What is a gesture? A meaning-based approach to defining gestural repertoires

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Abstract

Current systems of categorizing ape gestures are typically subjective, relying on human intuition. We have systematized the features on which categorization depends (movement; body part; one/both limbs; use of detached object; rhythmic repetition; contact with recipient), showing that a potential repertoire of over 1000 gestures is physically possible, as large as the lexicon of some languages. In contrast, little more than a tenth of these gestures is used in chimpanzee communication. The striking overlaps in repertoire found between populations and even species of great ape are evidently not a result of a restricted set of possible gestures. Using the reactions of signallers to identify which gestures are intended to be different by the apes themselves, we revised the current classification, making some new distinctions and abolishing others previously considered important, giving a final repertoire of 81. A small number of gestures are used deictically, such that the recipient must pay attention to specific locations to satisfy the signaller; raising the possibility of a stepping-stone to the evolution of reference.

Keywords

communication; *Pan*; intentional gesture; repertoire; deixis

Highlights

- We provide a meaning-based categorization of the chimpanzee gestural repertoire
- Chimpanzees could employ over 1000 gestures, but only use 12% of these.
- We use signaller reactions to identify features salient in determining meaning.
- A sub-set of gesture types is employed deictically to refer to external locations.

1. Introduction

All great apes, including humans, employ a rich range of communicative signals that includes facial expressions, body postures, vocalizations, and gestures. Gestures were described among the first field studies of great apes by Goodall (1968), Schaller (1963), Nishida (1980), and Plooij (1978); but it was more recent work (Tomasello et al., 1985, 1989, 1994; Leavens et al., 1996; Leavens & Hopkins, 1998) that highlighted that, unlike many animal signals, chimpanzee gestures are used intentionally. That is, they are used towards a specific recipient and with a particular goal in the signaller's mind. From these captive studies of chimpanzees, the field expanded to include all four non-human ape species (bonobo: Pika et al., 2005; gorilla: Tanner & Byrne; 1996, Pika et al. 2003; Genty et al., 2009; and orang-utan: Liebal et al., 2006; Cartmill & Byrne, 2007), as well as the first studies in the wild of gestural catalogues (chimpanzees: Hobaiter & Byrne, 2011a, 2011b; gorillas: Genty et al., 2009).

But what is a gesture? In the 21-years since Tomasello et al.'s 1985 chimpanzee paper the field has exploded: a Google scholar search returns 273 articles on nonhuman primate gesture published between 1985-2016. Some areas of the field remain remarkably consistent: for example, there is broad agreement that a gesture should be a physical movement that is not mechanically effective, and definition should incorporate a measure of the signaller's intention to communicate (Tomasello et al., 1985; Pika et al., 2005; Liebal et al., 2006; Tanner & Byrne, 1993; Genty et al., 2009; Hobaiter & Byrne, 2011a; Roberts et al., 2012, 2014; Frohlich et al., 2016). After that, the consensus starts to crumble. Should gestures be physical movements of the hand and fingers only (Leavens & Hopkins, 1998; Leavens et al,. 2010; Pollick & De Waal, 2007; Roberts et al., 2012, 2014); could they include movements of the head (e.g. Tanner & Byrne, 1996), body postures (e.g. Genty et al., 2009), or facial movements (Cartmill & Byrne, 2007). Given their use as communicative signals it is particularly worrying that there is little agreement on how we should discriminate one gesture from another. Even within a narrow definition focused on hand and finger movements, is a *reach* with the palm up the same as a *reach* with the palm down? How do we parse out the variation that results from a change in the signaller's body posture (standing or sitting), or from their environment (e.g. arboreal versus terrestrial), from the variation that results from the ape deliberately encoding differences – perhaps subtly – in information? Frequency of observation may impact a researcher's choice of whether to distinguish a gesture as a specific form, which is problematic, since a gesture may be rare because the context in which it is typically used is rare yet have a distinct meaning that is biologically important (e.g. gestures used in consortship see Hobaiter & Byrne, 2012).

The result of these ambiguities has been a field with a wide range of different gestural repertoires, split to varying levels (c.f. Genty et al., 2009 with Hobaiter & Byrne 2011a).

Typically the approach has been to group by the morphological features that we, as human observers, see as salient. For example: in our 2011 catalogue of chimpanzee gestures (Hobaiter & Byrne, 2011a) we distinguished *arm shake* (small repeated back and forth motion of the arm), *hand shake* (repeated back and forth movement of the hand from the wrist), and *feet shake* (repeated back and forth movement of the feet from the ankles), on the basis of the body parts involved; but we lumped shaking with one arm or shaking with both arms as being part of essentially the same gesture, *arm shake*. Perhaps because humans are themselves great apes, this subjective approach has been quite productive. However, the categorisations remain arbitrary, and the level of splitting has at times been inconsistent (for example: we differentiated *arm shake* and *hand shake*, but described the single gesture *arm raise* as including raise either the arm or the hand; Hobaiter & Byrne, 2011a). Indeed, whether the body part that was employed in performing the movement formed part of a gesture's definition at all was not consistent (for example: *arm shake* was distinguished from *hand shake* and *leg shake* by virtue of the body part, but *hand beckon* was not distinguished from *arm beckon* or even, feasibly, *leg beckon;* instead, *beckon* was defined only by the movement performed, irrespective of body part; Hobaiter & Byrne, 2011a). As a result, on paper, there appeared to be little systematic consistency in how to define a gesture, or to distinguish what might represent a new gesture type, rather than a variant of the same gesture.

Since great ape gestures are meaningful, it might be that a more relevant categorisation of signals could be provided by considering their usage from the signaller's perspective. For example: does any shaking movement, irrespective of the type or number of limbs involved, consistently convey the same intended meaning? We use the term 'meaning' deliberately. Many systems of animal communication involve the transfer of detailed information: for example, primate alarm calls may encode not only the type of predator, but also the level of risk (Schlenker et al., 2016a) or its location (Cäsar et al., 2013; Schlenker et al., 2016b). Assessing the effect of a signal on a recipient is sufficient to assess information transfer. Whether the signaller intends to achieve this effect on signaller behaviour remains unknown, and thought frequently not to be the case (Seyfarth & Cheney, 2003). Great ape gesture is different, because it is intentional. Signallers select their gestures based on a specific recipient and its state of attention; they pause and wait for a response; and – where unsuccessful – persist in signalling until they have achieved the desired change in recipient behaviour. In doing so great apes meet the criteria for 1st order intentional communication (Dennett, 1987). There is evidence for the 1st order intentional (hereafter intentional) use of one or two signal types in a very few non-ape species (e.g. grouper: Vail et al., 2013; macaque: Gupta & Sinha, 2016), but compare this with the extensive body of evidence for the intentional use of a large repertoire of gestures within all ape species in both captivity (chimpanzee: Tomasello et al., 1985, 1989, 1994; Halina et al., 2013; bonobo: Pika et al., 2005; gorilla: Tanner & Byrne; 1996, Pika et al. 2003; Genty et al., 2009; and orang-utan: Liebal et al., 2006; Cartmill & Byrne, 2007) and the wild (chimpanzee: Hobaiter & Byrne, 2011a,b, 2012, 2014; Roberts et al., 2012, 2014; bonobo: Graham et al., 2016). This large data set of intentional non-human signal use provides us with a unique opportunity: we are able to ask what a great ape gesture 'means' in a human language-like sense (Grice, 1957; Hobaiter & Byrne, 2014; Moore, 2016; although c.f. Scott-Phillips, 2015, 2016).

To assess a signaller's intended meaning we must move beyond examining recipient response, and consider signaller behaviour. A signaller's intended meaning is an internal mental state, unavailable to external observers. To overcome this problem, we focus on what behavioural response by the recipient appears to satisfy the signaller. This response must both represent a plausible desire on the part of the signaller (thus, we exclude agonistic behavioural responses from the recipient that targeted the signaller; 'attack me' or 'chase me aggressively' are implausible desires), and lead to the cessation of communication (Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014).

Here we re-examine the gestural repertoire of the wild chimpanzee population of Budongo forest, Uganda, using intended meaning as well as physical form to categorize ape gestural signals. In linguistics 'distinctive features' represent the smallest unit of variation used to describe the structure of phonemes. We adopt a similarly systematic approach, using physical features within dimensions of variation in gesture morphology (for example: the type of movement made, whether it is repeated in a rhythmic fashion, and the body part involved) to define the potential repertoire of gestures (see Forrester, 2008 and Roberts et al., 2012 for similar morphological categorisations of gesture, focusing on body posture and limb and hand movements). We compare this with our own research group's existing chimpanzee catalogue, which has been split at both a low level that focused on movements and body areas (St Andrews Catalogue Short List: StAC_SL, based on the level of splitting seen in the 66 gestures identified in Hobaiter & Byrne, 2011a) and at a higher level that distinguishes, for example, hand versus arm use, and one limb (hand) versus two limb (hands) forms of the same gesture types (St Andrews Catalogue Long List: StAC_LL shown in the Sonso specific column of Table 1, Hobaiter & Byrne 2011a).

We then use evidence from the signaller's intended meaning, to explore which of the potential and actual distinctions have any communicative significance *from a chimpanzee's perspective*, and thus generate a systematic categorisation of chimpanzee gesture types.

2. Methods

2.1 Ethical statement

This was a purely observational study that did not contain any interventions. All research adhered to the ethical ASAB/ABS Guidelines for the Use of Animals in Research and was conducted in compliance with the applicable national laws (UNCST research permit: NS179).

2.2 Procedure

All observations analysed here were made on habituated wild chimpanzees (*Pan troglodytes schweinfurthii*), during field periods between 2007 and 2013 (see Hobaiter & Byrne, 2011a,b, 2012, 2014). The Sonso chimpanzee community at the Budongo Conservation Field Station, in the Budongo Forest Reserve, Uganda consisted of 81 individuals at the start of data collection. We used focal behaviour sampling (Altmann, 1974), filming all cases of gestural communication using a Sony Handycam.

We defined *gestures* as discrete, mechanically ineffective physical movements of the body observed during intentional communication (see: Hobaiter & Byrne, 2011a; 2014). Our criterion of intentionality (at least 1st order intentional use) was applied at the level of the gesture instance, not the gesture type: thus, for every instance of gesture analysed, we had evidence that the signaller gestured with the intention of changing the recipient's behaviour, as indicated by one or more of response waiting, audience checking, and/or persistence in communication (see Hobaiter & Byrne 2011a, 2014 for a detailed description of the methods used to assess intentional communication). The resulting data set included 4535 individual gestures from 72 individuals. Our original catalogue contained 66 gesture types, on the basis of gesture morphology, used to achieve 19 distinct meanings (Hobaiter & Byrne, 2011a, 2014). In the present analysis, we included 8 additional gesture types. Four were observed during the original field study, but at that time we lacked evidence for intentional use in the Budongo community, which is now available (field observations between 2011 and 2013): *bipedal rocking*; *bipedal stance*; *rocking,* and *thrust*. Four were created by splitting two previously lumped gesture types: *present genitals backwards*, *present genitals forwards* (formerly combined as *present sexual*), *reach palm*, *reach wrist* (formerly combined as *reach*).

We investigated signallers' intended meaning through analysis of Apparently Satisfactory Outcomes (ASOs; see: Cartmill & Byrne 2009; Hobaiter & Byrne, 2014). An ASO is an observable change in the recipient that apparently stops the signaller from signalling; an ASO must conform to some plausible biological function for the signaller. Where we found consistent patterns of use over multiple cases of communication, we used these as an empirical indication of what signaller's intend to mean by giving the gesture. (Typically, we required at least three cases from at least three signallers; where that was not the case the data are clearly indicated; see Hobaiter & Byrne, 2014 for a more detailed description of methods used to analyse meaning.)

Play represents a prolific context for gestural communication and all data, including play data, were used in morphological categorization of the gestures. However, signals given during play are not necessarily used with their non-play, 'real world' meaning; and outcomes within play may not reliably signal the gesture's meaning in a non-play context (Bateson, 1972/1955; Bekoff & Byres, 1981; Hobaiter & Byrne, 2014). In order to investigate the normal meaning of gestures we excluded gestural communication during play from analyses of intended meaning (as per Hobaiter & Byrne, 2014; gestures with a play-related ASO represented 49.2% individual gesture cases). We specified in each case where an analysis was conducted on data from communication that occurred outside of play. In addition, as our previous research has shown no effect of individual identity on gestural meaning (Hobaiter & Byrne, 2014), in the following analyses we combined individual data. Parametric analyses were carried out in SPSS v11, non-parametric analyses were calculated by hand, $\alpha = 0.05$ was required for significance. Means are given ± standard deviation, throughout. All statistical tests were two-tailed.

Table 1. Classification features for splitting gestures. The six initial features used to describe each gesture type within the catalogue; a value must be recorded for each feature in order to identify the specific gesture form (see Table S1).

Feature (n=values)	**Definition**	**Possible values**
Movement (36)	The physical movement of the gesture type.	Bend; bite; clap; cover; dangle; embrace; fling; grab; grab hold; grab pull; hit; jump; locomote; Look; move object; offer; posture; posture bipedal; push; raise; reach; rock; roll over; rub; scratch; shake*; shake object*; spin; splash; stroke; swing; tear off; throw; touch; touch hold; wave
Body part (11)	The area moved while gesturing. Unless specified in the analysis these terms include the use of both single and double-limbs; e.g. body part hand refers to the use of either one hand or two hands.	Arm; body; fingers; foot; genitals; hand; head; knuckles; leg; mouth; rump
Single/Double limb (2)	Where gestures involved movements of the limbs were one or both involved	Single; double
Detached object use (2)	Use of a detached object by the body part gesturing.	Yes; no
Rhythmic repetition (2)	A repetitive movement is produced with a regularly spaced rhythm indicating it is part of a single continuous gesture e.g. *tapping*	Yes; no
Contact (2)	The movement of the gesture requires physical contact with the recipient	Yes; no

* The distinction between a shake movement + detached object use, and a shake object movement, is that in shake the focus of the movement is to shake the limb; whereas in shake object the focus of the movement is to shake an object that remains attached (for example a sapling or branch).

3. Results

3.1 Initial Classification

Six features have regularly been used, in our own and other studies of great ape communication and behaviour, to describe and categorize gestures in their repertoire (e.g. Cartmill & Byrne, 2007, 2010; Genty et al., 2009; Graham et al., 2016; Goodall, 1968; Halina et al., 2013; Hobaiter & Byrne, 2011a, 2014; Hobaiter et al., 2013; Leavens & Hopkins, 1998; Leavens et al., 2010; Liebal et al., 2006; Pika et al., 2003, 2005; Plooij, 1978; Pollick & DeWaal, 2007; Roberts et al., 2012; Schaller, 1963; Tanner & Byrne, 1996; Tomasello et al., 1985, 1989, 1994). Together, these six features formed the basis of our initial categorization (Table 1). The features were as follows: (1) movement (n=36). Where chimpanzees made two different movements at the same time with different limbs, we treated them as two separate gestures produced together. Thus, if a chimpanzee were observed to swing with one leg and shake with the other, we would treat that as the movements of two separate gestures produced in tandem, rather than a single gesture with a 'swing-shake' movement. (2) Body parts (n=11); (3) single or double limb (n=2); (4) detached object use (n=2); (5) rhythmic repetition of movement (n=2); and (6) contact with recipient (n=2). So, for example, the gesture: *arm shake* was classified as [movement = shake; body part = arm; single/double limb = single; detached object use = no; rhythmic repetition = yes; contact with recipient = no]; the gesture *drum other* was classified as [movement = hit; body part = hand; single/double limb = double; detached object use = no; rhythmic repetition = yes; contact with recipient = yes]; and the gesture *object in mouth* was classified as [movement = offer; body part = mouth;

single/double limb = single; detached object use = yes; rhythmic repetition = no; contact with recipient = no].

By multiplying the possible values for each feature we constructed a matrix of the *hypothetical maximum repertoire size*: n= 6336. However, this included a large number of implausible options, for example: a beckon movement with the body part rump. We therefore excluded (a) the option of double limb use where only one existed (e.g. body or head); (b) the option of single limb use where the movement required two (e.g. clap); (c) the option of detached object use where it could not be employed by the body part (e.g. body, genitals); (d) impossible or physically improbable movement + body part combinations (e.g. spin + head; or bite + hand). This process left us with a remaining *possible maximum repertoire size*: n=1005.

We then examined n=4535 cases of gesture use within our catalogue using the 6 features described in Table 1 to assign each to one of the n=1005 possible gesture types. When categorized using these features, chimpanzees showed an *employed repertoire size*: n=124 (12.3% of the maximum possible). So, for example, the chimpanzees showed the movement shake with the body parts: arm(s), feet, hand(s), head, and leg(s) but not: rump, genitals, or foot.

3.2 Did the 6 initial features provided a sufficiently detailed categorization?

At first sight, this new morphological classification resembles our existing chimpanzee StAC long list, with a similar number of gesture types (StAC_LL n= 158). However, even within our short list (StAC_SL, n=72), a number of gesture types were lumped by the new categorization. Lumped gestures could be grouped into three sets; we examined each set individually, comparing the distribution of ASOs achieved for the newly lumped gesture types to determine if it was appropriate to combine them or if, based on the use of these gestures by the chimpanzees, we needed to specify additional features in our classification system. The 6-feature morphological classification no longer distinguished gestures:

(i) Where a movement of hitting is performed with both limbs and could be performed either simultaneously or with alternating hits. For example: *drum other* (alternating hits), is not distinct from *slap other 2-hands multiple* (simultaneous hits). Four such cases occurred (Table 2): in each case, both alternating and simultaneous gestures were used either exclusively in play or with three or fewer cases of use outside of play. Therefore, we find no justification from the chimpanzee behaviour to distinguish simultaneous from alternating hitting movements (Table 2) and so no requirement for an additional feature to discriminate simultaneous from alternating hitting movements.

(ii) Where locomotion, posture, or spinning movements are performed with the body as a whole. Three movement + body part combinations contained multiple gestures that were split in our original classification but were lumped by the new classification using the 6 features: [locomotion + body] lumps the two gestures: *gallop* & *stiff walk*; [posture + body] lumps the gestures: *bow* & *head stand*; and [spin + body] lumps the gestures: *pirouette, side roulade* & *somersault*).

Only the movement spin with the body part body provided sufficient examples of use outside of play for comparison, termed: *side roulade* (n=9) and *somersault* (n=15). In our original classification these gesture forms differed in the position of the body when it was spinning: extended out in *side roulade*, and curled up in *somersault.* However, the specific position in which the body was held was not differentiated in our new classification. As both gestures were used exclusively to achieve the ASO ‘Stop that’, we found no justification from the chimpanzee behaviour to distinguish gestures that involve the movement spin with the body (Table 2) and so no requirement for an additional feature to discriminate the specific position in which the body part was held.

Table: 2 Gestures lumped by the 6-feature classification that were previously split in the StAC Long list.

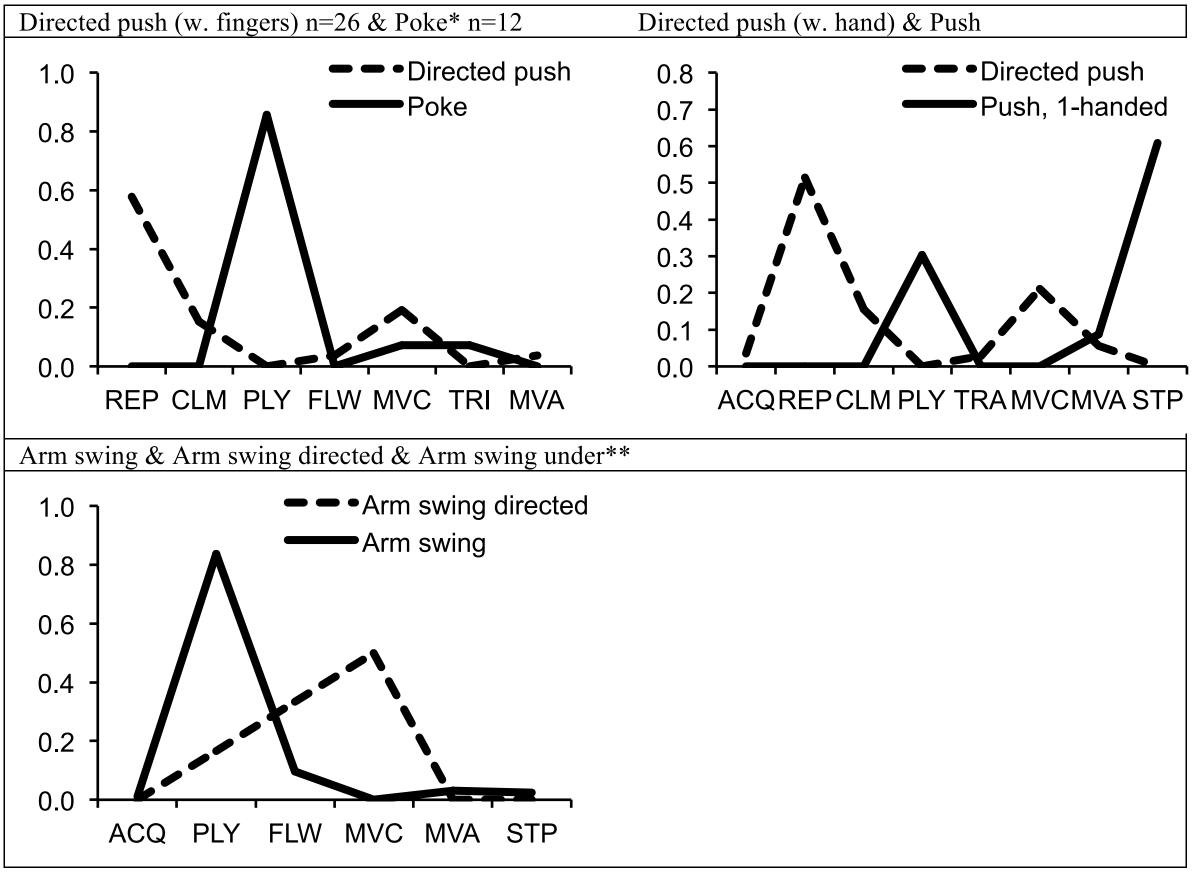
Gestures with simultaneous vs alternating hitting movement	**Locomotion and body posture gestures**
Kick 2-feet* & stomp 2-feet other**	Gallop** & stiff Walk***
Kick* & stomp other *	Bow*** & head stand*
Drum object** & slap object, 2-handed multiple***	Pirouette** & side roulade & somersault
Drum other** & slap other, 2-handed multiple*	

* ASO = play related in all cases; ** ASO = 3 or fewer cases of gesture use outside of play; *** 3 or fewer cases of gesture use

(iii) Where the gestures differed in directing or not directing the recipient’s behaviour.

We observed three cases of movement + body part combinations in which the difference that had previously been used to split them can be described as the signaller intending to direct the recipient’s behaviour: in other words, not just ‘Move away’ but ‘Move yourself *there*'. In each of the three cases we observed distinct differences in the distribution of the ASOs achieved by the gestures that would be combined by the features approach (Table 3). The gesture *directed push* performed with the fingers (n=26) was primarily employed to achieve the ASO 'Reposition' (n=15); whereas the gesture *poke* (n=14) was primarily employed in play (n=12). The gesture *directed push* performed with the hand (n=142) was also primarily employed to achieve the ASO 'Reposition' (n=73); whereas the gesture *push* (n=23) was primarily employed to achieve the ASO 'Stop that' (n=14). The gesture *arm swing* (n=166) was primarily employed in play (n=139) and outside of play (n=27) was used to achieve the ASO of 'Follow' (n=16); whereas the gesture *arm swing directed* (n=6) was primarily used to achieve the ASOs of 'Move closer' (n=3) and 'Follow' (n=2).

Table: 3 Distribution of ASOs in gestures lumped by the 6-feature classification that were previously split in the StAC Long list. The proportion of gesture cases used to achieve an ASO is plotted for movements produced with or without directedness. ASOs with *potentially similar meanings are plotted adjacent to each other*. ACQ = ‘Acquire object’; REP = ‘Reposition’; CLM = ‘Climb on me’; PLY = ‘Play’; FLW = ‘Follow’; TRA = ‘Travel with me (adult)’; MVC = ‘Move closer’; TRI = ‘Travel with me (infant)’; MVA = ‘Move away’; STP = ‘Stop that’. For clarity only ASOs for which the gesture was employed are labelled.



*3 or fewer cases of gesture use outside of play; **3 or fewer cases of gesture use.

From these clear distinctions in use we suggest that there exists an additional element of classification ‘deixis’. Given its use across several movement + body part combinations we consider this to be an additional feature that may categorize movements: Place indicated. However, as deictic indication refers to a potentially infinite number of points in the external environment it seems inappropriate to classify it as a specific physical feature of the gesture in the same way as a body part, or use of an object. We therefore suggest deixis be recorded but treated separately from the physical features of a gesture. We continue our current analysis focused on the six physical features previously defined.

3.3 Do the 6 physical features used to describe gestures in the repertoire modify the meaning of the gestures?

Here we describe the forms of the gestures used, and then employ the ASOs achieved outside of play to investigate whether the chimpanzees distinguish different meanings from the physical features (Table 1) that might modify the feature movement.

3.3.1 Does varying the body part with which a movement is performed modify the meaning of a gesture?

Of the 11 body parts, the hand was the most commonly employed in gesturing and was used to perform the greatest range of movements (Table 4); together the hand, fingers, and knuckles account for over half of all gestures produced (n=2678).

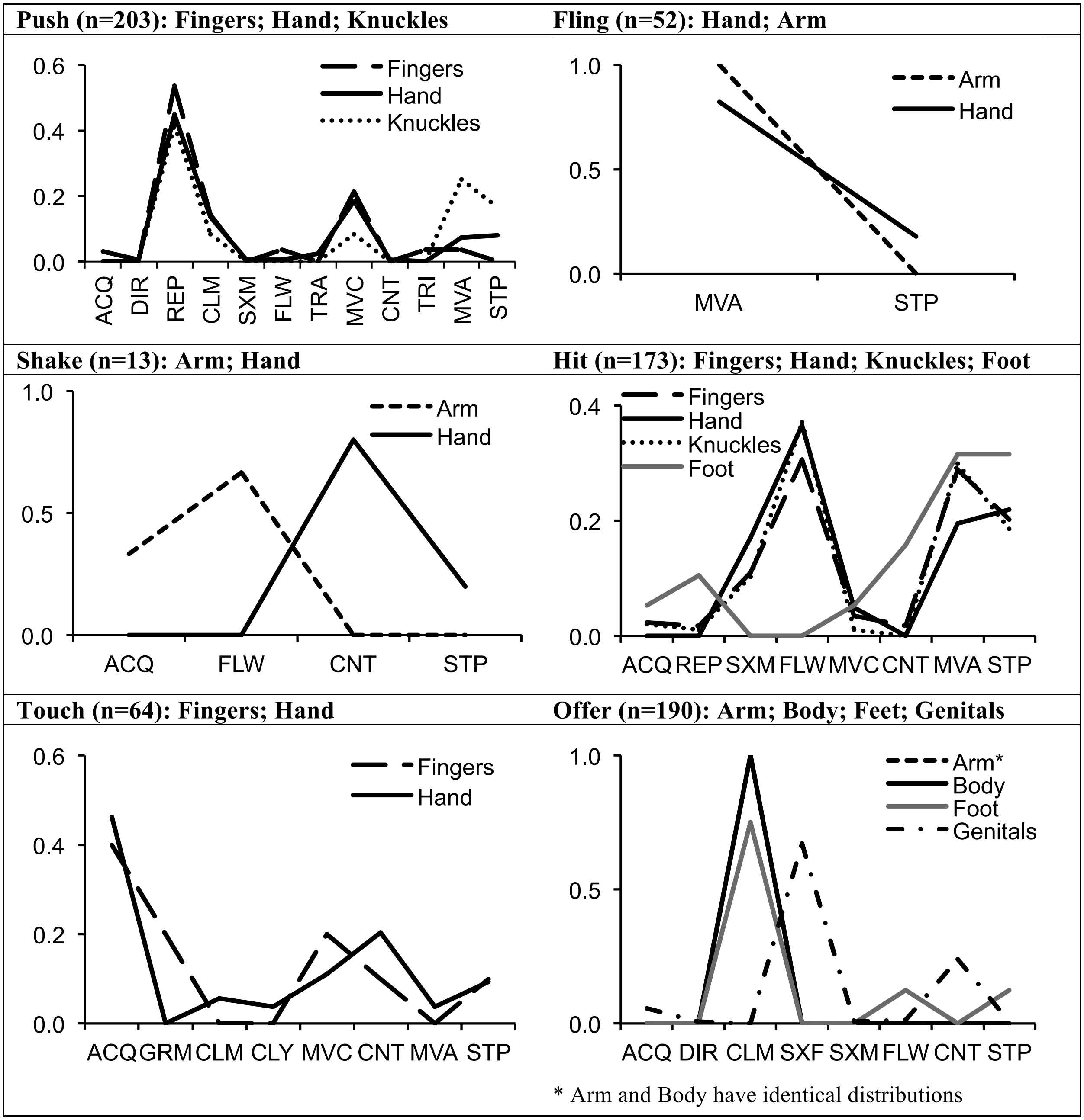
Table 4. Number of gesture instances and movement types per body part.

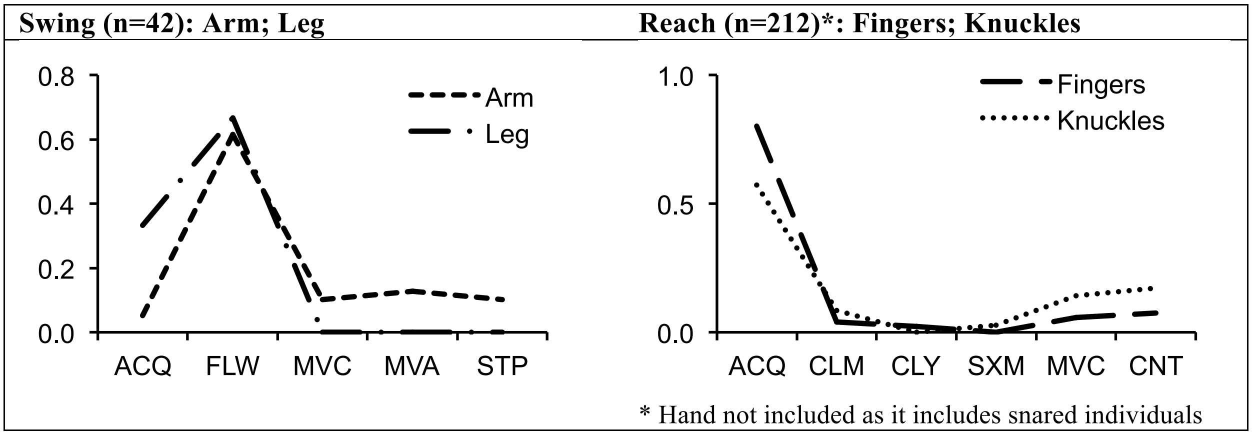
Body part	Instances; n	Movements; n
Mouth	114	4
Head	30	4
Arm	316	9
Hand	1991	17
Fingers	533	6
Knuckles	154	4
Body	540	10
Rump	32	1
Genitals	201	2
Leg	26	3
Foot	416	7

The majority of movements (22/36) were performed by only a single body part: for example, clap was performed only with the hands whereas rub was performed only with the rump. Six movements were performed with two body parts, and eight with three or more (body parts per movement: range = 1-6; mean = 1.9±1.5). When we excluded gesture cases that were (a) used during play, (b) with an ASO of unknown, or (c) where there were fewer than three examples of the specific movement + body part combination, the range of body parts per movement decreased (movements performed by a single body part = 18/26; body parts per movement: range = 1-4, mean = 1.5±0.9).

For the eight movements expressed using more than one body part we examined the pattern of ASOs achieved in non-play situations on a case-by-case basis. A visual inspection of Table 5 shows several cases of clear variation between the distribution of ASOs achieved by different body parts with the same movement, suggesting that chimpanzees attended to both the movement and body part when decoding the signaller's intended meaning.

Table 5. Distribution of ASOs produced by different body parts within a movement. The proportion of gesture cases used to achieve an ASO is plotted for the same movement produced with different body parts. ASOs with *potentially similar meanings are plotted adjacent to each other*. ACQ = 'Acquire object'; DIR = 'Direction attention'; GRM = 'Groom'; REP = 'Reposition'; CLM = 'Climb on me'; CLY = 'Climb on you'; SXF = 'Sexual attention to female'; SXM = 'Sexual attention to male'; FLW = 'Follow'; TRA = 'Travel with me (adult)'; MVC = 'Move closer'; CNT = 'Contact'; TRI = 'Travel with me (infant)'; MVA = 'Move away'; STP = 'Stop that'. For clarity only ASOs for which the gesture was employed are labelled.





For three movements, fling, swing, and reach the pattern of distributions between the body parts was very similar. Regardless of body parts, the movement fling achieved a primary ASO 'Move away' (>80% of use); the movement swing achieved a primary ASO 'Follow' (>60% of use); and the movement reach achieved a primary ASO 'Acquire object' (>50% of use). In the case of reach there was a difference between the frequency with which the primary ASO was achieved by the fingers (80%) or the knuckles (57%), with the latter often used to achieve secondary ASOs such as the affiliative 'Contact'. Similarly, in the case of the movements push, hit, touch, and offer, the ASO patterns suggested only minor variation between the different parts of the hand, in particular the knuckles from the hand and fingers, and more substantial discrimination between these and other body parts such as the feet or genitals. In push and touch all body parts achieved the same primary ASO ('Reposition' and 'Acquire object' respectively) with minor variation in the patterns of secondary ASOs (see for example: push with knuckles to achieve 'Move Away').

The two movements hit and offer showed more substantial variation, with different body parts achieving different primary ASOs. In the case of hit, the primary ASO for fingers, hand, and knuckles was ‘Follow’; whereas hit with the feet gave joint primary ASOs of ‘Move away’ and ‘Stop that’. Interestingly, this suggests that in non-play situations chimpanzees make little distinction between a *Slap* gesture (typically hands or fingers) and a *Punch* gesture (typically knuckles); but do discriminate these from foot based *Stomp* gestures.

With the movement offer, the primary ASO for arm, body, or leg was ‘Climb on me’, whereas for the genitals it was a request for ‘Sexual Attention’. However, a large category of the movement offer was excluded from these analyses: the gesture *present groom* (n=181), which is almost exclusively employed for the ASO ‘Direct attention’ (n=177). In *present groom* gestures the body part offered was typically not specified in coding leading to these cases being excluded as both movement and body part were required for this analysis. In both *present groom* and *present climb on me* the movement indicates a specific location, in this case on the signaller’s body. The distinction in meaning between these offer movements is seen not in the body part offered (in both *present groom* and *present climb on me* the foot or back could be offered). Instead the distinction in meaning was identified from the recipient’s behaviour (gesturing by the signaller stops when the recipient either (a) starts to groom in the specified location or moves existing grooming activity to that location, or (b) climbs on the signaller). As a result, the gestures *present groom* and *present climb on me* are now lumped as the single gesture *present.*

Finally, one movement – shake – showed near opposite patterns of distribution for the two body parts: arm, used to achieve the primary ASO 'Follow', and hand, used to achieve the primary ASO 'Contact'. All of the shake movements produced with the hands were of the contact gesture *shake hands* rather than a hand only version of the non-contact gesture *arm shake* (e.g. *hand shake*).

Thus, of the eight movements produced with one or more body parts, in five cases the same primary ASO was achieved irrespective of body part used. In a further two cases, the majority of body parts (particularly when grouped at the level of the fingers to arm) produced the same primary ASO. In one case the primary ASO varied strikingly; and here variation was seen not only in the body part but also in the gestural modality with physical contact made in one but not the other. As a result the decision on whether or not to lump body parts that were used was taken for each type of movement on a case-by-case basis.

3.3.2 Does physical contact with the recipient modify the meaning of a gesture?

Outside of play, only the movements hit and shake were employed with both contact and non-contact. The movement shake, as described above, includes both the non-contact *arm shake* and the contact *shake hands* gestures. Shake with contact (n=9) achieved a primary ASO of 'Contact' (n=7, 78%); whereas shake without contact (n=3) achieved a primary ASO of 'Follow' (n=2, 67%). The movement hit occurred in gestures such as *punch other, slap object, kick, stomp object*, etc. Hit movements with contact (n=134) achieved a different primary ASO ('Follow', n=53, 40%) when compared to hit movements without contact (n=40; primary ASO 'Move away', n=13, 33%). Three body parts produced hit movements both with and without physical contact to the recipient: hand, knuckles, and foot. In two cases the primary ASO achieved varied between the contact and non-contact forms; however, of the 10/14 primary and secondary ASOs achieved across the different body parts and levels of contact (Table 6) were a request for the recipient to 'displace' themselves ('Follow', 'Move away', 'Move closer', 'Reposition'), three were a request for 'Stop that', and one was for 'Sexual attention to a male'. As a result, we suggest that it is appropriate to maintain the splitting of movements that lead to contact with the recipient as opposed to an object, for example: *hit other* from *hit object.*

Table 6. Primary and secondary ASO of hit movements produced with and without physical contact with recipient.

Movement	Body part	Modality	Primary ASO (% of use)	Secondary ASO (% of use)
Hit	Hand	Contact	'Follow' (44%)	'Move away' (30%)
		Non contact	'Stop that' (65%)	'Move away' (29)
	Knuckles	Contact	'Move away' (33%)	'Follow'/'Move closer'/'Sexual attention to male' (22%)
		Non contact	'Move away' (57%)	'Stop that' (29%)
	Foot	Contact	'Move away'/'Reposition' (50%)	-
		Non contact	'Stop that' (40%)	'Move away' (27%)

3.3.3 Does the use of single or double-limb forms modify the meaning of a gesture?

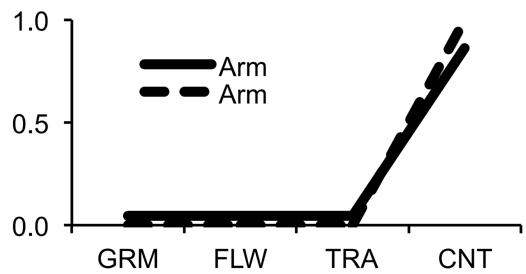
Nineteen movements were performed with both single- and double-limb forms of the same body part. Single-limb forms were more common across gestures types (single: mean cases per movement = 98.3 ± 109.6; double: mean cases per movement = 28.2 ± 45.9; paired t-test: $t=3.86$, $df=18$, $p=0.0011$). A greater proportion of the double-limb forms of the movements were used in play (proportion of single-limb forms in play: mean = 0.57±0.3; proportion of double-limb forms in play: mean = 0.74±0.3; Paired t-test: t=2.63, df=18, p=0.0169).

Outside of play, seven movements included three or more cases of both the single- and double-limb forms of the same body part employed towards a known ASO (Table 7). The primary ASOs achieved were the same in the single- and double-limb forms of 6 of the 7 movements. We further compared the frequency with which this primary ASO was achieved as compared to all other ASOs for the single and double limb forms and again found no differences between them (Embrace + arm/arms, primary ASO = 'Contact', Fisher's exact test n=30, p=0.545. Hit + foot/feet, primary ASO = 'Follow', Fisher's exact test n= 41, p=1.000. Hit + hand/hands, primary ASO = 'Follow', Fisher's exact test n=97, p=0.585. Move object + hand/hands, primary ASO = 'Follow', Fisher's exact test n=63, p=1.000. Raise + arm/arms, primary ASO = 'Acquire object', Fisher's exact test n=27, p=0.326. Shake object + hand/hands, primary ASO = 'Follow', Fisher's exact test n=313, p=0.443). The seventh case (grab pull + hand/hands) only contained an n=16 examples and showed no clear primary ASO in either single- or double-limb form (Table 7).

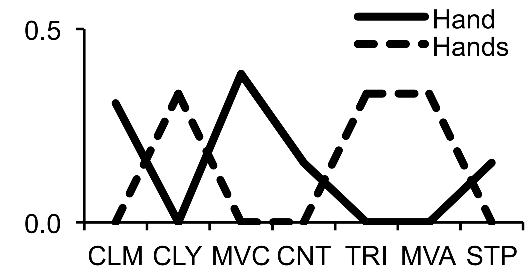
As a result, we suggest lumping single and double limb forms of the body parts used to produce gesture movements: for example, the gesture *arm raise* will include both use of single arm or double arms.

Table 7. Distribution of ASOs produced by single- and double-limb forms of movements. The proportion of gesture cases used to achieve an ASO is plotted for the same movement produced with a single-limb or double-limbs. ASOs with *potentially similar meanings are plotted adjacent to each other*. For clarity only ASOs for which the gesture was employed are labelled.

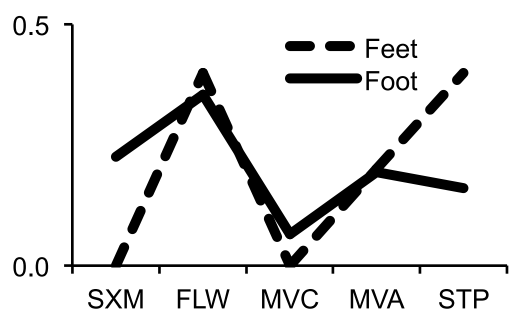
Embrace (n=30): Arm n=22, Arms n=8



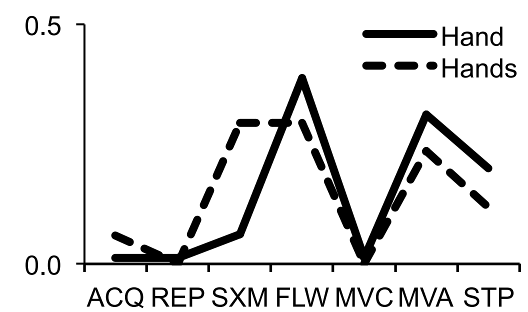
Grab pull (n=16): Hand n=13, Hands n=3



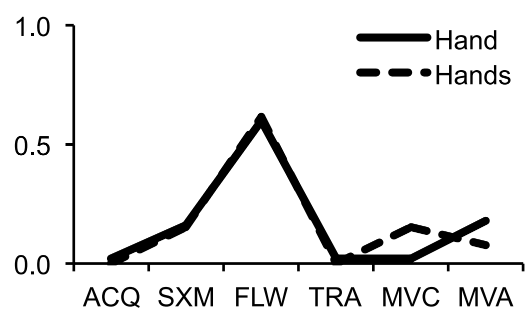
Hit (n=41): Foot n=31, Feet n=10



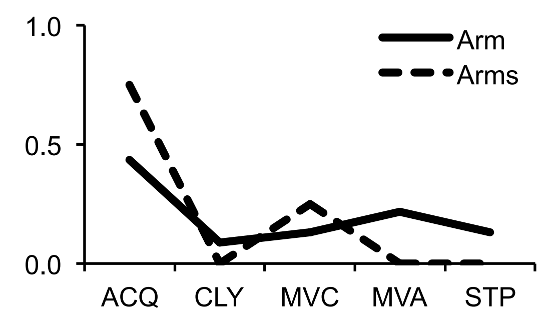
Hit (n=97): Hand n=80, Hands n=17



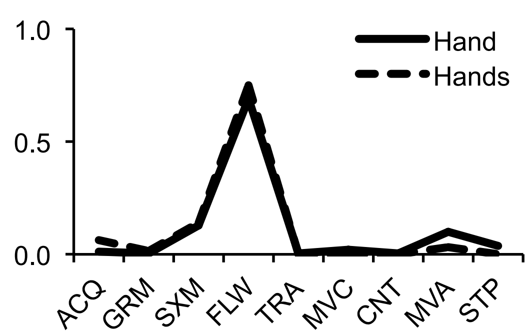
Move object (n=63): Hand n=50, Hands n=13



Raise (n=27): Arm n=23, Arms n=4



Shake object (n=328): Hand n=264; Hands n=64



ASO Key:

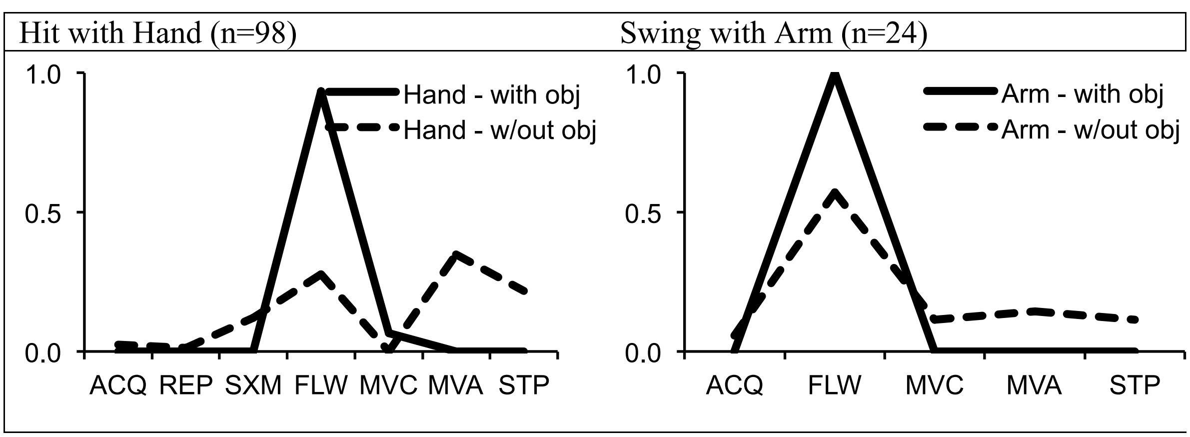
ACQ = Acquire object
DIR = Direct attention
GRM = Groom
REP = Reposition
CLM = Climb on me
CLY = Climb on you
SXM = Sexual attention to male
SXF = Sexual attention to female
FLW = Follow
TRA = Travel with me – adult
MVC = Move closer
CNT = Contact
TRI = Travel with me – infant
MVA = Move away
STP = Stop that

3.3.4 Does the inclusion of an object modify the meaning of a gesture?

Six movements were performed with the use of a detached object (hit, move object, shake object, swing, tear off, throw). Only two movements were performed both with and without object use: hit with the body part hand (with object n=15; without object n=83) and swing with the body part arm (with object n=4; without object n=35).

Outside of play, the primary ASO for hit with the hand without an object was ‘Move away’ (n=29, 35%), and with an object was ‘Follow’ (n=14, 93%). The primary ASO for swing with the arm both with (n=4, 100%) without an object (n=20, 57%) was ‘Follow’ (Table 8). As a result, we suggest that it is appropriate to maintain splitting of movements produced with and without detached objects, for example: *hit other* from *hit with object*.

Table 8. Distribution of ASOs in movements produced with and without a detached object. The proportion of gesture cases used to achieve an ASO is plotted for the same movement with and without a detached object. ASOs with *potentially similar meanings are plotted adjacent to each other*. ACQ = ‘Acquire object’; REP = ‘Reposition’; SXM = ‘Sexual attention to male’; FLW = ‘Follow’; MVC = ‘Move closer’; MVA = ‘Move away’; STP = ‘Stop that’. For clarity only ASOs for which the gesture was employed are labelled.



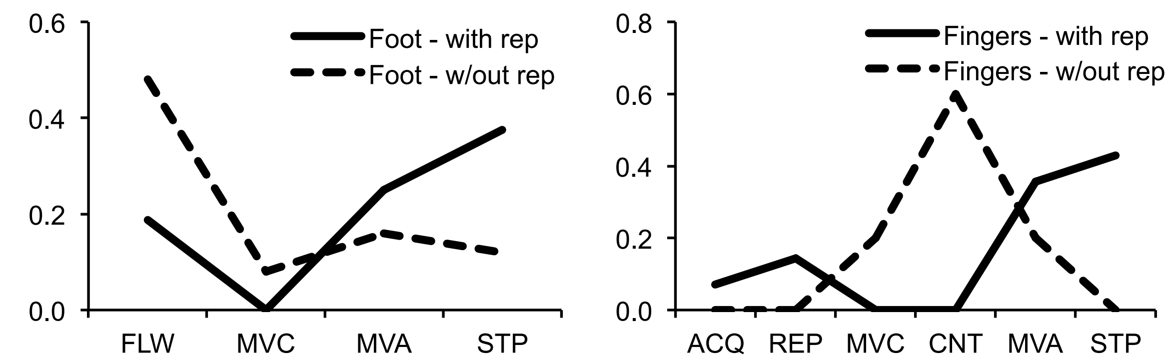
3.3.5 Does the use of rhythmic repetition modify the meaning of a gesture?

Twelve movements (n=1227 cases) were performed with rhythmic repetition; however, the majority of rhythmic repetition cases (n=908, 74%) were recorded in movements that were only performed with repetition (rock, rub, scratch, shake, shake object, spin, stroke, tear off, wave).

Outside of play, only two movements were employed with and without rhythmic repetition. The movement dangle was used both with and without repetition; however, only two cases were employed outside of play, one with and one without repetition. The movement hit was used with the body parts foot and fingers with both repetition and non-repetition of the movement (Table 9). We found differences in the primary ASOs for hit with either the foot (with repetition = ‘Stop that’; without repetition = ‘Follow’) or with the fingers (with repetition = ‘Stop that’; without repetition = ‘Contact’). As a result, we suggest maintaining the splitting of gestures that incorporate rhythmic repetition of the movement, for example: the gestures *tap* and *tapping*.

Table 9. Distribution of ASOs in movements produced with and without rhythmic repetition. The proportion of gesture cases used to achieve an ASO is plotted for the same movement with and without rhythmic repetition. ASOs with *potentially similar meanings are plotted adjacent to each other*. ACQ = ‘Acquire object’; REP = ‘Reposition’; MVC = ‘Move closer’; CNT = ‘Contact’; MVA = ‘Move away’; STP = ‘Stop that’. For clarity only ASOs for which the gesture was employed are labelled.

Hit with Foot: with repetition n=16; without repetition n=25	Hit with Fingers: with repetition n=5; without repetition n=14



3.4 Revising the catalogue of meaningful gestures for the chimpanzee

To summarize, our analysis of the appropriate categorization of chimpanzee gestures, based on the intended meanings of gestures, has the following consequences:

1 **No effect of simultaneous as opposed to alternating hit movements**

Outcome Lump gesture types previously split e.g. *drum* with *slap/punch multiple 2hands*

2 **No effect of body position on spin movements**

Outcome Lump gesture types previously split e.g. *pirouette, side roulade, somersault*

3 **Deictic gestures**

Outcome Allow for the coding of gesture types as deictic depending on the signaller and recipient’s movements.

4 **Body part impacts meaning of some movements but not others**

Outcome Lump body parts: fingers and hand

		Lump gestures *arm swing* and *leg swing*
		Lump gestures *slap, punch* as new gesture *hit*
5	**Physical contact with recipient impacts meaning of movement**	
	Outcome	Maintain split of movements on other versus on object
6	**Use of single- or double-limb forms impacts meaning of some movements**	
	Outcome	Lump forms for movements: embrace, move object, raise, shake object
		Maintain split form for movements hit and grab-pull
7	**Inclusion of object impacts meaning of movements**	
	Outcome	Maintain split of with/without object movement forms
8	**Repetition of movement impacts meaning of hit movements**	
	Outcome	Include splitting of single versus repeated hit movements

From this we generated a new standard St Andrews Catalogue for chimpanzee gestural communication, containing 81 gesture types (Table S1). In this catalogue, all gestures were distinguished based on the features for which there is evidence that they affect the primary meaning of the gesture. We suggest that gestures that are used to indicate (*directed reach)* that have the same physical form as gestures that are not used to indicate (*reach*) be considered to be the same type of gesture, but one that can be employed with or without an additional, non-physical, feature of deixis.

4. Discussion

Considerable importance has been attached to the discovery of the large overlap between the lists of gestures described for the different great ape populations, suggesting a predominantly species – and even family – typical origin (Hobaiter & Byrne, 2011a). One weakness of these claims is that commonality in gestures might simply result from a limited possible range of movements. Here we see that any such limitation is far from the case: the potential repertoire of physically possible combinations of the features extends to over a thousand types, of which only 12% are employed by chimpanzees in their gesturing.

Interestingly, from the perspective of a gestural theory of language evolution, a repertoire of a thousand signals would be (more than) sufficient for productive language. The original dictionary for Esperanto, for example, has around 900 root words (Zamenhof, 1905); while 'mother-in-law' languages (for example: Dyalŋuy used by Dyirbal speakers to communicate in the presence of relatives with whom there is a speech taboo) contain only a few hundred items (Dixon, 1972). The upper limit on the size of the chimpanzee gestural repertoire is clearly not set by the features used to distinguish among different gestures, and in a species that needed – and was capable of envisioning – an extended repertoire that could serve as a language there would be no need to change from a manual system of gesture in order to achieve it.

Building on previous morphological classifications of limb and hand movements in ape gesture (e.g. Forrester, 2008 and Roberts et al., 2012) we have taken a systematic approach to the chimpanzee gestural repertoire, employing six core features to discriminate all gesture types at the same level of classification. We then re-examined the catalogue produced taking into account the meanings for which the chimpanzee signallers employ these gestures. In doing so we were able to confirm the importance of categorizing by features such as the use of detached objects, and the use of rhythmic repetition; conversely, we were able to simplify the categorization scheme by discarding features that chimpanzee signallers did not use, for example the use of single- or double-limb forms across the majority of movements, and the use of simultaneous versus alternating hitting movements. Further empirical research is required to investigate gesture use across great ape communities and species, but we suggest that the use of meaning to classify gestures within great ape repertoires provides a powerful new tool for studies of great ape communication.

We have noted a small number of gestures that are used deictically (*present; push; reach; swing*), to indicate specific places, such that only when the recipient takes account of those places in its response is the signaller satisfied. (In contrast, with a gesture like *fling*, while it is necessarily directional in motion and requires a movement on the part of the recipient, the specific direction is not part of its interpretation: 'Move anywhere that's away from me' rather than 'Move away to there'.) The location in effect functions as an "empty slot" in the specification of the gesture. In previous attempts to describe the chimpanzee repertoire (e.g. Hobaiter & Byrne, 2011a; Hobaiter et al., 2013) we distinguished some gestures in which the location was always critical (treating *directed push* and *push* as separate gesture types), whereas in others (*arm swing*) its presence was optional. In the present review, we have distinguished gestures based on their physical features, and since the number of locations that can be indicated is, technically speaking, infinite, we could not use the location as part of the gesture classification system. Instead, we have coded a binary indication of deixis separately within a gesture type (e.g. *push:* directed = yes/no; *swing:* directed = yes/no).

Finding only a small number of deictic gestures is not greatly at variance with human communication, in which direction can be indicated by index-finger pointing, head movement, and in some cultures, lip pointing. As with these human gestures, a chimpanzee gesture may be employed with or without deixis. The physical form of a chimpanzee *reach palm* gesture that is used in dyadic communication to beg for the food that the recipient is holding is the same as the physical form of a chimpanzee *reach palm* that is used in triadic communication to indicate another individual or object (Hobaiter et al., 2012). These are distinguished not by physical form but by accompanying behaviour, such as apparently ostensive gaze and head movements. In the same way, in human communication an identical head movement, nod, may be used in dyadic communication as agreement, or in triadic communication to indicate a location to the recipient, for example where the signaller has their hands full. Although deixis functions referentially, indicating external entities by directional pointing, the referent itself is not encoded in the signal, as is the case with the words of language or symbolic gestures. Thus, in the case of a word in a language, for instance, a word can indicate – "point to" – its referent even when that is not physically present (e.g. the cake in the shop), or is abstract in nature (e.g. next Wednesday). Nevertheless, the possibility that deixis may over evolutionary time have been the root from which reference developed makes these few instances of particular interest.

The approach to defining gesture types that we offer is flexible, and could be employed to describe gesture types in all great ape species. Extending this approach to new species and sub-species may reveal new gesture types. If so, the current catalogue can be easily extended through the description of new movements, new movement + body part combinations, or the addition of single/double limb distinctions, detached objects, contact, rhythmic repetition, or deixis to existing ones. Crucially, using the reactions of signallers, to identify gestures that were intended to be different by the apes themselves, may allow a more appropriate categorization of signals – from an ape's perspective; offering us new means to investigate the evolutionary origins of linguistic features such as syntactic structure or reference.

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