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Language as a tool for social bonding: evidence from wild chimpanzee gestural, vocal and bimodal signals

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Abstract

The evolution of language has fascinated anthropologists, psychologists and biologists for centuries, seeking to infer language origins from the communication of primates, our closest living relatives. Capacity for intentional signalling is a key feature of transition to language in our hominin ancestors, facilitating complex social dynamics in complex social groups. However whether vocal, gestural and bimodal signals are differentiated according to intentional use and hence complex sociality has not been studied, making unclear the modality of language evolution. We addressed this question in wild chimpanzees. We found that larger social network size was associated with a larger network of gestural but not vocal or bimodal signals. Response waiting was more common in association with gestures than vocalisations, but elaborations were more common in vocal than gestural or bimodal signals. Overall, chimpanzees were more likely to manage weak social bonds through vocalisations, whereas strong social bonds were managed through gestures and bimodal signals. However, when social bonds were weak, gestures accompanied by response waiting were more likely to elicit approaches than vocalisations accompanied by elaboration, which elicited avoidance. This suggests that gestures were the primary modality of language evolution and that the use of more sophisticated gestural signalling led to evolution of complex social groups of hominin ancestors.

1. Introduction

Understanding whether language evolved to increase group cohesion and facilitate life in complex social groups is one of the most important questions in establishing the evolutionary pressures driving evolution of human social cognition [1, 2]. In order to determine origins of the language evolution, studies have primarily focused on examining communication of primates. Producing sounds by means of a vocal tract, is a primary characteristic of language, and therefore the bulk of studies of primate communication, have focused on vocal signals [3]. Vocalizations are functionally referential, and therefore like language can convey semantic meanings to the recipients, suggesting that language evolved from vocal modality of communication [4]. Further, it was argued that the combined vocalization-gesture system (conventionally referred to as bimodal communication) may have driven the evolution of language, whereby gesture and vocalization had different but complementary functions [5]. According to this hypothesis, language evolved from bimodal gesture-vocal signals because it can identify greater number of distinct messages than either vocal or gestural signals alone, and therefore like language can increase the complexity of messages that can be conveyed by communication [6].

However, recent theoretical approaches to language evolution posit that language evolved not from vocalizations or bimodal signals, but initially from gestures. Gestural communication, defined as socially directed movements of the head, body, hands or the body postures is an important ancestral feature of language evolution that humans share with their primate relatives [7]. Human language is underpinned by neurological structures that are homologous to the ones underpinning gestural communication [8]. Only humans and apes, use gestural communication as a primary modality of signaling, which was shown to be more flexibly deployed in social interactions than either facial expressions or vocalizations [9]. Here we examine whether the predecessors to language evolution can be found in wild chimpanzee gestural, vocal or bimodal signals.

In order to understand the homology in complexity of communication between humans' and apes' it is important to examine understanding of intentionality in signaling, defined as ability to appreciate that others have different thoughts from us, and that these thoughts affect their behavior [10]. In intentional signalling, the signaller has a goal and flexibly modifies communication to influence the comprehension state of the recipient [10]. This ability is one of the most important features of human communication and makes social relationships of humans so complex. The most important question is whether primates have understanding of intentionality in gestures, or if vocal and bimodal signals are also characterized by understanding of intentionality.

Studies of gesturing in captive chimpanzees have shown that they have some understanding of intentionality as evidenced by a signaler's audience checking (directing visual attention at recipient prior to signal), response waiting (directing visual attention at recipient after signaling) and elaboration of signals (using a new signal after the first signal in sequence) until their goal is obtained, or failure is indicated [11]. For example, chimpanzees can figure out if an experimenter knows, or does not know about the location of a hidden food and persist in gesturing until the experimenter finds the food [12]. Some studies have proposed that human contact is necessary for chimpanzees to have flexible, intentional communication [13]. This is because humans interact with chimpanzees in different ways than chimpanzees do amongst themselves, for instance, by attempting to direct their attention towards self or other objects or events. When humans display these behaviors toward captive chimpanzees, the apes may acquire different abilities to those of wild chimpanzees, that is, the enculturated apes may have specifically adapted to contact with humans [14]. However, research into intentionality underlying gestures in wild chimpanzees shows that intentional gestures are more ubiquitous than previously thought. Chimpanzees in the wild show complex use of gestures demonstrated by how chimpanzees make *sequences* of gestures, i.e. gestures produced consecutively, in response to another's behavior [15]. Chimpanzees show an awareness of whether or not the recipient of the gesture really understands the message the sender is trying to get across. If the recipient only partly understands the message, then the sender repeats the same gesture, while if the recipient does not at all understand the message, then the sender uses new gesture. These findings are significant because they show that gestures are not simply a result of emotional states felt by a chimpanzee but are choices designed to influence others, in order to achieve desired goal. Intentional gesture is not acquired in captivity, but is a trait shared with humans and other apes [13].

It is not only the gestural behavior that can shed light on our evolutionary origins; the vocal and bimodal signals are also important in ’decoding’ communicative and cognitive abilities [16]. To address understanding of intentionality in bimodal signals, Leavens & authors [17] showed that captive chimpanzees tailor use of bimodal and unimodal signals to success of communication acts with a human observer. Specifically designing playback experiments to capture the nature of intentional communication in alarm calls of wild chimpanzees, Schel & colleagues [18] showed that alarm calls experimentally elicited by a presence of a snake were socially directed, and used in tandem with audience checking and gaze alternations until the recipients were safe from the snake. These findings thus suggest, that chimpanzees are unique in having in common with us the propensity to use vocal and bimodal signals to alter the knowledge states of the recipient, which is a key feature important in the evolution of human communication [8, 18].

However, understanding intentionality in primate communication has been complicated by the methodological constraints of focusing on the signaler’s perspective, whereas recent studies point out the important role of intentionality from the point of view of the recipient. According to this perspective intentional signals influence knowledge states of the recipient because they augment the recipient’s capacity to process information about social relationships, whereby the recipient focuses on relevant information about ongoing and past social interactions to figure out the signaler’s goal. Intentionality in communication is required to form social bonds in socially complex species. However, absence of previous experience with the social partner may limit the ability of the recipient to process information about social relationships. Weak social bonds are ambiguous, and the high unpredictability of social interactions causes the recipient to perceive them as threat resulting in high likelihood of avoidance [19-21]. In this context, higher intensity signals attract attention because they have a high predictive value for the presence of threat, causing reflexive avoidance in response to physiological stimulus of physical characteristics [22]. In contrast, intentionality in communication can increase the positive evaluation of the social interaction, facilitating approaches and enabling two animals to engage in social interaction. This process gives rise to efficient social interactions between strongly bonded dyad partners, based on simple readouts of behavioral states, whereby recipients learn to respond to emotional state generated as a consequence of direct, repeated experience of the social interaction with the signaller.

Chimpanzees live in complex fission-fusion social system, whereby they split into subgroups of different composition and duration on a daily basis, leading to a presence of weak social bonds. Although the size of the chimpanzee communities on average is very large, ranging from 20-150, individual chimpanzees differ in the size of their social networks, with central chimpanzees in the communities having a large number of strong social connections, whereas peripheral chimpanzees have smaller numbers of strong social connections. An important avenue of research is to use social network analyses to examine how the social relationships of primates and intentionality in communication are inter-connected. Such analyses will reveal how primates use communication and other behaviours to facilitate life in complex social groups and whether primate communication was a predecessor to language evolution.

Here we examine this topic in wild chimpanzees and hypothesize that gestures are more effective in social bonding than either vocal or bimodal signals because they are more intentional. Chimpanzees (*Pan troglodytes schweinfurthii*) are among our closest living relatives and examining the association between communicative and social complexity in this species is particularly interesting because of the complexity of their fluid fission-fusion social system [23]. They are thus excellent model species to investigate patterns of sociality and communicative complexity so as to inform models of human social evolution. To this end we examined whether: 1) the complexity of the gestural, vocal and bimodal communication network is positively associated with the complexity of the social network; 2) gestural, vocal and bimodal communication differ in respect of 3) intentionality, 4) strength of social bond and 5) how weak social bonds are managed, and 6) social interactions are differentiated according to the rate of gestural, vocal and bimodal communication.

2. Methods

(a) Study site, data collection and coding

Habituated adult chimpanzees (6 males, 6 females) were followed over 9 month period at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (2006 – 2008). The observation duration for each subject is shown in Supplementary Information 1 [24]. Focal follows of 18-minute duration (9 scans at 2-minute intervals) recorded the activity of the focal individual; the identity, activity, and distance of the nearest adult neighbor relative to the focal subject as well as identity of all chimpanzees present within 10 m of the focal subject continuously recording communication using a digital video camera. Supplementary Information 1 gives description of the categories of behaviour coded [24]. For each communication event, we determined the social bond of the recipient towards the signaller from 8 social behaviours using the Composite Sociality Index [12] (Supplementary Information 1) [24].

(b) Social network analysis

We deployed Double Dekker Semi-Partialling Multiple Regression Quadratic Assignment Procedure (MRQAP) to examine the associations between communication networks, calculated as the frequency of behaviour per hour dyad partners spent within 10 meters [13] and the social networks calculated as the frequency of behaviour, when nearest neighbor, within 2 m per hour spent within 10 m. We considered six behaviors were both focal and non-focal subject were engaged in the same social behavior with each other (visual attention, proximity, feeding, resting travel, mutual grooming) and two behaviours which were unidirectional (giving and receiving grooming). The data entry and the results of these analyses are reported in Supplementary Information 1 [24]. Using matrices of social interactions, we calculated centrality measures using normalized degree centrality. This measure represents the average value of each row or column of the network matrix (i.e., the average value of that behavior for each focal chimpanzee). Since the network of social behaviors differed between dyads A to B and B to A, we calculated indegree (behaviors directed by conspecifics toward the focal chimpanzee) and outdegree (behaviors directed by the focal chimpanzee to conspecifics) separately. Further, we dichotomized and symmetrized social and communication networks, to obtain the measure of overall network size (the total number of edges connected to a particular node: n degree), we calculated the normalized degree (n degree) of social and communication networks, dichotomizing and symmetrizing social networks. For analyses of social interactions we first obtained composite sociality index using formula presented in Supplementary Information. Both A to B and B to A dyads were considered. Further, we computed the network of strong and weak bonds separately, using composite sociality index, whereby values above 1 represent dyads that have higher rate of social interactions per hour spent within 10 meters than average dyad (strong bond). Values below mean of 1 denoted dyads that have a lower rate of social bonding behavior per hour spent within 10 meters than average dyad (weak bond). To construct communication networks, we used rates of communication produced by the focal towards non-focal chimpanzee. In all analysis of centrality in social network, we included four control variables: proximity to oestrous female outdegree (duration of time focal subject spent in proximity to oestrous female per hour spent in the same party outdegree), proximity to kin outdegree (duration of time focal subject spent in proximity to kin per hour spent in the same party outdegree), sex (two levels: male, female), age (age of focal subject in years) (see Supplementary Information 2 for details of all models)[24]. UCINET 6 for Windows was used to carry out all data transformations and social network analyses.

(c) Generalized linear mixed models (GLMM)

In the analysis, only those events were included which occurred as first signal in the sequence. We included all behaviors potentially communicative (e.g. quadrupedal stance), unlike in our previous studies [25], excluding only the scratch behavior. This was done so as to take into account the influence of behaviors on social bonding that appeared to be communicative but were potentially non-intentional. To examine differences between gestures, vocalisations and bimodal signals, in the analysis we included five control predictors: signaller and recipient age (two levels: subadult, who was individual less than 15 years old, adult, all others) signaller and recipient sex (two levels: female, male), relatedness (two levels: non-kin, such as mother offspring dyads or siblings, father offspring dyads were largely unknown; kin). In those analyses where social bond of the recipient towards signaler was included, only adult recipients were considered. In the GLMM, three key variables of interest were: 1) communication type: vocalization versus gesture (two levels: vocalization, gesture), bimodal signal versus gesture (two levels: bimodal signal, gesture), bimodal signal versus vocalization (two levels: bimodal signal, vocalization); 2) intentionality of signaling: audience checking (two levels: absent, present), response waiting (two levels: absent, present), elaboration (two levels: absent, present); 3) recipient/ signaller bond (two levels: weak, strong); 4) recipient’s response (two levels: avoidance, approach); activity change (two levels: maintain ongoing activity, initiate activity change by directing movement and attention of the recipient). The data in GLMM, had a hierarchical structure: Level 1 (identity of signaller), Level 2 (identity of recipient of the gesture).The models were fitted using a binomial error structure with logit link. Signaller identity and signaller identity by recipient identity, were random effects for which random intercepts were used (see Supplementary Information 2 for details of all models not given in text of the manuscript) [24]. The results of predictors of intentionality by communication type are reported in Supplementary Information 1 [24]. We analyzed all data using SPSS 25.0 (SPSS Inc., Chicago, IL, USA). The datasets are available on Figshare [24].

3. Results

Overview of the communication events

Overall, we extracted from the footage 5328 potentially communicative behaviours. Out of these cases we excluded 1120 events which contained scratches or combinations of scratches with communication. The remaining dataset contained 3275 events of gestures, 509 bimodal combinations of gestures with vocalisations and 424 events of vocalisations. We coded 3046 of communication events for audience checking, 2979 events for response waiting, 3402 events for elaboration, 3206 events for recipient’s response and 3401 events for activity change. See Table 1 for presence and absence of these markers according to communication type.

Does complexity of communication network increase with social complexity?

Across all adult dyads in the community where there was some level of social interaction (values of CSI were above 0), the chimpanzees had a differentiated number of social bonds and this varied across two consecutive years. Of the total community size of 36 adult members in 2007, and 30 adult members in 2008, the mean ± sd number of all connections was 4.66 ± 3.67 and 9.08 ± 2.42 connections in 2007 and 2008 respectively, and this difference was statistically significant (Wilcoxon signed-rank test, T = 28, z = -2.375, p = 0.016, median 2007: 4, median 2008: 8.5). The mean ± sd number of strong connections in 2008 (6.75 ± 2.83 connections) was significantly higher than in 2007 (4 ± 3.31 connections): (Wilcoxon signed-rank test, T = 21, z = -2.214, p = 0.031; median 2008: 7.5, median 2007: 3). There was no difference in the number of weak social bonds in 2007 (the mean ± sd: 0.66 ± 1 connections) and 2008 (the mean ± sd; 2.33 ± 1.49 connections): (Wilcoxon signed-rank test, T = 19.50, z = -1.897, p = 0.094; median 2007: 0, 2008: 2.5) (see Supplementary Information for number of strong and weak social bonds per each focal chimpanzee across the consecutive years). Across 132 dyads of focal chimpanzees, animals directed communication at a dyad partner at a mean rate ± sd of 3.96 ± 11.06 gestures, 0.47 ± 4.79 vocalisations and 1.08 ± 2.87 bimodal signals. Chimpanzees used vocal, gestural and bimodal signals with the majority of their network members. The mean degree of gestures was 53% of connections to all network members, bimodal signals was 37.9% of connections and vocalisations was 12.1% of connections. We used node level regressions to examine whether centrality in the social network predicted centrality in the gesture, bimodal and vocalisation networks. We found that there was a significant positive association between social network size (composite sociality index n degree) and the size of the network of gestural communication (r^2=0.861, β= 0.680, p = 0.049), but not bimodal signals (r^2=0.669, β= 0.576, p = 0.099) or vocalisations (r^2=0.706, β= 0.090, p = 0.407) (Fig. 1).

Considering size of strong and weak social bonds networks separately, we found that size of strong social bond network positively predicted size of gesture (r^2=0.873, β= 0.803, p = 0.040) and bimodal signal (r^2=0.808, β= 0.896, p = 0.028) networks but not size of the vocal network (r^2=0.803, β= 0.514, p = 0.149). In contrast, size of weak social bond network negatively predicted size of vocal gesture network (r^2=0.903, β= -0.725, p = 0.049) but not the size of gesture (r^2=0.667, β= -0.325, p = 0.246) or bimodal signal (r^2=0.595, β= -0.498, p = 0.145) networks. Further, we used node level regressions to examine whether centrality in the social network based on social behaviour directed by non-focal subjects at the focal subject (composite sociality index indegree) was predicted by vocal, gestural or bimodal communication produced (communication outdegree) and received (communication indegree). We found that chimpanzees who received a higher rate of social behaviour also received gestural communication (gesture indegree: r^2=0.753, β= 0.661, p = 0.038) and bimodal communication (bimodal signal indegree: r^2=0.745, β= 0.804, p = 0.027) at higher rates than the chimpanzees who received a lower rate of social behaviour (composite sociality index indegree). However, chimpanzees who received social interactions at a higher rate did not receive vocalizations (vocalisation indegree: r^2=0.837, β= 0.713, p = 0.064) at a higher rate than the peripheral chimpanzees in the social network.

Do signallers differentiate use of gestures, bimodal signals and vocalisations according to strength of social bond with the partner and use of intentionality markers?

We used GLMM to examine the association between type of communication (vocal versus gestural, bimodal versus gestural, bimodal versus vocal) and the following predictors: strength of social bond of recipient towards signaller, absence and presence of intentionality marker considered separately (audience checking, response waiting, elaboration), controlling for signaller age, relatedness, signaller and recipient sex (Table 2).

Comparing vocal and gestural signals, we found that subadult chimpanzees were more likely to direct gestures at the partner than the adults, gestures were more likely used to communicate with kin than non-kin, and female than male recipient. Further, gestures were more likely directed at strongly bonded recipient to the signaller when compared with the weakly bonded recipient. Further, gestures were less likely to be accompanied by elaboration than vocalisations.

When comparing bimodal signals to gestures, the analysis showed that gestures were more likely produced by subadults when compared with adults, by males when compared to females, and towards female recipients than to male recipients.

Finally, comparing bimodal signals to vocalisations, we found that bimodal signals were more likely when the social bond of the recipient to the signaller was strong than when weak. We also found that bimodal signals were less likely to be accompanied by elaboration than were vocalisations.

Does vocal, gestural and bimodal communication differ according to how it manages weak social bonds?

We used GLMM to examine whether approach or avoidance was a more likely response to gestures between weakly bonded dyad partners in response to presence and absence of an intentionality marker (audience checking, response waiting, elaboration), while controlling for signaller age, relatedness, and the sex of signaller and recipient (Table 3). Comparing gestures to vocalisations, we found that when social bonds were weak, communication was more likely to elicit approach to than avoidance from kin compared to non-kin, when communication was accompanied by response waiting, when there was absence of elaboration, and when communication was gestural rather than vocal (Fig. 2). Comparing gestures to bimodal signals we found that approach was more likely than avoidance when communication was accompanied by presence of response waiting and absence of elaboration and when communication was gestural than bimodal.

Do audience checking, response waiting and elaboration between weakly bonded partners have a different effect on the recipient according to modality of communication used?

We used GLMM to determine whether approach or avoidance to communication accompanied by either audience checking or response waiting in social interactions between weakly bonded dyads occurred in response to vocal versus gestural, and in response to bimodal versus gestural signals, controlling for signaller age, relatedness, signaller and recipient sex. Comparing vocal and gestural signals, we found that chimpanzees were more likely to approach in response to communication made by kin than non-kin ($\beta = -14.222 \pm 0.858$, $p < 0.001$), when the recipient of communication was a male than a female ($\beta = -1.540 \pm 0.694$, $p = 0.028$), and when communication was gestural than vocal ($\beta = -3.690 \pm 0.832$, $p < 0.001$). Further, comparing bimodal and gestural communication, we found that approaches were more likely by male than female recipients ($\beta = -1.501 \pm 0.704$, $p = 0.034$) and when communication was gestural than bimodal ($\beta = -0.974 \pm 0.403$, $p = 0.017$).

Next, we used GLMM to examine whether approach or avoidance to the last gesture in an elaboration sequences between weakly bonded dyad partners occurred in response to gestural compared to vocal signals, controlling for signaller age, relatedness, signaller and recipient sex. We found that approach was more likely than avoidance when elaboration was produced by female than a male ($\beta = 14.859 \pm 1.191$, $p < 0.001$) and when elaboration was gestural rather than vocal ($\beta = -0.666 \pm 0.050$, $p < 0.001$).

4. Discussion

In this study, we hypothesized that gestures are more intentional than either vocal or bimodal signals and hence facilitate more complex social dynamics acting as a primary modality of language evolution. We deployed social network analysis to examine the associations between size of the social network and the size of the network of vocal, gestural and bimodal signals. We found that chimpanzees who had a larger number of social connections also had a larger number of connections maintained through gestures but not through vocal or bimodal signals. Using GLMM to examine this association, we found that chimpanzees directed elaborations and vocal signals at weak bonds, whereas they directed gestural and bimodal signals at strong bonds in absence of elaboration. Finally, to examine the effect of signals on the recipient, we found that when social bonds were weak intentional gestures elicited approaches, whereas intentional vocal and bimodal signals elicited avoidance. These data suggest that gestural communication is underpinned by understanding of intentions, whereas vocalisations and bimodal signals are underpinned simply by understanding of behaviour, suggesting that the capacity for intentional signalling in gestures facilitates more complex social dynamics of wild chimpanzees. On this basis we conclude that language as a tool for social bonding has primarily evolved from gestures to facilitate group cohesion in large and complex social groups of hominins.

If intentionality is important for managing weak, rarely reinforced relationships, then chimpanzees should direct communication that requires only behavioural understanding at individuals with whom they have strong social bonds and communication underpinned by intentionality at those with whom they have weak bonds. We found that gestural and bimodal signals were more likely in association with strong social bonds, whereas vocalisations primarily co-occurred with weak social bonds. The observed results are likely because gestural signals differ from vocal signals in the cognitive skills that need to be employed in processing of information due to the differences in intentionality. Forming social relationships in novel social conditions, such as interactions with weakly bonded dyad partners, requires the ability of the recipient to attribute goals to social interactions, by allocating memory to selectively focus on relevant information [26]. In contrast, direct social experience reinforces strong social bonds, facilitating understanding of behaviour. If vocalisations are primarily associated with weak social bonds, this would suggest that they are key for forming social bonds with group members. However, attention allocation involves frequent errors and this implies that it is less likely to be successful, biasing strategy towards less cognitively complex tasks that produce a higher chance of a successful outcome [27]. In this context, vocalisations are less cognitively demanding because they influence understanding of behaviour between weak social bonds, whereas gestures are more cognitively complex because they influence understanding of intentions between strong social bonds [28]. Although vocalizations appear to be more intentional than gestures because chimpanzees elaborated with vocalisations more often towards weak social bonds, these elaborations are likely expressions of emotional state of the signaller, rather than attempts to inform the unaware recipient of the goal of the interaction. For instance, when social bonds were weak only gestures accompanied by response waiting elicited approaches, whereas elaborations by vocalisations elicited avoidance. This could potentially indicate that elaborations of vocal signals were threats that were used to manage spatial positions in competitive contexts.

Although we acknowledge that not all vocalisations may function in this way (e.g. contact grunts of baboons may not [29]), in the context of our data, vocalisations appear to express signaller’s own emotional arousal, and cause the recipient to experience it through the vocal communication of a signaller, as a variation in the state of physiological activation, indicated by heart rate [30], cortisol secretion [31] or nasal temperature [32]. High intensity vocalisations (e.g. alarm call) influence recipient’s behaviour by increasing their heart rate and cortisol. The role of vocalisations in maintaining weak social bonds rather than forming new social connections is supported by the data showing that when social bonds were weak chimpanzees used gestures to initiate change of activity by the recipient, whereas vocalisations maintained ongoing activities. The fact that only vocalisations and not gestures or bimodal signals co-occurred with a longer duration of time spent feeding in close proximity, supports this suggestion. This is further supported by the results showing that the size of the social network increased in association with the size of the network of gestural but not vocal signals.

One interesting finding was that when weakly bonded dyad partners interacted, the intentionality markers had a different effect on the recipient, depending on the type of communication. Gestures accompanied by intentionality markers elicited approach, whereas with vocalisations accompanied by intentionality markers elicited avoidance. Social environments impose chronic and acute stress on processing of information. It is expected that when these challenges reach a certain threshold, the recipients will downgrade understanding of intention to understanding of behaviour. Acute stress has a larger detrimental effect on understanding of intention than chronic stress, in that in conditions of acute stress, understanding of behaviour is favoured over understanding of intention [33]. Visual attention, such as visually monitoring the dyad partners prior to communication (i.e. audience checking) or after communication (i.e. response waiting) is processed in the areas of the brain involved in both understanding of intention as well as understanding of behaviour [33]. Visual attention during chronic stress disinhibits understanding of intentions, leading to a greater capacity of the recipient to process information. In contrast, visual attention heightens acute stress, leading to a greater inhibition of intentional state of the recipient, and increased behavioural processing. In the context of managing weak social bonds, animals may exploit their repertoire of vocalizations to match that of an interaction partner to whom they actively pay attention to in a stimulus driven way. Use of intentionality markers in this context leads to a greater degree of overlap in the repertoire of vocalisations through enhanced ability of the dyad partners to actively match and synchronise their communication in condition of acute stress. If the motivational state of fear is reduced by a joint display of affect in response to behavioural convergence in vocalisations, the use of intentionality markers facilitates formation of social bonds by automatic attribution of value of ‘liking’ and ‘wanting’ [34, 35].

It could be argued that language evolution occurred in vocal communication because our study shows that chimpanzees used vocal signals to manage social relationships with weaker links, whereas gestures were used to manage strong social bonds. However, the value attribution in language occurs through cognitively complex processing. For instance, activation of brain areas such as the superior and middle temporal gyri in the left hemisphere which indicate abstract higher-level processes are present during normal language processing, but are reduced when speech sounds are artificially distorted to disrupt the connection between sound and meaning [36]. Gestural communication facilitates formation of the representations about goal of the social interaction with weak social bonds, suggesting a potential important role of these behaviors in language evolution. Psychopharmacological studies examining the influence of dopamine on language processes showed that dopamine enhanced value encoding in speech [37]. This suggests that cognitive processing of primate gestures might be affected in a similar manner to language processing. Cognitive skills underpinning gestural communication therefore probably preceded language evolution.

However, the claim for gestural origins for language confounds language capacity with language expression (and has no explanation for why it should have switched from gestures to voice in humans). Humans use speech/language not to manage close relationships (strong ties, which we deal with mainly by gestures) but to manage distant weak ones, just as our data suggest is the case of chimpanzees. Language as an adjunct to grooming to allow group size to increase beyond the limit at ~50 that we can manage via grooming. Although cognitive skills underpinning language, may have first evolved in gestural modality of communication, the language evolution may have occurred in the modality of the low intensity vocal signals once our human ancestors gained greater voluntary control over their vocal output to face challenges of acute stress. As familiar dyad partners repeatedly interacted in a goal directed way through novel, low intensity vocalisations, this innovation could produce group level differences in communication where small differences in morphology of the same type of low intensity vocalisation would produce ‘accents’. Such vocalisations acquired with familiar conspecifics may have been used with unfamiliar dyad partners to establish social bonds when exposed to acute stress as the dopamine is not released in response to habitual signals and the low intensity of signal would prevent overstimulation of the recipient and allow recognition of social distance between the signaller and the recipient when social bonds were weaker. This would allow transfer of value in non-aversive way during acute stress, for instance, signalling value information to the recipient about signaller's potential as a grooming partner giving rise to language evolution.

Through hominin evolution there has been an increase in both brain size and this is likely to have been accompanied by an increase in group size [1]. Dunbar [35] has argued that the pressure to maintain larger social groups through hominin evolution may have driven the evolution of language as a novel social bonding mechanism that is more time efficient than grooming. Between primate species, it has been shown that evolutionary increases in the size of the vocal repertoire in non-human primates were associated with increases in both group size and also time spent grooming [38]. This suggests that vocal communication may indeed play a key role in the evolution of social behaviour - larger groups are more complex to manage, and thus require a larger repertoire to maintain an increasing number of differentiated relationships. However, it is increasingly being recognised that gestural communication also plays a key role in regulating social behaviour, and systematic studies of the role of gestural communication in wild primates are in their infancy. This study examined how the gestures and vocalisations and bimodal signals in wild chimpanzees are related to the complexity of social network. There is currently an active debate as to whether human language evolved from vocal or gestural communication, and the finding that the use of gestural but not bimodal or vocal communication is related to a greater complexity of social network provides important insights into this debate. A key challenge of the future study of primate sociality is evaluating the relative importance of vocalisations, bimodal signals and gestures in the maintenance of primate social networks [39], and exploring how primates in groups of increasing size use these behaviours differentially to maintain their social relationships.

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Table 1. Occurrence of markers of intentionality according to type of communicative behaviour

	Gesture	**Vocalisation**	**Bimodal vocalisation with gesture**	**Total**
Audience checking present	2269	43	274	2586
Audience checking absent	396	8	56	460
Response waiting present	1876	35	204	2115
Response waiting absent	729	18	117	864
Elaboration present	606	47	55	708
Elaboration absent	2308	31	355	2694
Approach	2103	17	250	2370
Avoidance	679	31	126	836
Initiate activity change	1539	32	218	1789
Maintain ongoing behaviour	1372	33	207	1612

Table 2. Effects of social bond of recipient towards signaller and intentionality marker (audience checking, response waiting and elaboration considered separately) including control variables (signaller and recipient sex, signaller age, relatedness) on vocal, gestural and bimodal communication.

a) Comparison of vocal (reference category) versus gestural signalling

Model term	**Coefficient**	**Standard error**	**Significance**
Signaller age [subadult]	13.174	0.814	<0.001
Relatedness [non-kin]	-12.867	1.160	<0.001
Signaller sex [female]	0.839	1.020	0.411
Recipient sex [female]	2.641	0.978	0.007
Audience checking [absent]	1.674	2.229	0.453
Response waiting [absent]	-1.611	1.801	0.372
Elaboration [absent]	4.510	0.397	<0.001
Recipient/ signaller social bond [weak]	-1.690	0.559	0.003

b) Comparison of bimodal (reference category) versus gestural signalling

Model term	**Coefficient**	**Standard error**	**Significance**
Signaller age [subadult]	7.754	0.597	<0.001
Relatedness [non-kin]	-0.842	0.457	0.066
Signaller sex [female]	-1.448	0.451	0.001
Recipient sex [female]	2.114	0.585	<0.001
Audience checking [absent]	1.145	0.635	0.072
Response waiting [absent]	0.144	0.226	0.525
Elaboration [absent]	0.129	0.539	0.810
Recipient/ signaller social bond [weak]	1.113	0.712	0.119

c) Comparison of bimodal (reference category) versus vocal signalling

Model term	**Coefficient**	**Standard error**	**Significance**
Signaller sex [female]	-0.710	1.869	0.705
Recipient sex [female]	0.131	1.697	0.939
Audience checking [absent]	-0.343	1.446	0.813
Response waiting [absent]	1.711	1.572	0.279
Elaboration [absent]	-5.061	0.773	<0.001
Recipient/ signaller social bond [weak]	3.799	0.993	<0.001

Table 3. Effects of communication type: a) vocal versus gestural, b) bimodal versus gestural and intentionality marker (audience checking, response waiting and elaboration) including control variables (signaller and recipient age, signaller and recipient sex, relatedness) on approach and avoidance response to communication. Only those events were considered, whereby the recipient was weakly bonded to the signaller.

a)

Model term	**Coefficient**	**Standard error**	**Significance**
Signaller age [subadult]	-2.516	1.367	0.067
Relatedness [non-kin]	-17.082	1.818	<0.001
Signaller sex [female]	0.233	1.347	0.863
Recipient sex [female]	1.251	1.197	0.297
Audience checking [absent]	1.961	1.648	0.236
Response waiting [absent]	-4.953	1.514	0.001
Elaboration [absent]	4.083	1.282	0.002
Communication type [vocalisation]	-0.990	0.386	0.011

b)

Model term	**Coefficient**	**Standard error**	**Significance**
Signaller age [subadult]	-1.922	1.089	0.079
Relatedness [non-kin]	-1.880	1.105	0.091
Signaller sex [female]	-0.283	1.003	0.778
Recipient sex [female]	0.277	0.961	0.774
Audience checking [absent]	0.018	0.955	0.985
Response waiting [absent]	-2.174	0.847	0.011
Elaboration [absent]	2.793	1.015	0.007
Communication type [bimodal signal]	-1.332	0.647	0.041

Figure 1. Relationship between communication n degree and composite sociality index n degree

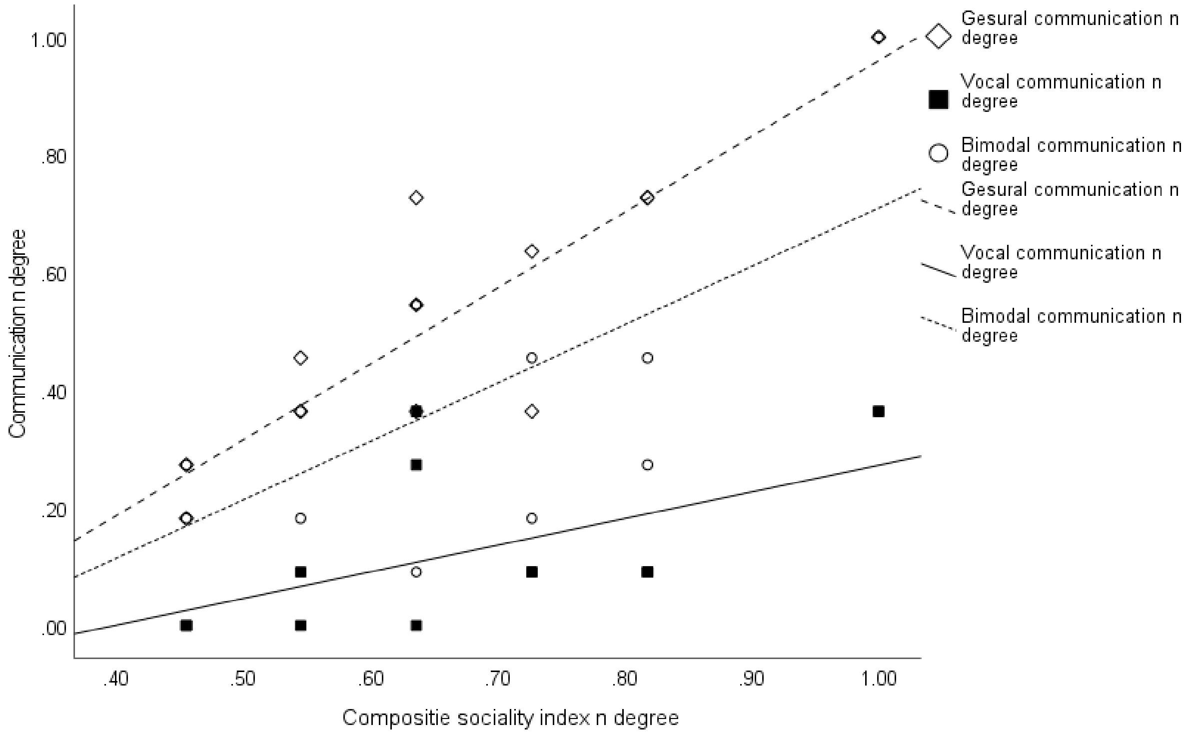

Fig. 2 Relationship between presence of intentional signalling accompanying communication type and response type of the recipient when social bonds of the recipient towards signaller are weak