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A structure-based repertoire of manual gestures in wild chimpanzees: statistical analyses of a graded communication system

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Abstract

Great ape gestural communication is considered important in understanding the evolution of human language as these share important features, namely, flexible and intentional signal use. Although gestural repertoires have been compiled for captive and wild primates, reports are largely qualitative. We quantify the morphological structure and variation of gestural signals identified in the repertoire of a community of wild chimpanzees. Gestures were classified on the basis of 29 morphological features, such as trajectory and orientation during the preparatory and stroke phases of a gesture. Hierarchical cluster and discriminant function analyses identified 30 morphologically distinct manual gesture types; the majority was subsequently correctly classified using a cross-validation technique, with incorrect classifications for rare gesture types only. Comparisons of this statistically determined repertoire with previous repertoires did not identify systematic variation between captive and wild chimpanzees. Moreover, consensus was not greater within studies of the same populations, highlighting the importance of systematic and well-documented inventories. Our morphologically based analyses indicate that manual gestures are best considered as graded rather than discrete communication signals, similar to some vocalisation systems. We discuss these findings in light of current theories of human language evolution.

Keywords: Chimpanzee; Gesture; Great ape; Communication; Repertoire; Structural inventory

1. Introduction

Insight into language evolution can be gained from the communicative systems of nonhuman primates (Slocombe, Waller, & Liebal, 2011), especially those of chimpanzees, our closest living relative (McGrew, 2010). Although not a ‘missing link,’ chimpanzees display a number of features considered characteristic of early human populations, such as fission–fusion social organisation and life at the forest–savannah interface (van Lawick-Goodall, 1968). The study of communication in chimpanzees contributes to our understanding of the probable communicative abilities present in our last common ancestor, helping to identify the evolutionary pressures that have shaped human communicative abilities (Tinbergen, 1963).

Studies of chimpanzee communication have primarily focused on compiling the vocal repertoire (Mitani, 1996). Signal repertoires are species-specific collections of ritualised actions or cues, deployed to change the behaviour of recipients (Bradbury & Vehrencamp, 1998). More recently, attention has shifted to gestures as a potential evolutionary precursor to human language (Slocombe et al., 2011). Manual gestures, defined as movements of the hands without the use of objects or a substrate, have attracted considerable attention because of the possibility of being an ancestral trait that humans share with their primate relatives (de Waal, 2003). It has been argued that manual gestures are governed by specific neurological structures homologous to the ones responsible for human language (Perrett et al., 1985). Only

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humans and other apes habitually use their hands to communicate (de Waal, 2003), and gestural communication in chimpanzees and bonobos shows greater flexibility than either facial or vocal signals (Pollick & de Waal, 2007).

Chimpanzee gestural behaviour has been studied in a few wild (Goodall, 1986; Hobaiter & Byrne, 2011; van Lawick-Goodall, 1968; McGrew, Marchant, Scott, & Tutin, 2001; Nishida, 1970; Nishida, Koichiro, Takahisa, Agumi, & McGrew, 2010; Plooij, 1978, 1979; Reynolds, 1963; Roberts et al., 2012; Sugiyama, 1969) and captive populations (van Hooff, 1971; Tomasello, Call, Nagell, Olguin, & Carpenter, 1984; Liebal, Call, & Tomasello, 2004; Pollick & de Waal, 2007). Gestures are used flexibly across a diverse range of contexts, including agonism, mating, grooming, and play (Pollick & de Waal, 2007; Roberts et al., 2012); in mother–offspring interactions, gestures are pivotal in negotiating nursing and food sharing, and coordinating travel (Plooij, 1978). While these studies provide important insights into overall repertoire, manual gestures have been mostly studied within the broader framework of all communicative bodily movements. Moreover, not all studies investigated whether the observed signals are intentional, as determined from the signaller directing gestures to recipients in flexible, goal-directed ways (see e.g. Roberts et al., 2012). However, it is important to determine whether the observed behaviours are voluntary because the distinction between simple behavioural actions, which may be used by others to infer intentions and meaningful gestural communication, lies in determining whether the action is used intentionally (Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979). For example, activities that regularly precede a particular event, such as those that indicate changes in activity state (i.e., between resting and locomotion), can become communicative to the receiver even though this signal is unintentional from the sender's perspective (Roberts, 2010; Roberts et al., 2012).

Previous research has identified broad consensus on the chimpanzee repertoire of manual gestures across captive populations (Pollick & de Waal, 2007). However, comparisons are constrained by the lack of relevant or comprehensive illustration and the subsequent difficulty of accurately matching written descriptions of visual signals across studies (but see Arbib et al., 2008 and Nishida et al., 2010). There are few direct comparisons using the same methodology, but between-group variation seems to primarily reflect the relative frequency of different gestures, which determines the probability of observing a specific gesture at any one site (Pollick & de Waal, 2007; Hobaiter & Byrne, 2011). However, identifying differences between wild and captive repertoires is important because it is unclear to what degree human contact and a captive setting might influence the ontogeny of gestural signalling (Tomasello & Call, 2004). For example, captive apes point to distal objects, an important capacity in prelinguistic human development (e.g., Liszkowski, Carpenter, & Tomasello, 2008) and a behaviour thought to be absent in wild great apes (but see Veà & Sabater-Pi, 1998).

Gestures are often categorised by context or perceived function rather than precise morphology because it can be difficult to disentangle gestures from noncommunicative actions. Gestures can also be more broadly defined as including locomotor activities (e.g., bipedal jump), orofacial movements (e.g., lip-lock), or object-directed actions (e.g., throw object) (e.g., Liebal et al., 2004; Hobaiter & Byrne, 2011), with the result that repertoire sizes can differ considerably across studies at the same location (up to threefold: Liebal et al., 2004; Pollick & de Waal, 2007). Previous studies have also been heavily biased towards the play context (Slocombe et al., 2011), which may not reflect the form and function of these gestures more broadly. Play also overrepresents younger individuals, whose gesture repertoire may differ from adults, at least in chimpanzees (Tomasello et al., 1984), although this is confounded by age differences in overall gesture production rates (Hobaiter & Byrne, 2011).

Detailed morphology can be informative but is largely neglected or only selectively considered, for example, in examining the potential ritualisation of taking actions into reach gestures. However, perceived morphological variation is often considered to lack communicative function, and subsequently, gesture variants are lumped together (Hobaiter & Byrne, 2011; but see Roberts et al., 2012). The underlying assumptions are that a human observer can identify and classify meaningful units (in a similar manner to the animals themselves) and also that similar morphological properties reflect similarities in function. Although analysing gesture function requires accurate identification of morphological characteristics of different gestures, there is no systematic method for analysing gestural signals based on their morphology (but see Forrester, 2008). This hinders comparison of repertoires within and across species, and contrasts with more standardised, bottom-up approaches for categorising human posture (e.g., see Coulson, 2008). Morphological classification provides objective criteria to classify graded signals and addresses subjectivity in the lumping/splitting of behaviours. Such an approach also separates form and function during classification of gestures, avoiding potential biases in the interpretation of meaning and circularity in the study of gesture function.

In this study, chimpanzee gestures are analysed quantitatively based solely on their morphological features and without a priori assumptions about context or function. The component features of gestures are classified statistically and clustered into groups (Bortz, 1993). For example, if a chimpanzee extends its hand towards a receiver, this action can differ in both intensity and form of hand and arm shape, with fingers either flexed or stretched, a smooth, sweeping movement or a forceful, stretched, and linear action, in either the vertical or horizontal plane. A bottom-up analysis provides a more rigorous, quantitative description for each gesture type in terms of morphology and movement configurations. For example, human posture can be quantified in terms of the degree of rotation of major joints that underlie the relative position of head, torso, and arms, and also the tempo, plane, and direction of these movements (Coulson, 2008; Gross, Crane, & Fredriskson, 2010).

Importantly, only structural descriptions of gestures can also determine the extent to which the gestural repertoire of chimpanzees is discrete or graded in order to relate overall structure to social and ecological factors (Marler, 1976). A repertoire may consist of only discrete signals (with no intermediates between adjacent elements) or fluid signals that change continuously and grade from one prototypical form to another. Graded repertoires are considered advantageous in open habitats with close range social interaction, while discrete repertoires better suit poorer visual conditions and less frequent direct social interactions (Marler, 1976). Moreover, the structural nature of a repertoire can also be informative about the cognitive processes underlying gesture production and the amount of genetic control (McGrew et al., 2001).

Here, we provide first systematic analyses of manual gestures of wild chimpanzees using a quantitative morphological approach. We establish an inventory of intentional manual gestures using standard clustering techniques and subsequent validation with discriminate function analysis. The resulting clusters are compared with previously reported repertoires to explore potential differences between and within groups. Finally, morphological variation is examined in relation to repertoire size in two other communication modalities, vocalisations and facial expressions, to explore social and ecological influences on chimpanzee gestural communication.

2. Methods

2.1. Study site and subjects

Manual gestures of one community of habituated East African chimpanzees were examined over an 8-month period (September 2006, April–July 2007, and March–May 2008) at the Budongo Conservation Field Station, Budongo Forest Reserve. Budongo is in western Uganda on the edge of the western Rift Valley (1°37′–2°00′N; 31°22′–31°46′E) at a mean altitude of 1100 m. The reserve covers an area of 793 km^2 composed of grassland and semideciduous tropical forest with predominantly continuous forest cover of 428 km^2 (Reynolds, 2005).

The chimpanzee community varied between approximately 72 and 79 individuals. We selected 12 adults (15–46 years of age) as focal animals, all habituated to human observers to a distance of approximately 5 m. Study animals were selected so that sexes and rank classes were equally represented (i.e., three high-ranking and three low-ranking males and females, as determined by long-term records, without limb injuries). All female focal subjects were parous (had previously given birth). All gesture types reported were observed in adult subjects. Focal animal data were complemented with ad libitum observations, including 15 events on subadult subjects in nonplay contexts.

2.2. Data collection

Focal and ad libitum samples were collected to establish an inventory of gestures. Focal animals were followed for 20-min intervals, so that each subject was sampled equally at different times of the day across the study period. Gestures and behavioural context (i.e., eliciting context and response by a recipient) were recorded continuously using a digital video camera recorder (SONY DCR-HC18E/HC32E) centred on the focal animal but taking a wider view to include any audience. In total, 250 h of focal footage was coded with mean±S.D.=17.21±1.29 h of focal data per subject (N=12) in good visibility conditions. This footage was subsequently reviewed, and any gestural events were extracted and subjected to analyses.

2.3. Video analysis

We first generated an inventory of gesture types from the available video recordings. We extracted N=218 manual gestures of sufficient quality to code morphological components. Gestures were defined as expressive movements of the limbs that are mechanically ineffective, i.e., the signaller did not affect a change in the recipient's behaviour by mechanical means (Pollick & de Waal, 2007). Additional criteria were that the behaviour was considered to be both (a) communicative in terms of consistently inducing a change in the recipient's behaviour and (b) intentional, as determined by the signaller monitoring the recipient's response during or after gesture production (Pollick & de Waal, 2007) or by the persistence and elaboration of gesture production when the recipient failed to respond (Bates et al., 1979; Roberts, 2010; Roberts et al., 2012). Using these conservative measures, some gestures were excluded from analyses. For instance, scratching was excluded because there was no indication of response monitoring, although scratching could be intentional (Pika & Mitani, 2006). For each event, the signaller and recipient (the individual at whom the signaller was looking during or immediately after gesturing) were identified, as well as the eliciting context and recipient's response.

The morphology of the manual behaviour was examined between successive rests of the hands from the moment the limb began to move to the moment it returned to the resting position. The entire event was divided into two sections: the preparation phase describes the action from the resting position to where a stroke phase begins, at the point of greatest remove from the resting position. The stroke phase describes the movement from this preparatory peak position until the retraction of limb to resting position (Kendon, 2004).

First, the entire data set was screened to determine behaviours that qualified as gestures and to compile a complete list of all morphological components of these behaviours. A total of N=29 components were identified (Table 1, see also ESM Table 1, available on the journal's website at www.ehbonline.org, for fuller descriptions of morphological details). Second, these morphological components were coded for all gesture events. Gestures can be executed in a dyadic way (in relation to a recipient) or in a triadic way (in relation to a recipient and an external object). For instance, arm orientation can be independent of the recipient's location ('Stiff Swing') or directed to a recipient

Table 1
Summary of coding scheme used to describe morphological components of gestures during (A) preparatory phase and (B) stroke phase (ESM, Table 1, available on the journal's website at www.ehbonline.org, for fuller morphological descriptions)

Preparatory	Motion descriptor	Location of movement			Relative to position
Phase					
	Unilateral/bilateral	Arm	Hand	–	–
	Rigidity	Arm	Hand	–	–
	Orientation	Arm	Hand	–	Recipient/object
	Flexion	Arm	Wrist	Fingers	Recipient/object[a]
	Strength of flexion	–	Wrist	Fingers	Recipient/object[a]
	Position	Upper Arm	Forearm	–	Recipient/object
Stroke					
	Executed/not executed	Arm	Hand	–	–
	Repetition	Arm	Hand	–	Object[a]
	Tempo	Arm	Hand	–	Object
	Location	Arm	Hand	–	Object
	Joint	Arm	Hand	–	Recipient/object
	Trajectory	Arm	Hand	–	Recipient/object
	Plane	Arm	Hand	–	Recipient/object
	Direction	Arm	Hand	–	Object
	Orientation	Arm	Hand	–	Recipient/object/target

[a] This may also be coded as the subject holding the referent object. See ESM, Table 1, available on the journal's website at www.ehbonline.org, for fuller morphological descriptions.

('Vertical Extend'). If the recipient is in front of the signaller, the arm extension will be horizontally towards the recipient; if it is above the signaller, the arm extension will be upwards. Gestures may rely on presenting specific parts of the limb, such as the inner part of the arm or hand. The recipient's distance may further determine the degree of extension of the limb. In this study, we report manual gestures that did not use objects for communicative purposes, although gestures with objects were included if the object was not integral to gesturing, for example, a mother holding something while raising her elbow to invite her infant to breastfeed.

To describe the context, we coded a range of potentially relevant external conditions. This included any action performed towards the signaller by other group members or any concurrent behaviour by the signaller during the production of a gesture, including other gestures, vocalisations, facial expressions, or noncommunicative behaviour. We also scored more general contextual categories, including grooming, travel, contact, foraging, sex, submission, and aggression (for detailed descriptions, see Roberts et al., 2012).

To examine the effect of a gesture on a recipient, any change in the behaviour of the recipient immediately after the signal was coded for each event, provided this change occurred within 30 s of gesture production and prior to any other event, which might have led to a change in a recipient's behaviour. Response categories included changes in proximity to the signaller or other subjects, changes in activity patterns, onset of communication, or changes in possession of a resource (for detailed categories, see Roberts et al., 2012).

2.4. Statistical analysis

Due to the limited sample size, observations were pooled across individuals to identify the repertoire, as in previous studies (e.g., Pollick & de Waal, 2007). To determine the statistically significant grouping of gestures into distinct clusters, we carried out a standard hierarchical agglomerative clustering analysis (HCA) based on the morphology data set (Table 1, ESM Table 1, available on the journal's website at www.ehbonline.org). We employed an average between-group linkage algorithm, assuming squared Euclidean distance as the metric of distance between elements of each cluster (e.g., Lattin, Carroll, & Green, 2003 for a detailed review of cluster algorithms). Hierarchical cluster analyses measure the interpoint distances between morphological features of all gestures to determine the similarity between gesture cases in terms of each of its specific characteristics. Gestures grouped together are similar to each other in morphological terms and different from gestures located in another cluster group (Sokal & Michener, 1958).

Multistate categorical variables were then converted into binary variables, representing the presence or absence of each state, and subsequently submitted to a simultaneous discriminate function analysis (DFA). The purpose of the DFA was to validate the results of the hierarchical clustering technique. The DFA identifies the linear combination of predictor variables (i.e., morphological features) that characterize the differences between gesture types. Predictor variables (i.e., morphological components) are combined into $n-1$ discriminant functions (where n is the number of gesture types in the analysis), which are plotted onto a two-dimensional graph to demonstrate the grouping patterns of gestures. Gestures can be assigned either to an appropriate group (i.e., the group assigned by cluster analysis) or to a different group, which produces the percentage of correct assignment into categories (Bortz, 1993). The results obtained from the DFA were then validated by using a 'leave one out' procedure, where the

Table 2
Gestures discriminated by HCA; percentage classification correct in DFA; cross-validation and confusions with other gestures (abbreviation given in parenthesis); and agreement across studies

Study 1				Cross study comparisons						
HCA	*N*	DFA	Cross valid	2	3	4	5	6	7	8
Arm beckon (Ab)*	3	100	67 (Ph)	*	*	*	–	*	–	*
Arm drop (Ad)*	2	100	100	–	*	–	*	–	–	–
Limp extend (Lh)*	25	100	100	–	–	–	^	–	–	–
Stretched extend (Pp)*	5	100	100	–	**	*	*	–	–	**
Cupped extend (Ap)*	9	100	100	*	*	*	*	*	–	*
Vertical extend (Pv)*	51	98	98 (Pp)	–	*	*	^	*	*	*
Arm flap (Af)*	25	100	100	*	*	*	**	*	*	*
Arm raise (Ar)*	10	100	70 (Ad/Se)	*	*	*	*	–	–	*
Backward sweep (Bs)*	12	100	100	–	–	*	–	*	–	–
Elbow raise (Er)*	8	100	100	–	–	*	–	–	–	–
Rounded sweep (Rs)*	2	100	100	–	–	–	^	*	–	*
Linear sweep (Fs)*	5	100	100	*	*	–	*	–	–	–
Forceful extend (Fe)*	5	100	100	*	*	**	^	–	–	*
Hand bend (Hb)*	20	100	100	–	**	**	***	**	*	*
Hand swing (Hs)*	6	67 (Af)	67 (Af)	–	–	–	^	–	–	–
Stretched reach (Pe)*	2	50 (Pt)	50 (Pf)	–	–	*	–	–	–	*
Hand reach (Ph)*	4	100	100	–	–	–	–	–	–	–
Sharp reach (Pt)*	3	100	100	–	–	–	–	–	–	–
Stiff extend (Se)*	4	100	100	–	**	–	^	–	–	–
Unilateral swing (Su)*	5	80 (Ss)	100	–	*	*	*	*	–	**
Fist flail (Ff)	1	100	0 (Fe)	*	–	–	^	–	*	**
Hand clap (Hc)	1	100	0 (Ss)	–	–	–	–	–	*	*
Flexed extend (Fw)	1	100	0 (Fe)	–	–	–	–	–	–	–
Backward extend (Be)	2	100	0 (Af/Hs)	–	–	–	^	–	–	–
Finger reach (Ps)	1	100	0 (Pe)	–	–	–	–	–	–	–
Swinging reach (Pf)	1	100	0 (Pt)	–	–	–	–	–	–	–
Fist extend (Sc)	1	100	0 (Su)	–	–	–	–	–	–	–
Stiff raise (Sd)	1	100	0 (Ar)	–	–	–	^	–	–	–
Bilateral swing (Sb)	1	100	0 (Su)	–	–	–	–	–	–	–
Stiff swing (Ss)	2	50 (Rs)	0 (Fs/Hc)	*	–	–	–	–	–	–
Repertoire size (*N*)			**20**	**8**	**15**	**14**	**18**	**9**	**5**	**16**
Mean Kappa agreement			**0.32**	**0.19**	**0.32**	**0.36**	**0.20**	**0.26**	**0.12**	**0.34**

N is number of cases. The presence and absence of identified matches for each gesture type are identified in the following seven studies: 2=Hobaiter and Byrne (2011); 3=Plooij (1984); 4=van Lawick-Goodall (1968); 5=Nishida et al. (2010); 6=van Hooff (1971); 7=Liebal et al. (2004); 8=Pollick and de Waal (2007). Asterisk next to gesture label indicates gesture type validated above chance level by DFA. See ESM Table 2, available on the journal's website at www.ehbonline.org, for definitions of HCA gesture labels and more detail on matching of gesture labels across studies.

* Gesture type described.

** Two labels matched.

*** Three labels matched.

^ Coded from video materials (Nishida et al., 2010).

discriminant functions are computed from all but a single case and then classified. The process is iterated until each case has been left out once.

Finally, we performed Fisher's Exact Tests on the uncorrelated morphological features of gestures, i.e., those that were not related to any other morphological components across all gesture types. Only those uncorrelated morphological features that had the highest correlations to both the first and second discriminant functions were examined to explore how these morphological features differentiated between gesture types. Since the value of correlations was relatively low overall, the cutoff value of 0.1 was used (on the scale of 0 to 1).

To assess agreement between our study and previously reported gestural repertoires, a Cohen's Kappa coefficient (Bakeman & Gottman, 1997) was calculated for each possible pairwise comparison between studies ($N=8$) and sites ($N=5$).[1] This method is well established and has been used in several other studies for comparisons of gestural repertoires (e.g., see Pika, Liebal, & Tomasello, 2005). The agreement between each possible pair of studies was calculated individually for each of 25 gesture types (i.e., those identified in at least one additional study). An exhaustive matrix was used to calculate agreements on inclusion of a gesture type (total gestures=25) and 'other' for disagreements when one study omitted a gesture type. These

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[1] Please note that reported reliability (Cohen's Kappa) relates only to agreement on the classification of gestures and not to the reliability of the data collection for each study.

analyses are based on an assumption that, if there is a species-typical repertoire, there should be some degree of agreement between different observers, despite differences in methodology. Although Cohen's Kappa is designed to assess reliability for multiple coders of the same events, this method allowed us to compare overall concordance between these gesture repertoires, allowing for differences in repertoire size, and both lumping and splitting in the classification of gestures types, between dyads. Next, mean gesture repertoire size and Kappa value were calculated by averaging the summed total gestures and Kappa for each individual dyad. All data analyses were performed using statistical package SPSS 17.0.

2.5. Interobserver reliability

A second coder correctly assigned video clips of randomly sampled gestural events to the correct label based on morphological descriptors alone (27/34, 79.41%; Cohen's Kappa=0.76, Bakeman & Gottman, 1997).

3. Results

3.1. Determining manual gesture types and contextual usage in wild chimpanzees

The number of cases contributing to each gesture type is presented in Table 2. Mean±S.D. number of gesture types contributed by each focal individual was 7.26±2.59, *N*=197 cases, 12 individuals; ad libitum data *N*=21 cases, 6 individuals; with a range of 5–12 gesture types per focal subject. For the cluster analyses, we were able to include *N*=218 gesture events. Hierarchical cluster analysis produced a tree representing 30 gesture types (Fig. 1). Overall, the morphological differences between gesture clusters were small; 22 gesture types (73%) were separated by a distance smaller than 5 (on the scale of 0 to 25), whereas three gesture types (10%) were separated by distance larger than 15.

The morphology of gestures was based on key morphological features, such as arm extend, swing, reach, and flail. For example, amongst the gestures within the group 'arm extend,' we found variants where the arm and hand were positioned vertically, with the inner parts of both arm and hand facing towards the recipient's body and held at the point of greatest remove, and others in which the hand was cupped and held upwards (Electronic Supplementary Materials, Table 2 for morphology descriptions of gestures identified by HCA and video clips of gesture types).

These gestures were produced intentionally in a flexible, goal-directed way. Gestures were significantly associated with the presence of the audience (binomial test, $p<.001$; $N=207/207$) or signallers' monitoring a recipient's response by looking at the recipient during (binomial test, $p<.001$; $N=173/191$) or after gesture production (binomial test, $p<.001$; $N=140/187$). There was also a significant presence of mutual visual contact between signaller and the recipient prior to gesture production (binomial test, $p<.001$; $N=134/182$).

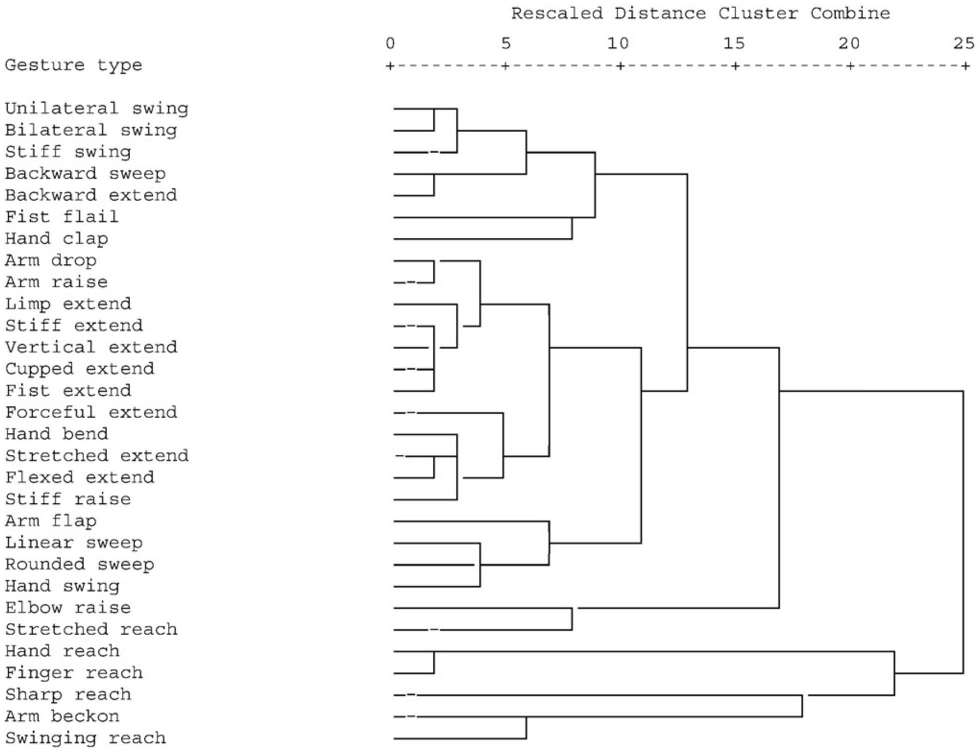

Fig. 1. Dendrogram of manual gesture types using average linkage between groups.

The gestures observed were produced across a variety of affiliative, agonistic, and mother–infant contexts primarily to elicit responses in a targeted receiver towards a third party or objects in the environment. For instance, amongst gestures that enforced signaller's requests for specific actions from a recipient, we observed 'Vertical Extend' to request that the recipient approach the signaller. Other gestures indicated a signaller's request for the recipient to perform behaviour towards an external item, object, or third party, such as 'Cupped Extend' to request handing over of a food item or body part and 'reach' gestures, in which the signaller appeared to request from a recipient to take an external object in the environment (ESM, Table 2, available on the journal's website at www.ehbonline.org).

In order to test whether the gestures were morphologically distinct and the HCA accurately represented the different gesture types, a DFA was conducted. For the DFA, 13 gesture cases were excluded as repetitions within the same gesture sequence, reducing the sample to N=205. Wilks' lambda confirmed that there were significant differences across the means of discriminant functions [Λ=0.000, χ^2 (696)=7575.81, p<.001], indicating that the DFA differentiated the gesture types identified by the HCA and that these gestures were morphologically distinct. We then cross-validated the classification of gestures using a leave-one-out procedure. The average correct assignment into the HCA gesture type by the DFA was 97.6% (N=199 out of N=205 gesture cases correctly classified, binomial test, p<.001) with a cross-validated assignment of 90.7% (N=186 out of N=205 gesture cases correctly classified, binomial test, p<.001). Thirty gesture types were classified above chance level by the DFA, but these were reduced to 20 with cross-validated classification. In the cross-validation DFA, 15 gesture types received 100% correct assignment, 5 gesture types were classified above chance level (between 50% and 98%), and the remaining 10 gesture types were classified below chance level at 0% (Table 2). Hence, in the absence of contextual information, it was possible to distinguish 20 of 30 gesture types from their morphological features alone. Not all gestures were discrete, but some were graded and contained morphological features intermediate between prototypical forms, although this may have been partially due to the sample size for some gesture types.

3.2. Morphological variability

The DFA identified 24 standardized canonical functions, of which 21 functions differentiated significantly between gesture types. The first two functions accounted for the greatest amount of variance: over 67% with canonical effect sizes of R^2=1.00 and R^2=0.99, respectively. The remaining functions represented small or moderate effects, accounting for a combined variance of 33%. The first four functions explained over 80% of the variance (eigenvalues and variances: factor 1: 286.23, 45.9%; factor 2: 131.81, 21.2%; factor 3: 57.08, 9.2%; factor 4: 44.93, 7.2%).

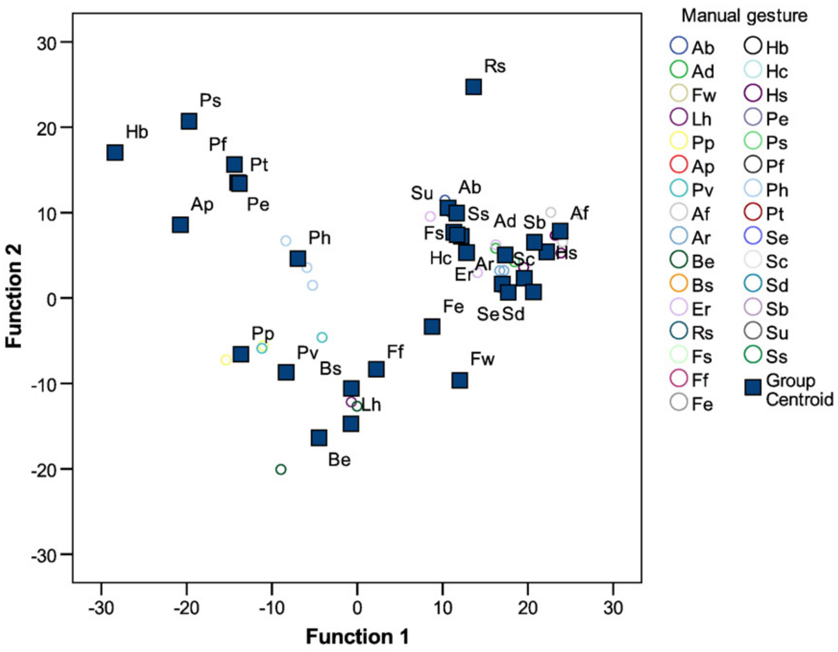

Fig. 2. The distribution of discriminant scores along two standardized canonical discriminant functions for all gesture types established by cluster analysis. Gesture abbreviations are as follows: Vertical extend (Pv); Limp extend (Lh); Arm flap (Af); Hand bend (Hb); Backward sweep (Bs); Arm raise (Ar); Cupped extend (Ap); Elbow raise (Er); Hand swing (Hs); Forceful extend (Fe); Stretched extend (Pp); Unilateral swing (Su); Linear sweep (Fs); Hand reach (Ph); Stiff extend (Se); Sharp reach (Pt); Arm beckon (Ab); Arm drop (Ad); Rounded sweep (Rs); Backward extend (Be); Stretched reach (Pe); Stiff swing (Ss); Fist extend (Sc); Fist flail (Ff); Finger reach (Ps); Bilateral swing (Sb); Swinging reach (Pf); Flexed extend (Fw); Hand clap (Hc); Stiff raise (Sd).

Table 3
Gesture types discriminated by DFA factor 1 and/or 2 and morphological features associated with these functions

		Arm flexed at wrist joint	Fingers stretch	Hand fully flexed to forearm	Hand move executed once	R facing exterior part arm/hand	Fingers flexed at PI joint	Hand vertical toward S	Wrist flexion relative to R	Finger flexion relative to R	R facing interior part arm/hand
Gesture	**DFA**	**+1**	**+1**	**+1**	**+1**	**+1 +2**	**+2**	**−1**	**−1, −2**	**−2**	**−2**
Arm beckon (Ab)	1, 2	**0.013**	**0.022**	**0.016**	**0.009**	-	**-**	-	-	**-**	-
Limp extend (Lh)	1, 2	0.001	0.001	0.001	0.003	**0.001**	0.009	0.001	**0.001**	**0.001**	0.001
Stretched extend (Pp)	1, 2	–	**0.002**	–	–	0.025	–	–	–	–	**0.012**
Cupped extend (Ap)	1, 2	–	–	–	–	0.001	**0.001**	0.005	**0.014**	0.011	**0.001**
Vertical extend (Pv)	1, 2	0.001	0.001	0.001	0.001	0.001	0.001	**0.001**	**0.001**	**0.001**	**0.001**
Arm flap (Af)	1, 2	**0.001**	**0.001**	**0.001**	**0.001**	0.001	0.009	0.001	0.001	0.001	0.001
Arm raise (Ar)	1, 2	–	**0.007**	–	–	**0.002**	–	0.005	0.001	0.006	0.006
Backward sweep (Bs)	1, 2	–	0.022	0.039	**0.001**	0.001	–	0.001	**0.004**	**0.001**	**0.001**
Elbow raise (Er)	1, 2	-	–	–	–	–	–	–	0.002	0.043	**0.043**
Rounded sweep (Rs)	1, 2	–	–	–	–	–	**0.033**	–	–	–	–
Linear sweep (Fs)	1, 2	**0.001**	**0.002**	**0.001**	–	–	–	**0.017**	0.011	–	–
Forceful extend (Fe)	2	**0.001**	–	**0.001**	–	0.025	–	–	0.011	–	–
Hand bend (Hb)	1	0.008	0.002	0.004	0.015	**0.001**	**0.001**	**0.001**	**0.001**	0.001	0.014
Hand swing (Hs)	2	**0.013**	**0.022**	**0.016**	–	–	–	–	–	–	–
Hand reach (Ph)	1, 2	–	–	–	–	–	–	–	0.027	–	–
Sharp reach (Pt)	1, 2	–	–	–	–	–	**0.033**	–	–	–	–
Stiff extend (Se)	1, 2	–	**0.006**	–	–	–	–	–	0.027	–	–
Unilateral swing (Su)	1, 2	–	–	–	–	–	–	**0.017**	0.011	–	–
Total gestures		8	11	9	6	9	7	9	13	8	9

Values are Fisher's Exact Test *p* values. Only values of *p*<.05 are given. Bold font=positive association, regular font=negative association, dash=not significant. S is signaller, and R is recipient. Only those gestures which were cross-validated above chance level by DFA and had significant correlation with morphological features associated with first and second discriminant functions are reported.

3.3. Discrete versus graded gestures

A DFA scatter plot of gesture types displays the discriminant scores as a measure of the overall similarities between the different gestures (Fig. 2). We observed considerable clumping of scores rather than general dispersion, suggesting that many gestures had few distinguishing features. Additionally, discriminant scores overlapped for a number of gesture types, indicating that the repertoire contained both discrete and graded signals. Gestures differentiated by the first two DFA functions were the most removed from one another. Function 1 discriminated between 18 gesture types; function 2 discriminated between19 gesture types (Table 3).

3.4. Key morphological features

To determine which morphological features best differentiated between gestures, we examined the DFA correlation coefficients for all morphological features (N=20 cross-validated gestures only, Table 3). Correlation coefficients indicated the magnitude of the contribution made by each morphological feature to differentiating groupings (high values=large contribution). No single feature loaded strongly on the functions that accounted for most of the variance (highest correlation coefficients: 0.32 and 0.37 for functions 1 and 2, respectively). Similarly, the largest absolute correlations between individual variables and discriminant functions were weak. The highest correlation coefficients were for functions with a weak influence on separation between gesture types (e.g., function 13: 0.76), indicating that no single morphological feature strongly differentiated between gesture types.

DFA correlation coefficients indicated precisely how morphological features influenced the differences between gesture types. Morphological features sharing the same sign of coefficients (e.g., positive or negative coefficients) contributed to separation in the same way; opposite signs indicated a contribution to group separation in different directions. The most distinctive features [i.e., had highest correlation (r>0.10) to either function 1 or function 2] are listed in Table 3. Overall, the discriminate functions that accounted for most of the variance discriminated between gesture types in a similar way (i.e., same sign of correlation coefficients), indicating similarity in morphology across gestures.

Whilst correlation coefficients indicated how morphological features influenced differences between gesture types in relation to each other, they do not identify differences in the frequency of association between gesture types and morphological components. Fisher's Exact Tests were performed on the uncorrelated morphological features that had the highest correlation (r>0.1) with functions 1 and 2 (Table 3). On average, the most salient morphological features for each function (those with highest loadings) were significantly positively associated with 24% of all gesture types (range 17%–39%). For instance, the gestures 'Vertical Extend' and 'Hand Bend' were significantly positively associated with the following morphological components: hand directed vertically towards signaller's body and wrist flexion relative to recipient, but were distinctive in the direction of their association with fingers flexion relative to recipient, fingers flexed at joint proximal interphalangeal, recipient facing exterior part of arm or hand, and recipient facing interior part of arm or hand (Table 3).

3.5. Comparison of chimpanzee gestural repertoires across studies and sites

We compared our statistically determined repertoire with previous reports of chimpanzees in both field and captive studies (see ESM, Table 2, available on the journal's website at www.ehbonline.org, for details[2]). This identified some previously unreported gesture types, such as 'Limp Extend,' 'Hand Reach,' and 'Sharp Reach.' Other gestures, 'Hand Clap' and 'Fist Flail,' were also only reported in one other group (Yerkes, ESM, Table 2, available on the journal's website at www.ehbonline.org). When considering agreement for collapsed repertoires across pairings of the study populations (ESM Fig. 1, available on the journal's website at www.ehbonline.org), the mean agreement reported for each research site was positively correlated with the total number of gestures reported at each site (Budongo N=27, K=0.43; Gombe N=21, K=0.41; Mahale N=19, K=0.38; Yerkes N= 16, K=0.37; Arnhem N=9, K=0.28; R=0.96, N=5, p=.009).

Comparison of the eight individual studies detailed in ESM, Table 2, (available on the journal's website at www.ehbonline.org), resulted in lower mean agreement than the preceding site comparison but also indicated that reported repertoire size impacted on mean Kappa values (Goodall K=0.36, N=14; Plooij K=0.34, N=16; Nishida K=0.20, N=11; Hobaiter K=0.19, N=10; Roberts K=0.32, N=25; Pollick K=0.34, N=16; Liebal K=0.12, N=5; van Hooff K=0.26, N=9: R=0.72, N=8, p=.041). However, the highest individual pairwise agreement (K=0.49) was between van Hooff and Goodall, which shared gesture types but were not closest in overall repertoire size (ESM Fig. 2, available on the journal's website at www.ehbonline.org).

4. Discussion

While previous research has focused on examining the morphological complexity of vocal behaviour and facial expressions (Parr, Cohen, & de Waal, 2005), this is the first systematic quantitative demonstration of such complexity in gestural behaviour beyond qualitative descriptions (Reynolds, 1963; van Lawick-Goodall, 1968; Sugiyama, 1969; Plooij, 1978, 1979; Nishida et al., 2010; Hobaiter & Byrne, 2011). Our study demonstrates that adult chimpanzees have a multifaceted and complex repertoire of manual gestures,

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[2] Nishida et al. (2010), Study comparisons only included reported gestures, while cross-location comparisons also included unlabelled gestures identified in their videos materials (indicated by underline in ESM, Table 2).

organised around prototypes, within which there is considerable variation. Boundaries were not always clear-cut, and gradation was apparent for several morphological components.

Chimpanzees in our study displayed at least 20 statistically discriminable gesture types in their repertoire, including some previously unreported or undifferentiated gesture types. We analysed only those 20 gestures cross-validated above chance level by a DFA procedure. However, a few of these validated-at-chance gesture types had previously been documented in great ape repertoires (Liebal et al., 2004; Pollick & de Waal, 2007), and additional observations would likely allow the remaining 10 gestures (identified by the HCA) to be validated. Gestures were produced intentionally and used across diverse contexts such as affiliation, antagonism, and maternal care. These gestures were primarily used to coordinate responses towards the signaller, third-party individuals, or objects, demonstrating that manual gestures have the potential to serve a range of functions during interactions (see also Roberts et al., 2012).

Our repertoire size of 20 gestures is in concordance with previous studies on captive and wild groups, validating structure-based repertoire assessments of gestural communication, which allow more standardised comparisons across populations and species. The high concordance between collapsed repertoires between sites compared to individual studies suggests that differences are due to sample size and categorisation biases rather than culturally acquired behavioural diversity (Genty, Breuer, Hobaiter, & Byrne, 2009). In general, gestural repertoires appeared uniform across sites; our post hoc comparisons indicated greater consistency across sites than across studies (Kappas are considered as fair and poor, respectively; Fleiss, 1981). There are clearly difficulties in objectively establishing the level of categorisation of gesture units, with variability in lumping morphological features between and within studies (ESM, Table 2, available on the journal's website at www.ehbonline.org). For instance, reaching gestures, categorised as one type by Hobaiter and Byrne (2011), were split into several gesture types by our analysis. Concordance across sites seems to be determined by sample size and categorisation of gesture units rather than specific location or captive/wild distinction. Recent analyses suggest that genetic differences cannot be ruled out as an explanation for some putatively 'cultural' differences in chimpanzees, including the 'Hand Clasp' (see Langergraber et al., 2011; but see also Lycett, Collard, & McGrew, 2010). The coherence reported for wild and captive gorilla groups also indicates a species-typical gesture repertoire rather than a more idiosyncratic, socially acquired repertoire (Genty et al., 2009).

However, for captive populations, social learning from humans may also play a role. Of particular theoretical importance is the pointing gesture, in which the signaller directs a recipient's attention to an external object or event in the environment. According to some definitions, this qualifies as referential communication and resembles human pointing, a capacity thought by many to be absent in wild chimpanzees (but see Pika & Mitani, 2006). In prelinguistic infants, pointing indicates the possession of cognitive skills required for language acquisition and rudimentary 'theory of mind' (e.g., Liszkowski et al., 2008). Here, we report a number of 'reach' gestures, in which the signaller appeared to request that a recipient give or take an external object in the environment. These gestures appeared morphologically and contextually similar to pointing observed in captive chimpanzees, who most frequently point with the whole extended hand. However, it is necessary to quantify the use and responses to these gestures to determine whether they have a communicative function homologous with human pointing.

The repertoire of manual gestures reported here is typical for adult chimpanzees in general and suggests shared ancestry with human gesture repertoire. For instance, gestures such as Arm Beckon (ESM: Video 1, available on the journal's website at www.ehbonline.org), Arm Flap (ESM: Video 7, available on the journal's website at www.ehbonline.org), Cupped Extend (ESM: Video 5, available on the journal's website at www.ehbonline.org), Hand Clap (ESM: Video 22, available on the journal's website at www.ehbonline.org), Vertical Extend (ESM: Video 6, available on the journal's website at www.ehbonline.org), and Forceful Extend (ESM: Video 13, available on the journal's website at www.ehbonline.org) are also present in the human gesture repertoire and appear homologous in both morphology and function (see Roberts et al., 2012, for analyses of functional similarity), although systematic comparisons are lacking. Our study suggests that the development of gestures is at least partially under genetic control. This suggests that the cognitive skills underlying usage of manual gestures may have been present in our last common ancestor and are shared within Hominoidea (Roberts et al., 2012).

The capacity afforded by gesture analysis at the morphological level would allow a more detailed examination in terms of how structural components correspond with intended meanings (see e.g,. Roberts et al., 2012). For instance, in humans, manual gestures with discrete form can represent words and concepts (emblems), while graded gestures tend to amplify information (illustrators). Future studies should consider the relation between morphology of gestures and function to determine how structural components of gestures correspond to effects in the recipients. Moreover, structural analyses would enable to examine the coherence in graded gestures across groups and individuals. Many human manual gestures appear biologically determined, but their precise morphological structure could be culturally variable (for instance, different types of pointing, Bullinger, Zimmermann, Kaminski, & Tomasello, 2011, see also McGrew et al., 2001). The organisation of signals within the manual repertoire suggests that chimpanzees may also have flexibility in the reproduction of precise morphology of gestures, as evidenced by a graded and mixed repertoire. Gestures are not structurally discrete but contain variants that are intermediate between the prototypical forms. A large range of signals may be a sign of cognitive complexity and a key prerequisite for the evolution of linguistic communication (Dunbar, 1998). For example, to acquire language, infants need precise voluntary control over their signal production and to link visual and auditory outputs to the corresponding motor outputs (Jürgens, 1998). Future studies of gesture production and usage should clarify whether gesture reproduction is truly flexible, whether gesture subtypes vary in relation to the signaller's affective states, and whether this variation is meaningfully perceived during interactions (e.g., Gross et al., 2010; Roberts et al., 2012).

Complexity of communication in a species, such as repertoire size, is likely to reflect the cognitive demands that result from the complexity of their social environment (e.g., Dunbar, 1998). For example, vocal repertoire size is positively correlated with both social and cognitive measures of complexity in primates (McComb & Semple, 2005). The gestural repertoire size identified here is comparable to the vocal and facial expression repertoires in captive and wild chimpanzees at around 20 to 30 different facial expressions and vocalisations (Parr et al., 2005). Concordance between gestural, vocal, and facial repertoires in chimpanzees is likely to reflect social organisation and the cognitive complexity needed to maintain relationships.

In addition, fission–fusion social systems are thought to increase social complexity and cognitive demands, as individuals must retain information about group members they see only infrequently. Chimpanzees and bonobos live in fission–fusion social systems, while gorillas live in stable, coherent groups. Chimpanzees have a similarly sized manual gesture repertoire to both the 18 gestures reported in bonobos (Pollick & de Waal, 2007) and the 20 in gorillas (Genty et al., 2009). However, chimpanzee repertoires contain more gestures that direct the movement and attention of a recipient towards an object or location in the immediate environment (Roberts, 2010; Roberts et al., 2012). This is usually done by means of an extended hand, but the gesture repertoire in gorillas is manually less directed (e.g., Genty et al., 2009). Manually directed gestures are important for understanding language evolution because these require a complex ability to infer and manipulate information from past and current context for understanding the intended meanings of gestures (Roberts, 2010; Roberts et al., 2012).

The chimpanzees in our study produced gestures that shared many morphological attributes. These gestures frequently co-occurred with vocal signals (Parr et al., 2005; Pollick & de Waal, 2007), which appear to be less graded (e.g., Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001). In human communication, gestures also tend to be more graded than vocal signals, particularly speech, although both channels of communication are used simultaneously to convey an idea or intention (Burling, 1993; Kendon, 2004). Research into multimodal communication is needed to better understand how vocalisations and gestures are combined in chimpanzees (Slocombe et al., 2011).

If the common ancestor of humans and chimpanzees lived in a habitat characterised by a forest–savannah interface, then it could be argued that the low degree of distinctiveness in gestures is a relatively recent shift towards flexible communication in the gestural domain, an adaptation to hominoids living in more open habitat (Marler, 1976). An alternative explanation is that the observed similarities have converged in relation to the demands of living in complex social groups. Nonetheless, chimpanzee vocal signals are relatively discrete, while gestural signals are relatively graded, while both channels of communication are complementary, as in human language. While great ape gestural communication clearly plays an important role in dealing with social complexity, it is likely to have also been pivotal in human language evolution.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2012.05.006.

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