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Laterality in the gestural communication of wild chimpanzees

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Keywords

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Laterality in chimpanzee gestural communication

Abstract

We examined hand preference in the intentional gestural communication of wild chimpanzees in the Budongo forest, Uganda. Individuals showed a tendency to be lateralized; on average, their absolute bias was around 0.25. Lateralization was incomplete even in individuals with major manual disabilities. Where individuals had a stronger preference, this was more often towards the right hand; moreover, as age increased, the direction (but not the extent) of hand preference shifted towards the right. While the gestural repertoire as a whole was largely employed ambilateraly, object-manipulation gestures showed a strong right-hand bias.

Introduction

Analyses of hand preference in great apes have focused disproportionately on food-related manipulation: for instance, picking up food,[1,2] getting food out of containers,[3,4] processing natural foods,[5,6] tool use while foraging,[1,7,8] and begging for food;[9-11] however, see Marchant and McGrew[12,13] for a broad analysis across limb functions. In chimpanzees, captive studies have often reported strong individual and population level right-hand biases,[3,9,11] whereas studies conducted in wild populations largely report ambilateral preferences in most manual tasks, with the exception of tool use. Tool use appears to be highly lateralized in each individual but in no consistent direction in the population.[8,12] In the light of recent evidence from human studies, that hand preference can vary markedly within individuals depending on the task in hand,[14] it has become increasingly important to examine great ape hand preferences in contexts other than feeding, ideally in wild populations living under ecologically relevant conditions.

In our species, right-handedness and left-hemisphere laterality for language have long been considered related, making studies of manual laterality in great ape communication an obvious starting point. Great apes have a rich, elaborate repertoire of gestures that they use in an intentional manner to communicate about specific goals to other individuals.[15-20] Recent studies of gestural communication in captive chimpanzees have reported both individual and population level right-handedness,[9,21] with an increase in right-handedness when gestures are produced together with vocalizations.[11] However, to date, work on hand use in gestural communication has been limited to captive groups, in particular to the use of gestures in begging and pointing for food; moreover, the strongest effects were found in individuals with a history of human rearing.[9,11]

We recently conducted the first systematic study of gestural communication in a wild community of chimpanzees. This presented us with the opportunity to examine hand preferences in a very large database of gestures, produced across a full range of situational contexts, by all ages and sexes, and under ecologically relevant conditions.

Method

We define gestures as discrete, mechanically ineffective physical movements of the whole body, limbs and/or head, used in intentional communication (i.e. directed to a specific audience and towards a specific goal). Chimpanzees employ a repertoire of at least 66 gesture types in their communication. We took it that a gesture was being used intentionally if it (or a sequence of gestures separated by <1sec) was accompanied by one or more of the following: checking of the recipient's state of attention, waiting for a response and, if none, then showing persistence or elaboration in further gesturing. (See Hobaiter & Byrne, 2011[20] for a full description of the repertoire and the criteria for intentional use.) A number of gesture types involve actions that would not easily reveal any lateral bias, for example: Clap (both palms brought together with audible contact), Pirouette (signaler spins on their vertical axis) and Present-sexual (signaler approaches backwards, exposing swelling or anus to recipient). We excluded these gestures, and restricted our analyses to gestures of the hand and arms.

Subjects

At the start of data collection in October 2007, the Sonso study community of chimpanzees consisted of 81 named individuals. Following Reynolds (2005),[22] we defined age groups as follows: infants (0-4yrs11mnths), juveniles (5yrs-9yrs11mnths), sub-adults (10yrs-13yrs11mnths♀/14yrs11mnths♂) and adults (14yrs♀/15yrs♂and over). Using these categories, the initial group composition was 32 adults (7 males and 25 females), 16 sub-adults (10 males and 6 females), 15 juveniles (6 males and 9 females) and 18 infants (3 males and 15 females). Over the course of the 22-month study, there were 10 deaths or long-term disappearances, 6 immigrations and 5 births, leaving the final total at 82.

A number of Sonso chimpanzees suffer from injuries caused by snare traps left in the forest by bush-meat hunters from the local villages. In some cases the snare traps sever tendons resulting in paralysis and in particularly severe cases may cause amputation of the limb. The limitations of individual chimpanzees were well known and data from individuals missing limbs or with damage to the whole hand or foot were examined separately.

Procedure

Observations were made on chimpanzees within the Sonso community during three field periods between October 2007 and August 2009 (October 2007–March 2008; June 2008–January 2009; May 2009–August 2009). We employed focal behaviour sampling (Altman, 1974),[23] and filmed all instances of intentional gestural communication; in each instance the data recorded included the signaler, recipient, gesture type, and limb(s) used; for a detailed method and analysis protocol see Hobaiter & Byrne 2011.[20]

Analysis

In any analysis of laterality it is important to ensure statistical independence in the data, and each datum must represent a choice of limb unaffected by external influences from the physical or social environment. For full details of the restrictions applied to the data set to ensure independence, see ESM: Independence in the data.

To measure the direction of hand preference, both for individual chimpanzees and within particular gesture types, we used the hand preference index (HI). HI is calculated as (R-L)/N, where R=frequency of right-hand use, L=frequency of left-hand use and N=total use. The index varies between -1.0 indicating complete left-hand use, through 0.0 (no preference), to +1.0 indicating compete right-hand use. Because the data are likely to include a different balance of use among the potential set of gesture types between one individual and another, and some gesture types may always be more lateralized than others, we needed to normalize the data to avoid confounding these effects. We dealt separately with (a) any possible effect of gesture differences in laterality upon individual chimpanzees' laterality estimates; and (b) any possible effect of individual differences in laterality upon laterality estimates for gesture types. Thus, we first calculated an individual's HI for each gesture type, and then calculated the individual's mean HI across gesture types. Similarly, we first calculated a gesture type's HI for each individual who contributed data, and then calculated the gesture type's mean HI across individuals.

To measure the strength of hand preference, irrespective of direction, we used the absolute hand preference index (ABS HI), calculated as ABS HI=$\sqrt{(HI^2)}$. This varies from 0.0 (no preference) to +1.0 (complete hand preference in either direction). As with the direction of hand preference, we calculated an individual's ABS HI after averaging across gesture types, and for gesture types after averaging across individuals.

In order to test whether or not individuals or individual gesture types were significantly lateralized in either direction we employed Goodness of Fit tests. This required us to pool an individual's data across gesture types (and across individuals in the case of gesture types), which runs the risk that pseudo replication may bias the findings; the results are discussed with this in mind. Goodness of Fit tests were only applied to individuals or gesture types that matched the requirement of a minimum expected 5-cases in each cell. In practice, as the null hypothesis was a 50/50 distribution between left and right hand use, this restricted the analyses to individuals or individual gesture types with 10 or more gesture instances. Then, where the data were sufficiently homogeneous, a pooled Goodness of Fit test was used to verify whether or not generalizations, that appeared possible from analyses of individual chimpanzees or individual gesture type, were significant when examined at a broader level of analysis. For example, we compared all object manipulation gestures with all non-object manipulation gestures, and male chimpanzees with female chimpanzees. All means are shown with standard deviation; all statistical tests are 2-tailed.

Results

We recorded a total of 5026 gesture instances produced with concurrent evidence of intentional usage, distributed across 66 gesture types. When restricted to gestures suitable for examining any laterality effects, this reduced to 1274 instances across 20 gesture types: our analyses are all based on this sample, to which 54 individuals contributed data (individual range=1-191 gestures, 1-15 gesture types).

Do individuals show a hand preference when gesturing?

Absolute hand preference strengths (ABS HI) ranged from 0.0 to 1.0: from no bias to complete hand preference. (To avoid pseudo replication, we averaged the hand preference scores for each of the gesture types a chimpanzee used.). For the population, the mean ABS HI was 0.38 ±0.32 (n=54). However, as can be seen in Figure 1, the only individuals that showed either zero or complete hand preference were those with less than four gesture instances, and individual variation in hand preference appeared very high with small samples. When we accordingly excluded individuals with fewer than 20 gesture instances the range of individual preference decreased, to 0.02-0.67 (n=21), and the population mean ABS HI became 0.25 ±0.15. An alternative way of estimating the true degree of lateral bias in this population is the mean, weighted by the number of gesture cases per individual, which gives an ABS HI of 0.26.

Are lateralized hand preferences in one particular direction?

Hand preference scores (HI) range from -1.0 to 1.0 (to avoid pseudoreplication, we averaged the hand preference scores for each of the gesture types a chimpanzee used.) For the population, the mean ABS HI was 0.15 ±0.48 (n=54). However, once again, individuals with very low numbers of gestures produce spuriously extreme hand preference scores (see Figure 2). If we consider only individuals with more than 20 instances of gesture use contributing to their individual hand preference index (n=21), 9 had a left-hand preference and 12 a right-hand preference (range of individual preference -0.31-0.67; population mean 0.10 ±0.28). Of these, only 5 were significantly lateralized, four to the right (Janet: n=28, g=5.31, df=1 p=0.02; Hawa: n=29, g=6.04, df=1, p=0.01; Zefa: n=47, g=7.91, df=1, p=0.005; Nick: n=85, g=20.63, df=1, p<0.0001) and one to the left (Zed: n=66, g=4.97, df=1, p-0.04); the group as a whole was too heterogeneous to combine (heterogeneity goodness of fit G: g=55.55, df=20, p=0.00003). Eleven of the individuals with 20+ instances of gesture use had hand indices of >0.25 or <-0.25, i.e. showed clear lateralization. Among this more lateralized group, two individuals showed a left-hand preference (HI range -0.3 – -0.36) and eight showed a right-hand preference (HI range 0.26 – 0.67); this difference was not significant (Exact binomial test two-tailed, n=10, p=0.109).

Is there an effect of age on individual hand preference

For this analysis, individuals were assigned to four age groups: infants, juveniles, subadults and adults. As the study was conducted across 3 years, individuals frequently contributed data to more than one age-group, so the total number of ‘individuals’ included in age related statistics (n=114) was larger than the actual number of chimpanzees in the population (n=54), and the sample size for each ‘individual’ was smaller than in other analyses. In this case, employing our previous restriction to individuals with 20+ gestures would eliminate the majority of individuals (from n=114 to n=15), so we relaxed the criterion to include individuals with 10+ gestures (n=38).

We found a significant effect of age on the direction of hand preference (One-way Anova: F=3.16, df=3,34, p=0.037), with individuals becoming more right-handed with age (Figure 3). There was no effect of age on the strength of hand preference (One-way Anova: F=1.34, df=3,34, p=0.261).

Do snare injuries determine hand choice?

We examined the gesturing of 8 individuals with major snare injuries (hand amputated or paralysed). Six of the snare-injured chimpanzees preferred their healthy hand; one preferred the snared-hand, but only 2 cases of gesture use were recorded; and one individual had severe snare-injuries to both hands. As a group the snare-injured individuals were more lateralized than healthy chimpanzees (healthy group: n=21, mean ABS HI=0.25 ±0.15, snare-injured group: n=8 mean ABS HI=0.68 ±0.32, t-test: t=5.07, df=27 $p<0.0001$). However, injured individuals varied greatly in their degree of hand preference (ABS HI snared individuals: range=0.12-1.0). Only 2 of the 4 individuals suitable for statistical testing with a binomial test (gesture cases $n>10$, individual data pooled across gesture types) were significantly lateralized (Zig: n=35, p=0.04; Kana: n=20, $p<0.0001$), both in the direction of the less injured hand.

Does lateralization vary among gesture types?

Within the 20 gesture types suitable for analysis of lateralization, strength of hand preference scores (ABS HI) for each type ranged from 0.0 to 1.0, with mean 0.38 ±0.32. (To avoid pseudo replication, we averaged, for each gesture type, the scores of each chimpanzee who contributed to the index.) However, as with the ABS HI scores for individual chimpanzees (Figure 1), variation in the ABS HI scores of gesture types decreased with an increase in the number of gesture instances. If analysis is restricted to gesture types with 20+ instances of the gesture type (n=8), the ABS HI range is 0.01-0.32 and the mean ABS HI is 0.20 ±0.11.

Within the repertoire we found no clear direction in hand bias: 10 gestures had HI index scores of less than zero, indicating some left-hand preference, and 10 above zero, indicating right-hand preference. The mean HI index for all gestures studied was 0.04 ±0.50 (n=20; see Figure 4); when gestures with fewer than 20 cases were eliminated, this rose to 0.17 ±0.15 (n=8).

While pooling individual data runs the risk of introducing pseudo-replication, we felt that given the low levels of hand preference within the population this might be worthwhile for investigating hand preference across gesture types. Twelve gesture types had 10 or more instances of use (after pooling across all individuals) and could be tested for hand bias with individual goodness of fit tests. Five of these showed a bias, one to the left (Arm shake: n=11 g=4.82, df=1 p=0.028), four to the right (Big Loud Scratch: n=222 g=4.63 df=1 p=0.031; Object Shake: n=261 g=5.85 df=1 p=0.016; Object move: n=103 g=6.13 df=1 p=0.013; Hand fling: n=44 g=7.58 df=1 p=0.006); all other gestures were non-significant (Slap object with object, Punch object/ground, Arm swing, Slap object, Reach, Leaf clipping, Arm raise). The variation across gesture types was too heterogeneous to pool into a single repertoire score (heterogeneity goodness of fit G=21.04, df=11, p=0.033), indicating that the use of different gesture types did not fit a single pattern of hand bias. However the fact that two right-biased gestures involved object use led us to carry out an additional analysis

We investigated whether or not object manipulation (OM) was a significant factor by separating OM gesture types from non-object manipulation (NOM) gesture types. OM gestures were found to be sufficiently homogenous to combine, and the combined OM set showed a significant right-handed bias (OM total G=11.98, df=2, p=0.003; pooled G=11.31, df=1, p=0.0008; heterogeneity G=0.67, df=1, p=0.414). NOM gestures were also found to be sufficiently homogenous to combine, but in this case the combined NOM set did not have a significant hand bias (NOM total G=19.54, df=10, p=0.034; pooled G=2.85, df=1, p=0.091; heterogeneity G=16.69, df=9, p=0.054).

Discussion

Communicative gestures of wild chimpanzees at Budongo show very flexible hand use: none of our subjects employed a single hand exclusively, and estimates of the strength of hand preferences decreased with increasing amounts of data. Nevertheless, none of these chimpanzees displayed perfect ambilaterality; there were consistent hand preferences even in individuals with extremely large sample sizes; and the community as a whole showed a slight right-hand bias.

If one requires that an individual's hand use be significantly lateralized to be classified as a preference, then our findings correspond to Level 1 in McGrew and Marchant's suggested framework 'most individuals in a group (or deme or species) are ambipreferent and only a minority of individuals are lateralised to either side to varying degrees'.[13] Perhaps one of the most striking examples of incomplete lateralization is seen in the snare-injured group of chimpanzees: although they had more pronounced hand preferences than healthy chimpanzees, individuals persisted in gesturing at times with their injured hand even in the face of massive physical deformity (e.g. complete amputation of one hand).

A possible explanation for this striking flexibility is that there is an environmental benefit for ambilaterality in chimpanzee gestural communication; in other words, being able to use either hand confers some advantage to a communicating individual. In termite fishing complete lateralization was found to confer a small but significant advantage, with 100% handed individuals more efficient in gathering termites;[8] this might explain the tendency towards lateralization in chimpanzee tool-use. The circumstances are different for gesturing, however. Feeding chimpanzees are rarely engaged in other activities, in marked contrast to gesturing chimpanzees who may well be grooming, travelling, or playing at the same time. In addition, tool use usually occurs on the ground, in open areas, whereas communication may occur anywhere: while hanging from a climber, or travelling through dense undergrowth. Under these conditions it may be that the ability to communicate with either hand - and, by doing so, to avoid having to stop any concurrent activity or locomotion - represents sufficient advantage in maintaining flexible use of either hand, even in the face of massive physical pressures such as permanent injury. Testable predictions of this theory include (a) an individual's manual lateralization should decrease when forced to operate in more difficult locations, for example when using tools to break into arboreal beehives; (b) an individual's gestural lateralization should increase in less complex environments with no other concurrent activities, for example in captivity.

Despite the strong evidence for ambilateral hand use in gestural communication in the wild Sonso chimpanzees, it is difficult to completely dismiss the pattern of small but consistently right-handed biases we have found. More individuals favoured their right-hand to some extent, whether we consider all individuals, only individuals with more than

20 cases of gesture use, or only individuals with stronger hand preferences. Mean population hand preference, after correcting for any bias from either individuals or gesture types, was to the right. Individuals become more right handed with age. The one gesture class that showed significantly lateralization, the object manipulation gestures, was lateralized to the right.

Our finding that right-hand use increases with age supports the similar findings from captivity[9] and suggests that this is not, as has been suggested,[13] simply an effect of human enculturation or exposure to a human designed environment.

Perhaps our most interesting finding is that of the striking right hand bias in object manipulation gestures, which highlights the potential task-specificity of hand preferences. Although several (less lateralized) gestures involve the use of an object or the ground *as a substrate* (for example, object slaps or stomps), in the case of the (lateralized) Object shake or Object move gestures, the object is *actively manipulated*. In captive gorillas, hand preferences for uni-manual actions have been found to be affected by target animacy, with inanimate targets eliciting increased right-hand use.[24] Those authors suggested that ape brain structures involved in object manipulations, such as tool use, may have served as a precursor to those involved in language processing, so that a pre-existing bias to left-brain processing led to the left-lateralization of language. Data from wild gorillas are consistent this suggestion. The hierarchically-organized food processing skills of wild gorillas have been noted as ‘syntactically’ structured, like a phrase-structure grammar.[6] And several of these food-processing routines showed significant right-handedness[5]. Our findings on chimpanzee gesture, however, suggest an alternative or additional explanation for human right-handedness: that language might have been ‘scaffolded’ on a primitive substrate for intentional communication in great ape gesture.

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Figure captions

Figure 1. Absolute hand preference index (ABS HI) for individual Sonso chimpanzees (n=54) plotted against each individual's total number of gesture instances, of the 20 gesture types coded for laterality. The mean across individuals, weighted by the number of gesture cases, is indicated as a single line.

Figure 2. Hand preference index (HI) for individual Sonso chimpanzees (n=54) plotted against each individual's total number of gesture instances, of the 20 gesture types coded for laterality.

Figure 3. Black bars represent mean absolute hand preference index (ABS HI) for each age group, plotted on a scale of 0-1; White bars represent mean hand preference index (HI), plotted on a scale of -1 to +1. Only individuals with 10 or more gesture instances contributed data to the group mean.

Figure 4. Hand preference index (HI) of individual gesture types (n=20), plotted against the frequency of observed instances.

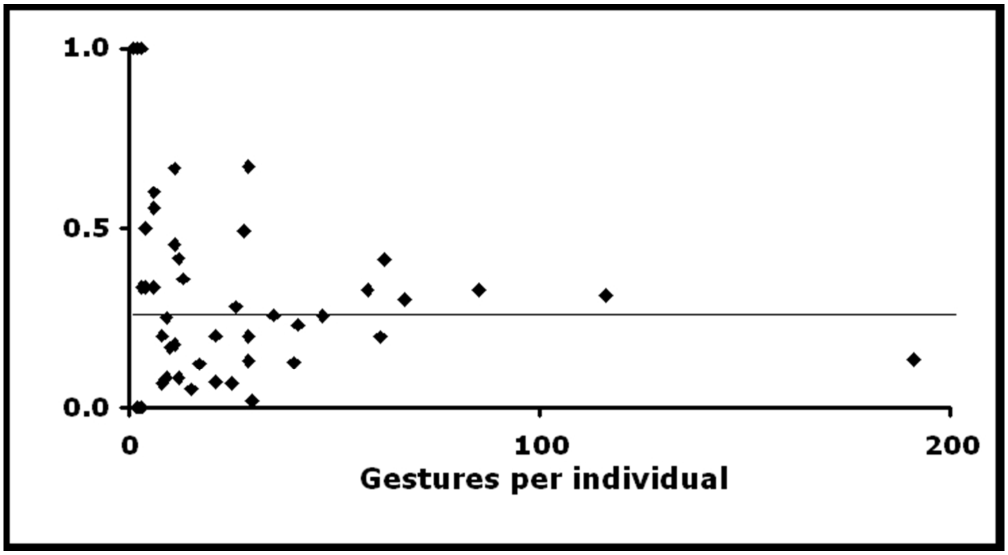

Fig 1
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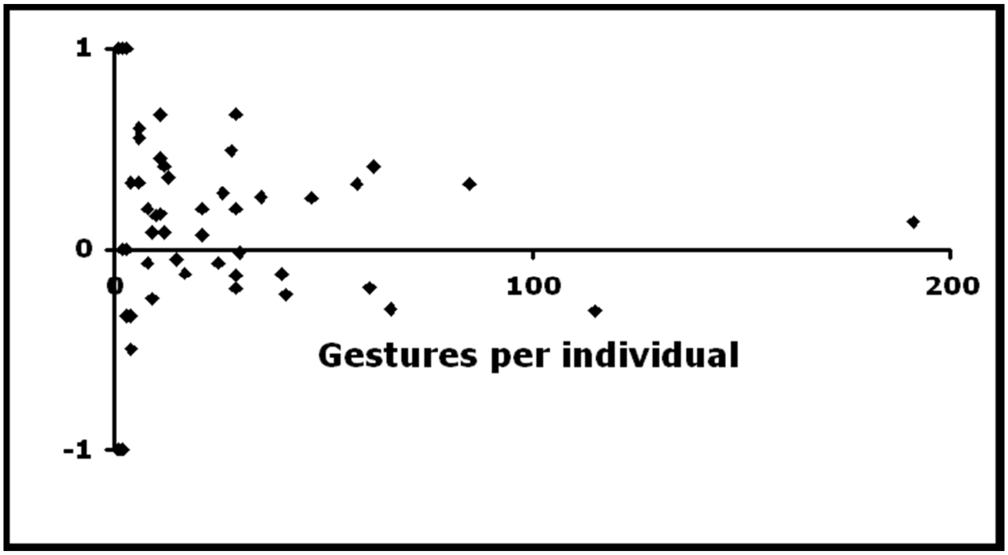

Fig 2
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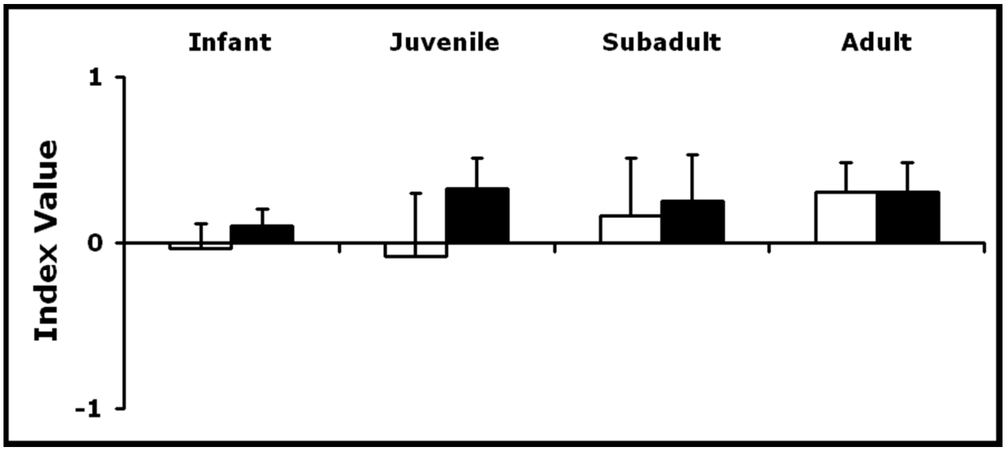

Fig 3
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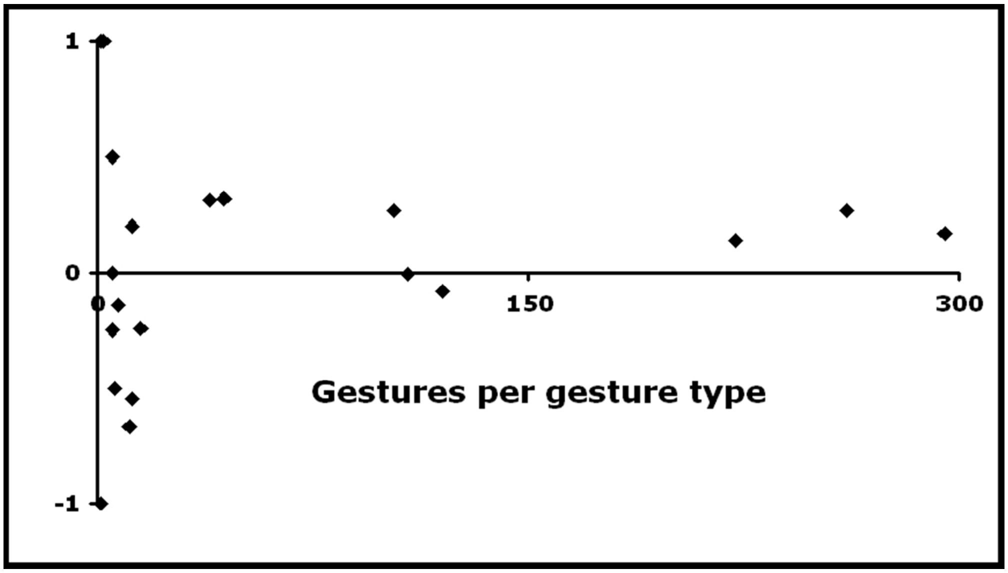

Fig 4
228x129mm (96 x 96 DPI)