human and human multimodal communication.

590

591

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602 The authors declare that they have no conflict of interest.

603

604 **Ethical approval**

605 This article does not contain any studies with human participants or animals performed by
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607

608 **Informed consent**

609 For this type of study formal consent is not required.

610

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