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Gestural communication of the gorilla (*Gorilla gorilla*): Repertoire, intentionality, and possible origins

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Abstract

Social groups of gorillas were observed at three captive facilities and one African field site. Cases of potential gesture use, totalling 9540, were filtered by strict criteria for intentionality, giving a corpus of 5250 instances of intentional gesture use. This indicated a repertoire of 102 gesture types. Most repertoire differences between individuals and sites were explicable as a consequence of environmental affordances and sampling effects: overall gesture frequency was a good predictor of universality of occurrence. Only one gesture was idiosyncratic to a single individual, and was given only to humans. Indications of cultural learning were few, though not absent. Six gestures appeared to be traditions within single social groups, but concordance in repertoires was almost as high between as within social groups. No support was found for the ontogenetic ritualization hypothesis as the chief means of acquisition of gestures. Many gestures whose form ruled out such an origin, i.e. gestures derived from species-typical displays, were used as intentionally and almost as flexibly as gestures whose form was consistent with learning by ritualization. When using both classes of gesture, gorillas paid specific attention to the attentional state of their audience. Thus it would be unwarranted to divide ape gestural repertoires into 'innate, species-typical, inflexible reactions' and 'individually learned, intentional, flexible communication'. We conclude that gorilla gestural communication is based on a species-typical repertoire, like those of most other mammalian species but very much larger. Gorilla gestures are not, however, inflexible signals but employed for intentional communication to specific individuals.

Key words Great ape, Gesture, Audience effects, Flexibility, Ontogeny

Introduction

Fifty years of modern research on the vocalizations of monkeys and apes has revealed many fascinating aspects of animal cognition, but has shown that the auditory communication systems of non-human primates are very unlike human language (Cheney and Seyfarth, 1996; Hauser, Chomsky and Fitch, 2002). Syntax is missing (but see Arnold and Zuberbuhler, 2006; Arnold and Zuberbuhler, 2008), and referential usage is limited to narrow classes of objects, such as major predators or foods. Referentiality appears to be functional rather than intentional (Cheney and Seyfarth, 1990; Hauser, 1996), and the best interpretation of functionally referential calls remains disputed (Owren and Rendall, 1997). Most striking of all, the vocal repertoire of monkeys and apes is to all intents and purposes fixed. True, the appropriate circumstances in which to call and the class of referent to which a call is given changes with experience (Seyfarth and Cheney, 1986), and a caller may learn when to keep silent, when to call and how loudly (Hauser, 1992). But call types themselves are species-typical, and the set cannot be augmented. Even home-rearing by humans intent on teaching the words of language produces almost no change in the vocal repertoire of the chimpanzee (Hayes, 1951; Kellogg and Kellogg, 1933). The productive, open characteristic of human language is entirely missing in non-human primate repertoires (Hockett, 1960).

Considerable excitement, therefore, has been generated by the discovery that gestural communication in great apes is more flexible and apparently under greater voluntary control. With human help, great apes were shown able to acquire repertoires of tens or hundreds of gestures, which were certainly not species-typical since they were part of American Sign Language (Gardner, Gardner and Van Cantfort, 1989; Miles, 1990; Patterson and Linden, 1981). The gestures of ‘ape language’ subjects were often used in ways that were unambiguously intentional, and no clear limit on repertoire size was noted. The potential for

productivity in great ape gesture has been confirmed by finding gestures unique to particular individuals, living in the social circumstances of normal captivity, both in chimpanzees (Tomasello *et al*., 1994; Tomasello *et al*., 1985; Tomasello, Gust and Frost, 1989) and gorillas (Tanner and Byrne, 1996; Tanner and Byrne, 1999). Direct comparison between vocal and gestural signalling in the two chimpanzee species has shown that gesture is far more flexible in its usage than vocalization (Pollick and de Waal, 2007).

The voluntary, intentional nature of gesture use has been described in all species of great ape. Contrary to the 'one signal, one function' approach so successful in animal communication research, including that on primate vocalizations, a means-ends dissociation between gesture and context was found in chimpanzees, bonobos, gorillas and orangutans (Call and Tomasello, 2007c; Liebal, 2007; Pika, 2007a; Pika, 2007b). Many gestures were used in more than one context, and several different gestures were often used within a single context; such flexibility is equally typical of the communication of young children (Bates *et al*., 1979; Bruner, 1972).

Gesturing of great apes is appropriately adjusted to the attentional state of the recipient. Silent, visual gestures are given mainly when recipients are looking; audible, visual gestures less so; and tactile (contact) gestures are given indiscriminately of the audience's attention (Call and Tomasello, 2007a, p.212-216; Tanner and Byrne, 1996). One gorilla developed the trick of hiding its 'playface' expression with its hands, which effectively delayed or prevented the onset of play with the partner (Tanner and Byrne, 1993). This neatly demonstrates the gorilla's voluntary manual control compared to its involuntary facial expression, and suggests some understanding of vision as an attentional state. When thwarted of its immediate aim an ape will often sequence several different gestures together (Call and Tomasello, 2007a, p. 209-212). The choice of gesture in such circumstances shows clearly that the ape is able to take account of the degree of understanding of the audience, not simply

the presence or identity of individuals (Cartmill and Byrne, 2007). When audience reactions show that gestures have been partly understood, the ape persists with the same gestures; when complete incomprehension is evident, the ape switches to a different set of gestures.

Despite flexible, intentional usage of an extensive and extensible repertoire, no sign of local 'languages' or dialects has been noted in great ape gestural repertoires. If non-human great apes have cultural traditions in their gestural communication, these must be subtle and quite unlike the differences between human languages. This finding leads to an obvious sequel question: if ape gestures are in the main not learnt culturally, how are they acquired? Josep Call and Michael Tomasello have coordinated studies of gesture in all genera of great apes, with an ultimate hope of gaining hints about the evolution of human language, and the answer they give is unambiguous: 'ontogenetic ritualization, in which individuals essentially shape one another's behavior' (Call and Tomasello, 2007a, p.216).

Ontogenetic ritualization (OR) is envisaged as progressive transformation of normal, functional behaviour, under the influence of unintentional reinforcement (shaping) by a partner, to become an intentionally-used signal (Tomasello, 1996). According to the theory, an ape originally uses a physically effective sequence of actions to order to achieve some goal from a partner. Over time, the partner begins to anticipate the whole performance on the basis of some early step in it, and thus responds in the appropriate way, in anticipation. As a result, that early step alone is reinforced and becomes 'ritualized' into a communicative signal. Thus, a physically ineffective action comes to be used communicatively to attain the goal for which the whole performance was originally used (Tomasello and Call, 2007, p.5-6). Characteristically, actions liable to be ritualized as communication in this way will derive from the starting movements of an action sequence that is capable of attaining the goal by direct physical means, or intention movements typically given before such a sequence.

Since conditioning by reinforcement is held to be the means of acquisition in OR, neither of the communicating partners need have any insight into the means of operation of the communication. Thus, while an individual might come by OR to use one action intentionally as a signal to influence another, no understanding of that signal as meaningful communication can be presumed. Therefore, when attempting to communicate the same intention, the partner would not automatically use the same gesture. This is quite different to the case of human language, where each individual is a 'speaker-hearer': if I have learnt what you mean by 'zug' I can immediately use 'zug' to you to convey that same meaning. In principle, any regularly occurring part of the original, physically effective sequence might become ritualized to function communicatively, so that different individuals might learn physically different actions for the same purpose. Thus the occurrence of idiosyncratic gestures, unique to a single individual within a group, can be readily explained. Such idiosyncratic gesture use has been noted in all studies of great ape gesturing, supporting the theory that ape gestures are acquired by means of OR (Call and Tomasello, 2007b). In contrast, no studies have detected the hallmark of cultural acquisition of signals: many gestures used extensively or universally within a single group or local population, but not elsewhere (for cases of single gestures that appear to be acquired culturally, see (de Waal and Seres, 1997; McGrew and Tutin, 1978; Nishida, 1980). Admittedly, in most studies one or two gestures have been noted as specific to a single group and not obviously explicable by particular opportunities of the local environment, but when variability among individuals was compared within and between groups it was found to be comparable (Call and Tomasello, 2007a, p.207). Tomasello and Call (2007, p.10) also distinguish attention-getters, gestures with no intrinsic meaning which function only to attract attention to the signaller's current mood, as shown by its involuntary facial expression, or to a second (meaningful) gesture. Many great ape gestures are indeed used in combination, but the majority of combinations are

repetitions of the same gesture or another of similar meaning; chimpanzees, at least, do not seem to use an attention getter to preface a meaningful gesture (Liebal, Call and Tomasello, 2004). This leaves somewhat in limbo the concept of attention getters: involved only in emphasising mood rather than conveying meaning gestures carrying no meaning, they are presumably part of an innate repertoire, but Call and Tomasello (1997) discuss them rather little. Instead, they conclude (p.216), 'the major learning process involved for ape gestures in clearly ontogenetic ritualization'.

Two other theories of gestural ontogeny have not been examined in such detail, however. Barbara King (King, 2004) proposes that, rather than ritualization by coincidental shaping in dyadic interactions, the manner in which gestures are used as communication is 'mutually constructed' in real time by all parties, in complex and subtle interactions. Although this approach is philosophically far from the animal learning theory employed by Tomasello and colleagues as the explanation of gesture ontogeny, it is similar in its Vygotskyan reliance on other social individuals as the engine of development. Differences between the two theories in testable predictions may, therefore, be nuanced and hard to detect.

Gestures might also derive from an ape's biological inheritance, as do communicative signals in most other species of animal. Call and Tomasello do mention that some gestures may be 'species-typical behaviors shaped by evolution not by learning', which they consider would be characterized by 'inflexible use across contexts' (Call and Tomasello, 2007a, p.204). However they, like all other researchers who have examined ape gesture, find flexible use of gestures to be the norm. Thus, they are inclined to dismiss any pervasive influence of species biology when it comes to ontogeny of the most interesting ape gestures, gestures used in a flexible way to communicate intentions.

We are less confident that it is appropriate to partition meaningful gestures into two mutually exclusive classes: i.e. innate, species-typical signals used inflexibly when elicited by circumstances, versus learned signals, flexibly deployed with careful attention to the audience's attentional state. Humans certainly gesture flexibly, and sometimes with full insight into the means of the gestures operation as communicative signals, yet many gestures are universal among people (Darwin, 1872; Eibl-Eibesfeldt, 1972). Equally, there is little doubt that a plover's 'broken wing' display towards potential predators is innate, since it is universal in the family Charadriidae (del Hoyo, Elliott and Sargatal, 1996). Yet piping plovers take account of a predator's direction of gaze (Ristau, 1991), and react flexibly to failure. Thus, if the first deployment of the broken wing display fails, the bird will repeat the display where it can better be seen by the predator that is causing concern.

Here we present a comparative analysis, aimed at determining which of the potential theories of ontogeny best accounts for gestural repertoires in a great ape species, concentrating on aspects where theories (in particular, ontogenetic ritualization and biological inheritance) most differ in their predictions. We examined gesturing in the western gorilla (*Gorilla gorilla*), the great ape whose repertoire of gestures among captive individuals has been found the largest, both in total and per individual (Call and Tomasello, 2007a, p.198). Several European zoos allowed us to study their gorilla groups, none of which had any contact with each other. In addition, we analysed data from the wild (Mbeli bai, Congo), based on a short-term study specifically of gesture (EG, RWB) and video records of gesturing made ad lib over a longer period (TB). The western gorilla has been studied previously by two independent research groups (Pika, 2007b; Pika, Liebal and Tomasello, 2003; Tanner, 1998; Tanner and Byrne, 1999), allowing us to make comparison also with repertoires at further sites.

We began by asking whether those gestures that gorillas use in an meaningful, intentional way are best understood typically as a result of ontogenetic ritualization, as argued by Pika, Call and Tomasello (Pika, 2007b, p.121, Call and Tomasello, 2007a, p.216)? We collected samples of potential gestural communication using a very broad definition of gesture, mainly excluding cases where the action was sufficient to gain the result by physical force alone. But then, we applied a strict set of criteria for intentional usage, discarding all cases that did not meet the following criteria: (a) Gesture was given in such a way that the potential audience could readily perceive it, e.g. silent gestures must be given when others could see them. (b) Gesture appeared targeted at a specific and plausible goal for the signaller, e.g. aimed towards attainment of something the signaller has already shown interest in, at the time of gesturing or in similar previous circumstances. (c) Subsequent behaviour of the signaller was consistent with that goal, e.g. persisting in goal-directed attempts if the result was not obtained, but ceasing to gesture when it was. (Note that there is no theoretical interest in investigating gestures used non-intentionally. It is not in contention that automatic and reflex-like gestures do exist, as part of the biological inheritance of many species including the human.) For any gesture whose deployment met these criteria, we examined whether the gesture's form matched the predictions of the theory of ontogenetic ritualization. That is, was the gesture similar in form to an early part of the behavioural sequence normally used to achieve the same goal by direct means, or similar to an intention movement given before this behaviour? Then, since ontogenetic ritualization proved an incomplete explanation for intentional gesturing in the gorilla, we went on to ask whether cultural learning also contributed to the ontogeny of gesture repertoires. A cultural tradition would be strongly suspected if a gesture was used by all individuals in one local population but in none at other sites, despite broadly similar social compositions and local living conditions. Where some gestures might be explained as originating in ontogenetic ritualization but others

cannot, we asked whether the two classes of gesture differed systematically. For instance, a different ontogeny might be reflected in: (a) Degree of intentionality, such as whether attention is paid to the potential audience's attentional state. (b) Flexibility, such as the means/ends dissociation noted by Call and Tomasello to be characteristic of flexible, intentional gesturing by great apes. (c) Range of meanings, such as the fixity or otherwise of meaning across different local populations. Finally, rather than this 'multiple-origins' approach, we asked whether any other single-origin hypothesis might account better for the observed patterns of usage.

Method

Subjects

Captive groups of lowland gorillas (*Gorilla gorilla gorilla*) were observed in three European zoos (Basel and Zurich, Switzerland and La Vallée des Singes, France), and wild gorillas were studied at Mbeli bai, Noubalé Ndoki National Park, Congo.

The gorilla group at La Vallée des Singes consisted of 10 individuals at the time of observation: 1 silverback (24 yr old), 3 adult females (24, 36, and 36 yr old), 2 adolescent males (6 and 8 yr old), 1 young female (5 yr old), 2 juvenile males (2.5 yr old) and 1 infant female (15 months old). The group at Basel Zoo comprised 11 individuals: 1 silverback (18 yrs old), 5 adult females (48, 46, 39, 18, 16 yrs old) 2 adolescent males (8 and 7 yrs old), 1 sub-adult female (7 yrs old), 1 young male (5 yrs old), and one infant (1 yr old). The group at Zurich Zoo comprised 9 gorillas: 1 silverback (31 yrs old), 2 adult females (31 and 27 yrs

old), 3 adolescent males (7-8 yrs old), 1 adolescent female (7 yrs old) and 2 infants (one male and one female, 3 yrs old). In Mbeli bai, gorilla groups in the local population totalled c.130 individuals, including single males and breeding groups (see Parnell 2002 for full details of the population).

Environment

The three zoo-based groups inhabited relatively similar environments, designed to allow enrichment and encourage behaviour as natural as possible within captive conditions, and differing mainly in details. Those gorillas observed at La Vallée des Singes were in an enclosure composed of an indoor facility (125 m^2) provided with ropes, suspended tyres and several separate compartments. Window-walls on one side allowed visitors to observe the gorillas when kept inside. The outdoor enclosure was a wooded island (3800 m^2), surrounded by a stream that provided natural separation between gorillas and visitors. The gorillas spent from around 9:30 until 17:00 outside. They were fed 6 times a day with various fruits, vegetables, nuts, cereals and tree cuttings, with water available ad lib. Basel Zoo gorillas lived in an entirely indoor enclosure divided in three parts (100 m^2) and provided with ropes, fake trees, and swings. Additionally, other objects such as buckets and paper were provided every day for enrichment. The gorillas were fed every hour with various fruits, vegetables, nuts, cereals, seeds, tree cuttings, eggs, fruit juice, and monkey cakes; water was available ad lib. Zurich Zoo gorillas had an indoor enclosure provided with ropes and tree trunks (108 m^2 + 20 m^2 backstage), and when weather allowed they also had access for several hours a day to an outdoor enclosure (110 m^2). They were fed every hour with various fruits, vegetables, seeds, and tree cuttings; water was available ad lib.

The habitat in which the wild gorilla population of Mbeli bai, Congo, was observed consists of an 13 ha open area of pools and semi-stable floating vegetation surrounded by forest, Gorillas and other mammals visit this "bai" to pull out and eat vegetation from the water. Several gorilla groups and lone silverbacks visit the bai, separately and sometimes together, and are observed at ranges from 10m to 0.4km from an 8m high observation platform. All individuals seem habituated to observation from this tower, but have not been followed into the forest in which they presumably spend most of their lives.

Procedure & Analysis

Captive gorillas were observed on average six hours a day (5-7 h); daily observation time for wild gorillas was determined by their visits to the bai, within a typical day of 9 h watching from the tower. We observed gorillas at La Vallée, Basel and Zurich for 25 days at each site, which resulted in 125-175 hours observation time per site. We recorded potentially communicative events on miniDV with a Sony Handycam (DCR-HC 24). EG & RWB observed Mbeli bai gorillas for a 7 week intensive period, which resulted in 240 hours gorilla observation time; however, during only a small fraction of this time did any gorilla engage in social activity. In addition, we analysed video material, including gorilla gestural communication, collected ad lib over a 3-year period by TB, for events that were potentially communicative.

To obtain video records, we focused attention on "potentially communicative" episodes, i.e. those involving at least two individuals in which interaction was apparently sought or initiated by one individual. The aim was to make a broad trawl, and the boundaries of behaviour that was selected as potentially communicative are therefore vague. Indeed,

much of the filmed material did not prove to involve use of gestural communication. In addition, episodes of solitary play were recorded.

Video records were then examined for the occurrence of potential gestural communication, and for each case a clip was made with I-Movie and indexed for analysis with Filemaker Pro. Potential gestures were identified on deliberately broad criteria, but attention was restricted to *non-mechanically-effective acts*, including body postures, body movements and movements of the limbs and head. In addition, the actions of the gorilla must have been *potentially detectable* by an audience, if there was one (e.g. visible movements, audible results of movements, or tactile pressure from body contact), and the actions should not serve to attain the presumed goal by *direct, non-communicative means*. This last criterion was straightforward to apply to non-contact actions, but ambiguity often remained in the case of putative tactile gestures, where it is hard for an observer to estimate the degree of force applied. Each potential gesture was coded for the situational context, sensory modality (visible/silent, visible/audible, tactile), and identity of signaller. We recorded any potential audience, whether the gesture appeared directed at a particular recipient and if so we noted the attentional state of that recipient and any response they gave to the gesture, as well as the outcome of the interaction.

These potential gestures were then filtered, by removing any instances that did not meet strict criteria for the intentional nature of their use. We consider a gesture to be, necessarily, an intentionally communicative act. However, in practice, clear indicators of the intention behind them may not accompany many or most uses of gestures. The position is further complicated by the possibility that individuals may sometimes choose to use gestures outside communicative contexts (e.g. in solitary play). Filtering only cases that include evidence of intentional use is therefore highly conservative: no doubt many genuine cases of gesture use were removed.

To be considered intentional, a gesture must be given by an individual in a goal-directed way. There must be some *plausibly desired result* to be obtained, and when this result is not gained immediately then *response waiting* is expected (Tomasello and Call, 2007; Tomasello *et al*., 1994), followed by *persistence and elaboration* in signalling, such as repeating the same gesture or using others (Cartmill and Byrne, 2007; Leavens, Russell and Hopkins, 2005). These criteria may appear harsh, but since in our study, as in most previous work, the majority of gestures were observed in the context of juvenile play, plausible playful goals were in fact relatively easy to imagine. More restrictive was the additional criterion that the gesture must be *directed at an appropriate audience*. What his means must necessarily vary with the modality of the gesture. Tactile gestures, by definition, involve contact with another individual, to whom the gesture is considered to be directed. Silent, visual gestures must be given when an appropriate audience is potentially able to see them, and the signaller must be oriented towards and looking at that individual or those individuals, either just before or at the time of the gesturing. (Of course, humans are capable of giving a gesture for a target audience without ever making them a focus of vision, for instance, in deliberately surreptitious signalling. We accept the possibility that our approach will occasionally miss the real target of a gesture, but there seems little alternative to this sort of simplifying assumption.) Audible gestures present the greatest problem for determining the intended target, since by their nature they are appropriate for use without determining whether the target audience is attending. In this case, we required only that the signaller should be oriented towards and looking at the presumed target individual, and that their subsequent behaviour should be consistent with that assignment. That is, if the target fails to orient towards the signaller, persistence with audible gestures or switching to the tactile modality is expected.

In addition, we restricted most analyses to gestures occurring singly. Where gestures were given in sequences, strings of gestures with no pause greater than 1 s, we used only the first gesture in the sequence to reduce problems of non-independence. Gestures used in the middle of rough-and-tumble play were also excluded, because of the difficulty of discerning their target audience and goal in the melee of close interaction. However, gestures initiating play sequences were included.

The resulting set of intentional gestures was then used to work out the (minimal) repertoires of individuals, and each gesture's approximate meaning for that individual. We examined patterns of gesture occurrence within and between social groups, in particular measuring the extent of idiosyncrasy and commonality within communities. (Since our procedure is conservative, and must inevitably underestimate repertoires, we also computed the distribution of the full set of 'potential gestures' to avoid falsely attributing absence to individuals and social groups.) And we charted the flexibility or rigidity of use of gestures, and whether signallers paid any attention to the attentional state of their audiences. Where some gestures could reasonably have been learnt by ontogenetic ritualization, whereas others could not, we examined these variables for both sets of gestures independently.

Results

We recorded 105 hours of gorilla behaviour that had the potential to show gestural communication, in which 9540 potential gestures were identified. Once the strict criteria for intentional usage were applied, the number of instances of gesture fell to 5254 cases. In each of these the gesture was definitely made in an intentional way; note however that some of the cases set aside may reflect communicative gestures that happened not to give evidence of

their intentional use during our observations. This procedure resulted in a repertoire of 102 different gestures (see Appendix). The juvenile class of animals (2-8 years) were responsible for using the highest number of gesture types (see Fig. 1), compared to a smaller variety used by infants (<2 years), or adults of either sex.

We compared the degree of sharing of repertoires between individuals of the same age class, both within and between social groups, using Cohen's kappa as a measure of concordance. Within groups, concordance was quite variable: La Vallée, adult females 0.45, juveniles 0.54; Basel, adult females 0.41, juveniles 0.53; Zurich, adult females 0.03, juveniles 0.58). The lower values for adults are presumably a consequence of underestimating repertoires, since adult gorillas gestured much less frequently than juveniles. Differences between groups in kappa values were not significant (Kruskal Wallis ANOVA on adult females, N=10, χ^2=2.47, df=2, p=0.29; on juveniles, N=31, χ^2=3.70, df=2,p=0.16). Concordance in repertoires between groups appeared broadly similar that found within groups: adult females, 0.30, juveniles 0.54. (In this case, pooling data from all three captive groups gave sufficient data also to estimate values for infants, 0.28 and for adult males, 0.42.) However, statistical comparison revealed that values were in fact significantly different: kappa values are significantly smaller between groups than within groups (Mann Whitney test on adult females, N_1=10, N_2=26, U=74, Z=-1.98. p≤0.047; on juveniles, N_1=31, N_2=83, U=724, Z=-3.58, p≤0.001).

The great majority of intentional gestures (85%) were found at more than one of the four sites we worked at, and many (39%) were recorded at all of them. The remaining 15% were found at only one site. In that case, absence might be due to local environmental conditions, or simply rarity of use causing a gesture to be missed in our sampling. The former was certainly true in some cases. Thus, at sites where gorillas were not provided with detached objects that could be easily manipulated, gestures involving objects were missing

(e.g. *Throw threat*, *Rope spinning*, *Push object*, *Shake object*, *Throw object*, *Head shake with object, Knock object*). In several other cases, although a gesture was missing from the corpus of intentional gesturing at a site, it was noted as used on occasions when we could not be sure of intentional use, including use within sequences of other gestures. In this case, apparent absence in the main corpus could readily explained as a sampling effect (e.g. *Stomp*, *Stomp object*, *Multiple stomp*, *Arm shake*). Finally, to test whether in general a gesture's frequency of use did indeed affect the chance of it being detected during our sampling periods, we correlated the total recorded number of instances of a gesture with the number of sites at which we noted it. The correlation was positive (Pearson's $r=0.43$, $p \leq 0.001$, $N=84$, excluding cases explained satisfactorily by local environmental variations; see Fig. 2). We therefore conclude that apparently patchy distributions across sites are generally an artefact of sampling or local environmental affordances, and the great majority of gorilla gestures are universal.

Since absences from certain sites are likely to be function of environmental and sampling effects, the possibility exists that 'idiosyncratic' or 'group specific' gestures might be falsely identified, artefacts of insufficient sampling. For a species with a large gestural repertoire, such as the Western gorilla, the repertoire recorded for an individual is liable to increase over a long period of observation (e.g. new gestures were still being found at the end of an 11 year study: Tanner, 1999). Our sampling was necessarily carried out over much shorter periods, and is thus unlikely to be sufficient to pick up the rarest gestures for all individuals. Only 17 gestures were recorded as used intentionally at only one site. To avoid false diagnosis of any idiosyncratic or group specific gestures, we examined all instances of *possible* gesture use for occurrence of any of these 17 gesture types, i.e. including cases where lacking positive evidence of intentionality and instances given in sequences of gesturing.

Using this procedure, we identified only 8 gestures that were each recorded solely within one local population (Table 1). Of these, only one was idiosyncratic, i.e. unique to a single gorilla, and that was a gesture performed only to a keeper not to other gorillas. Six gestures were group specific, i.e. each was used by more than one individual at the only site where it was observed. However, the group-specific nature of two of these may readily be explained by environmental affordances. *1-handed move object* was only found at Basel, where access was given to detached objects too big and awkward to carry but nevertheless moveable, and *water splash* was only found at Mbeli bai, where the place the gorillas were observed included large areas of shallow water. The lack of similar opportunities at the other sites might explain the absence of these gestures at them. Thus, we would point to only 5 gestures as showing a possible cultural ontogeny. One of these, *bite-wrist+arm-shake,* was performed by only one individual at Basel during our study, but was also noted in a film of the Basel Zoo gorillas in 1973, made and kindly loaned to us by Dr Jorg Hess, "Prerequisites of highly organized behaviour of gorillas in captivity". At that time, the gesture was given by a different and now dead individual, implying that vertical cultural transmission of gesture form can occur.

Subsequent analyses were restricted to gestures recorded as used intentionally at all four sites (see Table 2). We examined the form of each gesture, in relation to its apparent goal, in order to determine whether the gesture resembled in any way an action that could bring about that goal directly, or an intention movement that might be expected to precede such action. For example, the gesture *slap other* has the apparent function of initiating contact play, and could have become ritualized from a physically effective slapping action sufficient to achieve the same aim. Conversely, *pirouette*, moving forward while twirling the body about the vertical axis, which in our studies appears to function in terminating play, does not seem in any way related to physically effective ways of achieving that aim.

Those gestures, for which an origin in ontogenetic ritualization is plausible, appear to be derived from several different activities. Many appear ritualized from acts used in play, including chasing, wrestling and other contact play activities, into play start signals or an attention-getters (*One-handed Grab, 2-handed Grab, 2-handed Grab-pull, Grab-pull, Bite, Pounce, Punch, Push, 1-handed, Push, 2-handed, Slap other, Slap other, 2-handed, Touch, Embrace, Hit with object, Kick*; see Appendix for definitions of gestures). Others have come also to function as signals, but appear to have originated in grooming (*Stroking, Poke*), agonism (*Arm raise, Arms raise*, from attempted slapping), balance control (*Arm swing, Arm swing with object*, from actions useful during running), or physically manipulating others (*Arm swing under*, *Positioning*, from bodily moving another; *Arms wave*, *Reach*, from attempt to grab another; *Hand on, Hands on*, from acting to prevent another's movement; *Leg swing*, from kicking), carrying or manipulating objects (*Object on head*, *Rope spinning*, *Throw threat*, now apparently play start signals).

Other gestures could not be accounted for as derived from physically effective means of achieving their goal, with any degree of plausibility. In most cases, these gestures instead resembled parts of species-typical displays of the Western gorilla, such as chest beating or foot stomping (for example, *Tapping object*, *Clap*, *Body beat*, *Pirouette*, *Stiff walk*). Provisionally, we termed these gestures 'species-typical', to contrast with those which might result from ontogenetic ritualization of intention-movements or physically effective actions, which we termed 'potentially-ritualized' (Table 2 reflects this categorization; note that some gestures may function only as attention getters, and would be classed here with other species-typical gestures).

Following the approach of Call and Tomasello (2007), we estimated the flexibility of use of each gesture by recording the range of situational contexts in which it was used (i.e. playing, agonism, feeding, nursing, affiliation, sexual, travel). Both potentially-ritualized and

458 species-typical gestures were found in several contexts, although the spread was greater for
459 potentially-ritualized gestures (Fig. 3; χ^2=14.2, df=5, p≤0.05). To examine this association in
460 more detail, we compared the frequencies with which potentially-ritualized and species-
461 typical gestures were used in specific contexts. In both cases, the difference is quantitative
462 and not large (χ^2=126.6, df=6, p≤0.05; Fig. 4 shows percentage values). Potentially-ritualized
463 gestures were found in up to six contexts, rather than five for species-typical gestures, and
464 those gestures used in many contexts were generally rather more likely to be those which
465 may have derived from ontogenetic ritualization, but there was massive overlap. In most
466 contexts, a range of gestures of either type was used, and only for nursing and travel were
467 gestures exclusively ones that might have derived from ontogenetic ritualization.
468 Although repertoires of gorilla gestures were similar, if not identical, across groups as
469 well as individuals, it might be that this uniformity was restricted to gesture *form*. Because
470 gestures are used in very flexible ways, perhaps gestures acquire their meanings by individual
471 learning and thus the true extent of idiosyncrasy across individuals or local traditions would
472 be revealed only when gesture *function* was examined. To test this assumption, we selected
473 five potentially-ritualized and five species-typical gestures which had the highest frequency
474 of use across all three captive sites, as well as showing frequent use in the wild (see Table 2).
475 For all these 10 gestures, at least three individuals and in most cases more employed the
476 gesture in each of the three captive groups. This allowed us to analyse their meaning, in the
477 sense of the instrumental function, both between individuals in each group and between
478 groups. To assess the function of each gesture for each individual, we catalogued the
479 behavioural reactions of the recipient each time the gesture was used, excluding gesture
480 sequences from analysis. We used the conditions that apparently elicited the gesture, and the
481 reactions that the gesturing gorilla apparently sought from using the gesture, to indicate likely
482 functions, and were able to distinguish 10 distinct categories. These were: “Approach

invitation": Elicits the approach of a recipient, or indicates that signaller is about to approach, often followed by start of play. "Attention getter": Causes a recipient to stop current activity and turn around to look at signaller, in which case signaller gestures again. "Calm down request": Causes an excited recipient to calm its activity. "Chase invitation": Elicits chasing in play, either recipient starts chasing signaller or starts running away to be chased. "Contact play invitation": Invites an approach to body contact to start playing, usually rough-and-tumble or wrestling play. "Cuddle invitation": Invites recipient to cuddle, or to be cuddled. "Displace": Causes recipient to change its location or position. "Stop": Request for recipient to stop current activity. "Stop approach": Causes recipient to stop progressing towards or passing the signaller; usually recipient sits down or marks a pause. "Travel invitation": Elicits travel, e.g. mother's request to infant to start moving, infant's request to mother to ride. For all cases where sufficient evidence of the function of gesturing were available, we assigned one of these 10 categories (Table 3). Inter-observer reliability was examined by asking an independent observer to rate 50 clips, chosen spanning all gestures and individuals, for whether any of the 10 functions was appropriate or not; overall level of agreement was high, with a Cohen's Kappa value of 0.89. Note that the species-typical category is by no means dominated by attention-getters, although we found that attracting attention was a minor function for several gestures.

We first asked whether the pattern of inferred function genuinely differs among gestures, pooling data across all three social groups. Summing the totals of inferred function over all gestures provided a null hypothesis, against which the distribution of functions for actual gesture could be compared with chi-square as a goodness of fit tests. The results are shown in Table 3: in only one case was the distribution not significantly distinct, and that was the gesture for which least data were available, *punch object*. Gestures are used in such a way as to produce reliably different effects, which are somewhat consistent across sites.

However, as is evident from Table 3, no gesture has a single, simple meaning: gorilla gestures tend to be multi-purpose. Inspection of the assignments for each individual showed that this was true also for any one individual. On average, we found that gorillas at each zoo use one of these gestures for 4.5±1.7 functions, having examined an average of 34.6±27.5 instances at each zoo. If these data are split according to possible ontogeny, the numbers remain comparable: potentially-ritualized, 5.5±1.7 functions per individual per zoo, with 50.7±28.9 instances per zoo examined; species-typical, 3.6±1.1 functions per individual per zoo, with a much smaller number of instances to examine per zoo, 18.6±13.3. The precise balance of usage will inevitably depend on local circumstances, including social group composition and affordances of the enclosure, even if a gesture's meaning is identical in all groups. To examine the extent to which meaning is shared across groups, therefore, we looked at the commonest assignment in each of the three social groups, for each gesture: how often was that assignment the same in two or three of the groups, and how often was it unique (Table 4). As the table shows, meanings, in the sense of instrumental functions for which gestures are used, are extensively shared between socially isolated groups. Even in the cases where a gesture was used mainly for the identical function at only two out of three facilities, at the third it was also used for that function, merely less often. The only case where the function seemed more variable, was once again *punch object*, the gesture for which we had least response data, less than half the number of cases of any other gesture. The functions of a gesture were thus found to be very similar, not only between individuals of the same group but also between groups; this conclusion applied equally to potentially-ritualized and to species-typical gestures.

All the cases of gestural communication that we subjected to detailed analysis were pre-selected as showing intentional use, but we made no stipulation that the potential recipient should actually be *attending*. It was therefore of interest to see whether signallers

fine-tuned their choice of gesture, matching the modality of the gesture with the communicative problem, and whether they paid specific attention to the attentional focus of the recipient. For each gesture, we examined the recipient's attention towards the signaller. Since it is often not possible to be sure of the eye-gaze of gorillas, and gaze generally follows head orientation, we scored as "attending" individuals whose head was facing in the direction of the recipient, $\pm 45^0$ (see Fig. 5). For both silent-visible and tactile gestures, we found no difference in sensitivity to the audience according to whether the gesture had been categorised as potentially-ritualized or species-typical (silent-visual χ^2=3.69, N=1224, df=1, ns.; tactile χ^2=0.15, N=2112, df=1). Because no significant differences were found, we collapsed potentially-ritualized and species-typical gestures to examine the possibility of an association between gesture modality and audience attention. In this case, the association was significant: silent, visual gestures were used more often when the recipient was attending, compared to tactile gestures (χ^2=106.0, N=3336, df=1, $p \leq 0.05$). Audible gestures were all found to be of the species-typical type, and may include some attention-getter actions: in no case could a plausible origin for an audible gesture be envisaged from ontogenetic ritualization. Examining only species-typical gestures, we found an association between modality and audience attention (χ^2=13.6, N=1951, df=2, $p \leq 0.05$), with audible gestures at least as closely associated with recipients attending the signaller as silent, visual gestures.

Discussion

According to the dominant theory for the origin of gesture communication in great apes (Call and Tomasello, 2007a, p.216), the repertoire of an ape can be divided into two parts. Species-typical gestures can be recognized because they are used inflexibly, in a single or very limited range of behavioural contexts or simply to attract attention. But the largest number of great

ape gestures, those of most interest to the theory of animal communication, are non-species-typical gestures, used flexibly and intentionally to convey meanings. Such gestures, Tomasello and his collaborators have argued, are acquired by ontogenetic ritualization.

We questioned the aptness of this two-part division, for understanding the origins of the gorilla gestural repertoire. Since there is no doubt that all primate species give some gestural responses in an automatic and unintentional way, cases were only relevant where we could be sure that a gesture was made intentionally. We therefore used a strict criterion of intentionality of use, based on accepted characteristics: direction at a target individual able to perceive the gesture, response-waiting, and/or appropriate reactions to a failure to achieve the apparent goal. This greatly reduced the corpus of data, and no doubt some intentionally communicative gestures were thereby missed simply because of their rarity. Nevertheless, we identified 102 gesture types, broadly overlapping with those described in previous studies: the Appendix shows mappings to gestures identified in the two previous studies (Pika, 2007b; Tanner, 1998). The fact that we distinguished a higher number of gestures may have no great significance. Tanner described only 30 gestures among the San Francisco Zoo gorillas in an 11 year study, but she clearly analysed at a somewhat higher 'splitting level' (e.g. our *arm shake*, *arms shake*, *hand shake*, *hands shake* would all be coded as 'armshake'). In any case, her analysis was restricted to discrete actions of the hands, arms and head, and she worked with only one social group, so a lower number of gesture types is to be expected. Pika (2007) described 33 distinct gestures at two zoos, Howletts in the UK and Apenheul in the Netherlands, and she only studied 13 individuals between 1 year 3 month and 6 years 2 months old, so a smaller repertoire is again to be expected. And as with Tanner's study, Pika's classification was less fine-grained than our own.

To gain an overview of the usage of intentional gesturing, we compared the pattern across individuals, from idiosyncratic use by only one individual at one site through to

universal occurrence among individuals at every site. As with previous studies, we found very few gestures suggesting cultural acquisition, i.e. used commonly by several individuals at one site but entirely absent at other sites; we identified 6 such cases. Intriguingly, one of these was a gesture 'idiosyncratic' to single individuals at the same site in 1973 and 2006, suggesting vertical transfer of knowledge. Tanner (1998) describes three gesture types used by more than one individual in San Francisco Zoo that were not found in our study. However, she noted that all of these gestures had been seen elsewhere. 'Chest knock' was also used by the language-trained gorillas Koko and Michael; 'extended palm' has been observed in several zoos and has also been described in the wild mountain gorilla (Schaller, 1963); 'pat off' has been noted in other zoos, under the term 'patting' or 'swiping'. Pika (2007) describes two gestures as apparently cultural traditions at Apenheul Zoo, 'arm shake' (performed by 6 out of 7 individuals) and 'chuck up' (performed by 3 out of 7). However, the definition of 'arm shake' resembles Tanner's 'armshake', and a combination of our *arm shake*, *arms shake*, *hand shake* and *hands shake*, gestures we noted at several sites. Similarly, 'chuck up' resembles our *arms raise*, which we noted performed by at least three individuals in the wild at Mbeli bai, and also among gestures seen at La Vallée and Zurich but without evidence of intention. The lack of any general cultural influence on the ontogeny of gorilla gesture was also evident when we examined concordance of repertoires. Although the level of inter-individual concordance was higher within groups than between them, the difference was small and readily explained as a consequence of social and environmental differences in living conditions.

Idiosyncratic gesture use was even scarcer, with only one clear instance, and that given only to a keeper rather than to other gorillas. This finding is in apparent contrast to previous studies: Tanner (1998) described 13 gestures unique to single individuals at San Francisco Zoo alone; Pika (2007) noted 3 gestures idiosyncratic to single individuals at

Apenheul. This difference may, however, be illusory. Tanner did not restrict attention to cases where she had evidence of intention to communicate, and included in her glossary gestures made only in solitary play. In our study, many idiosyncratic gestures failed to meet the criterion of intentional usage, and much idiosyncratic gesturing was indeed made in solitary circumstances rather than socially. Tanner noted that several of the gestures made idiosyncratically in her study (and not found in ours) had nevertheless been described before. These included 'circle hands' (only Zura in Tanner's study, but noted in the wild by Schaller, 1963), 'foot back' and 'hands behind back' (only Zura in Tanner's study, but seen before at other zoos), 'head turn' (only Kubie in Tanner's study, described before in several zoos and in the wild by Schaller, 1963). In addition, 'hands on shoulder' was unique to Kubie in Tanner's study, but appears to match *hand on* in our work. The remaining 8 idiosyncratic gestures ('facewipe', 'finger down lips', 'go', 'hand between legs', 'hide playface', 'mouth/lips', 'teeth', 'wrist glance') were unique to Zura, a female who spent much time engaged in solitary gesturing. Since we studied groups at four separate sites, we had more data with which to refute the hypothesis of idiosyncrasy. For instance, one of the three gestures Pika et al (2005) observed only at Apenheul, 'object drum', closely resembles our *drum object (palms)*, which we found at several sites. We conclude that differences between studies are largely a result of difficulties in analysis stemming from fundamental qualities of the gorilla's repertoire: namely, that the potential repertoire is extremely large, and that many gestures are used rarely. The degree of idiosyncrasy is therefore always likely to be overestimated, especially in shorter studies and those restricted to one or a few sites. True idiosyncrasy is relatively rare, and may be associated more with solitary, playful gesturing than intentionally communicative contexts.

Most gestures, therefore, were distributed in a way consistent with a universal, species-typical repertoire. Where gestures were frequent, most or several members of all

gorilla groups used them. Rarer gestures showed a more patchy distribution of use, as would be expected: it may take years to record the full repertoire of a single individual (Byrne and Tanner, 2006). However, such a distribution might also be consistent with ontogenetic ritualization, provided the normal behaviour whose early stages or intention movements become ritualized is a highly predictable, natural sequence for any individual with a similar goal. For instance, if hitting with one arm is used to initiate a play-fight, the action of arm raising is a prime candidate for ritualization into a play-initiation signal, whereas the action of patting the top of the head is not. Thus the extent to which intentional gestures are related in form to actions that achieve the effects non-communicatively, or to intention movements regularly associated with them, is a critical issue for the theory of ontogenetic ritualization.

We therefore examined the precise form of each gesture, dividing gestures into (1) those whose form suggested or was at least consistent with intention movements and actions that would achieve the desired effect non-communicatively, and (2) those where the form was entirely different. In the latter case, we found that the gesture usually resembled a species-typical communicative display, in full or abbreviated form. We then examined whether these classes differed in the signaller's adjustment to the attentional state of the audience. Was the gesture modality appropriate for the audience's ability to perceive the gesture, with attention paid to the gaze direction of the recipient especially in the case of silent visual gestures, and tactile gestures associated more with cases where the recipient would be unable to see a distal movement? The two categories did not differ in these ways. For both, silent visual gestures were given overwhelmingly to individuals who were already looking, audible gestures slightly less so, and tactile gestures less still, although even they were used more often to individuals whose attention was focused upon the signaller. Similarly, no qualitative difference was found in the degree of flexibility of the two gesture classes: both were used in many situational contexts, and a range of each might be used in a single context. Gestures

whose form was consistent with acquisition by ritualization were used in a slightly larger number of contexts on average, and in some contexts species-typical gestures were less used, but the differences were only of degree. Just the same applied to gestural 'meaning', in the sense of the goal to which gesture use appears directed and whose accomplishment apparently satisfied the gesturer. Gorilla gestures are multi-functional, each typically used for several overlapping purposes, but the pattern of functions is characteristic of the individual gesture and not markedly different at different sites, for both species-typical and potentially ritualized gestures. Attention-getting was identified as a function for only a minority of case for any of the gestures examined in detail.

We also failed to detect other possible diagnostics of ontogenetic ritualization. The theory is essentially dyadic: it is the behavioural interaction between two familiar companions that serves to build up each new action as a communicative gesture. The resulting communication should, then, sometimes have a dyadic character: evidence that a particular gesture was used mainly with one other partner would be supportive of its origin by ontogenetic ritualization, but we found only one such case, and for this the other participant was a human caretaker. In principle, an individual might have learnt, by ontogenetic ritualization, to use quite different gestures to achieve the same ends when interacting with different partners. Signals derived by ontogenetic ritualization are *one-way* signals, and only by coincidence might one expect both participants to use an identical gesture for the same purpose to each other. Evidence that members of a dyad typically use different signals to each other for an identical purpose would be strongly supportive of ontogenetic ritualization. We found none. In the typical case, both members of a communicating dyad were able to use the same gesture for the same purpose: repertoires were extensively shared. It is of course entirely possible that a single agent might use such similar behavioural sequences with several partners, on different occasions, that each one begins to interpret the same action by

683 the agent as a communicative signal. And some patterns of behaviour are likely to be so
684 highly consistent across individuals, regardless of their previous experience and social group
685 composition, that ontogenetic ritualization may result in similar gestural forms becoming
686 used for similar functions in different individuals in different groups. But it is stretching
687 coincidence to believe that this should almost always happen, that no sign of an origin in
688 dyadic mutual reinforcement should be found, and that idiosyncratic uses of gesture should
689 be a rarity.

690 We conclude, therefore that it is unsafe to attempt categorization of great ape gestures
691 into a (cognitively uninteresting) species-typical, "innate" repertoire of gestures used
692 inflexibly, and a repertoire of learned (and often idiosyncratic) gestures deployed flexibly and
693 intentionally. All groups of western gorillas we studied showed very extensive and broadly
694 overlapping repertoires of intentionally used gestures. Pika (2007, p. 121) likewise noted
695 "high levels of agreement concerning the performance of gestures between groups". She
696 concluded that this was entirely consistent "with the hypothesis of Tomasello and Call
697 (1997), who claimed that apes acquire their gestures via an individual learning process called
698 ontogenetic ritualization". We cannot agree, for the case of the gorilla. Instead, we consider
699 the only reasonable conclusion is that the great majority of gorilla gestures are part of a
700 species-typical repertoire, albeit one of unusually large size.

701 This conclusion does not render gorilla or other great ape gestural communication a
702 less interesting object of study. These gestures are used intentionally in a flexible, goal-
703 directed way, with clear account taken of the attentional state of the audience: in these
704 characteristics, they are thus very unlike the more automatic bodily signals described for
705 many species of mammal, and more like some forms of human non-verbal communication.
706 Moreover, although the general function of each gesture is apparently species-typical, how
707 gorillas use their gestures is undoubtedly modified by contextual learning (Janik and Slater,

1997), just as the functional referents of biologically fixed vocalizations are refined by experience in monkeys (Seyfarth and Cheney, 1986; see Pika *et al*., 2003 for a similar conclusion). And the characterization of an individual ape's gestural repertoire as a subset of a very extensive, biologically determined species repertoire is intriguingly different to most other animal communication systems, although entirely consistent with how great apes perform 'gestural imitation' (Byrne and Tanner, 2006).

It remains a puzzle that gorillas do not regularly extend the repertoire of gestures given them by biology. There seems little doubt that their motor control (Byrne, Corp and Byrne, 2001) and social learning capacities (Stoinski *et al*., 2001) are sufficient for this to be possible. Even monkeys, with much less cortical control of manual action, have been found able to invent gestures and local cultural traditions have been described (Laidre, 2008). Given human help gorillas and other apes can acquire an extensive vocabulary of novel gestures, and use many of them referentially (Patterson and Linden, 1981), and the very limited signs of culturally learnt gesture in gorillas suggest that the possibility exists under natural conditions. We can only conclude that gorillas fail to 'see the point' of inventing new gestures to refer to novel situations: a limitation on imagination, rather than communication.

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Figure Captions

Figure 1. Age distribution of gorilla gesture. The percentage of the total gorilla repertoire used by each age class. Error bars represent standard deviation across sites.

Figure 2. Distribution as a function of usage frequency. The total number of observed instances of a gesture in (intentional) use, plotted according to the number of independent sites at which it was recorded.

Figure 3. Gestural flexibility. The frequency of gestures is plotted according to the number of contexts in which they are used. Grey bars represent species typical gestures, black bars potentially ritualized gestures. Error bars represent standard deviation across sites.

Figure 4. Context specificity of gestures. The frequency of gestures is plotted for each of the situational contexts in which they are used. Grey bars represent species typical gestures, black bars potentially ritualized ones. Error bars represent standard deviation across sites.

Figure 5. Sensitivity to audience. The percentage of gestures used as a function of the attentional state of the recipient for each sensory modality (visible, audible and tactile). Separate analyses are performed for potentially ritualized gestures (top) and species typical gestures (bottom). Black bars represent attending, grey bars represent not attending Error bars represent standard deviation across sites.

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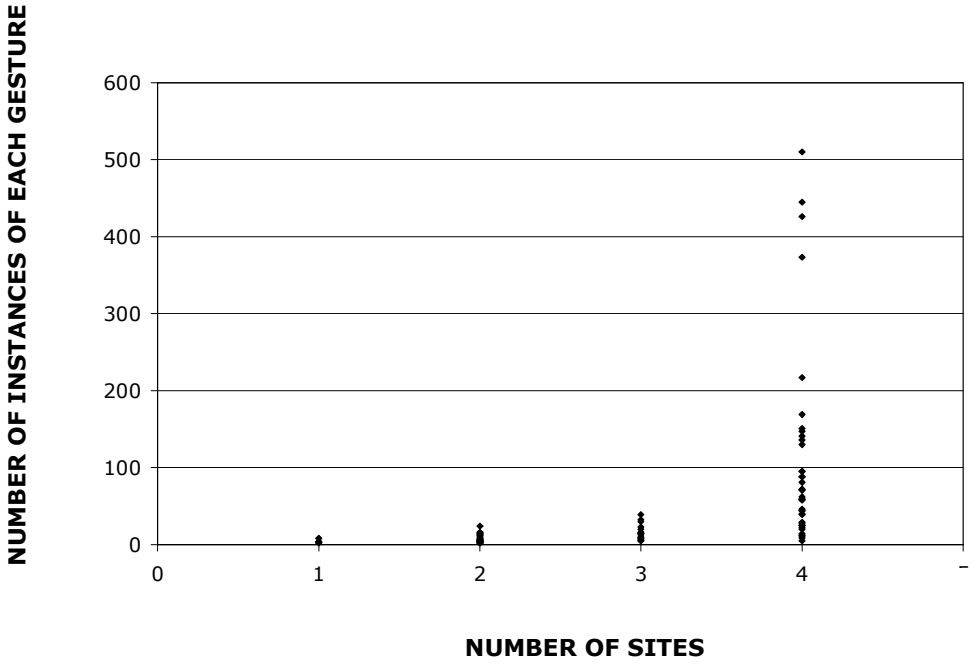

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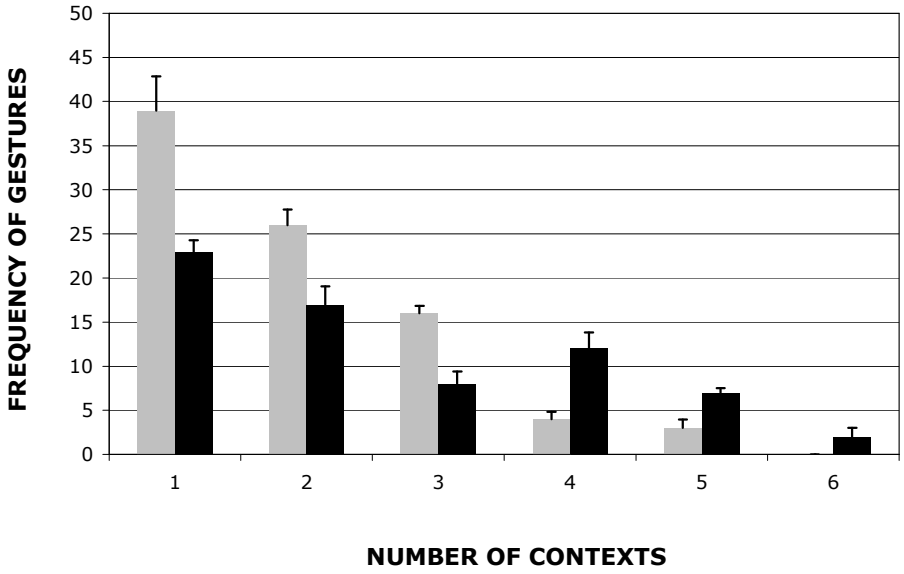

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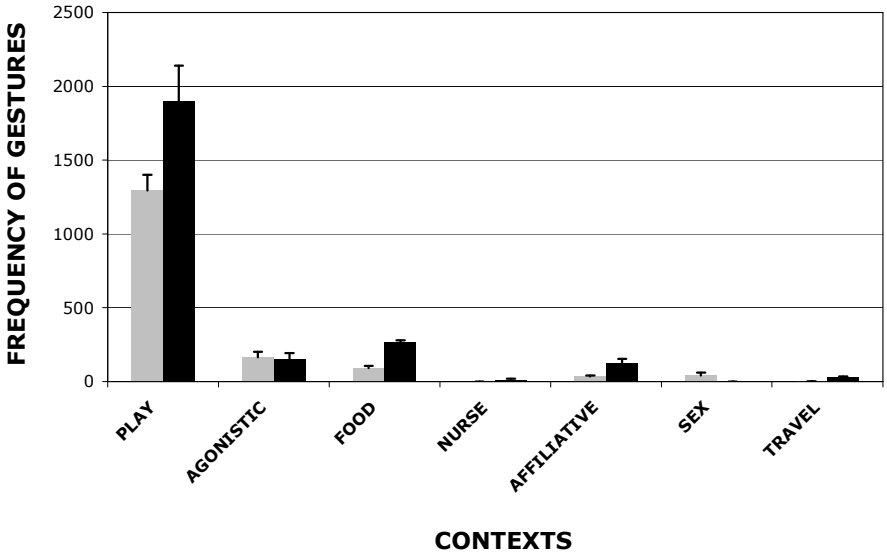

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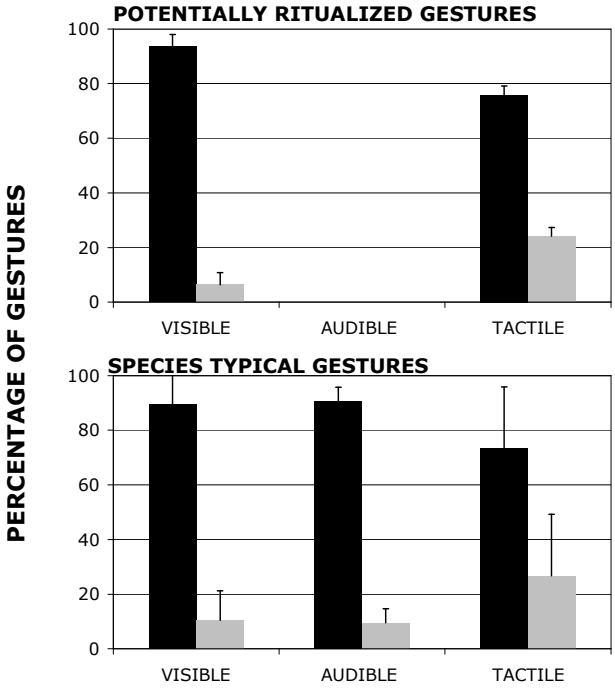

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Table 1. Gestures restricted to single sites.

	Number of Instances				Number of individuals			
	Basel	**La Vallée**	**Zurich**	**Mbeli**	**Basel**	**La Vallée**	**Zurich**	**Mbeli**
GROUP SPECIFIC GESTURES								
1-handed move object	**31**				4			
Water splash				**3**				3
Lick hand	**64**				3			
Bite + Arms shake on	**39**				4			
Arm swing under with object	**37**				4			
Arms swing with object	**11**				3			
Bite wrist+ Arm shake	**9**				2			
IDIOSYNCRATIC GESTURES								
Disco arms shake		**8**				1		

Table 2. Gestures recorded at all sites.

	Number of individuals						Number of Instances[1]				Number of Contexts[2] (max=7)			
POTENTIALLY RITUALIZED GESTURES	Basel (N=10)	La Vallée (N=10)	Zurich (N=9)	Mbeli (Age class)	Tanner & Byrne (1999) (N=7)	Pika et al. (2003) (N=13)	Basel	La Vallée	Zurich	Mbeli	Basel	La Vallée	Zurich	Mbeli
2-handed grab	1	4	6	Inf, SubA			2 [19]	6 [70]	43 [173]	11 [11]	1	1	1	2
2-handed grab-pull	4	3	6	SubA			4 [13]	3 [4]	20 [24]	1 [1]	1	1	2	1
Arm swing	3	5	4	Inf, SubA			5 [9]	25 [108]	7 [63]	7 [7]	3	2	1	1
Arm swing with object	1	3	1	SubA			1 [23]	6 [27]	1 [2]	1 [1]	1	1	1	1
Bite	5	6	8	Inf, SubA	1	11	28 [28]	13 [15]	49 [56]	5 [5]	4	2	3	1
Grab-pull	9	6	6	SubA, AdF	2	12	73 [73]	25 [26]	37 [41]	6 [6]	5	3	4	2
Hand on	9	6	5	SubA, AdF	5	7	37 [49]	32 [39]	15 [18]	4 [4]	4	4	3	2
One-handed grab	9	9	8	Inf,SubA, AdF	5	13	119 [126]	167 [173]	191 [223]	33 [33]	6	5	5	5
Positioning	2	4	2	Inf, AdF	5		9 [10]	9 [10]	3 [5]	4 [4]	1	3	2	2
Pounce	6	6	6	SubA, AdM			20 [33]	16 [22]	42 [60]	3 [3]	2	2	2	3
Punch	9	8	8	Inf,SubA, AdF, AdM		13	69 [74]	41 [46]	86 [110]	21 [21]	4	4	2	2
Push, 1-handed	9	8	9	Inf,SubA, AdF	5		30 [33]	30 [38]	79 [96]	12 [12]	5	1	4	2
Push, 2-handed	3	5	5	Inf, SubA		12	4 [6]	8 [10]	22 [26]	6 [6]	1	2	1	1
Reach	5	5	1	Inf	2	13	13 [21]	7 [10]	1 [1]	1 [1]	4	4	1	1
Slap other	8	5	8	Inf, SubA, AdF		13	109 [114]	132 [159]	140 [176]	45 [45]	4	4	3	3
Slap other, 2-handed	1	4	6	SubA			2 [11]	13 [19]	23 [30]	8 [8]	1	3	1	1
Touch	10	9	8	Inf,SubA, AdF, AdM	5	13	175 [187]	89 [94]	98 [129]	11 [11]	6	5	5	4

	Number of individuals						Number of Instances[1]				Number of Contexts[2] (max=7)			
SPECIES TYPICAL GESTURES	Basel (N=10)	La Vallée (N=10)	Zurich (N=9)	Mbeli (4 age classes)	Tanner & Byrne (1999) (N=7)	Pika et al. (2003) (N=13)	Basel	La Vallée	Zurich	Mbeli	Basel	La Vallée	Zurich	Mbeli
Body tapping	3	3	1	SubA			10 [35]	7 [30]	1 [3]	2 [2]	2	3	1	1
Body beat	4	5	5	SubA	5	10	6 [10]	42 [109]	8 [18]	3 [3]	1	2	1	1
Bow	3	1	2	SubA		2	19 [43]	5 [8]	4 [8]	1 [1]	3	1	1	1
Chest beat	9	6	7	Inf, SubA, AdF	5	13	123 [220]	166 [354]	79 [102]	77 [77]	4	5	2	4
Chest beat play	1	1	1	SubA			1 [4]	1 [4]	2 [6]	1 [1]	1	1	1	1
Clap	3	5	1	Inf, SubA, AdF	5	8	26 [70]	13 [26]	2 [2]	30 [30]	2	2	1	3
Drum object (palms)	4	5	5	Inf, SubA			57 [89]	48 [170]	39 [111]	3 [3]	2	2	1	1
Drum other	6	4	3	Inf,SubA			10 [12]	25 [25]	3 [3]	6 [6]	4	4	1	1
Gallop	5	7	6	SubA, AdF, AdM		10	33 [48]	35 [81]	49 [76]	13 [13]	3	5	3	3
Ice skating	1	4	2	Inf, SubA		10	2 [11]	15 [49]	3 [17]	5 [5]	1	2	1	2
Jump	2	1	1	SubA		10	5 [11]	1 [11]	4 [11]	2 [2]	2	1	1	1
Look	7	4	6	Inf,SubA, AdF, AdM			32 [36]	9 [17]	27 [33]	27 [27]	5	1	3	3
Pirouette[3]	6	5	4	Inf, SubA			11 [18]	82 [229]	5 [28]	38 [38]	2	3	1	1
Punch object	9	3	5	SubA, AdM	3		42 [68]	17 [53]	10 [30]	3 [3]	2	3	2	3
Slap object, 2-handed	2	3	4	SubA, AdM			2 [4]	14 [59]	19 [59]	4 [4]	1	1	2	2
Slap object 1-handed	4	5	5	SubA, AdF	4	13	29 [46]	11 [44]	11 [73]	8 [8]	3	2	1	2
Stiff gallop[3]	7	6	4	SubA			40 [47]	10 [21]	7 [7]	1 [1]	2	2	2	1
Stiff stance	7	3	4	SubA, AdM		2	51 [5]	4 [7]	6 [7]	27 [27]	3	2	2	2
Stiff walk	4	4	4	SubA, AdM			10 [10]	6 [10]	4 [5]	5 [5]	2	3	3	2
Stamp[4]	3	3	1	SubA		9	3 [9]	5 [12]	1 [2]	2[2]	1	1	1	1
Tapping object[3]	5	4	3	Inf, SubA			53 [88]	10 [27]	5 [17]	3 [3]	3	1	1	1
Tapping other	2	2	3	Inf, SubA, AdF, AdM	3	2	3 [4]	4 [4]	3 [3]	4 [4]	1	2	1	1

1. Number of individuals that were observed using gesture intentionally, with total single uses in square brackets. (Only age classes are available for Mbeli.)
2. Number of contexts in which a gesture was observed.
3. Gestures for which the rarity at some sites can be explained by a cultural preference of use at particular sites.
4. Gesture for which the rarity at some sites can be explained by a preferential use embedded in a sequence.

Table 3. Instrumental functions of gestures.

Function[1]	Throw object ***	Hand on ***	One-handed Grab ***	Slap other ***	Touch ***	Chest beat **	Drum object ***	Gallop ***	Pirouette ***	Punch object *	TOTAL
Approach invitation	3	0	0	0	1	1	6	0	0	0	11
Attention getter	3	0	6	8	32	0	4	1	0	2	56
Calm down request	0	**32**	25	11	29	1	0	1	0	0	99
Chase invitation	*16*	0	3	26	7	8	**19**	*21*	21	5	126
Contact play invitation	6	7	**111**	*49*	**39**	**28**	18	10	11	*7*	**286**
Cuddle invitation	0	12	8	5	25	1	1	0	0	0	52
Displace	**24**	3	*61*	**60**	*33*	*21*	15	**27**	0	**13**	*257*
Stop	5	13	4	39	13	3	0	0	**32**	0	109
Stop approach	2	6	16	0	3	0	0	0	0	2	29
Travel invitation	0	0	12	0	2	0	0	0	0	0	14
TOTAL	**59**	**73**	**246**	**198**	**184**	**63**	**63**	**60**	**64**	**29**	**1039**

1. For definitions of functions, see text.

Notation *, **,*** shows deviation from the overall distribution of assigned functions, i.e. from the distribution shown under “Total”, by the level of significance in a goodness of fit chi-square test (respectively: <0.1; <0.05, <0.01). Bold type is used for the commonest fucntion of a gesture, overall, and italic for the second commonest fucntion.

Table 4. Cross-site similarity in meaning.

Gesture type	Number of functions	Total frequency	Major function same in:
Throw object	7	59	La Vallée, Zurich
Hand on	6	73	All three groups
One-handed grab	9	246	All three groups
Slap other	7	198	2 groups
Touch	10	184	Basel, Zurich
Chest beat	6	63	Basel, La Vallée
Drum object	5	63	La Vallée, Zurich
Gallop	4	60	Basel, Zurich
Pirouette	3	64	All three groups
Punch object	4	29	Different in each

GESTURE NAME	DESCRIPTION	TANNER & BYRNE (1999)	PIKA et al. (2003)
VISIBLE ONLY			
1-handed move object	Grabbing an object with one hand and moving it away or pulling it forcefully		
2-handed move object	Grabbing an object with both hands and moving it away or pulling it forcefully		**Move**
Arm raise	Raising one arm above the head	**Up**	**Reach**
Arm shake	Shaking loosely one arm from shoulder joint	**Armshake**	**Arm shake**
Arm swing	Swinging arm back and forth on side, either once or repetitively	**Down**	
Arm swing under	Swinging arm back and forth from front of body to between legs	**Arm swing under**	
Arm swing under with object	Swinging arm back and forth from front of body to between legs while holding an object in hand		
Arm swing with object	Swinging arm back and forth on the side, either once or repetitively while holding an object in hand		
Arms raise	Raising both arms above the head		**Chuck up**
Arms shake	Shaking loosely both arms from shoulder joints.	**Armshake**	**Arm shake**
Arms swing	Swinging arms in front of body from one side to the other		
Arms swing with object	Swinging arms in front of body from one side to the other while holding object(s) in hand(s)		
Arms wave	Waving arms raised above head		
Bipedal run/walk	Running or walking bipedally.		
Bipedal stance	Standing upright on two legs		
Bite wrist+ Arm shake	Biting wrist of one hand while shaking loosely the opposite arm		
Body drum	Drumming own body part with fists.	**Chest knock**	
Body tapping	Tapping own body part repetitively with palm of hand		
Body tapping with object	Tapping own body part repetitively with palm of hand and an object placed between hand and body		
Bounce	Standing on four relaxed limbs and performing rapid up and down movements		
Bow	Bending forward upper body according to the body x axis while standing on two legs		**Bow**
Chest beat play	Drumming playfully on chest with palm of hands		
Disco arms shake	Shaking arms in a rotating movement towards self on one side of head		
Feet shake	Shaking feet loosely		
Gallop	Running with forelegs playfully stamping the floor (similar to a child imitating a horse galloping)		**Gallop**
Hand shake	Shaking hand loosely from wrist joint	**Armshake**	**Arm shake**
Hand shake with object	Shaking hand loosely from wrist joint while holding an object in hand		
Hands shake	Shaking loosely both hands from wrist joints	**Armshake**	**Arm shake**
Hands shake with object	Shaking loosely both hands from wrists joints while holding object in hands		
Head nod	Nodding head up and down in the body x-axis.	**Head nod**	**Bow**
Head rub	Rubbing head back and forth with palm of hands and/or forearms		
Head shake	Shaking head from side to side on horizontal axis	**Head shake**	**Bow**
Head shake with object	Shaking head from side to side with object in the mouth	**Head twirl**	**Bow**
Ice skating	Twirling movement of whole body around the body y axis while standing on four legs usually with head bent forward		**Ice skating**
Jump	Jumping from one location to another or springing on location		**Jump**
Leg rub	Rubbing extended legs back and forth with palm of hands while sitting		
Leg swing	Swinging leg back and forth		
Lick hand	Licking palm of hand frantically and repetitively		
Look	Staring intensively at another individual for several seconds		
Multiple stamp	Stamping the ground repetitively with foot, fast motion		
Multiple stamp, 2 feet	Stamping the ground repetitively with both feet alternatively, fast motion		**Stamp**
Object on head	Putting an object (usually straw or leaves) on head		
Pirouette	Twirling movement of whole body around the body y axis while standing on four legs. Progressive forward movement in space		
Pirouette with object	Twirling forward movement of whole body around the body y axis while standing on four legs. with an object held in mouth or covering body		
Push object	Pushing away forcefully an object with hand.		
Reach	Extending one arm towards another individual	**Away**	**Reach**
Rocking	Rocking movement of whole body usually while seated		
Rope spinning	Twirling whole body very rapidly around the y body axis, while hanging to a rope with one or two hands and one or two feet		
Shake object	Shaking fixed object forcefully with both hands		**Object shake**
Side roulade	Twirling side movement of whole body around body y axis while laying on the floor.		
Single Body tap	Slapping body part singly with palm of hand (except chest)		**Body slap**
Somersault	Twirling forward movement of whole body around the body x axis.		**Somersault**
Stiff gallop	Running with stiff forelegs		
Stiff stance	Standing rigidly with stiff limbs and forelimbs held tight, facial expression of tight lips usually occurs in sexual context.		**Stiff stance**

Stiff walk	Walking with rigid forelegs and usually head tilted on the side		
Stamp	Stamping the ground forcefully with sole of foot, often following or simultaneous to a Chest beat		**Stamp**
Stamp, 2-feet	Stamping the ground forcefully with sole of feet.		
Straw wave	Throwing straw over head with both hands		**Straw wave**
Tapping contralateral	Tapping shoulders or elbows repetitively and simultaneously with palm of hands and crossed arms	**Arm cross**	
Throw object	Throwing away an object towards another individual		**Throw**
Throw threat	Grabbing an object and performing a forward and forceful movement towards an individual.		

AUDIBLE AND VISIBLE

1-handed chest beat	Tapping chest repetitively with cupped hand	**Chest pat**	
Body beat	Drumming body part (except chest) with cupped hands or palm of hands.	**Body beat/Beat sides of head**	**Body beat**
Body beat with object	Drumming body part (except chest) with cupped hands or palm of hands with an object placed between hands and body part.		
Chest beat	Drumming chest with cupped hands	**Chest beat**	**Chest beat**
Chest beat with object	Drumming chest with cupped hands and an object placed between hands and chest		
Clap	Tapping both palms of hands against each other as human applause	**Clap**	**Clap**
Drum object (fists)	Drumming an object with fists		
Drum object (palms)	Drumming an object with palm of hands.		
Knock object	Hitting an object forcefully and multiply with fist or wrist.	**Knock**	**Slap ground**
Multiple stamp, 2-feet on object	Stamping an object repetitively with both feet alternatively, fast motion.		
Punch object	Hitting object forcefully and singly with fist or wrist.	**Backhand pound**	**Slap ground**
Slap object, 1-handed	Slapping forcefully and singly object with palm of hand	**Slap surface**	**Slap ground**
Slap object, 2-handed	Slapping forcefully and singly object with palm of hands.		
Stamp 2-feet, on object	Stamping an object forcefully with sole of feet		
Stamp object	Stamping an object forcefully with sole of foot, often following or simultaneous to a Chest beat		**Stamp**
Tapping object	Tapping an object repetitively with palm of hand		
Water splash	Hitting water with hands or fists		

TACTILE

2-handed grab	Grabbing another individual's body part with two closed hands.		
2-handed grab-pull	Grabbing another individual's body part with both closed hands and pulling towards self		
Bite	Gentle biting of another individual's body part, different from aggressive biting	**Bite**	**Formal bite**
Bite + Arms shake on	Biting other individual (usually its head) and shaking arms on the other's body		
Drum other	Drumming another individual with palms of hands.		
Embrace	Embracing another individual by wrapping both arms around its body, usually reciprocal		**Embrace**
Grab-pull	Grabbing another individual's body part with one closed hand and pulling towards self	**Tactile close**	**Grab-push-pull**
Hand on	Touching head of another individual with palm of hand and maintaining touch for several seconds.	**Tactile close**	**Hand on**
Hands on	Touching head of another individual with palm of both hands and maintaining touch for several seconds.		
Hit with object	Hitting another individual with object held in hand		
Kick	Kicking another individual with foot		
One-handed grab	Grabbing another individual's body part with one closed hand	**Tactile close**	**Grab**
Poke	Touching repetitively other individual's body part with finger		
Positioning	Pushing or pulling lightly then releasing another individual's limb in the direction of desired position, usually used in grooming	**Tactile close**	
Pounce	Jumping forward on another individual		
Punch	Hitting another individual forcefully and singly with fist or wrist		**Punch**
Push, 1-handed	Pushing away another individual with hand or arm	**Tactile close**	
Push, 2-handed	Pushing away forcefully another individual with two hands		**Push**
Slap other	Slapping forcefully and singly another individual with palm of hand.		**Slap**
Slap other, 2-handed	Slapping forcefully and singly another individual with palm of hands		
Stroking	Stroking another individual with gentle back and forth movement of palm of hand	**Tactile close**	
Tandem walk	Two individuals walk together, one individual over the other one		
Tapping other	Tapping repetitively another individual with palm of hand.	**Tap other**	**Prod**
Touch	Touching gently another individual's body part with palm of hand.	**Tactile close**	**Touch/Long touch**