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The repertoire, meaning and intentionality of gestural communication in wild chimpanzees

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Abstract

A growing body of evidence suggests that human language may have emerged primarily in the gestural rather than vocal domain, and that studying gestural communication in great apes is crucial to understanding language evolution. Although manual and bodily gestures are considered distinct at a neural level, there has been very limited consideration of potential differences at a behavioural level. In this study, we conducted naturalistic observations of adult wild East African chimpanzees (*Pan troglodytes schweinfurthii*) in order to establish a repertoire of gestures, and examine gesture use and comprehension, comparing across manual and bodily gestures. At the population level, 120 distinct gesture types were identified, consisting of 65 manual gestures and 55 bodily gestures. Both bodily and manual gestures were used intentionally and effectively to attain specific goals, by signallers who are sensitive to recipient attention. However, manual gestures differed from bodily gestures in terms of communicative persistence, indicating a qualitatively different form of behavioural flexibility in achieving goals. Both repertoire size and frequency of manual gesturing was more affiliative than bodily gestures; while bodily gestures were more antagonistic. These results indicate that manual gestures may have played a significant role in the emergence of increased flexibility in great ape communication and social bonding.

Keywords: gestural communication, gestural repertoire, repertoire, flexibility, intentionality, communicative persistence, chimpanzee, wild chimpanzee, Pan troglodytes, manual gesture, bodily gesture

Introduction

Several features of chimpanzee (and other great ape) gestural communication suggest that the intentionality and flexibility that underlies the evolution of human language emerged primarily in the gestural rather than vocal domain (Arbib et al. 2008; Corballis 2003; Corballis 2009; Hewes, 1973; Liebal and Call 2012). Firstly, the gestural repertoire is considered large relative to other forms of communication (Nishida et al. 2010; Pollick and de Waal 2007). Secondly, gestures are intentionally produced towards attaining specific goals, and are directed towards a recipient (Bard 1992; Leavens et al 2004; Cartmill and Byrne 2010; Roberts et al. 2013). Thirdly, gestures are flexibly used (Goodall 1986; Hobaiter and Byrne 2011a; Roberts et al. 2012a, 2013; Roberts et al. 2012b) and understood (Roberts et al. 2012a) across several different contexts. Finally, there is some evidence that manual gestures are lateralised at a behavioural level and that this reflects asymmetry at the neural level (Meguerditchian et al. 2010; Hopkins et al. 2012). However, it remains unclear whether different forms of gestural communication, such as brachiomanual gestures and grosser bodily postures or actions, should be considered as distinct at a behavioural and neural level (e.g. Pollick and de Waal 2007). Despite neurophysiological evidence for differences in the production and processing of manual and bodily gestures (Puce and Perrett 2003; Rizzolatti and Arbib 1998), there has been surprisingly limited attention to this distinction within behavioural studies of primate gesture.

Gestural theories for language evolution have posited that bipedalism was pivotal for the emergence of manual gestures, indicating that manual gestures are distinct from other postural signals (Armstrong and Wilcox 2007; Donald 1991). This distinction is potentially important because only humans and other great ape species have a large repertoire of manual gestures, while many primate species have postural signals (Arbib et al. 2008; Hinde and Rowell 1962). Some studies include bodily gestures, head movements, or facial expressions within their definition of gestural communication (Arcadi et al. 2004; Arcadi et al. 1998; Hobaiter and Byrne 2011a; Liebal et al. 2004; Tomasello et al. 1994), but in others the focus is limited to manual gestures, made with the arms and hands only, and without the use of objects or substrate (Pollick and de Waal 2007; Roberts et al. 2012a; Roberts et al. 2012b; Roberts et al. 2013). The current study aims to address this distinction by examining manual and bodily gestures in relation to the three defining features of gestural communication; repertoire and intentionality in production, usage and comprehension (e.g. Seyfarth et al. 2010).

Systematic comparisons across Pongidae indicate relative preservation of manual and bodily gestures across species (Hobaiter and Byrne 2011a; Scott 2013). Chimpanzee gestures such as hand clap, begging and beckoning are present in human gestural repertoire, although systematic comparisons with human gestural repertoire are missing (Roberts et al. 2012b). Gestures are important in regulating interactions, with around 30-50 manual gestures (e.g. arm raise) and a similar number for locomotory (e.g. jump) and bodily gestures (e.g. bowing) combined recorded in chimpanzees (e.g. Nishida et al. 2010; Hobaiter and Byrne 2011a; Roberts et al. 2012b). The gestural repertoire is relatively large, for example, 31 manual gesture types were identified compared to only 18 facial and/or vocal signals in captive chimpanzees and bonobos (Pollick and de Waal 2007). However, captive settings influence the cognitive skills underlying communicative behaviour during ontogeny (Call and Tomasello 1996) but most of our knowledge about chimpanzee gestural communication comes from studies of gestural behaviour in captivity (see e.g. Liebal et al. 2004; Leavens et al. 1996; Leavens and Hopkins 1998; Tomasello et al. 1984; Tomasello et al. 1985; Tomasello and Frost 1989; Tomasello et al. 1994; Tomasello et al. 1997). Studies of gestural communication in wild apes have been mainly focused on subadult subjects (Slocombe et al. 2011) or have not systematically applied intentionality criteria in identifying units of gestures. For instance, work on gestural communication of the Kasakela group of Gombe (Tanzania) in East Africa (Goodall 1986; van Lawick-Goodall 1968), later supplemented by observations on infants in the same community by Plooij (1979) give the first account of gestural behaviour in wild chimpanzees.

More recently, systematic field studies have identified a large repertoire of gestures that are used intentionally during chimpanzee interactions (Hobaiter and Byrne 2011a; Roberts et al. 2012a,b; 2013). Many acts, which are communicative to perceivers, do not necessarily involve complex cognitive processes since they are simply involuntary reactions and expressions of the signaller's internal emotional state. However, gestural communication involves complex cognitive processes because signallers use gestures intentionally, which implies that they may make informed choices which may be based on mental representations (Tomasello and Zuberbühler 2002). In intentional communication, the behaviour of the sender must involve a goal and some flexibility in the means for attaining it (Tomasello and Call 1997). Several operational criteria for defining intentionality have been used in the studies of gestural communication in great apes (e.g. Leavens et al. 2004; Liebal et al. 2004; Krause and Fouts 1997). One part of the supporting evidence for intentional gestures in great apes has been based on the influence of an audience on the propensity to produce gestures by chimpanzees (Leavens et al. 2004; Roberts et al. 2012b). Chimpanzee gestures are used effectively (Hobaiter and Byrne 2011b; Roberts et al. 2012a, 2013) and display high levels of responsiveness in recipients (Roberts et al. 2012a). Signaller sensitivity to the visual orientation of the intended recipient is also important for communication, especially for visual, silent gestures (Liebal et al. 2004; Roberts et al. 2012a, 2013). Some audible gestures have been labelled as 'attention getters' that serve to attract the recipient's attention (Tomasello et al. 1994). However, evidence for attention getting is inconsistent (Liebal et al.

2004). For example, the production of audible gestures did not differ according to the recipient's visual attention in wild chimpanzees (Hobaiter and Byrne 2011a).

Both captive and wild chimpanzees show flexibility in terms of communicative persistence when their goals are not met (Leavens et al. 2005; Roberts et al. 2013; Liebal et al. 2004). Intentional gestures are produced with the goal of eliciting a particular behavioural response in the recipient (Cartmill and Byrne 2010; Roberts et al. 2013). Gestures elicit a single, dominant response in recipient, more often than all other responses combined (Roberts et al. 2012a). Signallers stop gesturing when the response to a gesture matched the dominant response for a gesture, but continue gesturing when the response did not match the dominant response type to a gesture (Roberts et al. 2013).

However, recipients can make inferences about the goal of the signaller flexibly in presence of other accompanying contextual cues (Tomasello and Carpenter 2007; Seyfarth et al. 1980). For instance, while arm beckon gesture elicits 'approach' by a recipient, the gesture can be embedded within grooming or a mating context, determining subsequent interactions (Roberts et al. 2012a). Flexibility can be seen in the use of a gesture type across multiple contexts, or the use of multiple gestures within each context - so called means-ends disassociation (Bruner 1981). However, some gesture types are used more flexibly than others (Plooij 1978; Pollick and de Waal 2007). Manual gesture types differ in terms of their context specificity, and can be tightly, loosely or ambiguously associated with a dominant goal (Roberts et al. 2012a). Chimpanzees (and bonobos) were reported to have greater flexibility in their production of manual gestures across contexts than for vocal and facial signals (Pollick and de Waal 2007). Importantly, Pollick and de Waal (2007) state that this was not the case when gestures were defined more broadly to include locomotory or other bodily postures, but do not include any data or analyses to support this claim and most studies do not systematically compare manual gestures and other types of gestures (Liebal et al.

2004; Cartmill and Byrne 2010; Hobaiter and Byrne 2011a). This distinction is significant because reduced flexibility would be expected if some bodily postures are unintentionally communicative and are primarily intention actions, or emotional responses (Plooij 1978; Seyfarth et al. 2010).

Here we provide the systematic study of adult chimpanzee gestures in their natural habitat, making attempt to compare manual and bodily gestures. First, we examine the repertoire size of gestures in wild chimpanzees, comparing the gestural repertoire across individuals, studies and sites. Second, we examine the intentionality of gestures in terms of flexibility in production, usage and comprehension, to examine whether the distinction between manual and bodily gestures at the neural level is also evident at a behavioural level (Pollick and de Waal 2007). If manual gestures are produced more intentionally than bodily gestures, then we would expect manual gestures to be used to influence the recipients more flexibly than bodily gestures (Pollick and de Waal 2007). This flexibility may also be evident as increased sensitivity to audience attention states and more flexible contextual use (Tomasello et al. 1984).

Methods

Study site and subjects

The Sonso community of habituated East African chimpanzees at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (Reynolds 2005) was observed over an eight month period (September 2006; April – July 2007; March – May 2008). We examined the gestural communication of 12 focal adults (6 males, 6 females), characterized by a lack of any limb injuries (Roberts et al. 2012b). Additionally, ad libitum data on adult non-focal subjects was collected (N = 7 subjects, N = 54 events).

Data collection

Focal continuous individual follows and opportunistic, qualitative ad libitum samples were used to establish an inventory of gestures. A digital video camera recorder (SONY DCR HC32E), recorded continuously, with the camera focusing on the focal subject and conspecifics in proximity to capture the context (or in some instances, details of context were verbally described onto the videotape during the recording). In total 250 h of video footage was coded, with a mean ±SD observation of 17.21 ±1.29 h of data duration per focal subject (Roberts et al. 2012a).

Video analysis

Inventory of gestures

First, an inventory of gestures was established from video recordings of non-verbal behaviour with adequate quality footage (N = 4 886 cases) or verbal descriptions (N = 442 cases). Non-verbal behaviour was scored as gestural communication if it was a movement of the limbs, body, head or locomotory gait that was 1) intentional, as determined by signaller directing gesture at recipient and monitoring the recipient's response during and after gesture, or by persistence of gesture production when recipient failed to respond; and 2) communicative, in terms of being capable of reception, having a discernible function and consistently inducing change in recipient's behaviour by non-mechanical means.

In order to identify intentional gestures, we evaluated intentionality criteria for each gesture type separately, using pooled data from all subjects (but see Genty et al. 2009; Hobaiter and Byrne 2011a). Gestures were above the threshold of 60% of cases meeting criteria of intentional gesture. Moreover, in our final list of gestures, we included only those types represented by at least two events, or a single event for gesture types described in other studies (a total of 120 gesture types are identified, see Table 1). Categorisation of visual, manual gestures without use of objects, was previously made quantitatively based on N=29 morphological components (Roberts et al. 2012b). Other units of gestures were categorised qualitatively based on morphological similarity, naming gestures using a 'verb first' principle (Nishida et al. 2010). We assigned gestures to broad categories (e.g. head, leg, manual) to distinguish single gestures and their combinations (where more than one gesture is made simultaneously by the signaller, e.g. 'bite' and 'embrace'). Gestures were classified according to modality: 1) visual (silent) 2) auditory 3) tactile (physical contact between signaller and recipient). Moreover, gestures were classified in accordance to whether they occurred singly or in a sequence (more than one gesture made consecutively by one individual towards the same recipient, the same goal, within the same context, within a maximum of 30 s interval). For each gesture event the following data were recorded:

Signaller and recipient: The signaller was defined as the individual performing a gesture; the recipient was defined as the individual at whom the gesture was most clearly directed, as determined from orientation of head and body of the signaller during or immediately after performing the gesture. The signaller had to have the recipient within its field of view (up to 45 degrees body turn; Pollick and de Waal 2007). In those cases when no viable recipient could be detected by this method e.g. when there was no individual in the signaller's view but they were producing an auditory gesture, the recipient was identified from proximity rather than signaller orientation.

Visual attention: visual attention status of both signaller and recipient prior, during or after the gesture was scored as Attention Present (when one had the other within their field of view, up to 45 degrees body turn) or Attention Absent.

Function: we assigned gestures to a broad functional group based on following characteristics of signaller and recipient behaviour: affiliative (leading to increased cohesion between signaller and recipient, e.g. grooming initiation), defensive (appeasement in response to receiving or observing aggressive behaviour, includes reconciliation and reassurance), offensive (producing aggressive behaviour leading to physical aggression, retaliation, etc).

Context: to define context we examined all new conditions that confronted the signaller before and during the production of a gesture that might have led to the onset of gesturing, recipient behaviour, and the identity of the interactants involved in interaction. Contexts were categorised as 1) clinging (gripping another's belly or back with hands or hands and feet), 2) courtship (behaviour where individuals maintain monopoly of their sexual partner), 3) food (eating, observing others eat or sharing plant food or meat), 4) groom (using thumb or index finger to push through hair on another's body to pick at exposed skin, groom initiations), 5) hunt (stalking, pursing, capture and kill of prey), 6) inter-community (interactions in context of hearing other communities or patrolling their territory), 7) inter-party interactions (communicating or interacting in context of hearing another party), 8) nursing (sucking on the nipple of the mother), 9) third party aggression (observing aggressive behaviours between third party); 10) play (bodily contact, wrestling, chasing or tickling in a non-agonistic manner), 11) predator (observing dangerous animal in proximity), 12) reunion (meeting after separation), 13) ride (being transported by an individual, while gripping to its belly or back), 14) sex (mounting, stimulating genitals, copulating); 15) travel (walking, running with or following another in certain direction) and 16) water (drinking, observing others drink or sharing drinking hole).

Response: the recipient's behaviour was categorized as either Response Present (identified as the first change in recipient's behaviour observed following a gesture) or as Response Absent (Liebal et al. 2004). When there was no change in the recipient's behaviour, but the recipient continued an activity towards the signaller (e.g. approach), or the interaction with the signaller (e.g. groom), this was also coded as Response Present, on the assumption that the signal functioned to maintain an ongoing activity (Goodall 1986).

Statistical analysis

As a result of applying intentionality criteria in selection procedure of gestures we identified 3 237 gesture cases (including 307 verbal descriptions) from initial corpus of 5 328 non-verbal behaviours recorded. In order to calculate associations between gesture types, visual attention, context, function and response, we only included gesture types in analyses for which we had a minimum of five cases of independent gesture events (either only single gestures in all analyses of gesture production in relation to visual attention, or single gestures and first gesture in sequence), excluding gestures produced by non-focal subjects (with exception of analyses identifying the dominant response for a gesture at the group level) and gestures simultaneously combined with other types, or cases for which data on either response, function, context or attention was missing. Moreover, to ensure independence, for analyses of elaboration we examined second gesture in the sequence, relative to first gesture in the sequence only, including combined gesture if they occurred as second in the sequence. This produced a variable data set with different number of gestures and events eligible for inclusion in each analyses (see ESM Table 2 for the data set which formed bases of all analyses). In order to avoid pseudoreplication, we used the individual as the unit of analyses. We calculated individual frequencies and converted these into proportions for each individual for each gesture type (according to visual attention, context, function and response type) because the frequencies of gestures and production rates across contexts and so on, differed between individuals.

Overall gesture specificity (the degree of association between a given gesture and dominant context, dominant response and dominant function) or gesture/ context specificity for response was calculated as the mean of individual proportions for specificity for gestures overall. For each individual, gesture specificity was calculated as the mean of the proportion of total cases of each gesture type that co-occurred with the most common response, function or context type for that individual. We also calculated whether response to first gesture in sequence, matched or did not match the dominant response for a gesture identified at the group level (calculated from total frequencies of gestures). For each individual, the frequency of responses matching and non matching the dominant response for a given gesture was calculated and converted into individual mean proportions for analyses. Moreover, to examine how the gesture types differed in relation to response, we supplemented the data set with ad libitum data on non-focal subjects, and pooled mean proportions according to a given gesture type instead of by focal individual. For analyses by gesture type, mean specificity was calculated as the group average of individual specificity for a given gesture type in relation to response.

Finally, to examine consistency of repertoire overlap, with first calculated mean percentage overlap across individuals, sites and studies; calculating the percentage of individuals, studies and sites that displayed a gesture identified in Budongo repertoire; we then averaged this percentage across all gesture types. Cohen's Kappa was used to examine the consistency of the gestural repertoire across individuals and sites. This method has been widely used to compare gestural repertoires in other studies (e.g. Pika et al. 2005; Roberts et al. 2012b). Across individuals, the consistency (presence/absence of a specific gesture type) was calculated for each pair of subjects, and these Kappa scores were then averaged across all gesture types, and subjects. Across sites, the consistency was calculated for each gesture type between pairs of studies, and the Kappa scores were then averaged across all gesture types to give a mean Kappa score for each pair of studies. This method allowed us to compare the consistency of the gestural repertoire detailed at different sites, whilst allowing for differences in repertoire size and 'lumping' and 'splitting' in the classification of gesture types. All tests were non-parametric and exact probabilities were used (Mundry and Fischer 1998). All statistical tests were performed using Wilcoxon signed-ranks test (unless otherwise specified), all tests were two tailed, with an alpha level of 0.05. Medians and interquartile ranges (between the top of the lower quartile and the bottom of the upper quartile: IQ) are reported. All data analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.).

Results

Repertoire size

Using established criteria for intentional gestural communication of the initial 5 328 cases of non-verbal behaviours recorded, we excluded 2 091 cases, represented by behavioural events that did not meet our intentionality criteria (ESM Table 1). This excluded behaviours such as quadrupedal stance (N = 331), gentle, moderate or vigorous scratch (N = 1 121), peering at object (N = 7) and peering at recipient (N = 12). Of a total of 3 237 cases which fulfilled the criteria for an intentional gesture (Table 1), 88.6% (2 867 cases) were performed as single gesture event and 11.4% (368 cases) occurred as a combination of gesture events (two or more gestures performed simultaneously, e.g. 'bite' and 'embrace'), gesture combinations were not analysed. The total number of gestures recorded, forming corpus of 3 237 cases of both single and combined gestures, was 3 631.

Gestures were categorised into 120 types, consisting of 65 (54%) manual gestures and 55 (46%) bodily gestures (Table 1). The median (IQ) number of gestural events per focal subject was 238.5 (158.25 – 450.75). The median (IQ) focal subject repertoire size was 52 (41-55). For manual gestures, the median (IQ) repertoire size was 24 (20.25-28.5). Similarly, for bodily gestures, the median (IQ) was 24.5 (19-30).

INSERT TABLE 1 HERE

Repertoire homogeneity across individuals, studies and sites

The average percentage overlap in gesture types across all individuals was 40% overall, and 41% and 39% for bodily and manual gestures respectively. Eighteen gesture types were performed by only a single individual (15% of all gesture types observed) of these six types were represented by more than a single event and twelve types were represented by a single event (Table 1). Cohen's Kappa was used to examine the consistency of the gestural repertoire across individuals, with low consistency in categorisation in specific gesture types produced overall (Kappa scores from 0.21-0.30, median = 0.25, IQ = 0.22-0.27). This was true both of manual gestures (range 0.15-0.33, median = 0.23, IQ = 0.20-0.26) and bodily gestures (range 0.13-0.32, median = 0.23, IQ = 0.21-0.29), with no significant difference between these two categories, $T = 35$, $N = 12$, $P = 0.79$.

We used previously published data (Goodall 1986; van Lawick-Goodall 1968, 1967; Liebal et al. 2004; van Hooff 1971; Nishida et al. 2010; Plooij 1984; Plooij 1979, 1978; Pollick and de Waal 2007) to examine the average overlap in gesture types across three field sites (Budongo, Mahale and Gombe) and the average percentage overall was higher than for overlap across individuals (83.5%). However, the overall consistency of the gestural repertoire between dyads of sites was low, with a range of Kappa scores from 0.02-0.17 for the three comparisons (Budongo-Mahale, Budongo-Gombe and Mahale-Gombe) and for both manual gestures (-0.001-0.18) and bodily gestures (range of 0.09-0.11). There were eight gesture types recorded in Budongo, which were not reported in other wild chimpanzee sites (e.g. Hand clap, Drag self, Limp extend) and ten gesture types which were reported in other sites, but which were not recorded in adult chimpanzees in Budongo (e.g. Bite self, Scratch dry leaves, Table 1).

The percentage overlap in gesture types across studies of gestural communication in the wild was 81.6% overall (Goodall 1986; Hobaiter and Byrne 2011b; van Lawick-Goodall

1968, 1967; Nishida et al. 2010; Plooij 1984; Plooij 1979, 1978; Roberts et al. 2012b). There were 8 gesture types recorded in this study, which were not reported in other studies and 27 gesture types which were reported in other studies, but which were either rejected or not recorded in this study (Table 1), although this comparison does not take into account the focus on different age classes across these different studies (for more detail see ESM, Table 2)

Repertoire size and use across contexts and functions

Production of gestures across contexts

Overall, the greatest number of different gesture types occurred in the context of grooming (median frequency = 10, IQ = 8-10.75), followed by ride (median = 6.50, IQ = 3.50-7.25) and travel (median = 6, IQ = 4 - 8). For manual gestures, the greatest number of gesture types occurred in the context of grooming (median = 6, IQ = 5-6, Fig. 1), followed by play (median = 4, IQ = 1.25-8.25). For bodily gestures the greatest number of gesture types occurred in the context of grooming (median = 4, IQ = 3-4, Fig. 1), inter-party interactions (median = 4, IQ = 2-6) and reunion (median = 4, IQ = 4-5). In the context of grooming, there were significantly more manual gestures types than bodily gesture types (T = 66, N = 11, P = 0.001). Similarly for clinging, there were significantly more manual gesture types (median = 1, IQ = 1-2.75) than bodily gesture types (median = 0, IQ = 0-0; T = 21, N = 6, P = 0.03). There were no significant differences in the number of gesture types across all the other contexts.

INSERT FIGURE 1 HERE

The overall pattern of usage remains fairly consistent in terms of the frequency of gesture events across the different contexts, the highest proportion of total gestures occurred in the context of grooming (median = 0.26, IQ = 0.18-0.34), followed by food (median = 0.10, IQ = 0.06-0.19). For manual gestures, the pattern was the same, with the highest proportion of gestures occurring in the context of grooming, and then food (Fig. 2). For bodily gestures, the highest proportion of gestures again occurred in the context of grooming, but followed by reunion (Fig. 2). A significantly greater proportion of manual gestures, as compared to bodily gestures, occurred in the context of grooming ($T = 69$, $N = 12$, $P = 0.02$), clinging ($T = 21$, $N = 6$, $P = 0.03$) and play ($T = 36$, $N = 8$ (4 ties), $P = 0.008$). There were no statistically significant differences in the proportion of manual and bodily gestures occurring across the other contexts.

INSERT FIGURE 2 HERE

Specificity of gestures to context

On average, both manual (median number of contexts = 1.6, IQ = 1.29 – 1.77) and bodily (median = 1.64, IQ = 1.40 – 1.94) gesture types were produced within a small number of contexts, with a maximum of 6 and 7 different contexts observed for individual for manual and bodily gestures respectively. Overall there was a high proportion of gestures associated with the dominant context (median proportion specificity for dominant context = 0.84, IQ = 0.82-0.87). This remained the case when manual (median = 0.85, IQ = 0.80-0.87($T = 0$, $N = 12$, $P < 0.001$) and bodily gestures were considered separately (median = 0.84, IQ = 0.81-0.87 ($T = 0$, $N = 12$, $P < 0.001$), and there was no significant difference between their context specificity ($T = 42$, $N = 12$, $P = 0.85$).

Production of gestures across functions

Overall, gestures types were categorised as affiliative (median = 18.5, IQ = 13 – 20.75), offensive (median = 8.5, IQ = 6.25-9.75) or defensive (median = 6, IQ = 4.25-7). There was an influence of function on the number of gesture types (Friedman's ANOVA, χ2 (2, N = 12) = 15.95, P < 0.001). Individuals produced a higher number of affiliative gesture types, as compared to offensive gesture types (T = 0, N = 12, P = 0.001), and more offensive than defensive gesture types (T = 41, N = 12, P = 0.03). For bodily gestures alone, there was no influence of function (affiliative: median = 6.5, IQ = 4 – 9; defensive: median = 4, IQ = 3 - 5 and offensive: median = 5, IQ = 3 – 7.75) on the number of gesture types produced (Friedman's ANOVA, χ2 (2, N = 12) = 3.73, P = 0.16). However, for manual gestures there was an influence of function on the number of gestures types produced (Friedman's ANOVA, χ2 (2, N = 12) = 19.70, P < 0.001). There were significantly more affiliative gesture types (median = 10.5, IQ = 7.5-13.5) as compared to offensive gesture types (median = 3, IQ = 2 - 5; T = 0, N = 11 (1 tie), P = 0.001), but offensive and defensive (median = 1, IQ = 1-2); did not differ (T = 55, N = 11 (1 tie), P = 0.051). When comparing bodily and manual gestures, in the affiliative function, there was greater number of manual gesture types than bodily gestures types (T = 61, N = 11 (1 tie), P = 0.01). For the defensive function, however, there was a greater number of bodily gesture types than manual types (T = 10.50, N = 12, P = 0.02). There was no significant difference in number of gesture types across offensive function (T = 8, N = 9 (1 tie), P = 0.09).

Overall the average proportion of events associated with each function type varied between affiliative (median = 0.60, IQ = 0.46-0.64), offensive (median = 0.26, IQ = 0.17-0.32) or defensive (median = 0.16, IQ = 0.12-0.21) function (Friedman's ANOVA, χ2 (2, N = 12) = 16.17, P < 0.001). A greater proportion of events was associated with affiliative function than an offensive function (T = 1, N = 12, P < 0.001), and for offensive than defensive function (T = 65, N = 12, P = 0.04). There was no significant association with function, in terms of the proportion of bodily gestures occurring in affiliative (median = 0.45, IQ = 0.30-0.51), offensive (median = 0.32, IQ = 0.19-0.42) or defensive (median = 0.25, IQ = 0.14-0.39) function (Friedman's ANOVA, $\chi 2$ (2, N = 12) = 4.98, P = 0.08). However, the proportion of manual gestures did differ between functions (Friedman's ANOVA, $\chi 2$ (2, N = 12) = 18.50, P < 0.001) and was higher in the affiliative function (median = 0.72, IQ = 0.62-0.80), than for an offensive function (median = 0.16, IQ = 0.13-0.29), (T = 1, N = 12, P = 0.001), with likelihood higher for offensive than defensive functions (median = 0.06, IQ = 0.02-0.09), each other (T = 72, N = 12, P = 0.007). When comparing the proportion of bodily and manual gestures occurring in each function, a greater proportion of manual than bodily gestures occurred in the affiliative function (T = 77, N = 12, P = 0.01), bodily gestures were more frequent for the defensive function (T = 4, N = 12, P = 0.03), but there was no difference for the offensive function (T = 15, N = 11 (1 tie), P = 0.12).

Specificity of gestures to function

When gestures were categorised as having an affiliative, defensive or offensive function, there was a high proportion of gestures associated with the dominant function (median proportion specificity for dominant function = 0.97, IQ = 0.95-0.98). Signallers produced gestures associated with the dominant function more often than all other gestures combined for both manual (median = 0.97, IQ = 0.94-1.00) (T = 0, N = 12, P < 0.001) and bodily gestures (median = 0.97, IQ = 0.95-0.97; T = 0, N = 12, P < 0.001) and these did not differ (T = 44, N = 12, P = 0.73).

Moreover, there was significant difference in specificity for dominant function and dominant context; the specificity was higher for the dominant function, than for the dominant context, both for bodily (Wilcoxon signed-ranks test: T = 1, N = 12, P = 0.001) and manual gestures (Wilcoxon signed-ranks test: T = 0, N = 12, P < 0.001). Further, there was no significant correlation between function specificity and context specificity for bodily gestures ($r = -0.16$, $N = 12$, $P = 0.60$) but there was positive correlation for manual gestures ($r = 0.57$, $N = 12$, $P = 0.049$).

Recipient's responses to gestures and gesture/context combinations

Overall, the responsiveness of recipients was high, with a median proportion of 0.86 (IQ = 0.81-0.90) gestures receiving a response from the recipient. Both manual and bodily gestures were highly likely to lead to a response by the recipient (manual: median proportion = 0.87, IQ = 0.82-0.93, $T = 0$ $N = 12$, $P < 0.001$; bodily: median proportion= 0.80, IQ = 0.61-0.90; $T = 0$, $N = 12$, $P < 0.001$), and these did not differ ($T = 60$, $N = 12$, $P = 0.11$). Moreover, there was a high proportion of single gestures associated with the dominant response (most frequently observed across all individuals; median = 0.69, IQ = 0.63-0.77). Both manual (median proportion specificity for dominant response = 0.67, IQ = 0.40-0.81; $T = 12$, $N = 12$, $P = 0.03$)) and bodily gestures were associated with a single dominant response significantly more than all other responses combined (median = 0.71, IQ = 0.67-0.79 $T = 1$, $N = 12$, $P = 0.001$), and these did not differ ($T = 31$, $N = 12$, $P = 0.57$).

At the level of the most commonly seen gesture types ($N = 45$ gesture types with more than N = 5 cases), there was tight single gesture specificity overall for a dominant response type (median percentage specificity = 75.0, IQ = 53.5-100). However, when considering the specificity of each gesture type separately, 27 (60%), 10 types (22%) and 8 types (18%) were tightly, loosely and ambiguously associated with dominant response, respectively (see Table 2). Both manual (median percentage specificity = 75, IQ = 60-87.5) and bodily gestures (median = 81.2, IQ = 42.5-100) were tightly associated with a dominant response. The distribution of gesture types across loose, ambiguous and tight specificity categories, differed for both manual gestures (15 tight, 7 loose, 3 ambiguous; Chi-square goodness-of-fit test: χ^2 (2, *N* = 25) = 8.96, *P* = 0.01) and bodily gestures (12 tight, 3 loose and 5 ambiguous; Chi-square goodness-of-fit test: χ^2 (2, *N* = 20) = 6.70, *P* = 0.04.

INSERT TABLE 2 HERE

For gesture/ context combinations the dominant response (assigned at the level of gesture type, Table 2) was significantly more likely than all other responses combined for both manual (median proportion matching dominant response = 0.65, IQ = 0.46-0.78; T = 10.50, N = 12, *P* = 0.02) and bodily gestures (median = 0.69, IQ = 0.61-0.78; T = 1, N = 12, *P* = 0.001). There was no significant difference in specificity of response to gesture/ context combination when comparing manual and bodily gestures (T = 36, N = 12, *P* = 0.85).

The likelihood of a response matching the dominant response for a gesture alone did not differ from that of gesture/ context combinations for either manual (median = 0.67, IQ = 0.40-0.81; T = 37, N = 11 (1 tie), *P* = 0.77) or bodily gestures (median = 0.71, IQ = 0.67-0.79; T = 14, N = 12 *P* = 0.19). Further, there was no significant correlation between response specificity and context specificity for either manual (*r* = -0.15, *N* = 12, *P* = 0.65) or bodily gestures (*r* = -0.17, *N* = 12, *P* = 0.59).

Directing visual attention towards the recipient and response monitoring

Signaller's were visually oriented towards the recipient prior to the production of almost all gestures, with no difference between manual (median proportion of gestures with signallers visually oriented = 1.00, IQ = 0.96-1.00) and bodily gestures (median = 0.93, IQ = 0.86-1.00; (*T* = 38, *N* = 10 (3 ties), *P* = 0.07). Following the production of the gesture, there was no difference in the signaller's visual attention towards the recipient (response monitoring) for both manual (median proportion of gestures with recipient visually oriented = 0.75, IQ = 0.65-0.81) and bodily gestures (median = 0.57, IQ = 0.49-0.87; $T = 58$, $N = 12$, $P = 0.15$).

Adjustment of modality to recipient's visual attention

Recipients were almost always visually attending to the signaller prior to gesture production, but prior attention was higher for manual (median proportion = 0.88, IQ = 0.79-0.98) than for bodily gestures (median proportion = 0.78, IQ = 0.63-0.88; ($T = 73$, $N = 12$, $P = 0.005$). There was an influence of the visual attention state of the recipient on the modality of gestures for both bodily and manual gestures. For bodily gestures, when the recipient was not attending prior to the gesture, auditory gestures were more commonly produced (median proportion of auditory gestures when recipient not attending = 0.99, IQ = 0.91-1.00) than either tactile gestures (median = 0.00, IQ = 0.00-0.01, Fig. 3) or visual gestures (median = 0.01, IQ = 0.00-0.06; Friedman test, χ^2 (2) = 21.33, P <0.001). The proportion of bodily auditory gestures was significantly higher than bodily visual gestures ($T = 78$, $N = 12$, $P < 0.001$). For manual gestures, when the recipient was not attending, tactile gestures were produced more frequently (median = 1.00, IQ = 0.67-1.00) than either auditory gestures (median = 0.00, IQ = 0.00-0.00) or visual gestures (median = 0.00-0.33; Friedman test, χ^2 (2) = 18.57, P <0.001, Fig. 3). The proportion of manual tactile gestures was significantly higher than manual visual gestures ($T = 0$, $N = 9$ (2 ties), $P = 0.004$).

INSERT FIGURE 3 HERE

Communicative persistence

Frequency of production of single gestures versus sequences

Most gesture cases were made as a single gesture, rather than occurring within a sequence. Of the 3,191 focal gesture cases recorded, 1,971 cases (62%) were made as single gestures and 1,220 cases (38%) occurred within gesture sequences. These sequences contained up to 29 gestures (median sequence length = 2; IQ = 2 - 3). This was also the case both for manual gestures (median proportion of single gestures = 0.89, IQ = 0.68-0.93, $T = 0$, $N = 12$, $P < 0.001$) and bodily gestures (median = 0.69, IQ = 0.62-0.73, $T = 3$, $N = 12$, $P = 0.002$). However, single gesture cases were more likely to occur as manual gestures than bodily gestures ($T = 75$, $N = 12$, $P = 0.002$). Conversely, sequences were more likely to occur as bodily gestures than manual gestures.

Repetition and elaboration within sequences

When examining the structure of the gesture sequences overall (comparing only the initial and second gesture in sequences), signallers both repeated the same gesture (37%) and elaborated using different gestures (63%). This included elaboration by a single gesture (50%), a combination of gestures (9%); and augmentation (repeating and adding additional gesture, 4% of events). For manual gestures, signallers continued signalling more often by elaboration (83%) than by repetition (17%); $T = 0$, $N = 11$ (1 tie), $P = 0.001$). Similarly, elaboration (90% of events) was more common that repetition (10% of events) for bodily gestures (; $T = 0$, $N = 12$, $P < 0.001$). Manual and bodily gestures did not differ in the proportion of elaboration within sequences ($T = 23$, $N = 11$ (1 tie), $P = 0.41$).

Influence of recipient's response on production of sequences

Sequences were no more likely to be produced when the response of the recipient to the first gesture in a sequence did (median = 0.50, IQ = 0.47-0.51) or did not match (median = 0.50, IQ = 0.49-0.53) the dominant response type of that gesture; ($T = 12N = 7$ (5 ties), $P = 0.81$). However, for sequences that were initiated by a manual gesture, a higher proportion of the sequences were produced when the response to the first gesture did not match the dominant response type (median proportion of response = 1.00, IQ = 1.00-1.00) than when the response did match,(median = 0.00, IQ = 0.00-0.00; *T* = 54, *N* = 11 (1 ties), *P* = 0.004). In contrast, sequences initiated by a bodily gesture occurred following a matching (median = 0.83, IQ = 0.64-1.00) rather than non-matching response (median = 0.17, IQ = 0.00-0.36; *T* = 0, *N* = 11 (1 ties), *P* = 0.002). A higher proportion of manual than bodily gesture sequences were used in persistence, i.e. sequence production following an initial response that did not match the dominant response type for that gesture type (*T* = 0, *N* = 9 (1 tie), *P* = 0.004).

When comparing single gestures and sequences, bodily sequences were no more likely to be produced than bodily single gestures (median = 0.71, IQ = 0.67-0.79) when the response matched the dominant response type (*T* = 24, *N* = 12, *P* = 0.47). However, for manual gestures, single gestures (median = 0.67, IQ = 0.40-0.81) were more likely to be produced than sequences when the response matched the dominant response type (*T* = 66, *N* = 11, *P* = 0.001).

Meaning homogeneity within sequence

The next set of analyses examined whether the gestures types used within sequences had a dominant meaning, matching dominant meaning of the first gesture. For bodily gestures, there was no significant difference in the average proportion of gestures with the matching meaning (median = 0.57, IQ = 0.41-0.69) and non-matching meanings (median = 0.43, IQ = 0.31-0.59; *T* = 23, *N* = 11 (1 tie), *P* = 0.41). In contrast, for manual gestures, gestures matching in meaning (median = 0.71, IQ = 0.50-1.00) were significantly more common than those non-matching (median = 0.29, IQ = 0.00-0.50, *T* = 40, *N* = 9 (3 ties), *P* = 0.04). Sequences of manual gestures were significantly more likely to have gestures with matching meaning as the first gesture in the sequence than bodily gesture sequences (*T* = 4.5, *N* = 11 (1 ties), *P* = 0.008).

Influence of context on production of single gestures and sequences

In terms of context, single manual gestures occurred more often in affiliative contexts (median 0.74, IQ = 0.63-0.79) than offensive/ defensive contexts (median 0.26, IQ = 0.21-0.37; $T = 6$, $N = 12$ $P = 0.007$). However, single bodily gestures were no more likely to occur in affiliative contexts (median 0.49, IQ = 0.41-0.64) than offensive/ defensive contexts (median 0.51, IQ = 0.36-0.59; $T = 30$, $N = 11$ (1 tie), $P = 0.83$). There was a marginally significant trend for single manual gestures, as compared to single bodily gestures, to occur more often in affiliative contexts ($T = 64$, $N = 12$, $P = 0.052$).

In terms of the proportion of affiliative and offensive/ defensive gestures in gesture sequences, the proportion of affiliative gestures in manual gesture sequences (median = 0.79, IQ = 0.35-1.00) was significantly higher than the proportion of affiliative gestures in bodily gesture sequences (median = 0.28, IQ = 0.17-0.39, $T = 72$, $N = 12$, $P = 0.007$). Conversely, the proportion of offensive/ defensive gestures in bodily gesture sequences (median = 0.73, IQ = 0.61-0.83) was higher than the proportion of agonistic gestures in manual gesture sequences (median = 0.21, IQ = 0.00-0.65).

Moreover, when comparing single gestures and sequences for the influence of context, bodily gestural sequences, as compared to single bodily gestures, were significantly more likely to occur in an offensive/ defensive context ($T = 1$, $N = 12$, $P = 0.001$). In contrast, there was no influence of context on manual gestures. Manual gestural sequences, as compared to single manual gestures, were not significantly more likely to occur in affiliative contexts ($T = 46$, $N = 12$, $P = 0.62$).

Influence of meaning specificity on production of single gestures and sequences

Single manual gestures did not have tight meanings (median = 0.51, 0.44-0.69) significantly more often than ambiguous/ loose meanings combined (median = 0.49, IQ = 0.31-0.56; $T = 39$, $N = 11$ (1 tie), $P = 0.64$). However, single bodily gestures were significantly more likely to have tight meanings (median = 0.85, IQ = 0.76-0.93) than ambiguous/ loose meanings (median = 0.14, IQ = 0.08-0.24; T = 78, N = 12 P < 0.001). Single manual gestures were significantly more likely to have ambiguous/ loose meanings than single bodily gestures (T = 78, N = 12 P < 0.001). For bodily gesture sequences, there was no significant difference in the proportion of gestures initiating the sequence associated with an ambiguous/ loose meaning (median = 0.73, IQ = 0.45-0.83), and a tight meaning (median = 0.27, IQ = 0.17-0.75, T = 21.5, N = 11 (1 tie) P = 0.33). Similarly, for manual gestures initiating a sequence, there was no significant difference in the proportion of ambiguous/ loose gestures (median = 0.50, IQ = 0.38-0.71), and those with a tight meaning (median = 0.50, IQ = 0.29-0.63, T = 12, N = 8 (4 ties) P = 0.44). There was no significant difference between bodily and manual gesture sequences in terms of the proportion of ambiguous/ loose initial gestures (T = 29.5, N = 11 (1 tie) P = 0.78). When comparing single gestures and sequences, bodily sequences were more likely to be ambiguous/ loose than single bodily gestures (T = 76, N = 12 P < 0.001) but ambiguity did not differ between single gestures and sequences for manual gestures (T = 54, N = 12 P = 0.27).

Discussion

The ability to flexibly influence the recipient by use of intentional, meaningful gestures may have underpinned language evolution (Hewes 1973). Here we build up on several previous studies of captive chimpanzees (van Hooff 1971; Liebal et al. 2004; Pollick and de Waal 2007; Scott 2013; Smith and Delgado 2013; Tomasello et al. 1985; Tomasello et al. 1994; Tomasello et al. 1997) and those conducted in the wild (van Lawick-Goodall 1967, 1968; Goodall 1986; Nishida et al. 2010; Plooij 1978, 1979; Plooij 1984; Hobaiter and Byrne, 2011a; 2012a; Roberts et al. 2012a, b; Roberts et al. 2013; Pika and Mitani 2006) to examine the repertoire and flexibility of production, usage and comprehension of gestural communication in wild chimpanzees. Our results indicate that whilst overall chimpanzee gestural communication is intentional, there are some important differences in the flexibility of manual and bodily gestures.

Overall, our results indicate that chimpanzees have a diverse repertoire of both manual and bodily gestures. Previous research on wild chimpanzees identified 66 gesture types lumped into broad categories from 115 gesture subtypes. In our study we identified 120 gesture types, including 65 manual and 55 bodily gestures. Individuals used around 43% of all gesture types within their repertoire, higher than previously reported for this same community of chimpanzees, where approximately 15% of 66 gesture types were used within each individual's repertoire, with the average adult repertoire (8%); the smallest of all age classes (Hobaiter and Byrne 2011a). The difference in findings between these two studies may be due to differences in the criteria for inclusion of gestures within the repertoire, the active observation of adult individuals in this study and differences in the categorisation of gesture types. While in our study, gesture categories were also broad, containing multiple subtypes (Roberts et al. 2012b), quantitative approaches to gesture classification indicate that gestures are made up of multiple morphological components, which overlap across gesture types (Roberts et al. 2012b; see also Forrester 2008). Reported differences in overall repertoire size and form are therefore partially the result of the differences in the level of detail used in qualitatively categorising gestures when these are often graded signals (van Hooff 1967; Roberts et al. 2012b).

Both manual and bodily gestures were highly diversified across individuals and sites. There was a low level of agreement in the occurrence of manual and bodily gesture types both within individual repertoires and across study sites. This suggests that there is no more flexibility in chimpanzees' capacity to produce manual than bodily gestures (Pollick and de Waal 2007). As in previous studies, we identified a few idiosyncratic gestures - seven bodily and ten manual - that were unique to a single individual (Tomasello et al. 1994), although some of these gestures also occurred infrequently or were reported within other study populations (Hobaiter and Byrne 2011a; van Lawick-Goodall 1968; Nishida et al. 2010; Plooij 1984; Whiten et al. 1999). However, some gestures are tightly associated with a dominant context, so that individual variance may correspond to the likelihood of different forms of social interaction (for example, play, mother-offspring, mating or agonism). For example, our data indicate that adult chimpanzees produce manual and bodily gestures most frequently within the context of grooming (approximately 25%, then food related contexts, approximately 10%). Hobaiter and Byrne's (2011a) study also included subadults and reported play as the dominant context of gesture production (around 50% of all gestures, see also Liebal et al. 2004; Tomasello et al. 1985).

Chimpanzee gestures are produced intentionally; signallers attend to the recipient prior to and following gesture production for both manual and bodily gestures (Liebal et al. 2004; Leavens et al. 2004; Roberts et al. 2012a). Signallers are also sensitive to recipient's visual state. When the recipient was not attending to the gesture, bodily auditory gestures were more common than bodily visual gestures. Manual tactile gestures were also more common than manual visual gestures when the signaller was not attending. These findings are broadly consistent with previous evidence of signaller sensitivity to attention and gesture modality, although in these studies bodily and manual gestures were not considered separately (Genty et al. 2009; Hobaiter and Byrne, 2011a; Liebal et al 2004). The pattern of bodily auditory gesture usage, however, provides only weak support for the notion of 'attention-getting' gestures, since we did not examine influence of context on modality of gesture production (Hobaiter and Byrne 2011b; Liebal et al 2004; Tomasello et al. 1994). For instance, while the visual attention of recipient prior to the gesture was less common for bodily than manual gestures, more auditory manual gestures were produced than visual when recipient was attending. Chimpanzees may therefore use auditory manual and bodily gestures as a means of intimidation within an agonistic context whether recipients are or are not visually oriented towards the signaller. For instance, auditory gesture such as hitting object when produced in close proximity, in full view of the recipient.

Both manual and bodily gestures were effective, leading to equally high levels of behavioural change in the recipient. Moreover, categorisation of manual and bodily gesture types in relation to their association with a dominant response indicates that bodily gesture types were no more likely to be categorised as tightly associated with a response than manual gestures (Roberts et al. 2012a). Both manual and bodily gestures occurred more often as a single gesture than a sequence (62%), a similar result to previous findings (e.g. 64% of adult gestures were single; Hobaiter and Byrne 2011b). However, single manual gestures were more likely to occur as manual than bodily; suggesting that manual gestures were more effective.

More importantly, the key marker of intentional communication is communicative persistence, defined as the use of communication in which the sender has a goal, and continues signalling until the goal is obtained or failure is clearly indicated (Leavens et al. 2005; Golinkoff 1986). While manual and bodily gestures were both meaningful; eliciting the dominant response more often than all other response types combined, there was a much higher proportion of communicative persistence following manual gestures than bodily. Manual sequences were frequently associated with a response that did not match the dominant response to the first gesture in the sequence. In contrast, bodily sequences were dominated by a response that did match the dominant response to the first gesture. Thus, signallers continued gesturing following the first bodily gesture, even when they achieved their desired goal (the dominant response). This suggests that some bodily gestures were influenced by the emotional state of the signaller, rather than the signaller’s intention to communicate.

The elaborations within sequences also indicate the flexibility of gesturing, in particular, in their role in effectively influencing the recipient (Roberts et al. 2013). If communicative persistence is unintentional, then diffuse, uninformative elaboration occurs (Golinkoff 1986). In contrast, when the elaboration is intentional, then the use of informative signals are seen - these refer to the role of the recipient in the pursuit of the desired goal (Warneken et al. 2006). In accordance with previous research, both manual and bodily gestures were followed by elaboration rather than the repetition of original signals (Hobaiter and Byrne 2011b; Roberts et al. 2013). However, the less intentional character of bodily gestures is supported by the lack of fine-tuning of usage of gestures in elaboration sequences to elicit the desired response in the recipient. Our study shows that in manual sequences, the second gesture did match the meaning of the first gesture in the sequence. This was not the case for bodily sequences, suggesting bodily elaborations were not informative for the recipient in terms of the desired goal of the signaller.

However, sequences accounted for only 11% of manual gestures and only 31% of bodily gestures in the current study (a similar rate as previously reported for gestures overall for adults in the same community; Hobaiter and Byrne 2011b and for captive chimpanzees: around 30%, Liebal et al. 2004; Tomasello et al. 1994). Overall manual gestures were more often produced in affiliative contexts than bodily gestures, and the bodily gestures were more often produced in defensive contexts than manual gestures. However, the sequence production of manual gestures was independent of context, whereas bodily sequences were highly reliant on agonistic context (offensive and defensive combined). Further, overall sequences were equally likely to follow gesture types with a tight or ambiguous specificity to a dominant response, as previously reported for captive chimpanzees (Liebal et al. 2004). While, manual sequences were independent of the meaning specificity, ambiguity was higher for initial gestures within a bodily sequence than for single bodily gestures. This suggests that while context and meaning specificity were unimportant for production of manual gestures, these were the determining factors for bodily gestures. In contrast manual gesture sequences relied on recipient's response. However, not all gesture sequences are produced following communicative failure, as sequences can also be used to regulate dynamic interactions, for example, during play (Hobaiter and Byrne 2011b; McCarthy et al. 2012). Nonetheless, the inclusion of bodily gestures on criteria hinged on visual attention may identify less flexible gestures, in particular those which are ambiguous and antagonistic (Tomasello et al. 1984; Liebal and Call 2012). Future studies should examine communicative persistence at the level of gesture type to determine whether communicative persistence is less typical of bodily gestures overall or only for certain gesture types.

If flexibility is examined in terms of the influence of context on the response to a gesture, then the gesture/ context combinations did not vary in their association with the dominant response from gestures alone for neither manual nor bodily gestures (Roberts et al. 2012a, Roberts et al. 2013). This reflects the fact that we only observed first response to a gesture. Previous research also postulated that semantic meanings of gestures, as seen in first response to a gesture, are independent of the accompanying context (Cartmill and Byrne 2010; Roberts et al. 2012a). However, both manual and bodily gestures were used across a range of contexts and to achieve a number of goals. Overall both were function and context specific, although specificity for context was lower than for function for both manual and bodily gestures. Thus manual and bodily gestures had either affiliative, offensive or defensive functions, but were used across a number of different contexts such as grooming, play and, reunion. However, if voluntary control underlying gesture usage is considered in terms of the number of gesture types used within a context, then the manual specificity for function was related to specificity for context, but bodily function was independent of the accompanying context. This may partially reflect the type of contexts within which bodily gestures were often observed. For example, bodily gestures were more frequently observed than manual in the context of reunion, with a broad range of affiliative, defensive and offensive interactions observed in this context (Pollick and de Waal 2007; Roberts et al. 2012a).

However, overall individual specificity for context or function of manual gestures did not differ from bodily gestures. Thus, bodily gestures were no more flexible than manual gestures, in terms of usage across several contexts, as previously reported for vocal and facial signals relative to manual gestures in captive chimpanzees (Pollick and de Waal 2007). However, this is likely to be an oversimplification. For example, there is evidence that chimpanzee alarm calling is sensitive to the knowledge states of recipients, and does not seem to be closely tied to degree of risk or affective state of the sender (Crockford et al. 2012). In addition, captive chimpanzees can use novel vocal signals (raspberry, kiss and extended grunt) to attract the attention of human interactants (Wallez et al. 2012). However, while these vocal signals are both flexible and novel, they are also clearly highly context specific.

Although manual and bodily gestures are both associated with specific contexts, this does not necessarily indicate that their production is also closely tied to specific emotion states (as has been suggested for facial and vocal signals; Parr et al. 2005; Pollick and de Waal 2007; Arbib et al. 2008). For example, some postures are likely to be functionally related to a specific context, such as presenting a body part during grooming interactions. Moreover, as social interactions are underlined by emotions, it may not be useful to use context specificity to try and disambiguate intentionally communicative actions and indicators of internal states (e.g. Parkinson 1996).

Given the pivotal role of manual gesture production in theories of language evolution, it is important to try and understand how and why manual gesture usage differs from other forms of communication. Our findings indicate that manual gestures may be distinct in a number of interesting ways, especially once context is also taken into account (Scott 2013; Roberts et al. 2013). While all gestures were intentionally directed and effective, there was only evidence for communicative persistence for manual gestures, indicating a qualitatively different form of behavioural flexibility in achieving goals (e.g. Bruner 1972). Manual gestures were used more in affiliative contexts, while bodily gestures were more likely to occur in agonistic contexts in terms of both repertoire size and frequency of production. While both grooming and play both require frequent interpersonal adjustments (Hobaiter and Byrne 2011a; McCarthy et al. 2012), they also facilitate social bonding (e.g. Crockford et al. 2013). The selective pressure for maintaining complex social relationships within large social groups may have taken place within manual gestures (e.g. Dunbar 1996).

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Caption figures

Fig. 1 Average frequency of manual and bodily gesture types occurring in each context type per subject

Fig. 2 Average proportion of manual and bodily gestures used in each context type per subject

Fig. 3 Modality of bodily and manual gestures across recipient attention prior to gesture production

Captions tables

Table 1. Audio-visual repertoire of gestural communication in wild, adult chimpanzees, in Sonso community at Budongo Forest, Uganda

Table 2. Specificity of gestures to dominant response by gesture type. Gestures categorised as loosely (50-70%), ambiguously (below 50%) and tightly (above 70%) associated with dominant response.

Footnotes tables

Table 1. *, Detailed descriptions and videos accompanying these gesture types can be found in Roberts et al. (2012a); M, category contains gesture types merged with others based on cross validation (Roberts et al. 2012a): forceful extend with flexed extend, hand swing with backward extend, unilateral swing with bilateral swing, linear sweep with stiff swing, unilateral swing with fist extend and arm raise with stiff raise; A, auditory gesture type (possible reception via simply auditory channel); I, idiosyncratic gesture type represented by multiple events; 1, idiosyncratic gesture type represented by single event; +, video clip accompanying gesture type is absent; underlined, gesture types coded by first author from original footage contained in Nishida et al. (2010), named after video clip; italics, gesture type reported in other sites but unrecorded in this study; bold, gesture types recorded in this study, not reported in other sites; (2), gesture types recorded by Hobaiter and Byrne (2011a), see ESM Table 3 for details.

Table 2. Only single, non-combined gestures were examined, excluding 'no response'.

Captions Electronic Supplementary Material

ESM Table 1. Responsiveness and intentionality of behaviours rejected as gestures

ESM Table 2. Corpus of data on single gestures and sequences analysed in this study (excluding dependent, non-focal, combined gestures, represented by fewer than 5 cases per gesture type)

ESM Table 3. Comparison of gestural repertoire across different studies

Footnotes Electronic Supplementary Material

ESM Table 1. Only single, independent events were analysed (see methods); *Type of other scratch recorded was unknown and not analysed

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