Roberts, SGB and Roberts, AI

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Title page

Visual attention, indicative gestures and calls accompanying gestural communication are associated with sociality in wild chimpanzees

Authors: Sam George Bradley Roberts[1*]† & Anna Ilona Roberts[2]†

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Affiliations:

[1]School of Natural Sciences and Psychology, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF

[2]Department of Psychology, University of Chester, Chester; Parkgate Road, Chester CH1 4BJ, UK

†Equally contributing authors

S.G.Roberts1@ljmu.ac.uk, anna.roberts@chester.ac.uk

*Corresponding author: Sam Roberts. email: S.G.Roberts1@ljmu.ac.uk or anna.roberts@chester.ac.uk

Abstract

The challenges of life in complex social groups may select for complex communication in order to regulate interactions among conspecifics. Whereas the association between social living and vocalizations has been explored in nonhuman primates, great apes also have a rich repertoire of gestures and how the complexity of gestural communication relates to sociality is still unclear. We used social network analysis to examine the relationship between the duration of time pairs of chimpanzees spent in close proximity (within 10 m) and the rates of gestural communication accompanied by visual orientation of the signaller, one-to-one calls, indicative gestures (collectively self-relevance cues) and synchronized pant-hoot calls. Pairs of chimpanzees that spent a longer duration of time in close proximity had a higher rate of visual gestures accompanied by these behaviours. Further, individual chimpanzees that had a greater number of close proximity bonds had a larger social network maintained through gestures accompanied by synchronized pant-hoot calls. In contrast, the network size maintained through gestures unaccompanied by these behaviours was not positively associated with either close proximity bonds in pairs of chimpanzees, or individual differences in sociality. These results suggest that self-relevance cues and synchronized pant-hoot calls accompanying gestures may increase the efficiency of gestural communication in social bonding and that multimodal communication may have played a key role in language evolution.

Key words: chimpanzees, gestural communication, self-relevance cue, visual attention, social network, synchronized call

Significance statement

Like humans, nonhuman primates use gestures to communicate with others, but how combinations of gestures with visual orientation of the signaller, indicative gestures, one-to-one calls and synchronized calls are related to social relationships is poorly understood. We demonstrate that use of these behaviours accompanying visual gestures in pairs of wild chimpanzees was related to the amount of time pairs of chimpanzees spent in close proximity. Central individuals in the community had a larger network of relationships maintained through gestures accompanied by synchronized pant-hoot calls. Thus, these behaviours may increase the efficiency of gestural communication in social bonding. More broadly, these results illustrate the importance of different types of communication in managing different types of social relationships in nonhuman primates and other species.

Introduction

The association between sociality and communication has long been of interest both in understanding complex sociality in nonhuman animals and also in developing theories of how language evolved in humans (Arbib, Liebal, & Pika, 2008; M. Corballis, 2009; R. Dunbar, 2012; Freeberg, Dunbar, & Ord, 2012; Pollick & de Waal, 2007). Individuals maintaining complex social relationships may require more complex communication to regulate interactions with group members (Freeberg et al., 2012). Complex social relationships have been defined as '*those in which individuals frequently interact in many different contexts, and often repeatedly interact over time'* whilst complex communicative systems have been defined as '*those that contain a large number of structurally and functionally distinct elements (e.g. large display repertoire sizes) or possess a high amount of bits of information'* (Freeberg et al., 2012; K. Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009; Silk, 2007; Silk et al., 2010b). Although in primates individuals can maintain social relationships and communicate with partners who do not reciprocate their investment into the social relationship, reciprocated social relationships are a key feature of complex sociality (Foerster et al., 2015; Mitani, 2009). Language does not leave a direct fossil trace, and therefore studies of communication and sociality in nonhuman primates can provide insights into factors that have shaped the evolution of language in humans (Byrne et al., 2017; W. T. Fitch, 2010; Pollick & de Waal, 2007; Sam G. B. Roberts & Anna I. Roberts, 2016; Robert M Seyfarth & Cheney, 2014). In this study we explore the association between the complexity of sociality, defined as the presence or absence of reciprocated close proximity ties, and gestural communication of wild chimpanzees to provide insight into the origins of language.

Many theories of language evolution propose that nonhuman primate vocalisations provided the starting point for the development of more complex vocal communication seen in humans (Crockford, Wittig, Mundry, & Zuberbuehler, 2012; Enard et al., 2002; Engh, Hoffmeier, Cheney, & Seyfarth, 2006; W. T. Fitch, 2010; W. T. Fitch, de Boer, Mathur, & Ghazanfar, 2016; Anne Marijke Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013; Robert M Seyfarth & Cheney, 2014; R. M. Seyfarth et al., 2010). Studies of nonhuman primate vocalisations have focused on examining the association between specific vocalisations such as alarm calls and external entities (A. M. Schel & Zuberbuhler, 2009; R. Seyfarth, Cheney, & Marler, 1980) and exploring the overlap between the properties of nonhuman primate vocalisations and human language (T. Fitch, 2005; Robert M Seyfarth & Cheney, 2014). More recent studies have examined whether there is a relationship between vocalisations and sociality (Arlet, Jubin, Masataka, & Lemasson, 2015; McComb & Semple, 2005). Grooming is one key behaviour nonhuman primates use to maintain relationships, but vocalisations are more efficient in reaching more recipients at a greater distance, and thus some researchers have proposed that vocalisations can act as a form of ‘grooming at a distance’, helping nonhuman primates meet the challenges of living in a complex social group (Arlet et al., 2015; Fedurek, Machanda, Schel, & Slocombe, 2013). For example, there is an association between pant-hoot chorusing and social bonds in wild chimpanzees (Fedurek et al., 2013).

However, nonhuman primates – especially the great apes - also have a rich repertoire of gestures which they use in a flexible and intentional way to communicate with conspecifics (Byrne et al., 2017; K. Hobaiter & Byrne, 2011; Roberts, Vick, & Buchanan-Smith, 2012; Tomasello, Call, Nagell, Olguin, & Carpenter, 1984). Whilst recent findings have shown that vocalisations in nonhuman primates are produced more flexibly than initially thought (Crockford et al., 2012; Anne Marijke Schel et al., 2013), nonhuman primates show greater flexibility in their use of gestural communication, in that the association between the gesture type and behavioural context is much weaker (Byrne et al., 2017; Catherine Hobaiter & Byrne, 2014; Roberts, Roberts, & Vick, 2014). Nonhuman primates use gestures intentionally - they communicate with the recipient and adjust their communication in a flexible and dynamic way

(Byrne et al., 2017; D. A. Leavens, Russell, & Hopkins, 2005; Roberts, Roberts, et al., 2014). Because of this greater flexibility of gestural communication as compared to vocal communication, many researchers propose that gestural communication may have played a key role in language evolution (Arbib et al., 2008; Call & Tomasello, 1994; M. Corballis, 2009; Gillespie-Lynch, Greenfield, Lyn, & Savage-Rumbaugh, 2014; Pollick & de Waal, 2007; Tomasello et al., 1984). For instance, flexible gestural communication has only been recorded in great apes who are our closest living relatives, whereas vocalisations are present in many different taxa (Pollick & de Waal, 2007). The flexible use of gestures may have facilitated language evolution since the gesture areas but not vocal areas correspond to language areas in the human brain and primates may flexibly modify their behaviour to increase the efficiency of social bonding (M. C. Corballis, 2003; Freeberg et al., 2012; McComb & Semple, 2005). Thus, if communication systems play a key role in helping animals navigate the complexities of social life, there should be an association between gestural communication and sociality (Pollick & de Waal, 2007; Sam G. B. Roberts & Anna I. Roberts, 2016).

As one of the closest living nonhuman primate species to humans, chimpanzees are an ideal species to examine the association between sociality and gestural communication (Byrne et al., 2017; T. Fitch, 2005; McGrew, 2010). Chimpanzees have a fission-fusion social system where the broader community fissions into smaller sub-groups on a daily basis (Aureli et al., 2008; Eckhardt, Polansky, & Boesch, 2015; Goodall, 1986). Thus chimpanzees frequently interact with a broad range of social partners across a number of different behavioural contexts and the patterns of interaction between pairs of chimpanzees changes with the fissioning of the broader community into sub-groups. Chimpanzees use a complex system of vocalisations and some studies have demonstrated a link between these vocalisations and different aspects of sociality (Fedurek et al., 2013; Fedurek & Slocombe, 2013; Mitani & Gros-Louis, 1998). Chimpanzees also have a complex system of gestural communication and thus far research has been focused on establishing the repertoire, examining flexibility in use and assessing evidence of intentionality (Byrne et al., 2017; Catherine Hobaiter & Byrne, 2014; C. Hobaiter, Byrne, & Zuberbühler, 2017; D. A. Leavens & Hopkins, 1998; Pika, Liebal, Call, & Tomasello, 2005; Roberts, Vick, & Buchanan-Smith, 2013; Roberts, Vick, Roberts, Buchanan-Smith, & Zuberbühler, 2012; Roberts, Vick, Roberts, & Menzel, 2014).

More recently, using the same dataset as used in the present study, Roberts and Roberts (A. I. Roberts & S. G. B. Roberts, 2016; Roberts & Roberts, 2017; Sam G. B. Roberts & Anna I. Roberts, 2016) explored how different aspects of communication in wild chimpanzees are related to sociality. Overall, rates of both gestures and vocalisations were positively related to the duration of time pairs of wild chimpanzees spent in close proximity (Sam G. B. Roberts & Anna I. Roberts, 2016). Further, there were important differences between the different modalities of gestures, such as visual (e.g. arm raise), tactile (e.g. embrace), auditory short-range (can be heard within 10m e.g. tap object) and auditory long-range (can be heard more than 10m away e.g. drum) (A. I. Roberts & S. G. B. Roberts, 2016). Auditory gestures are classified as such because the gesture itself makes a sound. These auditory gestures may or may not be accompanied by a vocalization. Higher rates of visual gestures (as compared to tactile or auditory gestures) were associated with time spent in close proximity (A. I. Roberts & S. G. B. Roberts, 2016). Overlap in the gestural repertoire was also related to duration of time pairs of chimpanzees spent in social behavior (Roberts & Roberts, 2017). However these studies, or any other studies of nonhuman primate gestural communication, have not examined the association between sociality and one key aspect of gestural communication - the extent to which gestures are accompanied by cues that direct recipient’s attention and facilitate responding to signaller’s gestures (‘self-relevance cues’). In this framework, the integration of self-relevance cues and gestural communication increases the degree of self-relevance of the perceived gestural communication (Sander, Grafman, & Zalla, 2003). For instance, when there are several individuals in close proximity, accompanying the gesture with a self-relevance cue may enable the recipient to perceive that the gesture is directed at them and respond to it more effectively than if a self-relevance cue accompanying the gesture is absent. Thus one aim of this study is to examine the association between the rate of gestures accompanied by these self-relevance cues and the duration of time pairs of chimpanzees spend in close proximity.

A key challenge for group living animals is detecting whether communication is directed at them, or at another conspecific and to respond to communication effectively (Engh et al., 2006; Grèzes & Dezecache, 2014). This is especially true for chimpanzees detecting gestural communication in a dense forest habitat. Chimpanzees often accompany their gestures with a set of cues that may help receivers better coordinate behaviour with the signaller (K. Hobaiter & Byrne, 2011; Roberts, Roberts, et al., 2014). In line with previous literature in this area, we term these set of cues 'self-relevance cues', as they are all cues which enhance the relevance of the signaller's communication to the recipient – the target of the communication (Grèzes, Adenis, Pouga, & Armony, 2013; Grèzes, Philip, et al., 2013; N'diaye, Sander, & Vuilleumier, 2009; Sander et al., 2003; Soussignan et al., 2013). For example, previous research on human communication has demonstrated the processing of emotional expression is influenced by whether or not the signaller's gaze is directed at the recipient. Thus gaze direction acts as a self-relevance cue, indicating that the emotional expression is directed at the recipient (N'diaye et al., 2009; Soussignan et al., 2013). In this study we examine how the rate of gestural communication accompanied by three different self-relevance cues is associated with sociality. *Visual orientation of the signaller* has long been used as an indicator of the target of communication, both in research on nonhuman primate gestural communication and in human communication (D. A. Leavens, Hostetter, Wesley, & Hopkins, 2004; D. A. Leavens et al., 2005; N'diaye et al., 2009; Roberts, Roberts, et al., 2014). Gestures in which the signaller is oriented towards the recipient act as a cue to the recipient that the gesture is directed at them.

Further, gestures accompanied by vocalisations draw the intended recipient's attention towards the signaller – so-called 'attention getters' (Gillespie-Lynch et al., 2014; Hopkins, Taglialatela, & Leavens, 2007; D. A. Leavens et al., 2004; Taglialatela et al., 2015). These vocalisations are given by the signaller alone at another single recipient (*one-to-one call*) (Sam G. B. Roberts & Anna I. Roberts, 2016). Finally, *indicative gestures* refer to movements of the hand or arm towards the recipient without physical touch (e.g. arm beckon) (Catherine Hobaiter & Byrne, 2014; Roberts, Vick, et al., 2014). Again, there is evidence in both humans (Grèzes & Dezecache, 2014) and nonhuman primates (Catherine Hobaiter & Byrne, 2014; Roberts, Roberts, et al., 2014) that indicative gestures act as a cue to the recipient that the gesture is directed at them and facilitate processing of the gesture. Because of their manual nature, all indicative gestures are visual gestures. In addition to these self-relevance cues, chimpanzees can also accompany their gestures with synchronized pant-hoot calls that can function to socially bond and coordinate behaviour with several individuals simultaneously (*synchronized call*). These calls are produced jointly by several individuals at the same time. The simultaneous and rhythmically matched production of the sound and the gesture can act as an alternative mechanism to the gestures accompanied by self-relevance cues as it may not require mutual attention and one-to-one coordination to regulate social bonding. In this paper, we refer collectively to gestures with all types of cues (Mutual attention, One-to-one call, Indicative gesture, Synchronized call) as gesture with a cue. All of the gestures that did not include a use of self-relevance or synchronized cue were classified as gesture *no cue*.

One important feature of gestural communication is the conspicuousness of the signal. Primate gestures vary from loud vigorous sounds made by slapping or drumming their hands against objects, tactile behaviours such as strokes on another individual's body part, to more subtle visual behaviours such as waving a hand from a distance (Liebal, Call, & Tomasello, 2004). For recipients, detecting and responding appropriately to more subtle visual gestures could be a more difficult task than detecting and responding to more vigorous auditory gestures. Use of the cues, however, can facilitate maintenance of social relationships through more subtle gestures. In humans, simultaneous presentation of the gesture and multimodal cues (e.g. vocalizations) improves the detection and recognition of more subtle gestures (Van den Stock, Grèzes, & de Gelder, 2008). It is therefore reasonable to assume that the cues will be more important in managing social relationships through visual gestures than managing social relationships through tactile or auditory gestures. However, the relationship between the use of cues across modalities of gestures and duration of social behavior has not been examined.

In addition, the effectiveness of gestural communication in maintaining social relationships may vary as a function of the type of social cues. For instance, in humans the efficiency of social bonding increased when partners were positioned in sight of each other (i.e. Skype conversation) rather than out of sight (i.e. telephone conversation) (Vlahovic, Roberts, & Dunbar, 2012). In chimpanzees, the use of pant-hoot call accompanying visual gestures was associated with longer duration of time spent in social bonding behavior than the use of gestures for mutual grooming and travel (Sam George Bradley Roberts & Anna Ilona Roberts, 2016). However, it is currently unclear whether there is a relationship between the type of the cue and the efficiency of gestures in managing social relationships despite its importance in furthering our understanding of how communicative complexity is linked to social complexity in both primates and humans.

In this study we examined the effect of self-relevance cues whilst the recipient was visually attending to the signaller to take into account influence of visual attention on duration of time spent in proximity. Thus for *visual orientation of the signaller, one-to-one calls and indicative gestures*, there had to be mutual visual contact between the signaller and the recipient for the gesture to be classified as being accompanied by a self-relevance cue. For *synchronized call,* we included all the individuals within 10m as involved in the call, as pant-hoots can influence social bonding with many individuals simultaneously when compared with one-to-one calls such as pant-grunts (Fedurek et al., 2013).

In line with the definition of communicative complexity given above, all of these gestures accompanied by cues can be considered as more complex than gestures unaccompanied by these cues (Freeberg et al., 2012). Gestures accompanied by self-relevance cues contain both the gesture itself, and also the self-relevance cue making it clearer to the intended recipient the gesture is directed at them and facilitating responding to the gestures. In contrast, gestures accompanied by synchronized cues enable individuals to bond on a larger scale without the need for dyadic coordination in behaviour. Thus if there is a link between social complexity and communicative complexity, more complex communication in the form of gestures accompanied by cues may be expected to be associated with pairs of chimpanzees spending a longer duration of time in proximity, per hour spent in the same party. As the different cues have different acoustic and physical properties, the different cues may be differentially associated with sociality (A. I. Roberts & S. G. B. Roberts, 2016). However, the underlying similarity between all these cues is that they enhance the efficiency of the communication in social bonding (Grèzes, Adenis, et al., 2013; Grèzes, Philip, et al., 2013; Soussignan et al., 2013). We therefore examine both the overall use of gestures without the cues and then how gestures with the cue improve association of the gestures with sociality. As previous research has shown patterns of sociality are differentially related to the different modalities of gestural communication (A. I. Roberts & S. G. B. Roberts, 2016), we examined how different cues accompanied by different modalities of communication were associated with proximity. For consistency with previous research using the same database and population of chimpanzees as the current study, we categorized gestural communication into visual, tactile, auditory short-range and auditory long range modalities (A. I. Roberts & S. G. B. Roberts, 2016). Full definitions of the cues, gesture modalities and gestures included in each category are provided in Table 1.

Based on the above definitions of the cues, we used social network analyses to explore the association between rates of cues accompanying gestural communication and sociality in wild East African chimpanzees (*Pan troglodytes schweinfurthii*). Network analysis allows for examination of the association between communication and sociality both at the level of the social network as a whole, and of individual variation in sociality and communication (Lehmann & Dunbar, 2009; McCowan, Anderson, Heagarty, & Cameron, 2008; Sueur, Jacobs, Amblard, Petit, & King, 2011; Wey, Blumstein, Shen, & Jordan, 2008). In the first set of analyses, we explored how the rate of gestures accompanied by cues was associated with the duration of time pairs of chimpanzees in the same party spent in close proximity. In this analysis, using a social network approach allows us to have the dyad as the unit of analysis (Sueur et al., 2011), rather than analyzing each gestural event separately using a generalized linear mixed modelling approach (Prieur, Barbu, Blois-Heulin, & Pika, 2017). Thus we examined how the duration of proximity between pairs of chimpanzees was associated with characteristics of the communication between those pairs of chimpanzees. As previous findings have shown that the rate of visual gestures is most strongly associated with the duration of proximity (A. I. Roberts & S. G. B. Roberts, 2016), we predicted that pairs of chimpanzees that spend a longer duration of time in close proximity will have a higher rate of visual gestures accompanied by the cues.

In the second set of analyses, we examined how individual differences between rates at which the 12 focal chimpanzees accompanied their gestures with the cues were associated with individual differences in centrality in the social network (i.e. the number of proximity bonds the focal chimpanzees had with conspecifics). As previous findings have shown that synchronized communication plays a role in maintaining social bonds across larger numbers of individuals both in humans (Tarr, Launay, Cohen, & Dunbar, 2015; Tarr, Launay, & Dunbar, 2016; Weinstein, Launay, Pearce, Dunbar, & Stewart, 2016a, 2016b) and in nonhuman primates (Fedurek et al., 2013; Mitani & Gros-Louis, 1998), we predicted that individual chimpanzees with a higher rate of gestures accompanied by synchronized vocalizations will have a higher degree of centrality. In addition to specific types of gestural communication, demographic factors also play an important role in nonhuman primate sociality, with rates of proximity higher between kin, between similar age chimpanzees, between chimpanzees of the same sex and between reproductively active individuals (K. Langergraber et al., 2009; K. E. Langergraber, Mitani, & Vigilant, 2007; Mitani, 2009). We therefore controlled for these demographic factors in all our models.

Methods

Study site and subjects

The Sonso community of East African chimpanzees (*Pan troglodytes schweinfurthii*) at the Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (www.budongo.org) was studied in September 2006, between April and July 2007 and March and June 2008. Instances of communication and social relationships of the 12 focal subjects (6 adult males and 6 adult females) who did not have any limb injuries and were well-habituated for detailed data collection. Full details of the study site, subjects and data collection protocol have been described previously, so only essential information is provided here (Roberts & Roberts, 2015; Roberts, Roberts, et al., 2014; A.I. Roberts et al., 2012). The study was approved by the University of Stirling Ethics committee. The data collection and methods for this study were approved by the Budongo Conservation Field Station research committee (Prof. Klaus Zuberbuehler). The research was non-invasive and all methods were performed in accordance with the Association for the Study of Animal Behaviour guidelines.

Data collection protocol

Quantitative focal animal follows were conducted to examine the patterns of social relationships and communication for each of the focal individuals. The focal animals were chosen systematically and the behaviour of the focal subjects was recorded during a standardised observation period. We aimed to sample each individual equally at different times of the day and study period, and at least once every week. Consecutive samples of the same focal subject were taken at least 20 minutes apart in order to avoid dependency in the data set. The behaviour of the focal and non-focal individuals was recorded for the individuals who were present in the same party. Individuals belonged to the same party if they were a part of the group of individuals who were found within a spread of about 35 m. Behavioural data collected in this study came from the following sources: First, 18 minute focal follows, which consisted of 9 scans at 2 minute intervals of focal association patterns. These recorded the identity of individuals present within 10 m and more than 10 m from the focal individual, the bodily orientation between the focal subject and the nearest neighbour, the bodily orientation between the focal subject and the dominant individual in the party, the proximity between the focal subject and the nearest neighbour, and the proximity between the focal subject and the dominant individual in the party). Individuals within 10m of the focal were classified as being in close proximity. Secondly, the instantaneous sampling of associations was accompanied by data collection of gestures. A digital video camera recorder was used to record the gestures continuously, with the camera centred on the focal animal but also taking a wider view to include interactants within the visible presence of the focal individual. Communication was recorded in real time and for each gesture instance, the identity of the signaller and the recipient, the description of the response and the functional context of signal production was spoken onto the camera. The proximity and gestural data were collected at the same time by two different observers. The recording of association patterns was conducted by the experienced field assistant, who did not know the aims of the study. The field assistant is subject to inter-observer reliability test annually, with results consistently above 0.85 Spearman’s rank correlation coefficient, r_s. The video recording of the gestures was carried out by AR.

Video analyses of gestural communication

Instances of social behaviour which appeared communicative were first viewed on a television and coded. A full description of the coding scheme used for this dataset and a detailed discussion of intentionality in gestural communication can be found in Roberts et al. (Roberts, Roberts, et al., 2014; A. I. Roberts et al., 2012). Briefly, from full initial catalogue of social behaviour, specific instances of social behaviour were recorded as an act of gestural communication if it was an expressive movement of the limbs or head and body posture that met the following three criteria. First, the behaviour was mechanically ineffective – a gesture always elicited a change in the recipient’s behaviour by non-mechanical means, rather than by for example physically manipulating a limb of the recipient into a desired position. Second, gestures were communicative – at the level of the gesture type, communication was consistently associated with a change in the behaviour of the recipient after the signal. Thus gestures always occurred in social circumstances – a chimpanzee turning its back simply to change position would not be considered a gesture, whereas a chimpanzee turning its back to initiate being groomed would be considered a gesture. Third, instances of behaviour had to be intentional to be classified as a gesture. Noting the criteria used in previous studies (Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; Byrne et al., 2017; D. A. Leavens et al., 2005), intentionality was scored for each gesture type separately, using pooled data across all subjects. Gestures above the threshold of 60% of cases were classified as intentional (Roberts, Roberts, et al., 2014). This criterion enabled us to eliminate the behaviours where there was no consistent association between the behaviour type and intentional use when considering the following criteria:

i) The presence of an audience; ii) Response waiting (the signaller directs a gesture at a recipient and observes the recipient's response during and after the gesture)

These two criteria for intentionality of gestures were coded following the schema suggested by Tomasello et al. (1985) who gave following example to explain the intentionality of gestures: ‘a child might be struggling to open a cabinet, crying and whining as s/he struggles. Seeing this, the mother might come to the rescue and open the cabinet. This is a perlocutionary act because, while communication may be said to have occurred, the "sender" (the child) did not intentionally direct any behavior towards the mother. If, on the other hand, the child has turned its attention from the cabinet to the mother and whined at her, the whining now becomes a social-communicatory act with the intention of obtaining adult aid’. Following this description of intentional communication, we used the presence of an audience as one clear criterion for intentionality. In this dataset, all cases of gesturing included the presence of an audience within 10 meters. Secondly, response waiting was shown by the presence of bodily orientation by the signaller towards the recipient during the gesture as described by Tomasello et al. (1985) citation above. Visual attention between the signaller and the recipient was first recorded using 6 categories of bodily orientation: (1) the recipient is in signaller's view of vision and recipient's bodily orientation relative to signaller's is either: (a) recipient is facing the signaller with the side of the body (b) recipient is facing the signaller with the chest or (c) recipient is facing the signaller with the back (2) the recipient is out of signallers view of vision and the recipients bodily orientation relative to signaller's is one of the three: a) recipient is facing the signaller with the side of the body (b) recipient is facing the signaller with the chest or (c) recipient is facing the signaller with the back. In the sample of 545 sequences of gestures (consisting of adult to adult gestures only) the mean percentage ± SD [95% CI] of cases of all gesture types when recipient was in view of the signaller during production of the gesture was 91.5 ± 18.5%, [87, 95]. Of the remaining gesture cases (when the recipient was not in view of the signaller) the mean percentage ± SD [95% CI] of cases of all gesture types associated with the presence of recipients' bodily orientation towards signaller (recipient facing signaller with the chest or the side of the body) was 6.9 ± 15.4% [3, 10]. Finally, the mean percentage ± SD [95% CI] of cases of all gesture types where neither signaller nor the recipient were in view of one another during production of the gesture was 1.5 ± 11% [0, 3]. This shows that the gestures in our dataset were intentional according to the previously established criteria for defining intentionality in preverbal humans by Tomasello et al. (1985).

iii) The signaller persists in gesture production when the recipient fails to respond

Gesture events were scored in accordance to whether they occurred singly or in sequences, defined as one or more than one gesture made consecutively by one individual, towards the same recipient, with the same goal, within the same context, and made within a maximum of 30 seconds interval to ensure independence. Following Hobaiter and Byrne (2011; see also Townsend et al., 2016) persistent sequence is when the chimpanzee produces a gesture then after a pause (1-5s) it produces another gesture. Chimpanzee produces a rapid sequence when there is no pause between gestures. Of a total of 545 sequences per focal individual, the mean number ± SD [95% CI] of single gestures was 32.0 ± 32, [11.69, 52.47], for persistence sequences, the same variables were 4.41 ± 5.85, [0.69, 8.13] and rapid sequences 8.9 ± 9.09, [3.14, 14.69].

We grouped gestures qualitatively based on characteristics of the morphology (i.e. the presence/absence and type of bodily movement, bodily posture, head movement, leg movement, locomotory gait, manual movement). A complete description of the gestural repertoire, with video clips for each gesture type can be found in Roberts et al. 2012 and 2014 (Roberts, Roberts, et al., 2014; A. I. Roberts et al., 2012). This procedure has been widely used to identify distinct gesture types both in chimpanzees (K. Hobaiter & Byrne, 2011; Liebal et al., 2004; Pollick & de Waal, 2007; Tomasello et al., 1984) and in other nonhuman primates (Byrne et al., 2017; Genty, Breuer, Hobaiter, & Byrne, 2009). The broad morphological categories (e.g. head, leg and manual) were used to distinguish between single gestures and their combinations (where more than one gesture was made simultaneously by the signaller, e.g. 'bite' and 'embrace'). Consistent with previous research (A. I. Roberts & S. G. B. Roberts, 2016), gestures were classified according to the sensory modality (visual, tactile, short-range auditory, long-range auditory, Table 1). Additionally, gestures were classified as to whether they were accompanied by simultaneous production of vocalisations. For each instance of a gesture, the following data were recorded: identity of the signaller (the individual performing a gesture) and the identity of the recipient (individual at whom the gesture was most clearly directed, as determined from the orientation of the body of the signaller during or immediately after performing a gesture, i.e. the signaller had the recipient within its field of view).

The reliability of the coding scheme for communicative function of the gesture (e.g. gesture type, context and response) has been assessed in our previous studies (A. I. Roberts et al., 2012; Roberts et al., 2013). Here we examined instances of gesturing recorded between adult individuals (Bakeman & Gottman, 1997). The subsample for reliability scoring was taken from a corpus of 545 sequences (1044 instances) of gesturing. A subset of gestures from video was coded by a second coder in accordance with schema presented in previous studies in the field (K. Hobaiter & Byrne, 2011). Here the gesture rates were examined in relation to association patterns (duration of time dyad partners spent within 10 meters per hour spent in the same party and the number of dyad partners with whom chimpanzees maintained proximity). The proximity of the partners was not taken from the footage, but was independently recorded on the check sheet at 2-minute intervals by the field assistant and therefore the reliability coding could not be influenced by the observation of proximity. The second coder assigned a random sample of 45 gestures to categories of gesture modality.

Cohen’s Kappa coefficient showed that reliability was excellent for modality of signaling (K = 0.95) (Bakeman & Gottman, 1997). A sample of 50 gestures was coded by a second coder for intentionality (response waiting and persistence) and the Cohen’s Kappa coefficient showed good reliability (K = 0.74) (Bakeman & Gottman, 1997). Finally, a sample of 55 gestures was second coded for the presence or absence of the cues accompanying gestural communication. The Cohen’s Kappa coefficient again showed good reliability (K = 0.74) (Bakeman & Gottman, 1997). The reliability for intentionality and the cues is lower than for modality, but is in line with previous research in this area (K. Hobaiter & Byrne, 2011). Further, given the analysis is carried out on the overall communication patterns between dyads, any slight disagreement between observers about the intentionality or presence of the cues for individual gestural events is unlikely to have a large effect on the overall pattern of results.

Behavioural data

Previous studies on this population of chimpanzees have shown that the mean distance between signaller and the recipient before communicating gesturally is 6.4 m (Roberts & Roberts, 2015). In the current study, instances of gestural communication when the intended recipient of the gestural communication was within 10 m of the signaller were included in the analyses. This enables us to avoid excluding those communication patterns that are important for social bonding but are often used at a larger distance (e.g. to initiate or maintain travelling), whilst controlling for the ability of the recipient to perceive the signal (Sam George Bradley Roberts & Anna Ilona Roberts, 2016). There is not a single, agreed measure of bondedness within or between species (R. I. Dunbar & Shultz, 2010). Our measure of proximity bonds (duration of time spent in proximity within 10 meters, per hour spent in the same party) has been validated in previous studies on this population of chimpanzees, which demonstrated that pairs of chimpanzees who spend the longest duration in proximity within 10 m also have higher durations of other indices of social bonding such as duration of time spent within 2 meters, resting, travelling, grooming, visual attention, gestures and vocalisations (A. I. Roberts & S. G. B. Roberts, 2016; Sam George Bradley Roberts & Anna Ilona Roberts, 2016). Thus, this measure of proximity bonds appears to capture important aspects of variation in social behavior between conspecifics. Further, the duration of proximity between pairs of chimpanzees has been used in other studies to measure the nature of their social relationships (Fedurek et al., 2013; K. E. Langergraber et al., 2007; Mitani, 2009)

We analyzed gesture events both accompanied and unaccompanied by the cues. In this selection, only those events were taken into account which were independent, i.e. they were solely visual, auditory or tactile (not taking into account the modality of the cue) and accompanied by one cue only (not taking into account mutual visual attention). Since self-relevance cues (e.g. indicative gesture) were not counted unless visual orientation was also present, these self-relevance cues were additional/compounded cues. For synchronized calls the presence of mutual attention between interactants was not taken into account. The detailed description of all cues can be found in Table 1. Only those gestures unaccompanied by any of the cues listed were scored as lacking cues (no cue) and this includes synchronized calls. Gestures unaccompanied by cues were included in the models to compare the strength of association of gestures accompanied by and unaccompanied by cues with the presence and absence of proximity bonds. Thus the models examine whether the rate of gestures accompanied by cues was significantly associated with proximity, taking into account the rate of gestures unaccompanied by cues.

Next, to ensure that the sampling procedure did not bias our results, we examined whether there was a similarity in association patterns between scans taken at 2 minutes (scan 1), 4 minutes (scan 2) and 18 minutes (scan 9) of the focal sample (A. I. Roberts & S. G. B. Roberts, 2016). These analyses showed that there was no significant difference in the number of times the focal and non-focal subjects were in close proximity between scan 1 (Median = 2, IQ range = 0 - 5) and scan 2 (Median = 2, IQ range = 1 – 5, Wilcoxon signed-ranks test, *T* = 411.50, *n* = 132, *p* = 0.435). The aim of this analysis was to examine the likelihood that there was a change in group composition during the 2 minute interval. Since the analysis showed that there was no change in composition between scans 1 and 2, it did not seem reasonable to assume that the result would be different if differences in the focal-partner proximity were examined between scans 2 and 3, 3 and 4, etc. Thus, we did not undertake such additional analysis. However, there was a significant difference in the number of times the focal and non-focal subjects were in close proximity between scan 1 and scan 9 (Median = 2, IQ range = 1 – 4; Wilcoxon signed-ranks test, *T* = 2656.50, *n* = 132, *p* = 0.011). Similarly, there was no significant difference in the number of times the focal and non-focal subjects were in the same party between scan 1 (median = 5, IQ range: 3 - 10) and scan 2 (median = 5, IQ range: 3 - 10; Wilcoxon signed-ranks test, *T* = 218.50, *n* = 132, *p* = 0.571), whilst there was a significant difference in the number of times the focal and non-focal subjects were in the same party between scan 1 and scan 9 (median = 5, IQ range: 2 - 10; Wilcoxon signed-ranks test, *T* = 1460, *n* = 132, *p* = 0.010). These results demonstrate that the adjacent scans were similar both for 10 m associations and party level associations. These scans were therefore treated as continuous data sampling and used to calculate durations of proximity between pairs of individuals. If chimpanzee A and chimpanzee B were recorded as being in 10 m proximity at Scan 2, they were assumed to have been together for the 2 minutes preceding Scan 2, as 10 m associations between pairs of chimpanzees do not change significantly between adjacent scans. However, the first and final sample scans at 1 minute and 18 minute interval differed for both 10m associations and party level associations. This suggests that these scans were independent, as were the focal samples preceding and succeeding the 18 minute focal follow. Thus each separate 20 min focal follow can be considered as an independent sampling of the chimpanzees' association patterns.

Based on these behavioural data, we calculated association measures for proximity (duration of time pairs of chimpanzees spent within 10 m, per hour spent in same party) and communication (rate of communication between pairs of chimpanzees, per hour spent within 10 m). These measures have been previously described (Sam George Bradley Roberts & Anna Ilona Roberts, 2016) so only the detailed calculation for the dyadic association measure is presented here as an example. The dyadic association measure (DA) is the duration of time the focal subject A spent in close proximity (within 10m) to the non-focal subject B, per hour spent in the same party, or:

$DA_{AB} = [(P10_{AB}*2)* 60)] /PSP_{AB}*2$

where $P10_{AB}$ = the number of times A was in close proximity (within 10m) to B

PSP_{AB} = the number of times A was in the same party as B

2 = duration of instantaneous subsample interval in minutes

60 = the number of minutes in an hour

Attribute measures

Demographic factors such as age, kinship, sex and reproductive state can influence chimpanzees' propensity to associate with each other. The genetic relationships in the study group were established by previous research, enabling us to categorize chimpanzee dyads according to maternal kinship (mother offspring dyads) presence or absence (Reynolds, 2005). Moreover, the age of most subjects in the community is known from long term project records. In the wild, chimpanzees reach physical and social maturity between ages 15 – 16 years old (Goodall, 1986). We classified dyads of chimpanzees as belonging to the same (5 years or less age difference) or a different (above 5 years age difference) age class following previous studies (Mitani, Watts, Pepper, & Merriwether, 2002). Chimpanzee dyads were also categorized according to similarity of reproductive status. First, the reproductive status of the female was scored on the basis of the size of the sexual swelling, i.e. an enlarged area of the perineal skin varying in size over the course of the menstrual cycle. The reproductive status of the female was recorded as oestrous if during the observation period the female exhibited maximum tumescence and was observed mating with the males. All focal males were observed to mate with the females and therefore assumed to be reproductively active. Sex similarity was also scored based on observable morphological characteristics referring to sex, with dyads classified as composed of same sex or opposite sex pairs. Further details of the categorization of attribute data can be found in Supplementary Table 1

Social Network Analysis

The different networks were created using the behaviour categories described above. Each network matrix was composed of 12 rows and 12 columns, with each row and column denoting a different focal chimpanzee. Each cell of the matrix represented the value for the duration or the rate of occurrence of that particular behaviour for a specific pair of chimpanzees (e.g. the duration of proximity between Bwoba and Kutu, per hour they spent in the same party). The communication networks used in this study were weighted - that is each cell consisted of a continuous value representing that behaviour, rather than a 1 or a 0 indicating the presence or absence of a tie. The networks were also directed, in that they represented the rate of behaviour made by the focal Bwoba to Kutu, as well as the focal Kutu to Bwoba. For example, the rate of gestures produced by Bwoba and directed at Kutu may be different than the rate of the gestures produced by Kutu and directed at Bwoba.

The behavioural network related to the duration in minutes of proximity (within 10 m) between specific pairs of the focal individuals, per hour that pair were in the same party. Across the 132 chimpanzee dyads, dyads spent a mean of 21.16 (range 0 - 60) minutes in close proximity (within 10m) with conspecifics, per hour spent in the same party. In this network, 95.5% of potential connections to group members were present (range 82 – 100%). As with previous studies on this population of chimpanzees (A. I. Roberts & S. G. B. Roberts, 2016; Sam G. B. Roberts & Anna I. Roberts, 2016) a binary proximity network was created, whereby dyads who displayed values of proximity association equal or above the mean plus half standard deviation (equal or above 30.3 minutes spent in close proximity per hour spent in the same party), were scored as 1 if the proximity was reciprocated (i.e. both A to B and B to A dyads displayed values of proximity association equal or above the mean plus half standard deviation). These dyads were termed ‘preferred reciprocated close proximity bonds’. Dyads who had values below 30.3 minutes of proximity, or where the proximity was not reciprocated, were scored as 0. In this network of preferred reciprocated close proximity bonds, only 15.1% of potential connections were present (range 0 – 46%). The communication networks consisted of the rate of different type of communication between pairs of the focal individuals, per hour that pair of chimpanzees spent within 10m. For example, the rate of visual gestures accompanied by one-to-one calls between Bwoba and Kutu was used as the weighted, directed value of communication for this dyad in the ‘visual gestures with one-to-one call’ network.

The centrality measures were calculated from these network matrices, using normalized degree centrality (Croft, James, & Krause, 2010). We calculated the normalized degree centrality for each individual chimpanzee, i.e. the average value of each row or column of the strong proximity bond network matrix, where dyads of individuals who had values of proximity association equal or above the mean plus half standard deviation, were scored as 1 (‘close proximity bonds’). The networks used in this study are directed and therefore in-degree and out-degree were calculated separately for each behaviour. Out-degree is a measure that denotes behaviours directed by the focal chimpanzee to conspecifics. In contrast, in-degree denotes behaviours directed by conspecifics towards the focal chimpanzee. In these analyses, the proximity network was directed because some strong proximity bonds were not reciprocated and therefore in-degree was used in all models.

All data transformations and analyses were carried out using UCINET 6 for Windows (Borgatti, Everett, & Freeman, 2014). In order to examine the normalised mean degree across proximity and communication networks, networks were dichotomized and symmetrized. Normalised mean degree is the mean proportion of all possible ties which are present. In order to dichotomize the network, all values larger than zero are scored as 1 (tie present) and all values of zero were categorised as absent. In symmetrisation, a tie is scored as present if there is a 1 in either of the two cells corresponding to each pair of individuals (cell *i, j* or cell *j, i*).

The observations that were used to create the network are not independent of each other and thus general standard inferential statistics cannot be used. Instead, analyses using randomisation tests are used, where the observed value is compared against the distribution of values generated by a large number of random permutations of the data. The proportion of random permutations in which a value as large (or as small) as the one observed is then calculated, and this provides the *p* value of the test (Borgatti, Everett, & Johnson, 2013). The type of randomised test used to examine the relationship between different behavioural and communication networks was MRQAP regression (Multiple Regression Quadratic Assignment Procedure) (Borgatti et al., 2013). MRQAP regression resembles standard regression as it allows for the examination of the relationship between a numbers of different predictor variables (e.g. different communication networks) on a single outcome variable (proximity network). In our analysis this outcome variable was a binary one – whether or not a dyad was classified as having a preferred reciprocated close proximity bonds, scored as a 1 or 0. As with a standard regression analysis, MRQAP produces standardized coefficients and standard errors for the predictor variables. With a binary outcome variable, positive coefficients indicate that a higher value for that predictor variable (e.g. a higher rate of visual gestures accompanied by self-relevance cues) is associated with the presence of close proximity bonds.

As MRQAP is a modified form of regression analysis for network data, we used a hierarchical approach to building these models, as is common practice in standard forms of multiple regression (Field, 2013). We first constructed a model containing only the demographic variables - age difference between dyads, sex difference between dyads, whether the dyads were kin or not kin and reproductive similarity (Supplementary Table 1). We then added gestural communication not accompanied by cues, before in the final model adding gestural communication accompanied by cues. As in standard regression, we used the F statistic to assess the significance of the change in R^2 between each model. Using this approach allowed us to examine whether gestures accompanied by cues explained significantly more variance in proximity bonds than either a model just containing demographic variables, or a model containing demographic variables and gestures unaccompanied by cues.

There are a number of different types of MRQAP regression and we used Double Dekker Semi-Partialling MRQAP regression as it is more robust against the effects of network autocorrelation and skewness in the data (Dekker, Krackhardt, & Snijders, 2007). In these MRQAP analyses, we used 2,000 permutations. In our node-level regressions, similar procedure was used, whereby 10,000 random permutations were used to determine the association between number of predictor variables (e.g. the out-degree for visual gestures) on a single outcome variable (proximity in-degree). Moreover, in order to assess autocorrelation between attribute data (e.g. the total duration of observation) and network data (e.g. visual gesture network) we used Geary's C statistic. A value of 1.0 for the Geary statistic indicates no association between variables, values of less than 1.0 indicate a positive association and values over 1.0 indicate a negative association.

Results

The rate of gestures with cues predicts the presence of reciprocated close proximity bonds

In this study, a mean of 12.52 (range 8.33 – 18.63) hours of focal footage per individual subject was examined. The definitions of categories of cues and modalities of gestures are given in Table 1. The descriptive statistics on the rate of production and mean degrees of gestures (the percentage of potential connections chimpanzees had with others) accompanied and unaccompanied by cues are provided in Table 2. The details of sampling effort can be found in Supplementary Table 2. We used MRQAP regression to examine whether rates of gestural communication accompanied and unaccompanied by cues were a predictor of the presence of preferred reciprocated close proximity bonds, building up the models in a hierarchical method. For full details of all models, including insignificant findings, see Tables 3 – 4.

To examine the overall association between cues and the presence of preferred reciprocated close proximity bonds, initially we pooled all gesture types and examined whether gestures accompanied and unaccompanied by cues were significantly associated with proximity bonds (Table 3). In Model 1, none of the demographic variables were significantly associated with the presence of proximity bonds. Model 2 included the rate of gestures unaccompanied by cues – again none of the predictor variables were significantly associated with the presence of proximity bonds and including the rate of gestures unaccompanied by cues did not significantly improve the amount of variance explained, with the R^2 only increasing from 0.049 in Model 1 to 0.056 in Model 2, F (1, 126) = 0.934, $p > 0.05$. In contrast, when the rate of gestures accompanied by cues was added in Model 3, there was a significant increase in the R^2 to 0.135, F (1, 125) = 11.416, $p < 0.001$. The rate of gestures accompanied by cues was significantly associated with the presence of preferred, reciprocated close proximity bonds between pairs of chimpanzees (r^2=0.135, β=0.329, p = 0.009). There was no statistically significant association between the rate of gestures unaccompanied by cues and the presence of preferred, reciprocated close proximity bonds (β = - 0.074, p = 0.204, Table 3, Figure 1).

Given that overall rate of gestures accompanied by cues was associated with close proximity bonds, we then examined which categories of gestures accompanied by cues were significantly associated with proximity bonds, taking into account all combinations of modalities and cues (Table 4). We again used a hierarchical model building approach, comparing a model containing only demographic variables (Model 4), to one including the rate of gestures of different modalities unaccompanied by cues (Model 5) to a model including the rate of gestures of different modalities accompanied by self-relevance cues (Model 6) and finally to a model including the rate of gestures of different modalities accompanied by synchronized cues (Model 7). In Model 5, the rate of visual gestures unaccompanied by cues (visual no cue) was significantly higher in dyads with a close proximity bond. However, overall there was no significant improvement in the R^2 between Model 4 and Model 5, F (4, 123) = 1.924, $p > 0.05$. In contrast, including the rate of gestures of different modalities accompanied by self-relevance cues significantly improved the R^2 in Model 6 compared to Model 5, F (7, 116) = 3.204, $p < 0.01$. In this model, only visual gestures accompanied with self-relevance cues were significant predictors of preferred, reciprocated close proximity bonds. Pairs of chimpanzees that had preferred, reciprocated close proximity bonds had higher rates of visual gestures accompanied by one-to-one call (β=0.171, p = 0.044) and indicative gestures (β=0.352, p = 0.045; Figure 2). In contrast, in Model 6, the rate of visual gestures unaccompanied by cues (visual no cue) was significantly negatively associated with the presence of proximity bonds (β= -0.254, p = 0.043). Further, for tactile gestures, auditory short-range gestures and auditory long-range gestures, the rate of gestures either accompanied or unaccompanied by cues was not significantly associated with the presence of preferred, reciprocated close proximity bonds. Finally, in Model 7 including the rate of gestures of different modalities accompanied by synchronized cues again significantly improved the R^2 in Model 7 compared to Model 6, F (2,114) = 5.227, $p < 0.01$. In this model the higher rate of visual gestures accompanied by one-to-one call (β=0.175, p = 0.046), indicative gestures (β=0.355, p = 0.028) and synchronized calls (β=0.254, p = 0.005) positively predicted presence of preferred, reciprocated close proximity bonds. Dyad partners who had a higher rate of visual gestures unaccompanied by the cue were less likely to have a preferred, reciprocated close proximity bond with each other (β=-0.252, p = 0.031; Figure 2).

Gestures accompanied by self-relevance cues are associated with proximity centrality

We used node-level regressions to examine the predictors of proximity in-degree by the n degree of gestures accompanied and unaccompanied by cues (the percentage of all potential connections chimpanzees had with others). The focal chimpanzees with a high proximity in-degree had a larger number of connections maintained through gestures accompanied by presence of the cues (r^2=0.596, β= 1.440, p = 0.016, Supplementary Table 3). In contrast, the size of the social network maintained through gestures unaccompanied by presence of cues was not associated with proximity in-degree (β= -0.635, p = 0.166).

Finally, for communication networks accompanied by self-relevance cues, we calculated normalized degree and examined its relationship with proximity in-degree. First, we combined all gestures accompanied self-relevance cues in one model (indicative gesture, one-to-one call, mutual attention, Supplementary Table 4). The only positive predictor of proximity in-degree was the network size of the visual gestures accompanied by mutual attention (r^2 = 0.675, β= 2.895, p = 0.039). Second, we combined gestures accompanied by self-relevance cues with gestures accompanied by synchronized cues according to each modality of synchronized cue entered separately (visual and auditory). In a model combining visual, tactile and auditory gestures accompanied by self-relevance cues (indicative gesture, one-to-one call, mutual attention) and visual gestures accompanied by synchronized cue, the positive predictor of proximity in-degree was the network size of the visual gestures accompanied by synchronized call (r^2 = 1, β= 2.739, p = 0.038). The size of the tactile mutual attention network was negatively correlated with the proximity in-degree (β= - 5.075, *p* = 0.019, Supplementary Table 5). In a similar analysis, using auditory long-range gestures accompanied by synchronized cue, instead of visual gestures accompanied by synchronized cue, the pattern was similar. There was a positive correlation between proximity in-degree and the network size of the auditory long-range gestures accompanied by synchronized cue (r^2 = 1, β= 2.083, *p* = 0.045). However, there was a negative correlation between proximity in-degree and the size of the tactile mutual attention network (β= - 4.324, *p* = 0.022) and the size of the auditory long-range mutual attention network (β= - 3.297, *p* = 0.011, Supplementary Table 6).

Discussion

Many nonhuman primates live in social groups and it has been proposed that these complex groups require complex communication systems (Freeberg et al., 2012). Whilst there has been much focus on nonhuman primate vocalizations (T. Fitch, 2005; R. Seyfarth & Cheney, 2010; R. M. Seyfarth et al., 2010), less is known about how nonhuman primate gestural communication is related to sociality (Byrne et al., 2017; Sam G. B. Roberts & Anna I. Roberts, 2016). Integration of self-relevance cues such as visual attention, indicative gesture or one-to-one vocalisation with the gestures can increase the degree of self-relevance of perceived gestural communication (Sander et al., 2003). It is hypothesized that self-relevance cues facilitate social bonding because they make it clearer to the recipients that the gesture is directed at them and facilitate processing of the gesture. In addition, synchronized cues such as pant-hoot call accompanying use of a gesture are produced jointly with group members, with simultaneous, rhythmically matched sound production and movement. These features are predicted to increase efficiency of social bonding in large social networks by removing the need for one-to-one social coordination. In this study we examined whether the rates of gestures accompanied by cues as compared to the rates of gestures unaccompanied by cues, both overall and by modality, were a better predictor of sociality of wild chimpanzees. The complexity of sociality was measured by the presence of reciprocated, proximity bonds (time pairs of chimpanzees spent within 10 m per hour they spent in the same party) between dyad partners. There were two key findings. First, pairs of chimpanzees that spent a longer duration of time in proximity (those that had preferred, reciprocated close proximity bonds) had a higher rate of gestures accompanied by cues, per hour they spent within 10 m. In particular, a higher rate of visual gestures accompanied by cues was associated with close proximity bonds. Second, individual chimpanzees who had a greater number of close proximity bonds produced a higher rate of gestures accompanied by cues, and specifically a higher rate of gestures accompanied by synchronized pant-hoot calls.

Previous research on this population of chimpanzees has shown that pairs of chimpanzees that spend more time in close proximity have a higher rate of gestural communication (A. I. Roberts & S. G. B. Roberts, 2016; Sam G. B. Roberts & Anna I. Roberts, 2016). The current findings extend this research by demonstrating that it is not just the overall rate of gestural communication that is associated with proximity bonds, but specifically the rate of gestural communication accompanied by cues. When considering separately from gestures accompanied by cues, gestures unaccompanied by the cues did not predict the presence of proximity bonds. Thus in a combined model which included both the rate of gestures accompanied by cues and the rate of gestures unaccompanied by cues, only the rate of gestures accompanied by cues was associated with the presence of proximity bonds between pairs of chimpanzees.

Likewise, the results of the current study extend previous research showing an association between visual gestures and proximity bonds (A. I. Roberts & S. G. B. Roberts, 2016) by demonstrating that the rate of visual gestures accompanied by cues predicts the presence of proximity bonds. In contrast, the rate of visual gestures unaccompanied by cues was negatively associated with proximity bonds. Visual gestures may be particularly well-suited to coordinating behaviour between pairs of chimpanzees when interacting at close proximity – for example when pairs of chimpanzees are forced into close proximity due to the clumped nature of the food resources such as fig trees (A. I. Roberts & S. G. B. Roberts, 2016). In contrast to loud auditory gestures, visual gestures are not aversive to recipients when both signaller and recipient are close together. By producing these visual gestures at a higher rate, pairs of chimpanzees in close proximity to each other may be able to coordinate their behaviour more effectively (A. I. Roberts & S. G. B. Roberts, 2016). The predictability of conspecifics' behaviour is a major modulator of stress in group-living animals (Robert M Seyfarth & Cheney, 2013) and a higher rate of visual gestures may increase this predictability and facilitate social interaction in chimpanzees (A. I. Roberts & S. G. B. Roberts, 2016). These visual gestures may operate in a similar way to grunts in Guinea baboons, where a high rate of grunts helps regulate social behaviour when baboons are interacting in close proximity (Maciej, Ndao, Hammerschmidt, & Fischer, 2013).

However, for visual gestures to be effective in increasing the predictability of conspecifics' behaviour, recipients need at a minimum to detect the gesture is directed at them, rather than another conspecific (Engh et al., 2006). By accompanying their visual gestures with self-relevance cues such as visual attention, one-to-one call or indicative gesture, signalers can make it clearer to the recipient that the gesture is directed at them, and thus better coordinate their behaviour with the recipient. In turn, this has a potential to increase the effectiveness of communication, resulting in pairs of chimpanzees that spend a greater duration of time together, per hour in the same party. Previous research across both nonhuman primates (Byrne et al., 2017; Roberts, Roberts, et al., 2014) and humans (Grèzes & Dezecache, 2014; N'diaye et al., 2009) has examined how these 'self-relevance' cues affect how the signaller detects and responds to communication, but has not directly examined how use of these cues is associated with sociality in wild nonhuman primates. The current results suggest that it is specifically visual gestures accompanied by self-relevance cues that may play a key role in coordinating social behaviour in wild chimpanzees. In contrast, the rate of tactile and auditory gestures accompanied by self-relevance cues was not positively associated with proximity bonds between pairs of chimpanzees. One reason for this may be because visual gestures are harder for signalers to detect than tactile gestures, in which the signaller makes direct physical contact with the receiver, or auditory gestures in which the noise produced by the gesture can draw the receivers attention towards the signaler (Gillespie-Lynch et al., 2014; Hopkins et al., 2007). Whilst this study did not examine the response of the recipient to the gesture, previous research has shown that not only can self-relevance cues help recipients detect communication is directed at them, it can also trigger brain activity associated with preparing an appropriate response to the signal from the large set of potential action opportunities (Grèzes & Dezecache, 2014). Further research in this area could explore whether visual gestures accompanied by self-relevance cues, as compared to those unaccompanied by such cues, are more efficient in eliciting appropriate responses from recipients, as has been shown for other complex forms of gestural communication in chimpanzees such as persistence and elaboration (Byrne et al., 2017; Roberts, Roberts, et al., 2014; Roberts, Vick, et al., 2014).

However, visual gestures accompanied by self-relevance cues demand a high degree of inter-individual coordination through proximity and mutual visual contact. Thus, these interactions may be less efficient in socially bonding with a larger number of social partners. When visual gestures accompanied by self-relevance cues were included in one model with visual gestures accompanied by synchronized calls, the model explained a greater amount of variation in social relationships. Thus, visual gestures accompanied by synchronized calls may be more effective in meeting the demands of maintaining social relationships in primates.

In addition to variation in the duration of time pairs of chimpanzees spent in close proximity to each other, there were also important individual differences between the focal chimpanzees, with some focal individuals maintaining proximity to more numerous conspecifics, as measured by network centrality. The focal individuals with high network centrality had a higher rate of gestures accompanied by synchronized pant-hoot calls, per hour they spent within 10m of conspecifics. This finding builds on previous work showing an association between pant-hoot chorusing and social bonds in chimpanzees (Fedurek et al., 2013; Mitani & Gros-Louis, 1998) and suggest that accompanying gestures with synchronized calls may be particularly important to coordinate behaviour and maintain social relationships with multiple individuals simultaneously (Fedurek et al., 2013; Sam G. B. Roberts & Anna I. Roberts, 2016). Research on humans has shown that synchronized vocalizations such as singing and laughter are associated with the release of endorphins, which in turn helps social bonding (Manninen et al., 2017; Tarr et al., 2016; Weinstein et al., 2016a, 2016b). In a similar way, synchronized vocalizations in chimpanzees may provide a time-efficient way to form and maintain social bond with numerous conspecifics, particularly for individuals with numerous social partners (Arlet et al., 2015; Fedurek et al., 2013; Sam G. B. Roberts & Anna I. Roberts, 2016). How baseline rate of vocal behavior without a gesture could influence effectiveness of maintaining chimpanzee social relationships is thus an important avenue of research for future studies, which could compare how overall gesture and vocalization are associated with the presence of social bonding.

Overall, these findings support the link between communication and social complexity (Freeberg et al., 2012). Higher rates of more complex communication (gestures accompanied by cues, as compared to gestures unaccompanied by cues) were associated with greater sociality in wild chimpanzees. However, the results also suggest that different types of communicative complexity may be differentially suited to different types of social interaction, enabling nonhuman primates to meet the challenges that come from living in a complex social group (Gillespie-Lynch et al., 2014; Sam G. B. Roberts & Anna I. Roberts, 2016). Whilst visual gestures accompanied by self-relevance cues may help chimpanzees coordinate their behaviour and regulate proximity at a dyadic level, synchronized pant-hoot calls may be more effective at coordinating behaviour of multiple individuals over larger distances (Sam G. B. Roberts & Anna I. Roberts, 2016). Further tests of the link between communication and sociality could focus on how different types of communication are used to maintain and regulate different types of social relationships, rather than on simply the overall association between social and communicative complexity (McComb & Semple, 2005). Further, if using complex communication helps animals meet the challenges of living in social groups (Freeberg et al., 2012), individual variation in communication patterns could be related to both social integration in the group and to fitness outcomes (Robert M Seyfarth & Cheney, 2013, 2015; Silk et al., 2010a).

More broadly, these results have important implications for our understanding of the evolution of language. Nonhuman primates in larger groups spend a greater percentage of their day grooming, but the amount of time that can be devoted to grooming is limited (R. I. M. Dunbar, 2010). Thus as group size increased through human evolution, it has been theorised that synchronized vocalisations (Pearce, Launay, & Dunbar, 2015; Weinstein et al., 2016b) and language played an important role in maintaining social bonds and group cohesion (R. Dunbar, 2008). Other researchers have argued that gestures or multi-modal communicaiton may have been important precurors to language (Arbib et al., 2008; M. Corballis, 2009; Gillespie-Lynch, Greenfield, Feng, Savage-Rumbaugh, & Lyn, 2013; Taglialatela et al., 2015). Our results suggest that both gestures and synchronized vocalisations may be important in enabling chimpanzees to meet the time and cognitive challenges of maintaining a large set of differentiated social relationships. In particular, the use of self-relevance cues may enhance recipients’ detection that communication is directed at them and thefore increase the efficiency of gestural communication in faciliating social interaction. Through the course of human evolution, increased flexibility in the use of different types of mutli-modal communication to maintain different types of social relationships may have enabled larger groups of hominins to maintain social cohesion, acting as an alternative to other mechanisms that require physical contact, such as grooming and as a precusor to human language (R. Dunbar, 2012; Freeberg et al., 2012).

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Table 1. Ethogram of behavioural categories

Category	**Definition**
Modality	
Visual gesture[a]	Gesture perception is possible only by looking at signaler. Gestures included were: *Arm beckon, Arm flap, Arm raise*, Bob, Bow, Crouch, Crouch run, Crouch walk, Dangle, *Forceful extend, Hand bend*, Jump, *Limp extend, Linear sweep*, Lower head, Lunge, Present genitals, Present leg, Present mount, Present rump, Present torso, Rock, Roll over, Run stiff, Slap self, Sniff, Stationary stiff, *Stiff extend*,

	Stretched extend, Swagger bipedal, Swagger quadrupedal, Tip head, Touch self, Turn back, Turn head, *Unilateral swing, Vertical extend,* Walk stiff, Wipe
Tactile gesture	Gesture perception is possible via physical contact. Gestures included were: Bite, Embrace, Grab, Hold hands, Kiss, Locomote tandem, Pull another, Push by hand, Push by rump, Rub, Shake limb, Slide, Stand tandem, Stroke by mouth, Tap another, Thrust genitals, Tickle, Touch backhand, Touch innerhand, Touch long
Auditory short-range gesture	Sounds produced by the gesture can be heard within short distance from the signaller up to 10 meters. Gestures included were: Clip by mouth, Smack lip, Tap object
Auditory long-range gesture	Sounds produced by the gesture are audible at a distance of more than 10 meters away from the signaller. Gestures included were: Beat, Bounce, Drum, Knock, Pound, Shake mobile, Shake stationary, Stamp quadrupedal, Stamp sitting, Sway, Swing
Cue	
Visual orientation of the signaller	Signaller produces a gesture whilst in visual contact with the recipient, without simultaneous production of indicative gestures or calls. Visual contact was defined as when the signaller had the recipient within its field of view (up to 45 degrees body turn). The recipient also had to be in visual contact with the signaller.
One-to-one call	Signaller produces a gesture with simultaneous production of one-to-one call (produced by one signaller at one recipient) and without simultaneous production

	of indicative gestures or synchronized calls. The recipient of the gesture was an individual at whom signaller was bodily oriented during production of the call. Vocalisations included were pant-grunt, pant, scream, bark. The recipient also had to be in visual contact with the signaller.
Synchronized call	Vocalisation accompanying a gesture is produced simultaneously by a signaller and by other individuals who are present within 10 meters. Here cases of simultaneous production of indicative gestures or one-to-one calls by a focal subject were excluded. Vocalisations included were pant-hoot call.
Indicative gesture	Signaller produces a gesture with simultaneous production of indicative gesture (movement of the arm and hand towards the recipient, without physical touch) and without simultaneous production of one-to-one calls or synchronized calls. Indicative gestures included were: arm beckon, arm flap, arm raise, forceful extend, hand bend, limp extend, linear sweep, stiff extend, stretched extend, unilateral swing, vertical extend. All indicative gestures were visual gestures. The recipient also had to be in visual contact with the signaller.
No cue	Signaller produces a gesture without simultaneous production of one-to-one calls or synchronized calls or indicative gestures and whilst not in mutual visual contact with the recipient.

Note: Description of gesture types, accompanying video clips and criteria used to establish whether a nonverbal behaviour can be classified as a gesture can be found in (Roberts, Roberts, et al., 2014; A.I. Roberts et al., 2012). Nonverbal behaviours were only considered to be a gesture if they were mechanically ineffective, communicaive and intentional.

[a]Visual gesture types classified as indicative gestures are indicated in italics.

Table 2. Rate of gesture production per hour spent in close proximity (within 10 m) and normalized degree (the percentage of potential connections chimpanzees had with others)

Modality	**Type of cue**	**Rate**	**Rate overall range**	**Normalized degree (%)**	**Normalized degree overall range (%)**
Visual	Mutual attention	0.48	0 - 20	33.3	0 - 73
	One-to-one call	0.10	0 – 3.91	15.1	0 - 64
	Synchronized call	0.05	0 - 4	9	0 - 27
	Indicative gesture	0.09	0 - 5	15.1	0 - 46
	No cue	0.40	0 - 20	31.8	0 - 73
Tactile	Mutual attention	0.17	0 - 10	16.6	0 - 55
	One-to-one call	0.02	0 – 1.82	4	0 - 27
	No cue	0.14	0 – 17.65	6	0 - 27
Auditory short-range	Mutual attention	0.16	0 – 10.43	10.6	0 - 36
	No cue	0.24	0 – 22.50	13.6	0 - 36
Auditory long-range	Mutual attention	0.11	0 – 7.50	12.1	0 - 36
	Synchronized call	0.32	0 - 15	21.2	0 - 46
	No cue	0.01	0 – 0.97	4.55	0 - 18
All gestures combined	Cue	1.53	0 - 40	46.9	9 - 100
	No cue	0.81	0 – 22.94	36.3	0 – 82

Table 3. MRQAP regression model showing predictors of proximity between N = 132 dyadic relationships of the chimpanzees. Significant P values are indicated in bold. Dyads of individuals who had values of proximity association equal or greater than the mean plus half SD, were scored as 1 (‘strong ties’), if the proximity was reciprocated (i.e. both A to B and B to A displayed values of proximity association equal or greater than the mean plus half SD) whereas dyads who had values less than then mean plus half SD were scored as 0 (‘weak ties’).

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	*P*
Model 1 (R^2 = 0.049)			
Age similarity	0.133	0.120	0.169
Sex similarity	-0.025	0.118	0.396
Kinship similarity	-0.078	0.214	0.346
Oestrous similarity	-0.132	0.152	0.242
Model 2 (R^2 = 0.056)			
Age similarity	0.125	0.121	0.176
Sex similarity	-0.038	0.122	0.398
Kinship similarity	-0.077	0.213	0.365
Oestrous similarity	-0.138	0.152	0.236
All gestures combined no cue	0.088	0.010	0.165
Model 3 (R^2 = 0.135)			

Age similarity	0.103	0.115	0.209
Sex similarity	-0.051	0.114	0.365
Kinship similarity	-0.068	0.206	0.341
Oestrous similarity	-0.131	0.135	0.207
All gestures combined no cue	-0.074	0.010	0.204
All gestures combined with cue	0.329	0.010	**0.009**

Table 4. MRQAP regression models showing predictors of proximity between N = 132 dyadic relationships of the chimpanzees. Significant P values are indicated in bold. Dyads of individuals who had values of proximity association equal or greater than the mean plus half SD, were scored as 1 (‘strong ties’), if the proximity was reciprocated (i.e. both A to B and B to A displayed values of proximity association equal or greater than the mean plus half SD) whereas dyads who had values less than then mean plus half SD were scored as 0 (‘weak ties’).

Attribute category/ rate of gesture sequence per hour spent in close proximity	Standardized coefficient	Standard error	*P*
Model 4 (R^2 = 0.049)			
Age similarity	0.133	0.120	0.169
Sex similarity	-0.025	0.118	0.396
Kinship similarity	-0.078	0.214	0.346
Oestrous similarity	-0.132	0.152	0.242

Model 5 (R^2 = 0.105)			
Age similarity	0.120	0.123	0.174
Sex similarity	-0.040	0.120	0.388
Kinship similarity	-0.072	0.211	0.363
Oestrous similarity	-0.164	0.149	0.185
Auditory long-range no cue	0.087	0.288	0.214
Auditory short-range no cue	-0.043	0.016	0.303
Tactile no cue	-0.032	0.022	0.434
Visual no cue	0.208	0.018	**0.035**
Model 6 (R^2 = 0.250)			
Age similarity	0.086	0.111	0.234
Sex similarity	-0.076	0.113	0.290
Kinship similarity	-0.078	0.205	0.262
Oestrous similarity	-0.149	0.137	0.155
Auditory long-range no cue	0.152	0.318	0.065
Auditory short-range no cue	-0.051	0.018	0.245
Tactile no cue	0.045	0.026	0.223
Visual no cue	-0.254	0.040	**0.043**
Auditory long-range mutual attention	-0.203	0.086	0.076
Auditory short-range mutual attention	0.216	0.047	0.098

Tactile mutual attention	-0.292	0.098	0.083
Tactile one-to-one call	0.028	0.202	0.232
Visual indicative gesture	0.352	0.149	**0.045**
Visual mutual attention	0.413	0.055	0.067
Visual one-to-one call	0.171	0.079	**0.044**
Model 7 (R^2 = 0.313)			
Age similarity	0.094	0.114	0.195
Sex similarity	-0.045	0.112	0.353
Kinship similarity	-0.066	0.200	0.298
Oestrous similarity	-0.138	0.133	0.160
Auditory long-range no cue	0.156	0.316	0.053
Auditory short-range no cue	-0.052	0.018	0.232
Tactile no cue	0.042	0.025	0.226
Visual no cue	-0.252	0.037	**0.031**
Auditory long-range synchronized call	-0.061	0.022	0.182
Auditory long-range mutual attention	-0.191	0.084	0.075
Auditory short-range mutual attention	0.189	0.044	0.105
Tactile mutual attention	-0.269	0.094	0.096
Tactile one-to-one call	0.005	0.200	0.328
Visual indicative gesture	0.355	0.143	**0.028**
Visual mutual attention	0.394	0.053	0.062
Visual one-to-one call	0.175	0.078	**0.046**
Visual synchronized call	0.254	0.105	**0.005**

875

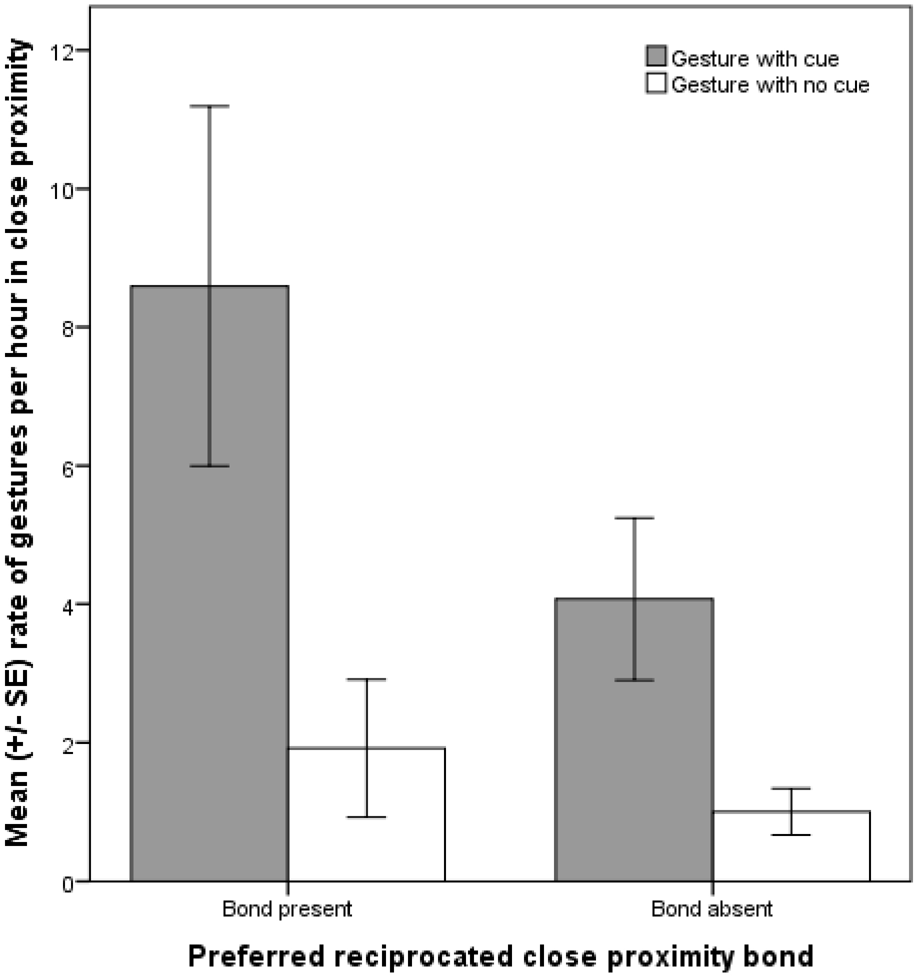

Fig. 1 Mean rate (+/- 1 standard error) of gestures with and without cues in dyads with and without preferred reciprocated proximity bonds. Preferred reciprocated proximity bonds were defined as when dyad A to B and B to A spent 30.3 or more minutes in close proximity, per hour spent in the same party.

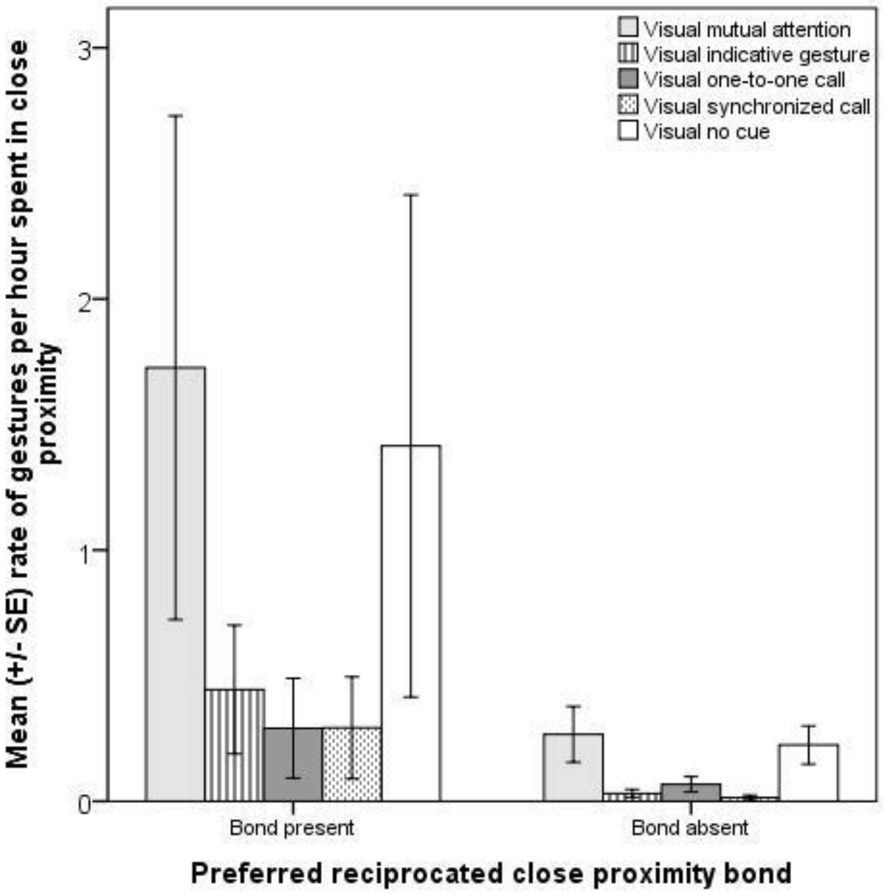

Fig. 2 Mean (+/- 1 standard error) rate of visual gestures in dyads with and without preferred reciprocated proximity bonds. Preferred reciprocated proximity bonds were defined as when dyad A to B and B to A spent 30.3 or more minutes in close proximity, per hour spent in the same party.

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