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Intentional gesturing increases social complexity by allowing recipient's understanding of intentions when it is inhibited by stress

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Abstract

Examining the links between intentional communication and social relationships provides insights into the cognitive skills needed to manage a differentiated set of social bonds. Great apes gesture intentionally, but how this intentionality relates to sociality is still unclear. Stress in the form of dominant audience members inhibits understanding of intentions downgrading cognition to understanding of behavior but intentional communication may enable social bonding in stressful conditions. We examined the associations between gestural communication, sociality, stress and the outcome of interactions in wild chimpanzees. Social network size was positively associated with intentional but not non-intentional communication. When a dominant bystander was present with whom the recipient was weakly bonded, and gesturing was non-intentional, recipients produced avoidance response towards signalers to whom they were weakly bonded, indicating understanding of behavior. Signalers used intentional gestures more frequently to recipients who were stressed, and intentional gestures evoked approach behavior by the recipients, indicating understanding of intentionality. These results suggest that the presence of dominant bystanders is stressful, inhibiting understanding of intentionality. However, intentional gestures facilitate social bonding by allowing understanding of intentions. The cognitive skills underpinning intentional gestures may therefore play a key role in enabling primates to meet the demands of sociality.

Key words: intentional gesture, social network, chimpanzee, audience checking, response waiting, elaboration, dominant bystander

1. Introduction

An understanding of intentionality, defined as the ability to appreciate that others have different thoughts from us, and that these thoughts affect their behavior [1] is central to being human and is what makes our social relationships so complex. Studies of primate gestural communication (e.g. movements of the hands, head and body) have shown that they have some understanding of intentionality as evidenced by a signaler's use of 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 [1]. This cognitive flexibility is required to monitor and manage social relationships in a dynamic social environment. Primates must not only keep track of their own relationships, but also monitor third party relationships between other group members, as changes in these relationships (e.g. a change in dominance rank) can have implications for their own position in their group.

Although intentionality in gestural communication has been considered from the standpoint of the signaller, recent studies argue for the important role of intentionality in gesturing from the recipient's perspective [2]. For recipients, understanding of intentionality, is cognitively demanding because it requires use of selective attention to focus on social goals of individual importance, as represented in the working memory [2]. This capacity allows the recipient to respond flexibly in novel social conditions, when the absence of direct experience with the social partner would limit the complexity of social relationships. In this context, intentional gesturing facilitates understanding of intentionality by increasing the ability of the recipient to process information about the social and ecological environment.

However, examining understanding of intentionality from recipient's perspective is not straight forward; it is difficult to disentangle whether primates use gestures to influence recipient’s intentional states (i.e. what the other knows – indicating second order intentionality, or formal theory of mind) or behaviour (i.e. what the other does without the involvement of knowledge – indicating simple first order intentionality). Examining social interactions in the context of social stressors can enable us to draw firm conclusions about mental capacities underlying the processing of information by the recipients. Exposure to social stressors dysregulates dopamine dynamics to downgrade functioning of the higher order brain structures that are involved in understanding of intentionality, such as the prefrontal cortex [3]. In contrast, the lower level structures based on the understanding of behaviour such as the striatum are not inhibited by stress [3].We hypothesize that gestures that are intentional in form (gestures accompanied by presence of audience checking, response waiting, or elaboration) as opposed to gestures that are non-intentional in form (when these features are absent) allow understanding of intentionality by releasing it from inhibition. This intentionality in communication, as seen in chimpanzee gestural communication, may enable primates to maintain more complex social relationships.

The complexity of a social group in primates depends on the complexity of social relationships between animals, as the social group itself is an emergent property of these micro-level interactions [4]. Primates allocate differentiated amounts of time into affiliative interactions such as grooming with both related and unrelated group members, giving rise to networks of strong (frequent interactions) and weak (infrequent interactions) social bonds [5]. For individual primates, the level of social complexity can be measured by the size of their social network. In smaller networks, primates form relatively strong ties with all network members, with frequent interactions based on multiple different behaviours. However, as network size increases, the social bonds primates have with other individuals become on average increasingly weak, with less frequent interactions and an increasing dissociation between different behaviours, as primates use different types of behaviours to maintain the different types of ties [4]. These weaker, indirect ties are cognitively complex to manage, and this is especially true for central group members who have affiliative interactions with many conspecifics, as compared to peripheral individuals who have fewer interactions. Thus, in more complex social networks one may predict that there will be increased use of intentional gestures because of the need to use increasingly sophisticated strategies to maintain an increasing number of weaker social ties.

Group living inevitably leads to stresses arising from competition over resources such as food and mates [6]. Displacement activities such as scratch, are a common group of behavioural measures used to identify anxiety [7], which can be used to complement measures based on behavioural data such as communication patterns [8]. A range of studies have shown that scratch rates increase markedly above baseline levels in situations that induce anxiety such as following aggression [7], or the presence of a dominant bystander in close proximity [6].

One of the primary mechanisms to offset stress, both in humans and primates, is social affiliation. The close social bonds of subordinates with the dominants are a direct response to the competition over resources, buffering individuals from stress. However, the greater time and cognitive constraints on forming social relationships in complex social networks imply that not all individuals will have a strong bond with the dominant group members. Subordinates who are in close proximity to a dominant group member with whom they have a weak bond should experience higher stress, as they are at a higher risk of competition and aggression.

In response to stressful events primates form a less diverse grooming network: they avoid unfamiliar conspecifics and focus a greater proportion of their grooming effort on a smaller number of strongly bonded conspecifics [9]. This suggests that the level of stress primates experience affects how they manage their social relationships. Stress increases the ambiguity of social interactions, particularly for weakly bonded conspecifics who may show incongruent responding where desirable interactions may appear undesirable, causing inhibition [3]. Thus, in stressful conditions, one may predict that there will be increasing avoidance of weakly bonded dyad partners, as primates prioritise social interactions with the strongly bonded conspecifics [9]. However, the use of intentional gestures may facilitate approaches towards weakly bonded conspecifics by enabling perception that the interaction is desirable. Further, surprising low probability events (i.e. novel signal, secondary context, higher intensity) also potentially upregulate cognitive processing, signifying their use should also co-occur with the use of intentional gestures [10].

Studies show that intentional gestures play an important role in sociality. For instance, chimpanzees preferentially direct right-handed over left-handed gestures at weakly bonded conspecifics, which elicits a response at a higher rate than if the gesture was left-handed [8]. However, it remains unclear how primates process social information received in the context of intentional and non-intentional gestures. We hypothesised that intentional gestures upgrade understanding of behaviour by allowing intentional processing as a more sophisticated form of cognition [11]. To test this hypothesis we observed social interactions in the fluid fission-fusion social system of wild chimpanzees (*Pan troglodytes schweinfurthii*) and examined if: 1) the complexity of the communication network is positively associated with the complexity of the social network; 2) a weak bond with the dominant bystander is a source of stress for the subordinate recipient (using scratching rates as a measure of stress); 3) a weak bond with a dominant bystander influences the perception of social interactions as undesirable as seen in response to threatening or aversive events, and intentional gestures change that perception; 4) intentional gestures influence the convergence in gesture repertoire.

2. Methods

(a) Study site, data collection and coding

We collected data on adult, habituated chimpanzees (six male, six female) at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda for 9 months (2006 – 2008). The observation duration was similar across subjects (mean number of hours ± standard deviation = 18.03 ± 0.67, see Supplementary Information 1). We conducted focal follows of 18-minute duration (9 scans at 2-minute intervals) and recorded the activity of the focal individual; the identity, activity, bodily orientation and distance of the most dominant individual; and the nearest adult neighbor relative to the focal subject. We also recorded the identity of all individuals present within 10 m of the focal subject. This was accompanied by continuous recording of communication using a digital video camera. We coded video recordings according with description given in Supplementary Information 1, Table 2. For each gesture, the social bond of the dominant chimpanzee towards the recipient and the recipient towards signaller was determined using the Composite Sociality Index [12] – see Supplementary Information 1 for details.

(b) Generalized linear mixed models (GLMM)

For the key inferential statistics, we used independent events from our dataset, i.e. communicative signals that occurred as a first in the sequence and that were not a scratch. To test factors influencing the intentional communication, we included three control predictors: age difference (two levels: different age category when there was more than 5 years age difference between individuals in the dyad, same age category when there was no more than 5 years age difference between individuals in the dyad), signaller sex (two levels: female, male), recipient sex (two levels: female, male). The same control variables were included when testing the effect of intentionality marker (audience checking, response waiting and elaboration combined) and other variables on the recipient's response (two levels: avoidance, approach), additionally including oestrous status of the dyad (two levels: reproductive dyads included dyads of male and oestrous females when on the day of signalling female was in oestrous showing sexual swelling and mating with the males, non-reproductive included all other dyads,). We did not control for influence of oestrous status of the dyad in all models (Table 2), because this measure was correlated with the strength of the social bond of the recipient with the signaller, but not with the reciprocated bonds (Table 1). Further, all communication in this context occurred between unrelated dyads, including in the dataset adult to adult communication only. In all GLMM, we included the following predictor variables: context of signal production (two levels: secondary context for gesture type, primary context for gesture type), modality (two levels: visual, auditory or tactile), dominant/ recipient bond (two levels: weak, strong), recipient/ signaller bond (two levels: weak, strong), recipient orientation (two levels: away, towards). In all GLMM, the data had a hierarchical structure composed of Level 1 (identity of signaller) and Level 2 (identity of recipient of the gesture). The models were fitted using a binomial error structure with logit link. The random effects included were the signaller identity and the signaller identity by recipient identity: for these effects, random intercepts were used. All data analyses were performed using SPSS 25.0 (SPSS Inc., Chicago, IL, USA).

(c) Social network analysis

Double Dekker Semi-Partialling Multiple Regression Quadratic Assignment Procedure (MRQAP) was used to determine the relationships between behavioral networks calculated as the frequency of behaviour per hour dyad partners spent within 10 meters [13]. This was to take into account any potential collinearity issues due to the significant correlations that may arise between different variables. In MRQAP regressions, we included four control variables: age similarity (two levels: different age category when there was more than 5 years age difference between individuals in the dyad, same age category when there was no more than 5 years age difference between individuals in the dyad), sex similarity (two levels: different sex male-female dyads vs same sex male-male or female-female dyads), kinship (two levels: non-kin vs kin, where kin included only mother/ adult son dyads as these were the only related dyads in the dataset), oestrous similarity (two levels: reproductively inactive denoted non-mating partners such as un-oestrous female-male or male -male dyad, reproductively active denoted potential mating partners such as oestrous female-male dyad). We tested the effect of overlap in repertoire on the rate of intentional and non-intentional gestures according to modality of the signal as visual, tactile, auditory short-range and auditory long-range. We used the Cohen's Kappa coefficient between each dyad of the whole repertoire of gestures to create a matrix of agreement in the repertoire of gestures between pairs of chimpanzees – see Supplementary Information 1 for details.

Further, we examined whether the strength of the social bond between the dominant bystander and the recipient of gesturing predicted the rate of scratching produced by recipient in the presence of the bystander. To this end, we included in the analysis only those instances of social bonds when interactions between adult subjects occurred in the presence of a bystander. In the case of one dyad, the social bond varied between years; in this case, we used the social bond in the first observation year. In order to examine the relationship between rate of scratching produced by the recipient of signaling in the presence of the signaler and intentionality of gestures, we transposed the scratching network (exchanged the rows and columns so that i becomes j, and vice versa). We used network matrices to calculate 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 was directed, indegree and outdegree were calculated separately. Outdegree refers to behaviors directed by the focal chimpanzee to conspecifics, whilst indegree refers to behaviors directed by conspecifics toward the focal chimpanzee. Second, to obtain the measure of overall network size (the total number of edges connected to a particular node), we calculated the normalized degree (n degree) of social and communication networks, dichotomizing and symmetrizing social networks. In the analyses, we used 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). The details of all social network models can be found in Supplementary Information 2. UCINET 6 for Windows was used to carry out all data transformations and social network analyses.

3. Results

Overview of social networks

In the overall social bonding network, the chimpanzees were connected to a majority of all other focal individuals—66.6% of potential connections to group members were present (range 46–100%). In terms of the behavioural measures, per hour spent within 10 meters, chimpanzees directed overall a mean (range) of 1.71 (0–32) intentional and 0.33 (0–15.8) non-intentional gestures at the dyad partner. The mean degree (range) of intentional gestures was 48.4% (18–100%) of connections to all network members and non-intentional gestures was 24.2% (0–64%) of connections.

Does communicative complexity increase with social complexity?

We used node level regressions to examine whether centrality in the social network predicted centrality in the intentional gesture network. 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 intentional communication (presence of audience checking, response waiting, elaboration combined n degree) (r^2=0.700, β= 0.718, *p* = 0.044, Fig. 1) but not the size of the network of non-intentional communication (absence of audience checking, response waiting, elaboration combined n degree) (r^2=0.736, β= 0.124, *p* = 0.391).

Examining predictors of composite sociality index indegree by 1) intentional and non-intentional communication in- and outdegree and 2) approach and avoidance in- and outdegree we found that chimpanzees who received a higher rate of social bonding behaviour received communication accompanied by intentionality markers (audience checking, response waiting, elaboration combined) at a higher rate (r^2=0.902, β= 0.900, p = 0.028) than the peripheral chimpanzees in the social network. Further, chimpanzees who received a higher rate of social bonding behaviour responded with approach at a higher rate (r^2=0.992, β= 2.032, p = 0.046) than peripheral chimpanzees in the social network.

Finally, examining predictors of approach response produced in response to signalling (approach indegree) by intentional and non-intentional communication indegree, we found that chimpanzees who received a higher rate of intentional communication approached signallers at a higher rate than the chimpanzees who received a lower rate of intentional communication (r^2=0.993, β= 0.956, p = 0.005).

Do chimpanzees experience higher stress in the presence of a weakly bonded dominant bystander?

Using MRQAP regression, we examined whether the strength of the social bond between a dominant bystander and the recipient of the signalling predicted the rate of scratching produced by the recipient. We found that recipients scratched at a higher rate in the presence of a dominant bystander who was weakly bonded to them than in the presence of all other dyads (r^2=0.078, β= 0.165, p = 0.042).

Do chimpanzees direct intentional gestures at recipients who experience higher stress?

Using MRQAP regression we examined whether rate of intentional and non-intentional gestures (considered for each marker separately) predicted the rate of scratching produced by the recipient of the signalling who was in the presence of the signaller. Signallers who received a higher rate of scratch by the recipient of gesturing directed a higher rate of gestures accompanied by audience checking (r^2=0.088, β= 0.207, *p* = 0.035) and response waiting (r^2=0.107, β= 0.263, *p* = 0.027) at the recipient of gesturing as compared to those signallers who received a lower rate of scratching by the recipient. Further, signallers who received a lower rate of scratching by the recipient of gesturing directed a higher rate of gestures unaccompanied by audience checking (r^2=0.088, β= -0.154, *p* = 0.029) and response waiting (r^2=0.107, β= -0.197, *p* = 0.014) at the recipient of the gesturing as compared to chimpanzees who received a higher rate of scratching. The production of elaboration was not associated with the scratch behaviour of the recipient.

Is avoidance more common in response to weakly bonded dominant bystander (stress source), weak social bond of recipient towards signaller, and absence of intentionality marker?

GLMM was used to examine the predictors of whether the recipient of gestural communication approached the signaller, as compared to avoidance (Fig. 2). An approach by the recipient was significantly more likely than avoidance when the gestures involved intentional rather than non-intentional communication, when the gesture was made in a primary context for the gesture type than secondary context, and when the gesture was visual, as compared to auditory or tactile. Further, the recipients were more likely to approach the signaller when the dominant bystander was strongly bonded to them and when the recipient had a strong bond with the signaller. Males were more likely to approach than females and the approaches were more commonly produced towards females rather than towards males. Reproductive dyad partners were more likely to approach than non-reproductive dyad partners (Table 1).

Is intentional signalling more common in response to weakly bonded dominant bystander (stress source), weak social bond of recipient towards signaller, and presence of approach?

We used GLMM to examine whether the social bond between the dominant bystander and recipient, the social bond between the recipient and the signaller, the type of communication event and the recipient's response predicted presence or absence of intentionality marker accompanying gesturing (Fig. 3).

(a) Audience checking

Audience checking was significantly more frequent when there was approach than avoidance. Further, audience checking was more common when the recipient was a female, and when the modality of the signal was auditory or tactile compared to visual (Table 2a).

(b) Response waiting

Signals accompanied by response waiting were more likely to be associated with approach than with avoidance. Response waiting was more likely to occur when the gesture type was produced in a secondary context as opposed to primary context for a given gesture type. Further, response waiting was more likely to occur when gestures were auditory or tactile when compared with visual. Social bonding influenced use of response waiting: chimpanzees used response waiting when the social bond of the dominant bystander towards the recipient was weak as compared to strong. Further, the signallers also used response waiting, when the social bond of the recipient towards them was weak as compared to strong. In addition, there was an influence of recipient's sex and age on response waiting. Partners of a different age class and females were more likely to be targeted with response waiting than the same age partners or the males. When the recipient's attention was oriented away from the signaller, signallers were more likely to use response waiting than if the signaller was oriented towards them (Table 2b).

(c) Elaboration

Elaboration was more likely to be produced when signallers use gesture in a secondary-when compared with primary context. Chimpanzees were more likely to direct elaboration at the recipients who were strongly bonded to them, and when gesturing occurred in the presence of the dominant bystander who was weakly bonded to the recipient. Chimpanzees elaborated towards partners who were females and who were of a different age class to themselves. Further, the recipients were more often oriented away from the signaller than towards during elaboration. Elaboration was more commonly produced by the males than the females (Table 2c).

Does intentionality in gestures increase overlap in the repertoire of gestures?

Finally, we used MRQAP regression to examine whether overlap in visual, tactile and auditory signals (kappa value) between signaller and the recipient predicted the rate at which signallers directed intentional and non-intentional gesturing at the recipient. We found that signallers who displayed a higher overlap in repertoire of visual gestures with the recipient directed a higher rate of signals accompanied by an intentionality marker at the dyad partner (r^2=0.215, β= 0.436, p = 0.002) than the chimpanzees who displayed a lower overlap in the repertoire of visual gestures.

4. Discussion

The hallmark of increasingly large groups and complex sociality of primates is managing the weak social bonds between group members because it requires an understanding of intentionality. However, more complex sociality imposes higher stress through higher levels of competition for resources by dominant bystanders. Understanding intentionality is impaired during stress, causing understanding to be downgraded to a simple understanding of behaviour and a reduction in the size of a social network. We suggest that the use of intentional gestures facilitates complex sociality during stress, by enabling understanding of intentionality [2].

We used social network analysis to show that the complexity of the social network (total number of social connections produced and received) was positively associated with the size of the intentional gesture network (total number of connections produced and received through gestures accompanied by audience checking, response waiting or elaboration) but not non-intentional gesture network (total number of connections produced and received through gestures not accompanied by these markers) directed by chimpanzees in the social network. Examining mechanisms underlying this association, we explored the contexts in which chimpanzees experienced higher stress. We found that chimpanzees experienced higher stress in the presence of a weakly bonded dominant bystander and directed intentional gestures at conspecifics who were stressed. To identify whether intentional gestures played a role in reducing the influence of stress on cognitive processing, we used generalised linear models to examine audience effects on intentionality in gesturing. We found that use of intentional gestures was predicted by presence of stress source, weak bond of recipient towards signaller and presence of approach. Avoidance in response to signalling was common by weakly bonded recipients, when the recipients were stressed and when signalling was non-intentional. Finally, overlap in the repertoire of gestures was positively associated with the use of a higher rate of intentional but not non-intentional gestures. These results suggest that intentional gestures play a key role in sociality by allowing understanding of intentions during stress. These findings go beyond findings reported in previous research on wild apes where the function of intentional gestures was to transfer encoded meaning from the signaller to the recipient [14, 15].

One interpretation of our findings could be that chimpanzees responded to understanding behaviour rather than intentions. Understanding of behaviour demands that individuals adapt to the challenges of sociality by having to experience social interactions directly and this would limit the capacity of the recipient to respond flexibly in novel social conditions such as interacting with weakly bonded conspecifics. If chimpanzees only understood behaviour, then there should not be an association between the use of intentional gestures and the complexity of the social network. In contrast, we found that the number of social bonds in the network was positively associated with use of intentional but not non-intentional gestures, suggesting an understanding of intentionality.

The transition from small social groups, where primates can maintain strong social bonds primarily with related conspecifics, to large groups, where primates form social bonds with a large number of unrelated conspecifics, is believed to have been accompanied by an understanding of intentionality [4]. Such ability enables primates to integrate in real time perception and accumulation of information about social relationships to form representations of other's future behaviour. This in turn allows them to form social bonds in the absence of prior social interactions, whereby representations of the future goal state give rise to a positive emotional state and approach motivation [5]. In this study, chimpanzees who received a higher rate of intentional gestures approached a wider range of social partners at a higher rate. Our findings suggest that intentional gestures mediate the transition from less complex to more complex sociality of primates by enabling understanding of intentionality.

Given these results it is important to explore the mechanisms underpinning the relationship between size of the intentional gesture and sociality networks. Social complexity imposes stress due to a higher cognitive load of managing multiple social relationships, promoting processing based on understanding of behaviour and this is particularly true for central individuals in the network who manage a larger number of differentiated social bonds [16]. In our study, we show that chimpanzees who had a larger number of social bonds, received intentional gestures at a higher rate to facilitate understanding of intentionality.

Further, social complexity is believed to be associated with greater stress due to greater scarcity of resources in larger groups, and greater monopolisation potential by dominant group members. One important finding of our study was that recipients of signalling were more stressed when they interacted in the presence of a dominant bystander who was weakly bonded to them. The effects of stress on cognitive processing are well understood. Stress impairs information processing as shown by reduced attention to positive information about the social target [17], increased focus on familiar conspecifics [9], avoidance of unfamiliar conspecifics [18], increased perception that social interaction is undesirable [19]and increased negative emotions [20]. In line with these findings, our study shows that chimpanzees downgraded their cognition to an understanding of behaviour during stress experienced by the recipient of gesturing in the presence of a weakly bonded dominant bystander. When chimpanzees were stressed, the gesturing was non-intentional, and the bond of the recipient towards signaller was weak the recipients avoided the signallers, suggesting they perceived the social interactions as undesirable. If responses to intentional gestures were likewise readouts of behavioural state, then chimpanzees should respond to intentional gestures with avoidance and during stress. On the contrary, we observed that chimpanzees prioritised use of intentional gestures when recipients were stressed, the social bond of the recipient towards signaller was weak, and the chimpanzees approached conspecifics at a higher rate, suggesting the recipients perceived the social interaction as less threatening or positive. This evidence therefore strongly shows that intentional gestures disinhibited understanding of intentions, and this was particularly important when recipients were stressed.

It could be argued that elaboration was underpinned by an understanding of behaviour because chimpanzees used elaboration with strongly bonded dyad partners and during stress. Whereas both audience checking and response waiting were produced at a higher rate towards conspecifics who displayed a higher rate of scratching in the presence of a signaller, this was not the case for elaboration. The fact that chimpanzees used elaboration in secondary contexts, when the recipient's attention was directed away from the signaller and the response to the first signal in the sequence was not by approach, suggests that signallers influenced understanding of intentions rather than behaviour.

It is important to explore the breadth of strategies that chimpanzees use to facilitate understanding of intentionality. We showed that use of intentional gestures was correlated with the use of signals in their secondary contexts and higher intensity signals, suggesting that intentional gestures mediated the influence of these factors on cognitive processing of social interactions by the recipients. More importantly, we show that the intentional but not non-intentional gestures influence overlap in repertoire of visual gesturing. Previous studies have suggested that the repertoire is genetically fixed, and the overlap in gestures occurs in response to repertoire pruning as chimpanzees learn which signals are effective [21]. If the gesture repertoire was genetically fixed, then the overlap in the repertoire should occur among closely related dyads regardless of the use of intentional gestures, suggesting that chimpanzees only understand behaviour. In contrast, we infer that the repertoire of gestures was flexibly acquired, because the use of intentional gestures influenced overlap in repertoire regardless of relatedness. We propose that chimpanzees create novel gestures (e.g. structural modifications of manual signals) to enable an understanding of intentionality and the recognition of the 'goal' or 'why' of the social interaction that arises through novel gestures results in gesture learning, whereby chimpanzees recognise contingencies between signals and the outcomes in the context of tracking and responding to the signaller's goal.

Previous research used response waiting, audience checking and elaboration as a label that describes a behaviour, which functions to intentionally transfer meaning embedded in the signal [14]. Here we use these labels to imply a different cognitive process, namely that these behaviours function to release overactive indirect pathway from inhibition to allow understanding of intentionality as seen by approach of the recipient, when it is downgraded to understanding of behaviour. Visual signals are particularly interesting because they differ from high intensity signals such as tactile or auditory in the cognitive skills that need to be employed in processing of social information due to the lower intensity of emotional arousal associated with these signals, which makes them more adaptive in frequent one on one interactions between strongly bonded partners [22]. Use of an intentionality marker such as response waiting in conjunction with the visual gesture, may augment capacity of the recipient to process social information. This causes co-activation of neural networks and communicative convergence in both repertoire and context, whereby understanding of behaviour becomes operational over time through being exposed to the relevant positive associations that occur during understanding of intentionality. This supports efficient social interactions, whereby the recipient experiences simultaneous activation of positive emotional state through synchronised use of overlapping visual communication as well as activation of mental state through intentional signalling. For instance, we showed that approach is most likely in response to visual signals and also when signals are made in primary context and in conjunction with intentionality marker.

Our study reveals that chimpanzee use of intentional gestures facilitates social bonding by allowing two animals to approach each other and engage in a social bonding activity such as grooming that resembles strategies that humans employ in language use and comprehension. In language processing, at the initial stage of the interaction, the speech automatically activates representations of all possible interaction outcomes in the memory of the recipient until the appropriate outcome is strategically selected through controlled processing [23]. Our results seem to suggest that, like language, chimpanzee intentional gestures activate representations of desirable outcomes in the recipients. Whilst chimpanzee intentional gestures may include precursors to language, the origins of language evolution are still hotly debated [24]. Based on results of our study, we suggest that language evolution may have occurred to provide a more effective social bonding mechanism than gestures, to facilitate social bonding and group cohesion in increasingly large groups of hominins [25].

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Table 1. Effects of intentionality marker (audience checking, response waiting and elaboration combined), social bond, bodily orientation of the recipient, modality and context of signal production including control variables (signaller and recipient sex, age difference, oestrous difference) on recipient's response (avoidance or approach). All communication in this context occurred between unrelated dyads (non-kin).

Model term	**Coefficient**	**Standard error**	**Significance**
Oestrous difference [non-reproductive]	**-5.393**	**1.088**	**<0.001**
Age [different class]	**-3.864**	**1.933**	**0.048**
Signaller sex [female]	**14.328**	**1.667**	**<0.001**
Recipient sex [female]	**-4.340**	**1.111**	**<0.001**
Context [secondary]	**-3.301**	**1.033**	**0.002**
Modality [visual]	**5.933**	**1.130**	**<0.001**
Dominant/ recipient bond [weak]	**-5.488**	**1.063**	**<0.001**
Signaller/recipient reciprocated bond [absent]	**-6.103**	**1.734**	**0.001**
Recipient orientation [away]	1.250	0.669	0.064
Intentionality marker [absent]	**-5.949**	**1.058**	**<0.001**

Table 2. Influence of recipient's response, social bond (dominant with the recipient, recipient with signaller), context, modality, bodily orientation of the recipient and control predictors (age difference, signaller sex, recipient sex) on proportion of communication associated with a) audience checking, b) response waiting and c) elaboration. All communication in this context occurred between unrelated signaller and recipient (non-kin).

a) Audience checking

Model term	**Coefficient**	**Standard error**	**Significance**
Age [different class]	2.093	2.178	0.339
Signaller sex [female]	1.157	0.953	0.228
Recipient sex [female]	**4.615**	**2.228**	**0.041**
Context [secondary]	0.017	1.754	0.992
Modality [visual]	**-4.824**	**2.314**	**0.040**
Dominant/ recipient bond [weak]	2.279	2.149	0.291
Recipient/ signaller bond [weak]	0.172	0.681	0.801
Recipient orientation [away]	3.430	2.168	0.117
Recipient's response [avoidance]	**-2.563**	**0.871**	**0.004**

b) Response waiting

Model term	**Coefficient**	**Standard error**	**Significance**
Age [different class]	**13.848**	**2.132**	**<0.001**
Signaller sex [female]	-4.285	3.450	0.217
Recipient sex [female]	**5.926**	**1.945**	**0.003**
Context [secondary]	**4.248**	**1.090**	**<0.001**
Modality [visual]	**-10.929**	**2.223**	**<0.001**

Dominant/ recipient bond [weak]	**4.613**	**1.090**	**<0.001**
Recipient/ signaller bond [weak]	**3.184**	**1.524**	**0.039**
Recipient orientation [away]	**11.394**	**2.543**	**<0.001**
Recipient's response [avoidance]	**-9.293**	**1.826**	**<0.001**

c) Elaboration

Model term	**Coefficient**	**Standard error**	**Significance**
Age [different class]	**57.290**	**6.136**	**<0.001**
Signaller sex [female]	**-6.647**	**2.697**	**0.015**
Recipient sex [female]	**26.572**	**1.296**	**<0.001**
Context [secondary]	**28.309**	**2.769**	**<0.001**
Modality [visual]	-0.960	2.218	0.666
Dominant/ recipient bond [weak]	**26.478**	**3.833**	**<0.001**
Recipient/ signaller bond [weak]	**-25.606**	**1.687**	**<0.001**
Recipient orientation [away]	**14.977**	**0.529**	**<0.001**
Recipient's response [avoidance]	-0.061	0.400	0.879

Figure 1. Relationship between size of the social bond network (composite sociality index n degree) and the communicative complexity network (intentional communication n degree)

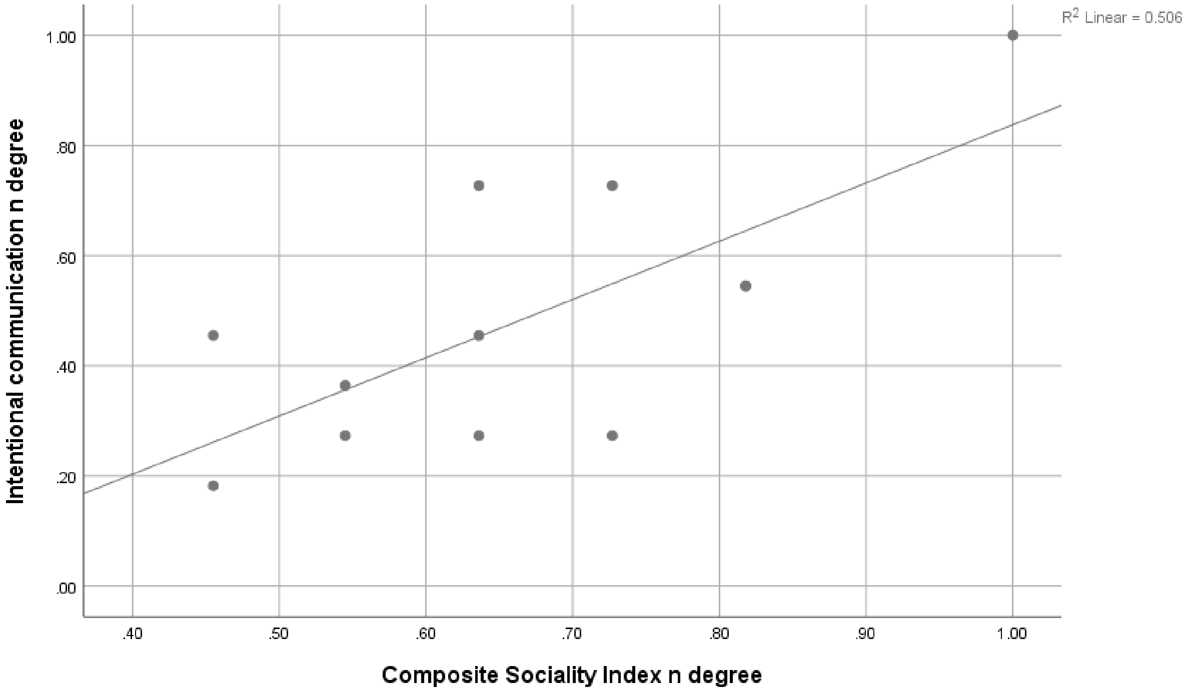

Figure 2. Relationship between use of intentional communication in wild chimpanzees (audience checking, response waiting, elaboration) and response by approach or avoidance

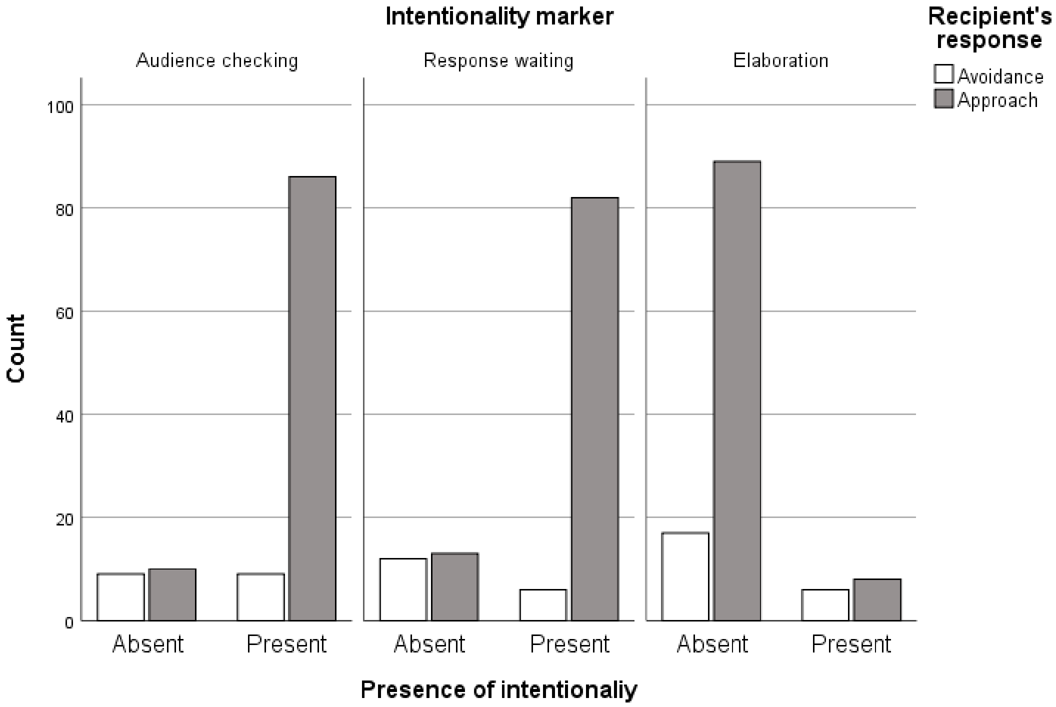

Figure 3. Influence of social bond between dominant bystander and the recipient of signalling on use of intentional communication: audience checking, response waiting and elaboration