Communication and cooperation in wild chimpanzees (*Pan troglodytes schweinfurthii*)

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ABSTRACT

Comparisons between animal and human communication are invaluable for understanding the evolution of language and, as our closest living relatives, chimpanzees can provide particularly important insights into this. Here I examined unimodal (UM) and multimodal (MM) communication in wild chimpanzees, in an integrated manner. I found that although MM signals were produced infrequently, and at lower rates compared to captivity, the vast majority of adult and sub-adult individuals did freely combine vocal, gestural and facial signals to produce MM signals. A total of 48 free MM signal combinations were observed, incorporating a wide range of different signal types from different modalities. Focusing on one specific vocal-gestural MM signal, I found that MM combinations and UM gestural signals were more successful in eliciting responses compared to UM vocal signals.

To investigate signal function more systematically I focused on one common grooming gesture, the big loud scratch (BLS), and tested several competing functional hypotheses. I found little evidence to support the hypotheses that this signal operates as an attention-getter, or as a referential signal. In contrast, my data suggested that in this community of chimpanzees, the BLS facilitates the negotiation of roles within a grooming bout. Groomers used BLSs to request grooming during grooming bouts and the BLS seemed to show willingness to groom, both to initiate a grooming bout, and potentially during a bout when groomees intend to start grooming their partner.

Finally, to explore the theoretical link between the evolution of communication and cooperation I tested whether, on an individual level, there was a positive relationship between communicativeness and cooperativeness in chimpanzees. In contrast to theoretical predictions, I found a significantly negative relationship between these two domains, indicating that more communicative chimpanzees were less cooperative. I explore several potential explanations for this highly unexpected finding.

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I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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CHAPTER 1: General introduction

What is communication?

Broadly, communication can be defined as the process by which a signal is coded and transmitted from one individual (sender) to another (receiver) (Marler, 1961), with this often resulting in modification of the behaviour of the receiver (Bradbury & Vehrencamp, 2011). Tinbergen (1963) proposed that in order to gain comprehensive understanding of communication (or any other behaviour), one can analyse this on four levels: 1) function, 2) phylogeny, 3) mechanism, and 4) ontogeny. The first two of these encompass 'ultimate' explanations (i.e. why this evolved), while the second two encompass proximate explanations (i.e. how this works). My aim was to explore phylogeny and function with my empirical research.

Throughout this thesis, my focus was on 'dynamic' signals (also considered 'events') that "have a limited duration and require an action by the signaller to initiate ('turn on') and to terminate the signal", as this differentiates these signals from 'state' signals, which have static features that cannot be 'turned off', such as feather colouration (Smith & Evans, 2013, p. 1390). As such, I did not record signals such as the swollen perineum of a female, as this could have a relatively long duration (over several days or weeks), and thus was deemed a state. The latter has also been described as a 'cue' (Maynard & Harper, 2003). Communication is especially critical for the survival of highly social species, which may live alongside, and interact with, many different individuals. In this case communication is key in contexts such as finding a suitable mate for reproduction, rearing offspring, finding food, and avoiding predators (Alcock, 2009). Further to communication, 'signalling behaviour' can be defined as behaviour that is, in most circumstances, adaptive and has been selected for by natural selection for the purpose of changing the behaviour of another individual (Davies, Krebs & West, 2012). Many researchers argue that communicative signals carry some kind of information, for example Smith (1997, p. 11) suggests communication is "any sharing of information between entities – in social communication, between individual animals"; while Bradbury and Vehrencamp (1998, p. 2) likewise pose it is the "provision of information from a sender to a receiver". However there is debate as to the definition of 'information' in this context (and this is often not defined at all), with some researchers encouraging the use of the term ‘influence’ instead of ‘inform’ when focusing on the signaller’s behaviour (e.g. Rendall, Owren & Ryan, 2009). The former refers to a more basic process, where the signal has the potential to influence or affect the probability of the receiver performing a certain behaviour, whereas the latter could be argued to suggest that beliefs or states of knowledge are altered.

Ultimately, signals are most effective (for the sender and/or receiver) when they are reliably given in the presence of a specific emotional, behavioural or external context. For instance, a ‘threat’ gesture may be most effective by reliably conveying the displeasure of the signaller, and reliably predicting the potential for further aggression, whereas an alarm call is most effective when reliably given in the presence of certain predators. Of course, this also means that there is the possibility that when there is a discrepancy between the interests of the sender and receiver, that sender may manipulate receiver through the use of deceitful signals. However, in general, through the course of evolution, receivers have shaped the nature of signalling behaviour in such a way that it is costly to be produced, minimising dishonest signalling (Zahavi, 1975; Grafen, 1990). Therefore, on the whole, signalling is usually beneficial for both the sender and receiver (Zahavi & Zahavi, 1999; Bradbury & Vehrencamp, 1998).

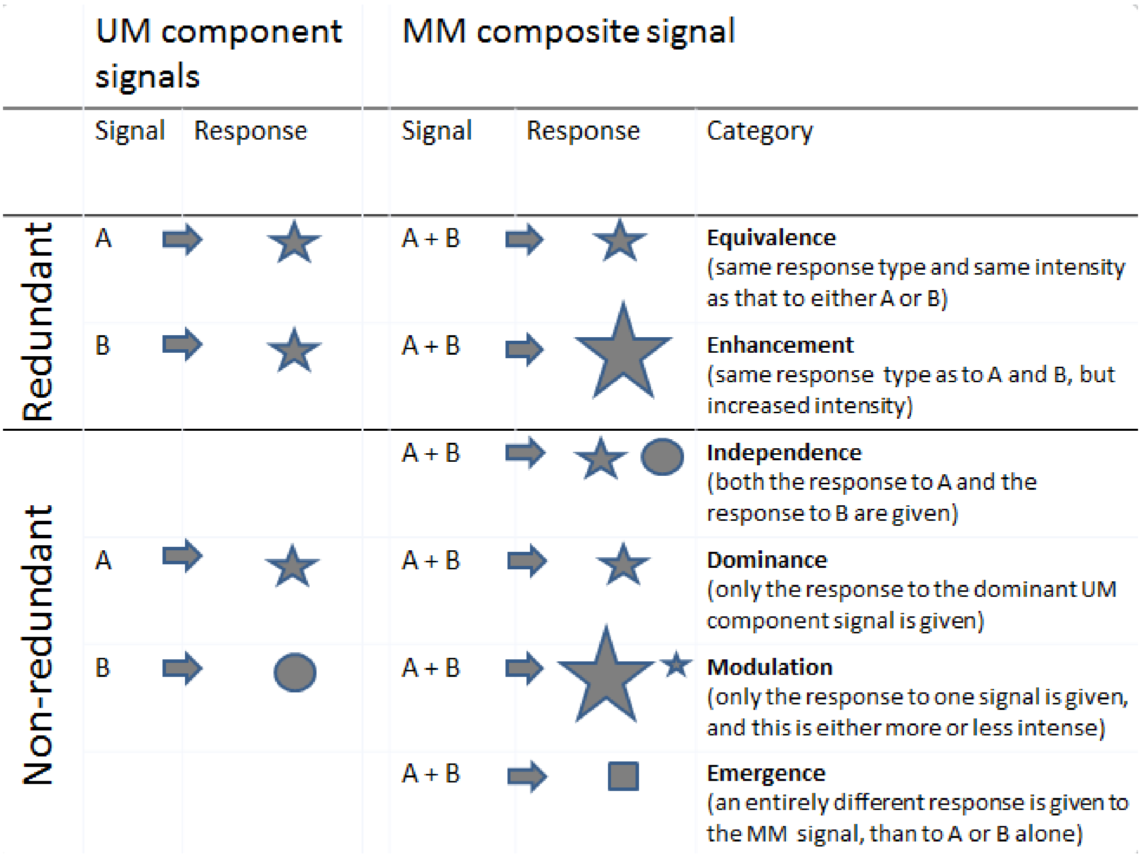
What is multimodal communication?

Most species produce communicative signals through a range of modalities, rather than simply emitting all their signals through one modality. For instance, some frog species produce advertisement calls, as well as ‘foot-flagging’ signals, as part of mating displays, and these can also be given simultaneously (Preininger et al., 2013), flies similarly make use of chemical, tactile, visual and acoustic signals in courtship displays (Colyott, Odu & Gleason, 2016), and stomatopods appear to combine chromatic cues with chemical cues in order to amplify threat displays (Franklin, Marshall & Lewis, 2016). These combinations of signals from different modalities have all been termed multimodal (MM) signals.

However, a definition of ‘multimodality’ is not quite this straightforward and important discrepancies and disagreements in the literature should be highlighted. First, it could be argued that ‘multimodal’ refers to the multiple channels through which the signal is *sent* (Partan & Marler, 1999). Contrarily, Higham and Hebets (2013) contend that the stimulation of two or more sensory systems of the *receiver* constitutes a MM signal; several other researchers agree that the perception and processing of the receiver is key (e.g. Ruxton & Schaefer, 2011). In contrast, Waller et al (2013a) advocate that rather than determining modality based on the sensory channels through which a signal is sent or received, that 'modality' should refer to the type of communicative act commonly described in the literature in a given species (e.g. gestures (manual and non-manual, see Chapter 2 for defined repertoire), vocalisations and facial expressions in chimpanzees). Whilst these three modalities could also be termed 'types' of communicative signals; in keeping with recent published studies (e.g. Taglialatela et al., 2011; Genty et al., 2014, Wilke et al., 2017), I have chosen to call them 'modalities' here. Waller et al (2013a) suggest that different cognitive processes or mechanisms may underlie different communicative acts, even if emitted through the same sensory channel (such as gestures and facial expressions, which could both be considered visual). For instance, chimpanzee gestures have often been suggested to involve more sophisticated cognitive processes (both from the sender and receiver), than facial expressions (Tomasello, 2008). A single act can also often emit sensory information through different channels (e.g. gestures such as hand-clapping, drumming, branch shaking etc.) and many vocalisations (i.e. whimper and whimper face; pant hoot and pant hoot face), necessarily produce salient audio and visual output), yet this type of multimodality is fixed as a function of signal production mechanisms and thus does not capture the flexible combination of different signals that is important in human communication. I therefore believe that, in line with Liebal et al (2013) and Waller et al (2013a), focusing on the combination of different communicative acts is more relevant for gaining insight into the evolution of our own multimodal communication system. Thus, I adopt this definition of multimodal signalling throughout my empirical investigations.

Alongside this, it should be explained that there is a distinction between signals that are inherently MM, and those that are not. 'Fixed' MM signals (Smith, 1977) are those whose component signals are necessarily combined due to the mechanics of signal production (e.g. the croaking produced by a frog and the eye-catching inflation of the throat sack). Conversely, 'free' (also referred to as 'flexible' or 'fluid') MM signals are those whose components may be produced separately (unimodally, UM) or combined flexibly with other signals (Marler, 1961; Tomasello, 2008). Thus ‘free’ combinations could be considered more cognitively interesting, if one is concerned with language evolution, as these have greater potential for flexible and intentional combinations.

Partan and Marler (1999) then offer a framework by which the function of MM signals can be determined (see Figure 1 below). This requires comparing recipient responses to the compound MM signal and the UM components in isolation. Broadly, MM signals can be categorised into (i) redundant combinations, where recipients produce the same response to the component UM signals and the MM signal, and (ii) non-redundant combinations, where recipients produce different responses to the component UM signals, with various patterns of responses to the MM signal possible (see Figure 1). One class of MM signals are particularly interesting from a language evolution perspective: emergent signals (Figure 1), where different responses are elicited by the component UM signals and the MM combination. This type of combination would allow more messages to be conveyed with finite means and may have been an important precursor to our open, generative system of language.



	UM component signals		MM composite signal		
	Signal	Response	Signal	Response	Category
Redundant	A	⇨ ★	A + B	⇨ ★	**Equivalence** (same response type and same intensity as that to either A or B)
	B	⇨ ★	A + B	⇨ ★	**Enhancement** (same response type as to A and B, but increased intensity)
Non-redundant			A + B	⇨ ★ ●	**Independence** (both the response to A and the response to B are given)
	A	⇨ ★	A + B	⇨ ★	**Dominance** (only the response to the dominant UM component signal is given)
	B	⇨ ●	A + B	⇨ ★ ★	**Modulation** (only the response to one signal is given, and this is either more or less intense)
			A + B	⇨ ■	**Emergence** (an entirely different response is given to the MM signal, than to A or B alone)

Figure 1. The classification of MM signals – based on Partan & Marler (1999). The same geometric shape indicates the same qualitative response; different shapes indicate different responses.

Several scientists have suggested that MM signalling can have several advantages over UM signalling for both producer and receiver. One benefit of a MM over a UM signal may be that a MM signal is often more easily detected, including an increased likelihood and speed of detection (Rowe, 1999) and providing insurance that the message will be received, especially in noisy environments (Partan & Marler, 2005). Likewise, a signal or display may be more memorable if it is more elaborate and incorporates several different modalities (Liebal et al., 2013). Message specificity can be increased, and more or different informational content provided in the signal. Thus, compound signals should be considered as unique, holistic signals, and it is worthwhile exploring the synergistic function of these, as these may be very different from that of the UM component signals (Figure 1).

Multimodal communication in non-primate species

It has been suggested that most animals produce MM signals (Hebets & Papaj, 2005; Rowe, 1999), with previous literature reporting MM signals in numerous taxa as diverse as ants (Uetz & Roberts, 2002), monkeys (Partan, 2002), and cowbirds (Cooper & Goller, 2004). This can involve the combination of a variety of different signals, such as seismic and visual signals (Hebets, 2008), or vocal and visual signals (de Luna, Hoedl & Amezquita, 2010; Partan, Larco & Owens, 2009). MM signals have also been reported across an array of contexts, including alarm behaviour (e.g. Partan, Larco & Owens, 2009), aggressive interactions (e.g. Schwarz, 1974) and courtship (e.g. Hebets & Uetz, 1999). Perhaps surprisingly, given the rich variety of communication research conducted with primates, it is research with non-primate species that has led the way in terms of MM research (Liebal et al., 2013).

Several elegant experiments have explored the function of MM signals, both free and fixed , and attempted to classify these based upon the framework of Partan and Marler (1999). One of these was carried out by Partan et al (2010) on wild grey squirrels, specifically in the context of alarm behaviour. Here, the researchers presented the squirrels with either a robotic squirrel producing only a bark, only a tail flag, or both combined. Each UM signal alone elicited alarm responses from the individual observing the robot, however when these were combined into a free MM signal there was a 'summation' (Partan, 2004) of responses, meaning the number of alarm responses given to the MM signal was almost exactly the sum of the number given to the UM signals. This is a clear example of a redundant signal (both UM components elicit the same response), which shows signs of enhancement. In contrast, other studies have documented MM signals which appear to be non-redundant. A study on wild frogs explored the free MM signal of 'foot-flagging' and advertisement calls (visual-acoustic signal), and both of these as separate signals, on the behaviour of the recipient, with the use of a model frog and playbacks (Preininger et al., 2013). It was found that different types of responses were given to the different stimulus types, suggesting that here acoustic and visual signals may be non-redundant. Furthermore, recipients showed more responses to the acoustic UM signal, than the visual UM signal, or the MM combination (indicating modulation). Finally, Acquistapace and colleagues (2002) demonstrated that in order to successfully determine whether another individual was male or female, a male crayfish required both chemical and visual cues. When these were both available, the male would respond with appropriate behaviour, however when only chemical cues were given, he showed no response. Unfortunately this study lacked a condition with visual cues alone, making it difficult to reliably classify this signal into Partan and Marler's framework. This highlights the importance of studying the responses to all the UM constituent signals, as well as the MM signal, in order to be able to draw conclusions about the potential function of the compound signal.

Although experimental paradigms are invaluable in allowing for controlled manipulation of conditions, observations, especially in a natural environment, can also provide important insight into signal function. A recent observational study by de Sa et al (2016) on frogs focused explicitly on multimodality from the receivers perspective. A MM courtship signal of females involved arm lifting and arm waving, usually integrated with tactile signalling. Here the signal given by the female was always the same, but in some instances both the visual and tactile components were received (considered multimodal), or occasionally only tactile (considered UM), when the visual component could not be detected by the male. The researchers found that the multimodal signal was three times more likely to receive a positive response from the male, than the UM tactile signal, suggesting that enhancement also occurs in this case; perhaps by increasing the accuracy of the transferred message. Observations have also been conducted on larger mammals. For instance, in captivity, the free MM courtship signals and behaviours of giant pandas seem not to significantly influence the response of the male mate in the short term; however the authors suggest this may be the case over a longer time-frame (Owen et al., 2013).

Overall, it is evident that many different species produce MM signals, across a range of contexts, and thus to gain a comprehensive understanding of a communication system, it is important to use methods that capture these combination signals (Partan & Marler, 1999).

Communication in non-human primates

Unimodal research: successes and limitations

In contrast to the pioneering work on MM signals in non-primate communication, a recent systematic review of primate communication literature found that the vast majority (95%) of studies only focused on a single communicative modality (Slocombe, Waller & Liebal, 2011). Before discussing the problems associated with this UM approach, it seems only fair to highlight the important progress that UM communication research in primates has made, as this has uncovered some key communicative capacities. In monkey species, this includes the alarm calls of vervet monkeys, that appear to function referentially (Seyfarth, Cheney & Marler, 1980), the gestures of macaques that seem to be used flexibly across a range of different contexts (Hesler & Fischer, 2007), and the facial expressions of capuchins that can provide valuable information to conspecific observers, and influence their future behaviour (Morimoto & Fujita, 2011).

In great apes, our more closely related relatives, complex communicative abilities have also been revealed in the last decades. In regards to communication, the term ‘complexity’ is used here to refer to the cognitive underpinnings and processes involved in the production of a signal, such as intentionality (and the varying orders of this; Dennett, 1983), referentiality, flexibility (Snowden, 1990), the free combination of signals (Hebets & Papaj, 2005), as well as other markers characteristic of our own 'highly complex' communication system.

More specifically UM research has revealed that great ape gestures are indeed used flexibly and intentionally (gorillas: Genty et al., 2009; chimpanzees: Hobaiter & Byrne, 2014; orangutans: Cartmill & Byrne, 2010), vocalisations can be used referentially (chimpanzees: Slocombe & Zuberbühler, 2005; bonobos: Clay & Zuberbühler, 2009), as well as intentionally (chimpanzees: Schel et al., 2013a), and facial expressions are argued to be under some volitional control, thus having the potential to be used to strategically influence others (Hopkins, Taglialatela & Leavens; 2011).

The studies outlined here demonstrate the advancements which have already been made in our knowledge of the communication of primates, yet the UM nature of this research, has had potentially damaging effects on language origin theories. Comparative research forms a key line of evidence for those interested in language origins, but many scholars have drawn comparisons between modalities that are likely confounded with a variety of methodological issues that apply to each modality differently (Slocombe et al., 2011). Those that argue that language has a gestural origin (e.g. Hewes, 1973), propose that language was preceded by a gestural form of communication and highlight the similarities between non-human primate gestures and human language in addition to the differences between primate vocalisations and language. For instance, they point to flexible and intentional use of gestures, which are also often used in relaxed social contexts (whereas vocalisations might be considered to be seen more often in urgent contexts), the fact that gestures are evolutionarily younger (present in apes but not monkeys), as well as the ability of primates to generate or learn new gestures. Historically they also emphasise the inflexible and unintentional nature of vocalisations – though recent scientific efforts in this area have been chiselling away at these claims (e.g. Schel et al., 2013a; Crockford, Wittig & Zuberbühler, 2015).

The 'opposing' team in this case are those that believe that our communication system has more commonalities and continuities with vocal primate communication than gestural communication (e.g. Zuberbühler, 2005). They draw on research showing that primate vocalisations can function referentially, and, more recently, that they can be intentionally produced (Schel et al., 2013a) and have the potential to be subject to vocal learning (Watson et al., 2015; Crockford et al., 2004). Further arguments include that vocalisations can be perceived as discrete signals (Fischer, 1998), and that rule-based combinations of these may exist (Outtara et al., 2009; Arnold & Zuberbühler, 2008). The contrasting lack of evidence that gestures are used to refer to external entities in the wild and studies showing that gestures are not combined into meaningful sequences are used to point out the weakness of gestural theories.

Such theories, which are strongly in favour of one or the other modality, may be premature, given these are based on UM communication research. Differing methodologies (e.g. observational vs experimental), study species (e.g. great apes vs monkeys) and environments (e.g. captive vs wild) for studying UM signals of different modalities means that there is a high probability that these confounds can account for several, perhaps even many, of the reported differences seen in the characteristics of gestures and vocalisations (Slocombe et al., 2011). Before drawing conclusions, an emphasis should be put on carrying out research which explores all communicative modalities side by side, within the same study. Researchers must also acknowledge and engage with the fact that signals from different modalities that are combined (into MM signals) could have different functions, and should potentially be treated as unique signals in themselves. In this respect, primate communication research is lagging behind research on other species, where MM signals have more frequently been documented and in several studies rigorously investigated with elegant experiments (see previous section).

In summary, the reliance on UM approaches in primate communication research is problematic for two main reasons. First, by ignoring signal combinations, we potentially have an inaccurate and incomplete understanding of primate communication systems and the complexities of their social worlds. Second, direct comparisons between modalities are confounded by a raft of methodological differences, so the theories of language origins that are built on a foundation of empirical evidence derived from UM comparative studies are on very unstable ground. Thus, we should make full use of the comparative approach by ensuring communication is studied in an integrated, objective and comparable manner; this has the potential to be a powerful tool in shedding light on the origins of our own complex communicative abilities. Indeed an increased focus on MM communication may ultimately lead to a MM origin of language theory (e.g. Slocombe, Waller & Liebal, 2011; Aboitz, 2012; Taglialatela et al., 2011). This would make some intuitive sense, given the multimodal format in which language is exchanged, and the fact that in humans and monkeys multimodal communication activates overlapping neural circuits (Aboitz & Garcia, 2009). Thus it could be posed that language evolved through an integrated combination of vocal, gestural and facial communication – bridging the ancient divide between the vocal and gestural theories, and fitting well with previous findings suggesting complexities in both vocal and gestural domains.

Multimodal communication in non-human primates

Whilst the vast majority of primate communication research is conducted in a UM manner, it is worth noting a few recent primate studies which *have* endeavoured to take a MM approach, and explored the responses to both the UM component signals and the MM composite. First, Micheletta and colleagues (2013) examined ‘lipsmacks’; an affiliative signal given by crested macaques, which can comprise visual and vocal components (combined into a free MM signal). In their observations in the wild they found that adding a soft grunt to the visual component of a lipsmack resulted in this being followed more frequently by affiliative contact, than the visual signal alone. They point out that the responses to the UM visual and MM signal were not found to be qualitatively different, but rather that the function appeared to be enhanced, potentially due to the higher salience of the MM signal. They concede, however, that it is difficult to categorise these signals as redundant or non-redundant as it was not possible to evaluate the function of both UM signals in isolation. Other studies that have equally made use of a MM approach have also included static signals, alongside dynamic signals. One of these is the investigation carried out by Rigaill et al. (2013) into the sexual signalling of olive baboons. Here they included sexual swelling size and colour, as well as olfactory, vocal and behavioural signals, finding that the latter three provided valuable information to males by advertising the beginning of the fertile phase of the female’s cycle. However, they did not operationally define multimodal signals, so it is unclear whether signals were temporarily overlapping (e.g. for auditory and behavioural), nor did they carry out any systematic investigation into the function of each of these signals alone. Nevertheless, they suggest that the use of multiple signals may provide additional information and increase the accuracy of assessment of mate quality. Similarly, Higham et al (2013) studied rhesus macaque sex skin colouration, vocal signals, hormone levels, and several other variables, in concert. Again it was concluded that these function to inform and influence mate choice, however it was also acknowledged that the data did not make it possible to explore the function of each signal separately, which, again, would have been ideal.

In great apes, multimodal studies are few and far between. In some cases researchers have looked at multiple modalities within a study, but have not gone on to also include signals given as combinations of these modalities. For example, Poss et al (2006) explored the gestures and vocalisations given by orangutans and gorillas, when these either had the attention of a human experimenter, or not. Both species showed flexibility in their communicative behaviour and seemed to modify their communication to manipulate the attentional state of the human, indicating that these signals were intentional. Thus, this study, although it did not examine combinations, presented data on two communicative modalities, under the same conditions, making comparisons across modalities plausible, and providing valuable insight into the function of these signals in these species.

Genty et al. (2014) investigated multimodal sequences in bonobos. Here the researchers focused on the ‘contest hoot’ vocalisation, which is frequently directed at specific individuals, and combined with ‘soft’ or ‘rough’ gestures into multimodal sequences, where the vocalisation and gestures were produced within 1 s of one another. ‘Soft’ gestures were those which were silent signals, produced without significant force, whereas ‘rough’ gestures were those performed with force, and could include physical contact. They found that multimodal sequences were no more effective at eliciting reactions than the contest hoot vocalisation given alone; however, interestingly multimodal sequences given by the alpha male did elicit significantly more responses than those given by non-alpha males. This suggests that these signals may have different functions for individuals at different positions in the dominance hierarchy and that it may be worthwhile including rank as an explanatory factor when exploring MM communication. The UM gesture component was context specific (i.e.

soft gestures were more often used in a play context; hard gestures in an agonistic context), providing additional cues about the nature of the interaction (though they did not look in more detail at the types of responses given to each of the different UM gesture types). They suggest the function of the MM sequence is to inform another individual of the intention to interact (conveyed through the contest hoot), and the type of interaction (conveyed through the type of gesture). Again, the authors recognise the importance of testing each signal's function alone, in future research. Although this point has been emphasised by numerous researchers, few studies look at MM signals in the sense of temporally overlapping UM signals (i.e. not sequences), and even fewer still include the exploration of UM versus MM signal function. The very limited number that have attempted this, have been carried out with chimpanzees in captivity, and are discussed in the second part of the following section.

Communication in chimpanzees

As chimpanzees (and bonobos) are our closest living relatives, research on chimpanzee communication is particularly relevant for informing language evolution theories. Chimpanzees are a powerful model by which to estimate the capacities of our last common ancestor (LCA) that lived approximately 6-8 million years ago (Langengraber et al., 2012). By studying extant apes we can attempt to map out the differences and similarities in communicative abilities of humans and our closest living relatives in order to discern which are the derived, uniquely human aspects of language, and which may have built on abilities already present in common ancestors. Nevertheless, it should be noted that although similarities in closely related species can represent homology, these could also be explained by convergence. In order to disentangle these two alternative explanations for similarities, it would be of great value to study other, closely related, species in the future (such as other great apes), following these initial explorations with chimpanzees.

Unimodal communication in chimpanzees

Previous research on chimpanzee communication has shown it has several interesting characteristics relevant to human language, as already very briefly touched on in the 'Communication in primates' section above. In the vocal domain, similarities with many other primate species have been found, including the finding that captive chimpanzees have functionally referential food calls that allow listeners to understand the value of a discovered food source (Slocombe & Zuberbühler, 2005). Importantly, evidence of flexible, socially mediated, vocal learning in functionally referential food grunts has also recently been documented in captivity (Watson et al., 2015). This is the first time this has been revealed in referential calls; this evidence adds to that of other chimpanzee vocalisations (e.g. pant hoots; Crockford et al., 2004), that have also demonstrated vocal learning, suggesting the structure of chimpanzee vocalisations can be modified to some extent. Furthermore, wild chimpanzee vocal production is sensitive to subtle social factors in that vocal signals are affected not only by the presence or absence of an audience but the identity, or class (e.g. high ranking male), or behaviour of individuals present (Slocombe et al., 2010; Schel et al. 2013b; Townsend & Zuberbühler, 2009; Fedurek & Slocombe, 2013; Laporte & Zuberbühler, 2010), and can be argued to be used intentionally (Schel et al., 2013a). Alongside vocalisations, gestures are frequently produced and have the hallmarks of intentional signals (Leavens, Hopkins & Thomas, 2004; Hobaiter & Byrne, 2014; Roberts, Vick & Buchanan-Smith, 2013). In addition, new gestures can be "invented", with some individuals and groups producing their own idiosyncratic variants (Goodall, 1986; Tomasello et al, 1985). Gestures are employed flexibly across a range of contexts (Hobaiter & Byrne, 2011a), with receivers using contextual cues in combination with the signal in order to respond in the appropriate manner. Further to this, one study has claimed to demonstrate the existence of a gesture given by wild chimpanzees which functions referentially (Pika & Mitani, 2006; but see Chapter 3). Facial expressions have not been studied as extensively from a cognitive perspective (Slocombe, Waller & Liebal, 2011); nevertheless, there is some indication that facial expressions in chimpanzees are under voluntary control, rather than being mere reflexive responses (Hopkins, Taglialatela & Leavens, 2011). Thus, it is clear that vocalisations, gestures and facial expressions are all important forms of communication for chimpanzees, and this previous UM literature has highlighted several features of communication that may have acted as building blocks for human language.

Multimodal communication in chimpanzees

As mentioned above, primate studies which focus on several communicative modalities within the same setting are rare; even rarer are those involving one of our closest living relatives, the chimpanzees. Here I will outline some of the first attempts at using a MM approach to explore chimpanzee communication. It should be noted that these were all in captivity.

Perhaps one of the first studies to look at UM and 'bimodal' communication was that of Leavens and colleagues (2004). This involved experiments where a food reward was handed to either the chimpanzee focal individual, a cage-mate within the same cage, or an individual in an adjacent cage. Communicative signals by the focal individual were recorded, including visual, auditory, and bimodal/MM visual-auditory signals. These were all directed towards the human experimenter and showed tactical use, with visual and bimodal signals being produced more often when the experimenters attention was towards the focal animal, and auditory (and 'disengagement') behaviours being given more when the human's attention was directed towards another individual. As the apes seem to be taking the experimenters attentional state into account when signalling, and appear to be actively trying to manipulate this with the appropriate signal modalities, this points towards an intentional use of these types of signals. Similar results were obtained in a later study by Leavens, Russell and Hopkins (2010), where complex signalling tactics seemed to be employed by the chimpanzees when the human experimenter showed differing attentional states. The authors point out that it is close to impossible to conclusively determine whether the chimpanzees were trying to manipulate the psychological state of the human, but that this problem is equally the case for any non-verbal organism, including human infants. As human babies are credited with having advanced appreciations pf psychological states from these types of experimenters, the same logic should apply for other great apes.

Focusing on conspecific interactions, Pollick and de Waal (2007) explored gestural as well as facial/vocal signals in captive chimpanzees and bonobos, and MM combinations of these (defined as signals within 10 s of each other). Concerning the production of these in chimpanzees, 55.9% of signals were found to be gestural, 22.5% facial/vocal and 21.6% a combination of these two. For this species it was found that a

MM signal was not more effective at eliciting a response than a gesture alone. However the authors did not test the responsiveness to facial/vocal signals alone (which could in themselves be fixed MM signals), nor did they control for context of the specific types of gestures; making it difficult to truly understand the function of these types of signals.

The common nature of MM signals in captive chimpanzee groups is further emphasised by Taglialatela et al. (2015) who recorded MM signals that comprised vocalisations and signals from other communicative modalities (such as gestures and facial expressions), but also behaviours (such as chase). This study found that approximately half of vocal signals produced were accompanied by another signal, from a different modality, or a behaviour (considered a MM signal). Furthermore these MM signals were more likely to be directed to another individual, than vocalisations alone, perhaps indicating that chimpanzees use these to achieve specific socio-communicative outcomes. Again there were a few limitations to this study, such as that signals and behaviours were both considered components of a MM signal, rather than only single communicative signals. For instance one signal/behaviour that was recorded to occur concomitantly to a vocal signal was ‘play’; this comprises a vast range of different behaviours and signals, and should likely be categorised separately to such MM combinations as a vocal signal and a ‘threat’ gesture. It would also have been intriguing to attempt to look at response to these UM and MM signals, as was done by Pollick and de Waal (2007), to delve deeper into their function.

Alongside these observational studies, only one study has experimentally investigated UM and MM signals in chimpanzees. Parr (2004) found that captive chimpanzees could successfully match corresponding facial and vocal elements of fixed MM signals (e.g. pant hoot vocalisation with a pant hoot face). It would be highly interesting to extend this research to understand the extent to which chimpanzees form cross-modal associations between elements of freely combined MM signals, including gestures. Parr also gave the chimpanzees the opportunity to demonstrate the modality they found most salient in fixed MM signals using a match-to-sample paradigm. When given an incongruous sample video (e.g. pant hoot face and scream vocalisation), she found that the chimpanzees preferred to attend to and match on the basis of the vocal signal for pant hoots and the visual signal for screams. This study is an important first step for future experimental research investigating MM communication in chimpanzees, and similar paradigms could be used to explore the specific qualitative outcomes or recipient responses to free MM signals and their component UM signals. Waller, Whitehouse and Micheletta (2016), recently pioneered such an approach, where crested macaque monkeys were trained to match signals with outcomes (e.g. affiliative grooming vs agonistic fight) and then tested on the outcome they predict for novel signals. Given that it is unlikely that robotic models are feasible to use to test MM signal function in chimpanzees, these kind of touchscreen based paradigms offer a promising alternative.

In summary, very little research investigating chimpanzee communication has thus far attempted to integrate several modalities, and explore these within one study. The research that has, has been carried out in captivity, and a clear operational definition of 'MM' is often absent. Equally only a single research group has attempted a systematic experimental exploration of recipient perceptions of UM and MM signals, and this did not include gestures (Parr, 2004). Finally, no study has attempted to document responses to specific component UM signals and compare them to responses to MM signals, which is essential to understanding the function of MM signals in our closest living relatives. Such empirical evidence will play a pivotal role in the formation of theories related to the likely origin of language. In the next section I will discuss, in a much broader manner, how our understanding of primate communication is used to influence our understanding of how our own communication system evolved.

Language evolution

The origins of human behaviour, including language, can be investigated through a diverse range of methods. In a multi-disciplinary arena, where the study of linguistics, genetics, computer modelling, functional morphology, neuroscience and developmental psychology, contribute to our understanding of language evolution, comparative research also plays an important role. For instance, research on evolutionary homologies provide information on the phylogenetic traits that humans and other animals share with their LCA. Comparative research with chimpanzees, and the identification of homologous traits we share with this species, is particularly helpful in allowing us to reconstruct the phylogenetic history of our own communication system. By doing this we can determine which facets of communication were already likely to have been present in our LCA (6-8million years ago), and which may be unique to the human lineage and critical in the evolution of our extremely complex communication system. Equally, the discovery of analogous traits can help us understand the evolutionary pressures that lead to the emergence of the same biological traits that evolved independently in phylogenetically distant species (Hauser, Chomsky & Fitch, 2002).

If comparative evidence from primates examining the ultimate function of communicative signals is going to usefully inform our understanding of the evolutionary pressures that might have made language adaptive, it is vital to first ascertain the function of human language. A recent experimental study by Redhead and Dunbar (2013) sought to test whether humans used language for social gossip, social contracts, mate advertising or factual information exchange. It was found that the primary function of language in everyday contexts is to talk about the social world. The researchers propose that language may have evolved primarily to facilitate ‘gossiping’, and once it was in place, it acquired other functions, such as non-social informational exchange. However, this prominent theory currently lacks empirical evidence, as it is difficult to test directly.

The function of communicative signals has also been studied in wild chimpanzees. Hobaiter and Byrne (2014) determined the likely desired outcome of numerous chimpanzee gestures, by observing which response satisfied the signaller, causing them to cease signalling. Thus, they could decipher the meaning, or function, of many of these intentional gestural signals, finding that the majority of these were imperative demands, often requiring movement of the recipient. Although this may indicate that a primary function of chimpanzee gestural communication is negotiation of social interactions, their methodology precluded the investigation of potentially declarative signals. Similarly, Roberts, Vick and Buchanan-Smith (2012) found that wild chimpanzees can infer meaning from gestures, taking the context of production into account, and again found that the primary function of the gestures studied was for directing the recipient’s movement or attention. In contrast, wild chimpanzee alarm vocalisations are produced intentionally, and seem to function to warn conspecifics about immediate danger (Schel et al., 2013a; Crockford, Wittig & Zuberbühler, 2015), indicating a potential declarative type of communication. Chapter 2 looks in more detail at the potential functions of one specific signal.

Whilst comparative evidence is undoubtedly an important piece of the language evolution puzzle, there is debate as to which aspects of language are best explored in other species. For instance, the structural properties of language, such as syntax and phonology, are often explored in non-human species. These are frequently studied together, as one important property of language is 'duality of patterning'. This refers to the combinatorial structure of language, which is found on two levels: phonology, where phonemes are combined into morpheme and words, and syntax, where morpheme and words are combined into larger structures (Hurford, 2008). This paves the way for our incredibly large, potentially infinite, lexicon of signals. Interest in this has led to studies on animal call combinations, which look to find any similarities to these two structures. Thus far there is no clear evidence for the existence of phonology, but promising support for syntax in animal communication systems (Collier et al., 2014). This suggests that syntax might be a simpler, more basic, process, which evolved before more sophisticated phonology.

Although considerable research effort has been dedicated to examining structural properties of language in other species, more recently the utility of this approach has been questioned and researchers encouraged to focus on the social-cognitive underpinnings of language (Scott-Phillips, 2015). Within this approach, researchers are trying to gain an understanding of the other cognitive faculties that are linked to language, or that are potentially necessary for language to become established. Three types of cognition have been proposed as precursors to language: orientation and navigation (e.g. Menzel et al., 2011), number (Cantlon & Brannon, 2007), and social cognition (Cheney & Seyfarth, 1990). Of these, social cognition has been argued to have the most support, as it deals with agents and actions, and having highly developed social cognition in place (e.g. building and maintaining bonds, and tracking others relationships, intentions, desires and beliefs) means that many of the crucial facets of language are already cognitively present (Seyfarth & Cheney, 2014). As part of social cognition, intentional signal production has been highlighted as an important ability crucial for language. By now there is ample evidence to suggest that chimpanzees demonstrate first order intentionality (characterised by voluntary control of signal production, with signals directed at specific individuals in order to achieve a goal) in their gestural communication (e.g. Leavens & Hopkins, 1998; Liebal et al., 2004; Roberts et al., 2014). Recently it has also been demonstrated that some types of chimpanzee alarm call also show this level of intentionality (Schel et al., 2013a); a significant discovery considering the long-held belief that signals in this modality are involuntary and emotional (Tomasello, 2008). Thus, although humans routinely show higher orders of intentionality in language production (Dennett, 1983), this research brings to light important similarities in the socio-cognitive domains in humans and chimpanzees, on which the higher orders of intentional communication may have been built, paving the way for language emergence. Finally, a similarly broad spectrum of socio-cognitive faculties may underpin engagement in cooperative behaviours (e.g. Frith & Frith, 2012), which have in turn been argued to be pivotal for language. This is explored in the following section.

Cooperation and the evolution of language

Several theories hypothesise a relationship between cooperation and communication. On the one hand there are those that suggest some basic form of cooperation must already be in place in order for complex communication to evolve, as individuals must have an urge to share information and intentions with others (Nowak & Krakauer, 1999). As words have been described as “cheap signals” (Zahavi, 1993), and could easily be used to deceive, there must be another reason why, on the whole, individuals trust and believe on another’s verbal utterances. Thus, complex communication (such as language) inherently implies a predisposition to cooperate (Grice, 1975); without this cooperative foundation at an individual and societal level, language may not be able to evolve and spread as an evolutionarily stable strategy. Similarly, cooperative breeding in the hominin lineage has been suggested to have driven the development of communicative processes, among other cognitive skills (e.g. Hrdy, 1999; Burkart & van Schaik 2010). From a somewhat different perspective, a very recent theory has also posed that cooperation allows for animals to acquire more protein, which in turn allows for bigger brains and advancements in cognitive and cultural traits, including communication (Coelho & McClure, 2016). Thus there seems to be ample indication that cooperative tendencies pave the way for the emergence of complex communication.

Equally, other theories postulate that more complex communication, which can be future-directed and dependent on detached representations (i.e. not necessarily referring to current events, objects and emotions), is essential for complex cooperation to be achievable (Brinck & Gaerdenfors, 2003). Without the help of symbolic communication, such as language, we would not be able to persuade others that a future goal is worth striving for, and be able to plan how this could be accomplished (Gaerdenfors, 2004). Likewise, communication is useful for establishing shared norms in the society; a vital prerequisite of more widespread cooperation (Fehr, Fischbacher & Gaechter, 2002), as well as finding and punishing free riders in the group (Smith, 2010), again potentially increasing cooperative tendencies. Several researchers have also attempted to model the emergence of cooperation using mathematical frameworks to investigate how measures of communicative production and processing complexity can influence cooperation over several 'generations' (e.g. Miller, Butts & Rode, 2002), finding that as communicative complexity increases, longer bouts of mutual cooperation are expected. Similar models have found that the number of communicative signals produced prior to a cooperative game, increased the use of cooperative strategies (Santos, Pacheco & Skyrms, 2011). These studies highlight the essential role of communication in making cooperation an advantageous and widespread behaviour.

When cognitive traits seem interdependent and might have co-evolved, several scholars underline the importance of considering these cognitive traits together (e.g. Pinker, 2010; Zlatev, 2016; Burkart & van Schaik, 2010). When two traits show such a close connection to one another, it is difficult to study and understand the evolution of these behaviours in isolation, as selection on one may have influenced and accelerated the evolution of "synergistic" traits (Szathmary & Szamado, 2008). Thus, the study of links and relationships between cognitive domains is highly informative and important if we are to uncover the evolution of our extremely complex behaviour.

Therefore, it is clear that the theoretical and empirical accounts of cooperation and communication outlined above, point to an evolutionary link between communication and cooperation. Although there is debate as to the directionality of any relationship, in this thesis I am not able to establish which of the theories has more credence, rather I simply aim to explore whether there is a relationship between these two traits in other species, perhaps most interestingly in chimpanzees, our closest living relatives, in order to discern whether ability in one truly correlates with ability in the other.

Cooperation in humans and chimpanzees

Humans are known to be hyper-cooperative and remarkably altruistic (Bowles & Gintis, 2011; Burton-Chellew, Ross-Gillespie & West, 2010); we help even unrelated strangers with apparent cost to ourselves. Instances of this include giving blood, donating money to charity, and giving aid to people in crises on the other side of the world. It is unlikely we will ever meet the people whom we are helping with this behaviour, and unrealistic to expect favours in return. Even from an early age it seems that humans have the propensity to help. Warneken and Tomasello (2006) found that of 24 18-month old children, 22 helped on at least one task (10 situations) where an adult was having trouble reaching a goal, with the majority needing only to see the adult focusing on a desired object, without gaze alternation or verbalisation. This suggests that this faculty is sophisticated even from an early age, and very young children are already motivated to help others.

On the surface, some acts of extreme human cooperation seem hard to explain as evolutionary stable strategies, so it is important to understand cooperation in terms of mechanisms that make seemingly selfless behaviour beneficial for the actor. Nowak (2006) proposes that there are five basic mechanisms that support the evolution of cooperation – these are kin selection, direct reciprocity, indirect reciprocity, network reciprocity and group selection. In general these behaviours may be costly for the actor to perform, whilst benefiting another individual; however the actor is also likely to ultimately gain benefits from this behaviour (for example through future reciprocation). Here, the focus will be on kin selection, and direct reciprocity, the mechanisms most commonly studied in animals, as well as humans. Kin selection means the individuals cooperating are genetic relatives, thus on a genetic level the actor benefits by increasing the fitness of individuals carrying shared genes. Direct reciprocity (also known as reciprocal altruism, e.g. Smith, 2010) refers to repeated encounters between two individuals, where one individual may help, or provide something positive for, another individual with cost to themselves, with the opportunity for the other individual to return this favour at the next encounter. It is unlikely that an individual will continue cooperating, if their partner does not do the same. Smith (2010) identifies another important mechanism of cooperation: mutualism, referring to a scenario where two individuals cooperating yields higher payoffs for both, than if either one were to “defect” and act alone. Again, here it may be costly for an individual to engage in this behaviour; however it will ultimately confer a benefit on both parties. It is important, when examining the spectrum of different cooperative behaviours, to be clear about the type of cooperation involved.

Whilst chimpanzee cooperation is not as frequent or extreme as human cooperation, they do engage in a range of behaviours that are argued to be cooperative in terms of mutualism or direct reciprocity. The most common way to investigate cooperation in “mutualistic” tasks, where two individuals work together to reach a common goal that neither can achieve individually, is to give captive individuals the ‘loose string paradigm’. Pioneered by Hirata (2003), this paradigm uses a food platform, which can be pulled into reach, only when both ends of the rope are pulled simultaneously. The ends are too far apart for both to be reached by one individual, so two individuals must work together to solve the task. If only a single chimpanzee pulls, the rope becomes detached from the food platform and the food remains out of reach for both individuals. In a series of experiments, Melis and colleagues found that when given the choice of different apparatuses, chimpanzees only recruited collaborators to help pull the platform when this was necessary to reach the food and they could not pull the platform into reach by themselves (Melis, Hare & Tomasello, 2006b). Thus, they understood the function of the collaborator, and were not particularly inclined to share a food reward which they could reach and take for themselves. It was additionally found that cooperation in this type of task may be mediated by the tolerance between the chimpanzee dyads; those with high tolerance outside the test (i.e. happy to share food) were more likely to cooperate in the test than those with low tolerance (Melis, Hare & Tomasello, 2006a). This makes sense in that if cooperation is not beneficial for both parties either immediately (as in this mutualistic task, where the mutually gained food reward must be shared) or in the future (direct reciprocity), then it is unlikely to prevail. Recently it has also been shown that, using a “stag-hunt” paradigm, where individuals have the simultaneous option of working alone for a low value reward, or working with another for a high value reward, chimpanzees only chose to work collaboratively for a better quality reward, and chose working alone over working with another individual when both strategies provided equal reward (Bullinger et al., 2011). This suggests chimpanzees are not intrinsically motivated to collaborate in a mutualistic task, unlike humans, which may find these cooperative interactions rewarding in themselves (e.g. Gräfenhain et al., 2009).

Captive chimpanzees also engage in cooperative acts characterised by direct reciprocity – where chimpanzees help a conspecific, even with no immediate reward for themselves, with the expectation that the partner will return the favour, in some form, in the future. Cues may be required to elicit this behaviour, such as the partner visibly requiring help, and actively trying to obtain the reward. When this is the case then chimpanzees are capable of assisting another chimpanzee to obtain food and non-food tokens (Melis et al, 2011). In this study it was not possible for recipients to directly reciprocate during the testing trials, however the authors nevertheless suggest that this type of helping may be driven by reciprocal mechanisms. Linking to this, there is some (albeit weak) evidence to suggest that chimpanzees are more likely to reciprocate favours to individuals that had recently helped them i.e. direct reciprocity (Melis, Hare & Tomasello, 2008). It has been suggested that in experimental conditions, reciprocity, as seen in the wild, may not necessarily arise because often experiments involve food items (perhaps a more competitive item), rather than grooming or agonistic support (Brosnan et al., 2009). The above evidence again suggests that chimpanzees may be reactive, rather than proactive, co-operators when it comes to direct reciprocity in captivity, and thus not necessary inherently motivated to cooperate, as humans seem to be.

In the wild cooperation in chimpanzees has been studied by looking at a range of behaviours that are suggested to have cooperative elements. Joint activities such as hunting may be considered mutualistic, with individuals more likely to catch a monkey by hunting simultaneously, than alone, and potentially showing signs of more sophisticated coordination (e.g. Boesch, 1994). More simply, however, individuals may monitor the state of the hunt and act in ways that maximise their own chances of catching a monkey at any particular time (Stanford et al., 1994), given the actions of others also engaged in the hunt. Boesch (2002) argues that in the Tai chimpanzee community, Ivory Coast, hunting behaviour is not merely driven by such selfish urges, as he describes that only rarely do individuals compete for the ‘best’ position (where they might be most likely to make the kill), and once the prey has been captured, the capturer immediately informs others by making a ‘capture call’; thus attracting others to share the spoils. Both boundary patrols and intercommunity encounters can also be considered mutualistic activities, with usually many individuals working together to achieve a common goal – that is to deter members from other communities from encroaching on their territory and gaining access to resources such as feeding trees and females, or to expand their own territory and access to more resources. This is an energetically costly behaviour (Amsler, 2010), and a high risk activity, especially if another community is encountered, and particularly for adult males, who are often at the forefront, and targets in such attacks (Muller & Mitani, 2005).

In contrast to hunting and boundary patrolling, behaviours such as supporting individuals in agonistic encounters, meat sharing and investing time and energy into grooming other individuals may be better understood within a direct reciprocity framework (Nowak, 2006). Chimpanzees have been shown to balance provision of grooming services over several repeated encounters with the same individual (Gomes, Mundry & Boesch, 2009), and appear capable of long-term reciprocation. Meat sharing is also often reciprocated over several successful hunts (Mitani & Watts, 1999, 2001). However, services do not have to be directly repaid in the same “currency”, as chimpanzee societies have been suggested to be akin to “marketplaces”, where services and goods are traded and exchanged (de Waal, 1982). Studies have shown that grooming increases food sharing from the groomee to the groomer (de Waal, 1997), with this effect being in line with an exchange model, rather than merely a reflection of the state of the relationship. Furthermore, males in the Ngogo community seem to exchange meat for agonistic support, (Mitani & Watts, 2001), and agonistic support for grooming, and vice versa (Watts, 2002), whilst males in the Tai forest, Ivory Coast, have been suggested to exchange meat for sex with females (Gomes & Boesch, 2009). It therefore seems likely that chimpanzees are able to store information regarding the services they have provided and received from different individuals, and this influences their future behaviour.

Summary of study aims

The overarching aim of this thesis was to systematically explore different aspects of wild chimpanzee communication and how this may be linked to cooperation. The empirical work presented in Chapters 2-4 addresses this objective. The aim of Chapter 2 was to document the repertoire of MM signals produced, and flexibly combined, by chimpanzees in their natural environment, for the first time. From this it could be established whether chimpanzees have the propensity and motivation to combine different modalities, potentially informing MM theories of language evolution. Secondly, I endeavoured to explore the individual and contextual variables affecting the rate of signal production and likelihood of eliciting a response for UM and MM signals, with vocal, gestural, facial and MM signals being collected side by side, with comparable methods. As seen in the literature discussed above, this kind of research has so far been lacking in primate communication studies, yet strongly encouraged by several scholars (e.g. Slocombe, Waller & Liebal, 2011; Taglialatela et al., 2011). Third, I focused on one specific MM signal and attempted to elucidate the function of this by comparing the responses to this to those of the UM constituent parts. Again, this is the first time this has been attempted with chimpanzees, or any primate species to my knowledge. This makes it possible to determine whether a MM signal is redundant or non-redundant, and make inferences as to its function. Hopefully this will lead the way for further use of comprehensive methodologies like this in primate communication, so that we ensure that our understanding of their communication systems is accurate and complete.

In Chapter 3 I single out one specific, and common, gestural signal (the big loud scratch, BLS) for a more detailed exploration into its function in dyadic grooming interactions. Grooming is a highly important cooperative social interaction, which requires negotiation between partners, thus it would be valuable to understand how this is coordinated. I test four hypotheses regarding the function of the BLS, including whether the BLS is used to (i) attract the visual attention of the partner, (ii) initiate grooming (iii) request grooming or a ‘present groom’ gesture from the partner and (iv) request grooming of a specific body area, and therefore could be regarded as a referential signal. The claim that BLS signals could function referentially has had a significant impact on debates surrounding language evolution, and thus it is crucial to test and attempt to replicate previous findings concerning this issue.

Chapter 4 aimed to empirically investigate the theorised link between communication and cooperation by looking at variation in these, on an individual level, in chimpanzees. I examined relationships between communicative and cooperative tendencies and how this relationship may be mediated by individual variables. From previous theories it would be expected that highly communicative individuals might engage in more cooperative activities.

CHAPTER 2: Production of and responses to unimodal and multimodal signals in wild chimpanzees

ABSTRACT

Animals communicate using a vast array of different signals in different modalities. For chimpanzees, vocalisations, gestures and facial expressions are all important forms of communication, yet these signals have rarely been studied together holistically. The current study aimed to provide the first comprehensive repertoire of flexibly combined (‘free’) multimodal (MM) signals, and assess individual and contextual factors influencing production of, and responses to, unimodal (UM) and MM signals in wild chimpanzees. In total, 48 different free MM signals were produced. MM signals were produced at a significantly lower rate than UM signals, but 22 of 26 focal animals were observed to produce free MM signals. The relative production rates of different types of UM and MM signals differed significantly between the behavioural contexts investigated, showing flexible use of signals across contexts. In contrast, individual factors such as age, sex, or rank of signaller did not appear to influence the type of signal produced or the likelihood of eliciting a response. Finally, I compared recipient responses to free MM grunt + gesture signals and matched UM component signals and found that these MM signals were more likely to elicit a response than a grunt alone, but were as likely to elicit a response as the gesture alone. The overall findings point to a widespread capacity for wild chimpanzees to flexibly combine signals from different modalities and highlight the importance of adopting a MM approach to studying communication.

INTRODUCTION

As covered in some depth in Chapter 1, multimodal (MM) signal production can be seen across a wide range of animal species (Hebets & Papaj, 2005), however, surprisingly, the majority of research takes a very narrow unimodal (UM) approach, focusing on only a single modality. This is particularly pervasive in primate communication (Slocombe et al., 2011), and the problems this brings include making comparisons across modalities difficult and biasing our understanding of the characteristics of signals in different modalities (Liebal et al, 2013; Slocombe, Waller, & Liebal, 2011). Moreover, the MM signals that most animals emit are not captured by unimodal methods, and an important aspect of potential complexity in animal signalling may be lost as a consequence (Partan & Marler, 1999). Thus, there is a clear need for more integrative and inclusive MM methods to be used when studying primate communication, similar to as those employed to study the communicative signalling of non-primate species (e.g. squirrels: Partan, Larco & Owens, 2009). I advocate that a MM approach which simultaneously investigates UM and MM signals using comparable methods is necessary to gain a comprehensive understanding of communication in any given species.

There are, however, some discrepancies and disagreements in the literature as to the definition of MM signals, as already outlined in Chapter 1. To briefly reiterate; throughout the empirical investigations of this thesis I focus only on 'dynamic' signals that "have a limited duration and require an action by the signaller to initiate ('turn on') and to terminate the signal" (Smith & Evans, 2013, p. 1390). In terms of modality, whilst I acknowledge contrasting definitions in the literature (e.g. Higham & Hebets, 2013), I adopt the definition advocated by Waller et al (2013a), and I define 'modality' as different communicative acts performed by chimpanzees i.e. facial expressions, vocalisations and gestures (as discussed in Chapter 1). Equally, I distinguish between 'fixed' and 'free' MM signals (Smith, 1977); where only 'free' MM signals are comprised of signals that can be produced in isolation (as UM signals), and can thus be flexibly 'mixed and matched'. Finally, there is variation in the literature as to how MM signals are operationally identified. Whilst fixed MM signals necessarily occur simultaneously, when considering free MM signals, some studies have looked for temporal overlap between signals (Partan, Larco & Owens, 2009), whilst others allow a margin of up to 10 s between the UM component signals comprising a MM signal (Pollick & de Waal, 2007). In line with Partan et al., 2009, I define MM signals as those with temporal overlap between the component signals.

In line with a framework offered by Partan and Marler (1999), the function of a MM signal can be determined by comparing recipient responses to the MM signal and the UM components in isolation. In the case of fixed vocal-visual MM signals, this has often been determined through careful experiments that use playbacks for vocal signals and animated models to test responses to visual signals. Although experiments remain optimum and have been applied to free MM signals (Partan, Larco & Owens, 2009), the function of these signals can also be examined by careful collection of observational data on recipient responses to the MM signal and its component parts when produced unimodally. Broadly, MM signals can be categorised into (i) redundant combinations, and (ii) non-redundant combinations, with possibilities for the responses to the MM signal to be different from those to the UM components (emergence) or more similar to those to one of the UM signals (dominance) (see Figure 1 in Chapter 1). Understanding the communicative abilities of primates is not only important for establishing a window into their complex social world and cognitive abilities, but also for understanding human language evolution. Mapping out the differences and similarities in communicative abilities of humans and our closest living relatives may help to discern which are the derived, uniquely human aspects of language and which may have built on abilities already present in common ancestors with extant primates. In addition, characteristics of primate vocal and gestural communication provide key lines of evidence for theories concerning whether language has vocal or gestural origins (Slocombe, Waller & Liebal, 2011). Amongst the primates, chimpanzees, our closest living relatives (alongside bonobos), provide the best model of what our last common ancestor may have been capable of, and thus play a critical role in informing debates on the evolutionary origins of human language (Hayashi, 2007; Watson et al, 2015; Schel, Machanda, Townsend, Zuberbühler & Slocombe, 2013; Taglialatela, Russell, Schaeffer & Hopkins, 2011; Hobaiter & Byrne, 2011a).

For chimpanzees, vocalisations, gestures and facial expressions are all important forms of communication, and previous UM research on these different types of signals have investigated characteristics such as intentionality (e.g. Leavens, Hopkins & Thomas, 2004; Schel et al., 2013a; Hopkins, Taglialatela & Leavens, 2011), referentiality (e.g. Slocombe & Zuberbühler, 2005; 2006; Crockford, Wittig & Zuberbühler, 2015), flexible use across contexts (e.g. Hobaiter & Byrne, 2011) and audience effects (e.g. Gruber & Zuberbühler, 2013; Leavens, Hopkins & Bard, 1996; Kalan & Boesch, 2015; Schel et al., 2013b; Slocombe & Zuberbühler, 2007; Slocombe et al. 2010; Townsend & Zuberbühler, 2009). On the surface, UM research indicates that gestures, vocalisations and facial expressions differ in terms of characteristics such as referentiality, intentionality and flexibility of use, as outlined in Chapter 1; however, few studies have attempted to examine these characteristics in a comparable manner in multiple modalities, so such conclusions may be premature (Slocombe et al., 2011). One study that has successfully examined different types of signal within a single experimental paradigm explored whether captive chimpanzees could selectively produce a signal appropriate to the attentional state of a human. Leavens, Russell and Hopkins (2010) showed that chimpanzees, whilst begging from a human experimenter, used more visual gestural signals, when the researcher was facing towards them and more tactile and vocal signals when they were facing away.

Despite the wealth of research on the production of vocal, gestural and facial signals in isolation, the combination of these signal types into MM signals in chimpanzees is virtually unexplored (Liebal et al., 2013; Slocombe, Waller & Liebal, 2011). As already outlined in Chapter 1, important exceptions to this include an experimental study probing recipient integration of signals from different modalities, which revealed that chimpanzees can cross-modally match facial expressions and vocalisations (Parr, 2004). Parr also found that either the vocal or facial components were more salient to the chimpanzees depending on the signal type (e.g. the vocal component of a pant hoot signal was more salient than the facial component). From a production perspective, a recent study by Taglialatela et al. (2015) indicated that approximately 50% of captive chimpanzee vocalisations were accompanied by non-vocal signals (e.g. gestures, fear grimace) or behaviours (e.g. chase, play), and that these combined signals were more likely to be directed towards another individual than vocal signals alone. This indicates that chimpanzees may use signal combinations from different modalities strategically to meet specific socio-communicative goals. Focusing on the combination of gestural signals with vocal or facial signals in captive chimpanzees, Pollick and de Waal (2007) found 21% of chimpanzee signals were MM. However, the operational definition of MM signals likely captured MM sequences as well as signals, as signals occurring within 10 s of each other were considered MM signals. Perhaps surprisingly, these signals were not found to be more effective in eliciting a response than UM signals. However, unfortunately, this study's findings are difficult to interpret as their analyses also suffer from pseudoreplication (Waller et al. 2013b). Despite variation in how these two studies define a MM signal, it seems in captivity, where visibility of group members is usually excellent, vocal, gestural and facial signals may be commonly combined into MM sequences or signals. The degree to which chimpanzees produce MM signals in their visually dense natural habitat, and whether in a wild setting MM signals are more effective at eliciting responses than UM signals, remains unknown. In addition, despite free MM signals having the potential to generate new meaning (emergent function; Partan & Marler, 1999) and to indicate cognitive complexity relevant to a language evolution perspective (Slocombe, Waller & Liebal, 2011), we are currently lacking a MM repertoire and an understanding of how common and varied such free combinations may be.

In this study I attempted to address these issues and systematically investigated the UM and MM communication of wild chimpanzees, by taking an integrated MM approach. I considered MM signals temporally overlapping combinations of vocal, gestural and facial signals. I aimed to provide the first MM signal repertoire, understand the individual and contextual factors that affect UM and MM signal production, and compare the recipient responses to MM and matched UM signals. The main expected findings and rationale for these is provided in Table 1.

Table 1. The expected findings, and rationales for each of these

Expected finding	**Rationale**
Signal production	
The rate of UM signal production will be significantly higher than the rate of MM signal production	Previously found in captivity by Pollick & de Waal (2007) and Taglialatela et al (2015)
The rate of MM signal production will be lower than that previously found in captivity	I use a stricter definition of MM (signals must be temporally overlapping) than previous captive studies
Younger, female or more subordinate individuals will show higher rates of MM signal production	These individuals may need more elaborate signals to elicit responses from other individuals, than older, male or

	more dominant individuals
Relative rates of UM vocal, gestural and facial signals will vary with context, with higher rates of gestures and facial expressions in contexts where visual signals are most visible for receivers	Captive chimpanzees (e.g. Leavens, Russell & Hopkins, 2010) modulate signal type dependent on the recipient’s visual attention
Recipient responses	
MM signals will elicit a significantly higher proportion of recipient responses compared to matched UM signals	Increased responses to MM signals have been repeatedly found in non-primate studies (reviewed in Liebal et al., 2013) as recipient’s are more likely to detect and attend to these more elaborate and salient signals
Recipient responses are more likely when the signaller is more dominant	Other individuals may be more likely to attend and respond to more dominant individuals as not doing so may result in aggression or other punishment
Recipient responses are more likely when there are more individuals in the vicinity	More individuals means there may be a higher likelihood of at least one audience member detecting and responding to the signal

METHODS

Study site

This study was carried out in Kibale National Park, located in western Uganda (0” 13’ - 0” 41’ N and 30” 19’ - 30” 32’ E) in 2013 - 2015. The study community occupies the hills and valleys surrounding the region of Kanyawara, which is situated at an elevation of approximately 1500 m, at the northwestern edge of the park. Kibale forest is a transitional semideciduous tropical forest between lowland rainforest and montane forest (Struhsaker, 1975), with the chimpanzees generally occupying an area of mosaic of semi-deciduous primary forest, secondary forest, grasslands and swamps (Chapman & Wrangham, 1993; see this paper for a detailed description of the site).

Study subjects

The study animals were a wild group of chimpanzees, the Kanyawara community. In 2013, the group comprised approximately 57 individuals (Muller & Wrangham, 2014), and occupied a median annual home range of 16.4 km² (Wilson, Kahlenberg, Wells & Wrangham, 2012). The community is entirely habituated and have been followed and studied regularly since 1987 by the Kibale Chimpanzee Project (Wrangham, Clark & Isabirye-Basuta, 1992; Georgiev et al., 2014). Specifically, the individuals included in this study were 13 males and 13 females; ages ranging 8 - 47 years (see Table 2). These individuals were chosen on the basis that they were easy to find and follow, ensuring that as much high quality focal time as possible could be collected for each individual. Dominance ranks were established by calculating a Modified David's Score, MDS (de Vries, Stevens & Vervaecke, 2006), for all individuals for which long-term field assistant data on decided aggressive interactions and submissive pant grunt vocalisations were available (these data were unavailable for some younger individuals - their rank is noted as NA). The mean MDS was calculated across the pilot (February – May 2013) and main study (June 2014 – March 2015) periods for each individual; this was done for males and females separately and all males were ranked above all females, as all of these males had dominated the females.

Table 2. ID, sex, age and rank of the 13 male and 13 female focal individuals

ID	Sex	Age (years)	Rank
AJ	M	39	4
AL	F	31	12

AT	M	14	7
AZ	M	9	NA
BB	M	47	5
BO	M	10	NA
ES	M	19	1
LK	M	31	3
LN	F	16	16
ML	F	16	14
NP	F	13	18
OG	M	12	NA
OM	F	8	NA
OT	F	15	19
OU	F	34	9
PB	M	18	6
PO	F	14	15
TG	F	33	10
TJ	M	18	2
TS	F	8	NA
TT	M	13	NA
UM	F	32	13
UN	M	9	NA
WA	F	22	17
WL	F	21	11
YB	M	40	8

Age in 2013 – the first year of data collection. Rank order based on Modified David's Score, where 1 is the highest ranking. NA indicates young individuals for whom these data were not available.

Equipment

All focal observational data were collected with a Panasonic HDC-SD90 camcorder, with a Sennheiser MKE 400 microphone attached. Recipient responses were recorded with a second camcorder – a Panasonic HDC-SD40. Videos were coded using Noldus Observer XT 10 event logging software (http://www.noldus.com/animal-behavior-research) for observational data.

Ethical note

The empirical research in this thesis complied with the ASAB guidelines for the use of animals in research; ethical approval was granted by the Biology Ethics Committee (University of York). The Ugandan Wildlife Authority and the Ugandan National Council for Science and Technology granted permission to carry out the study in Uganda.

Data collection

All data were collected February – May 2013, and June 2014 - March 2015, between 08:00 and 18:30. Focal animal sampling (Altmann, 1974) was employed in order to collect observational data on the 26 focal individuals. Focal animals were only sampled once a day and were chosen in a way that maximised the quality and spread of data across target individuals. Initially, once a party of chimpanzees were located, the target animal with the best visibility for clear filming was chosen as the focal individual, but later on in the study period target individuals with the least focal time were prioritised. At the beginning and end of every video observation the party composition was commentated onto the video. 'Party' was defined as all individuals within a 30 m radius of the focal animal (Slocombe et al., 2010).

Focal animal signal production

Focal samples consisted of 15 min of continuous video observation of one focal animal. The aim was to capture on video a complete view of all facial, gestural and vocal signals produced by the focal individual. Thus the camera was zoomed in as close as possible, whilst still capturing the whole body of the chimpanzee. The researcher commentated all vocalisations in real time, to ensure that even quiet vocalisations that could not be picked up by the microphone were recorded. If individuals moved out of sight and earshot during a focal observation, this time was coded as ‘out of sight’ (OOS) and excluded from any further analysis. Samples containing more than 10 min of OOS time were excluded from further analysis, meaning the analysed samples range from 5 - 15 min and all had a good level of visibility of the focal animal. As I was interested in social communication, only focal samples during which the focal individual was in a party were included in this analysis. This excluded times when mothers were alone with only their infants, as mother-infant communication could not be examined in the majority of the focal individuals, who were not mothers.

Recipient responses

To collect the response of other individuals to any signals produced by the focal individual, a second researcher used a camcorder to capture the signals and behaviour of as many of the individuals closest to the focal animal (within 5 m) as possible.

Video coding

Video coding with Observer XT 10 software was used to extract continuous details about the behavioural context and modality availability of the focal individual, as well as all their UM and MM signal production (see detailed definitions below). By coding the context and modality availability continuously I was able to calculate accurate rates of signal production in each context, as a function of the time each specific modality could be reliably detected. The types of behaviours elicited from individuals within 5 m of the focal individual, in response to each focal signal, were also coded from the videos (see detailed definitions of these responses below). Recipient responses were only coded for the 32 hours of video data for which a second observer was present to capture these on a second video camera.

Definitions

Behavioural contexts

Eight behavioural contexts were defined and coded, but only four occurred frequently enough across focal animals to be examined further in terms of signal production rates (rest, groom, feed, travel; see Table 3). For these four contexts, the requisite behaviour had to continue for at least 20 s (a break of up to 5 s was permissible during this time), after which breaks of up to 15 s were permissible, as long as the individual always returned to the original behaviour. For the repertoire and number of instances of different MM combinations (Table 7 and Appendix A), all contexts were included i.e. all available video time, in order to establish a more comprehensive picture of the types of signals that the focal individuals were motivated to combine.

Table 3. Description of the behavioural contexts of the focal individual

Behavioural context	**Description**
Rest	When the focal animal is sitting or lying down relatively still with eyes open, and for the majority of the time not feeding, grooming, or playing. Also includes time spent self-grooming (attending to their own body/fur – combing through the fur or picking at the skin to remove dirt or parasites).
Feed	When the focal animal is collecting and eating, or extracting moisture from, food (e.g. leaves, bark, fruit, honey). They may move short distances in the process of doing this. If they resume feeding after a period of chewing, this continues to be counted as feeding. If they chew for more than three min without resuming collecting and eating more food after this, this is coded as resting after three min of chewing.
Groom with other	When the focal animal is attending to the body/fur of another individual (or vice versa) – combing through the fur or picking at the skin to remove dirt or parasites.

Travel	When the focal animal is walking or running for the majority of the time (may sometimes halt for brief periods). Movement associated with play (such as chasing), feeding (such as moving short distances for foraging), displaying or aggression, is not regarded as 'travel'.
Other	Includes sleep (eyes closed and no movement), social play (Nishida et al., 2010), aggression (includes threats, chasing, physical violence, etc.), and display (includes charging, body swaying, branch shaking, dragging and throwing, etc.; see Nishida et al., 2010)

Some behaviours could occur simultaneously, thus there was a hierarchy when coding, with the more active (generally also rarer) behaviour being given precedence (e.g. travel>feed, display>travel, play>travel, aggression>travel, aggression>display, play>feed, groom with other>self-groom). It was occasionally the case that an individual would be involved in an agonistic interaction and then rest, feed, travel or groom immediately afterwards. In these cases behavioural contexts were still based on the current behaviour of the individual; thus it should be taken into account that rest, feed, groom and travel contexts could also include post-conflict periods.

Modalities available

This behavioural coding group was used to capture which type of signals produced by the focal individual could be coded reliably from the video at all times (see Table 4). It was frequently the case that only signals in one or two modalities could be accurately captured due to the orientation of the focal animal (e.g. face may not be visible) or distance of observer to the chimpanzee (e.g. quiet vocalisations may not be detected). This was coded so it could be taken into consideration when calculating rates of signal production.

To be coded as a 'modality available', the requisite modality had to be available for at least 20 s (a break of up to 5 s was permissible during this time), after which breaks of up to 15 s were permissible, as long as the original modality then became available again. The exception to this rule was when the modality could not be seen for the majority of the time, but in the short period for which it was available, a signal was produced (for instance an individual's face cannot be seen, they then turn around for 2 s, showing a 'play face', then turn away again); in this case it was coded as available for this short period, and the signal produced was also coded.

Table 4. Description of time each signalling modality of the focal individual was considered available

Modality available	**Description**
Vocalisations	Available if focal animal is <15 m away from the observer/camera and the exact location of the focal individual is known. Unavailable if the focal individual is >15 m away or <15 m but the exact location is uncertain due to dense foliage or the individual is in close proximity to many individuals so discriminating which individual vocalised would be very difficult.
Facial expressions	Available if the face can be seen from the front or side, or from any other angle that still allows sufficient sight of the mouth and eyes. Coded as unavailable when the mouth region cannot be seen at all.
Gestures	Available if majority of torso and arms are visible. Coded as unavailable when neither arm is visible, as half the gestures coded involved the arms/hands.
OOS	When no part of the focal individual's body can be seen, the location of the individual is unclear, and/or they are further than 15 m away.

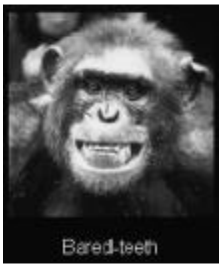
Focal individual signal production

I coded all vocal, gestural (manual and non-manual) and facial signals the focal individual produced (see Table 5). The duration of facial and gestural signals was coded; for vocalisations, which were commonly produced in bouts, the duration of the calling bout was recorded. Two or more vocalisations of the same type were coded as one continuous bout if they were produced within 10 s of one another (from the end of one to the beginning of the next). Eight different facial expressions were coded; these were based on the prototypical expressions described in Parr, Waller, Vick and Bard (2007), which are specific combinations of facial muscle movements (Action Units: ChimpFACS, Vick et al. 2007). I discussed exemplars with Dr Bridget Waller (certified FACS coder) prior to video coding in order to avoid any expressions that did not fit the prototypical descriptions. Forty common gestures were coded based on the repertoire proposed by Hobaiter & Byrne (2011a). Rare gestures were coded as ‘other manual gesture’ or ‘other non-manual gesture’ and described in the notes section. Similarly, owing to the size limits of the coding scheme, some gestures were combined under an umbrella term, for instance ‘manual contact with another individual’ included touch, hand on, punch, push, slap, tap, poke, hit. Fourteen different vocalisations were coded based on the repertoire proposed by Slocombe and Zuberbühler (2010).

Table 5. Descriptions of each of the focal individual signal types coded

Focal individual signal	**Description**
FACIAL EXPRESSIONS	
(Images taken from Parr, Waller, Vick & Bard, 2007, Figure 2, and Parr & Waller, 2006, Figures 1 and 2).	

Bared teeth display



Play face

Pant hoot face

Scream face

Alert face

Pout

Whimper face	
Ambiguous face	A facial expression is produced, but not similar to, or a variant of, any of the other listed facial expressions. Must be described in the notes next to this coded signal.

VOCALISATIONS

(Repertoire based on Slocombe & Zuberbühler, 2010)

Pant hoot	Species-typical long-distance vocalisation with four distinct phases: introductory phase (low frequency hoo calls), buildup phase (increasingly loud panted hoo calls with energy in both the inhalation and exhalation), climax phase (screams or roars), and letdown phase (resembles the buildup phase but with progressively decreasing energy). Calls often do not include all four phases; introduction and letdown are commonly omitted.
Pant grunt	Noisy, low-frequency grunts or barks, panted in a rapid rhythm with audible energy in both inhalation and exhalation.
Scream	Loud, high-pitched, harmonic vocalisation with varying degrees of tonality. They are almost always given in bouts, but the length of a bout can vary from a few seconds to several minutes. In most contexts acoustic energy is present only during exhalation, but during intense tantrums it is often present during inhalation as

	well.
Bark	Sharp, loud calls with abrupt onsets. They are often noisy and are generally low-pitched vocalisations.
Waa bark	A distinct loud, intimidating bark variant in which the sound ‘waa’ is clear. Acoustically distinct from the shorter barks and screams into which they often grade, waa-barks typically have a low frequency ‘w’ introduction at call onset, and then clear rise and short fall in pitch during the ‘aa’ element of the call. Waa-barks are produced in isolation or in short series.
Pant	Unvoiced, soft, low-frequency sounds. Temporal patterning is regular and rapid.
Grunt	Short, soft low-frequency calls given singularly or in short bouts.
Rough grunt	An umbrella term that describes the vocalisations produced by individuals when approaching, collecting, or consuming food. Acoustically, rough grunts grade from low-frequency, unvoiced, noisy grunts to high-frequency tonal squeaks.
Cough	Low-frequency vocalisation, similar to a grunt but rarely voiced. A short noisy signal with no harmonic structure.
Laughter	Noisy, low-frequency grunts and moans delivered in an irregular rhythm, reminiscent of hoarse, wheezing human laughter. Acoustic energy is audibly present in both inhalation and exhalation, with most voicing occurring during inhalation.
Whimper	A series of soft low-frequency hoo calls that can become

	higher in both frequency and amplitude as a bout progresses. The frequency and amplitude often rises and falls throughout a bout. Individual hoo calls are tonal signals with a variable number of harmonics.
Squeak	High-pitched, short calls often given in fast succession to form short bouts. The calls are tonal signals, often with clear harmonic structure.
Huu/Alarm call	Tonal calls with most energy at onset and a rise and fall in frequency over the call. Huu calls can be loud, sometimes carrying for more than 100m.
Soft hoo	Covers ‘travel hoos’ and ‘resting hoos’, as described in Gruber & Zuberbühler (2013).

MANUAL GESTURES

(Repertoire based on Hobaiter & Byrne, 2011a)

Brief manual contact with object or ground	Includes touch, punch, slap, tap, shake etc.
Manual contact with another individual	Includes touch, hand on, punch, push, slap, tap, poke, hit etc.
Manually displace object	Object is moved and released so that there is displacement through the air after moment of release. Object is displaced in one direction and contact is maintained through movement.
Arm raise	Raise arm and/or hand vertically in the air.
Arm shake	Small repeated back and forth motion of the arm.

Arm swing	Large back and forth movement of the arm held below the shoulder.
Arm wave	Large repeated back and forth movement of the arm raised above the shoulder.
Beckon	Hand is moved in an upwards sweep from the elbow or wrist towards signaller.
Big loud scratch (BLS)	Loud exaggerated scratching movement on the signaller’s own body.
Clap	Both palms moved towards each other and are brought together with an audible contact.
Drum belly	Slap belly with hand to make drum-like sound.
Embrace	Signaller wraps both arms around the recipient and maintains physical contact.
Hand fling	Rapid movement of the hand or arm in the direction of the recipient.
Hand shake	Repeated back and forth movement of hand from the wrist.
Hide face	Face is hidden by the hands and/or arms.
Leaf clip	Strips are torn from a leaf (or leaves) held in the hand using the teeth; produces a conspicuous sound.
Mouth stroke	Signallers palm and fingers are repeatedly run over the mouth area of the recipient.
Reach	Arm extended to the recipient with hand in an open, palm upwards position (no contact).

Shake hands	Signaller grasps recipient’s hand in their own hand and then makes small repeated back and forth movements from the wrist.
Water splash	Hand is moved vigorously through the water so that there is audible displacement of the water.

NON-MANUAL GESTURES

(Repertoire based on Hobaiter & Byrne, 2011a)

Bite	Recipient’s body is held between the teeth of the signaller.
Bow	Signaller bends forward from the waist while standing.
Dangle	To hang from one or both arms from a branch above another individual; this is audible as there is normally significant disturbance of the canopy.
Feet shake	Repeated back and forth movement of feet from the ankles.
Foot present	Sole of the foot is presented to the recipient.
Gallop	An exaggerated running movement where the contact of the hands and feet is deliberately audible.
Head nod	Repeated back and forth movement of the head.
Jump	While bipedal both feet leave the ground simultaneously, accompanied by horizontal displacement through the air.

Kick	Foot is brought into short hard contact with the recipient’s body in a movement from the hip with a horizontal element.
Leg swing	Large back and forth movement of the leg from the hip.
Look	Signaller holds an eye-contact position with the recipient; minimum duration 2 s.
Object in mouth approach	Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch).
Present climb on me	Arm or leg is extended to young recipient in order to facilitate them climbing onto the signallers body (normally mother to infant).
Present grooming	Body is moved to deliberately expose an area to the recipients attention which is immediately followed by grooming of the area.
Present sexual	Signaller approaches recipient backwards, exposing the swelling or anus to the recipients face (normally female to male, but sometimes a submissive gesture from male to male).
Roll over	The signaller rolls onto their back exposing their stomach, normally accompanied by repeated movements of the arms and/or legs.
Rump rub	Push/rub rump against the body/swelling of recipient.
Stomp (one or two feet; use notes)	Sole of the foot is lifted vertically and brought into a short hard audible contact with the surface being stood upon (e.g. ground or a branch).
Stomp other (one of two	As ‘stomp’ but contact is made with recipient.

feet – use notes)	
Walk stiff	Walk quadrupedally with a slow exaggerated movement.

Recipient response time and types

Recipient responses were coded from the beginning of the focal individual signal until 20 s after the signal had finished, from individuals within 5 m of the focal individual. During the recipient response time the number and identity of the individuals within 5 m of the focal individual were recorded. If another signal occurred within the 20 s after the first signal then the recipient response time was cut short for the first, with this only lasting until the beginning of the next signal. Similarly, if the recipient response continued after the 20 s (for example the signal elicited a long bout of grooming), this was also only coded for up to 20 s after the end of the focal signal.

Recipient responses comprised four groups: signal responses (facial, vocal, gestural and MM), movements, negative and positive responses (see Table 6). Signals by other individuals were only coded as responses if the recipient's facial expression or gesture was directed at the focal individual (as far as this was relevant and possible to discern). It was difficult to determine specifically to whom vocalisations were directed, so all vocalisations from recipients were counted as potential signals in response to the focal individual. Any signals or behaviours which were clearly in response to an unrelated signal or event were not coded as responses. For example, if the focal individual gave a big loud scratch (BLS) gesture, and immediately afterwards individuals in another party utter pant hoots, and then an individual within 5 m of the focal animal replies with a pant hoot, the pant hoot is not coded as a response to the BLS. Similarly, only an active change in behaviour of the recipient was coded as a response. For instance, if another individual was already vocalising, and then the focal individual produced a signal, and the other individual continued vocalising as before, this was not counted as a response to the focal animal's signal. Equally, 'terminating' behaviours were not coded, for example the cessation of playing or grooming. Behavioural responses (positive, negative) had to be directed towards the focal animal rather than a third party to be counted as a response to the focal animal's signal.

Table 6. Description of the types of recipient responses coded

Responses of recipients	**Description**
Facial, vocal, gestural or MM response	The facial expressions, vocalisations and gestures given by recipients were coded in the same way as those of the focal individual (see Table 5).
Movement response	Movement responses were coded when a recipient was clearly moving directly towards, or directly away from, the focal individual, by at least 2 m (excluding occasions where the recipient was merely passing). This was coded at the point the movement began.
Positive response	Positive responses from recipients included recipients grooming or playing (see description of these behaviours in Table 3) with the focal animal, or clearly desired responses e.g. ‘present climb on me’ is followed by the recipient climbing on the signaller. Grooming was coded as a response either when grooming was initiated, or the recipient changed where they were grooming (as was often the case when the focal individual presented a new body part).
Negative response	Negative responses from recipients included fearful or submissive responses (running away, a cowering body posture, showing fearful facial expressions, screaming), as well as mild (threats, non-directed display) or severe aggression (chasing, directed display, physical violence; see Nishida et al., 2010).

Calculation of signal production rates

A total of 121 hours of videos were coded. Of these, 111 hours were in groom, rest, feed and travel contexts and thus were used for the calculation of UM and MM signal production rates. To ensure that signal production rates were representative of an individual's behaviour, I set minimum amounts of time that an animal could have been observed to produce the relevant signal in key contexts in order to enter analyses.

For UM signals, rates were only calculated for UM facial, vocal and gestural signals for a specific context for an individual if they had at least 30 min of this modality available in rest, feed and groom, and at least 20 min in travel. For example, to have a rate for facial expressions in rest, that individual must have at least 30 min of facial expressions available during rest. Mean UM rate was the average of facial, vocal, manual gesture and non-manual gesture rates. Individuals must have contributed to all of these to have a mean UM rate calculated in a specific context. Those who did not meet this criterion had a missing value for UM rate in this context.

Rates were only calculated for MM combinations for a specific context for an individual if they had at least 15 min of this modality combination available in rest, feed and groom, and at least 10 min in travel. For example, to contribute a rate for vocal-gestural signals in travel, that individual must have at least 10 min of time where both vocalisations and gestures are simultaneously available in travel. Mean MM rate was the average of facial-gestural, vocal-gestural, fixed facial-vocal (pant hoot vocalisation and pant hoot face, whimper and whimper face, scream and scream face), free facial-vocal, and facial-vocal-gestural rates. Individuals must have contributed at least three of these MM combination rates to have a mean MM rate calculated in a specific context. Those who did not meet this had a missing value for MM rate in this context.

Mean signal production rates for the group (as reported in descriptive statistics and figures in the Results) were calculated as a mean of all the individual mean production rates that contributed to a particular analysis.

To assess whether the number of individuals in the party affected signal production, I calculated the average number of individuals in the party present during the periods from which signal rates were calculated for each type of signal produced by each individual. To do this, I first averaged the number of individuals recorded in the party at the beginning and end of every video. Second, for each signal type for which a rate was calculated for an individual, I took the corresponding videos that had contributed to the calculation of that rate and calculated a mean from the average number of individuals in the party across those videos.

Selection of dataset for comparison of responses to MM signals and UM components

Most previous non-primate research carried out within a MM framework, has focused on fixed MM signals and/or signals produced only in one specific context, for example alarm behaviour (e.g. Partan et al., 2009) or courtship behaviour (e.g. Uetz, Roberts & Taylor, 2009). In contrast, the signals I investigated were free MM signals, which were produced across a range of contexts (see Appendix B). As context was shown to heavily influence signal production (see signal production results below), I endeavoured to control for this by matching UM and MM signals based on signaller identity and behavioural context of production. I consider such matching of MM signals and UM component signals to be critically important in order to understand the function of the signals.

I focused on the free MM signal produced most frequently by the largest number of individuals, where matched UM component signals were also frequently produced by the same individuals: the grunt + gesture signal (vocal-gestural combination). It was not possible to examine more MM signal combinations as no other type of free MM signal, with sufficient matched UM components, was produced by a sufficient number of individuals.

For each of the MM signals I identified component UM signals that were matched to the MM signal in terms of the behavioural context during production. Up to five UM grunt signals and five UM gesture signals were matched to each MM signal. Where possible I also matched the number of individuals present within 5 m of the focal individual. For instance, if the individual PO produced a grunt + present groom MM signal in a groom context, with two individuals within 5 m, the responses to this signal could be compared to the responses to a UM grunt vocalisation from PO, in a groom context, with two individuals within 5 m of her, and a UM present groom gesture, in a groom context, with three individuals within 5 m of her.

Inter-coder reliability

To assess the inter-coder reliability of the video coding, a second independent researcher also coded 6.5% of the videos (7.75 hours, *N* = 31 videos each lasting 15 min, from a total of 15 individuals), having been provided with comprehensive instructions. Cohen's kappa was calculated; the mean Kappa value obtained was 0.81, indicating excellent levels of coder agreement (Fleiss, 1981). All reliability analyses were run using the Reliability Analysis function in Observer XT 10, which enables the comparison of two different Event Logs for one video.

Data analysis

I constructed linear mixed models (LMMs) and generalised linear mixed effects models (GLMMs) in order to test the hypotheses regarding signal production and recipient responses respectively. LMMs were used to investigate the influence of continuous and categorical variables on signal production rates, whilst GLMMs with a binomial error structure were used to investigate the influence of continuous and categorical variables on the occurrence of recipient responses (binary response variable: received one or more responses or no responses). Furthermore, because I had repeated sampling from the same individual, to control for pseudoreplication I fitted 'individual' as a random factor (Crawley, 2002) by conducting random intercepts models using the package lme4 (Bates & Maechler, 2009; https://cran.r-project.org/web/packages/lme4/index.html). I first assessed whether the full model could explain a significant amount of variation in the dependent variable, by comparing the full model to a null model containing just the intercept and random factors. To assess the significance of each explanatory variable or interaction term, I compared the full model with a reduced model excluding the variable or interaction of interest using a likelihood ratio test (Faraway, 2006). All models were run in R v. 2.15 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org).

As some data were not available for all individuals (e.g. dominance rank) or were missing in the majority of individuals due to methodology (e.g. facial expression was not available during travel, as the observer followed and filmed travelling chimpanzees from behind), I sometimes constructed several models in order to test the hypotheses thoroughly, and to maintain a high number of individuals in each model.

An alpha value of 0.05 was used to determine statistical significance throughout this thesis.

RESULTS

MM signals – repertoire, rates and responses

Overall the results show that across rest, feed and groom contexts MM signals were rare relative to UM signals (see Figures 2 and 4). Free MM signals were, however, produced by 22 of the 26 focal individuals, and I recorded a total of 48 different free MM signals, consisting of combinations that in total included six different facial expressions, nine different vocalisations and 16 different gestures (see Appendix A for MM repertoire).

Figure 2 shows that vocalisations and gestures were produced at a significantly higher rate alone (UM), than as part of a free MM combination. In contrast, facial expressions were produced at a higher rate as part of a free MM combination, than in isolation; though notably only four individuals contributed to the facial expression signal production rates.

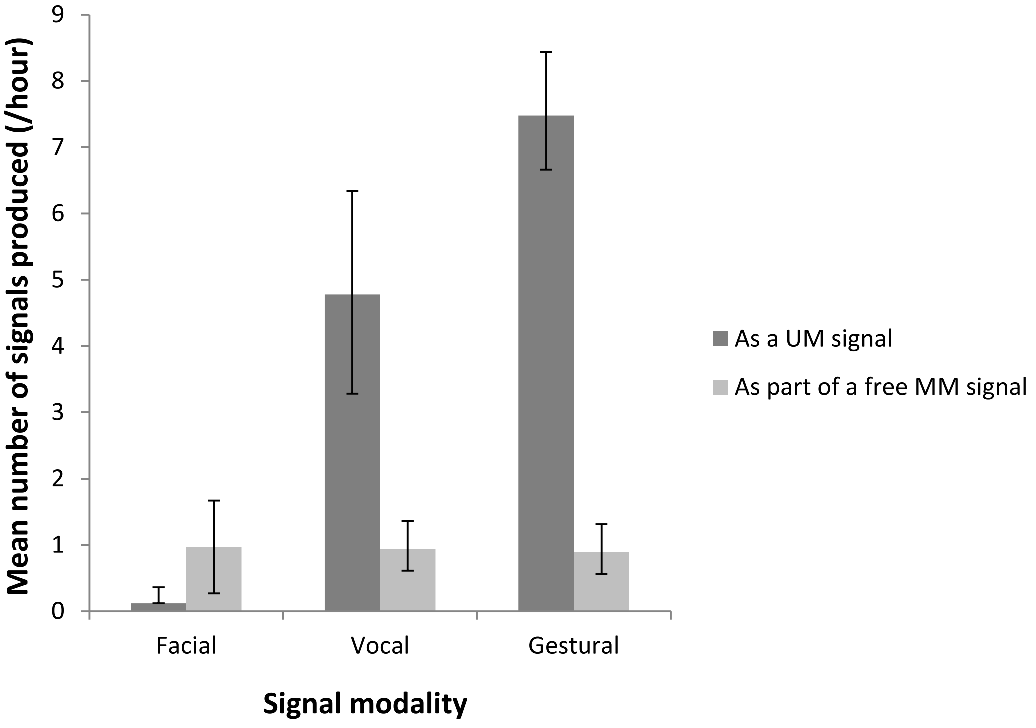


Figure 2. The mean signal production rate (per hour) for each of the three modalities as UM signals, and when these are combined into free MM signals, across the contexts of rest, feed and groom. Error bars represent bootstrapped 95% confidence intervals, based on 1000 iterations. Error bars that do not overlap represent a significant difference. Mean rate and confidence intervals derived from data of *N* = 23 individuals (vocal and gestural), and *N* = 4 (facial). UM vocal signals include fixed vocal-facial signals.

Vocal-gestural combinations were the most common free MM signals recorded, and free facial-vocal the least (see Table 7). The frequency of different types of responses the various different categories of MM signal elicited from those within 5 m are also shown in Table 7. Vocal-gestural signals were the most likely to elicit any kind of response, and the most likely of all the signal combinations to elicit a positive response. In contrast fixed facial-vocal signals received the highest percentage of negative responses.

Table 7. Occurrences of different MM combinations and responses to these

	Across all eight contexts			Across rest, feed, groom and travel contexts					
					Percentage of occurrences that elicited a response				
	MM signal combination	**No. of individuals**	**No. of occurrences observed (range for a single individual)**	**No. of occurrences with at least one recipient within 5 m**	**F, V, G or MM signal response (%)**	**Movement response (%)**	**Positive response (%)**	**Negative response (%)**	**No response (%)**
Free	F-G	14	47 (1-9)	5	20	20	0	0	60
	F-V	9	14 (1-4)	8	25	0	0	0	75
	V-G	15	53 (1-15)	46	20	9	41	4	26
	F-V-G	13	36 (1-12)	12	8	17	0	0	75
Fixed	F-V	20	95 (1-11)	57	35	4	5	12	56

The number of instances and number of individuals observed to produce different MM combinations, both free and fixed, across all eight behavioural contexts, with the range of number of occurrences a combination was produced by a single individual in parentheses. Also shows the number of occurrences where the signal was produced in rest, feed, groom or travel contexts with at least one recipient within 5 m, and of these, the percentage of these occurrences that elicited each of the four recipient response types, or no response. One signal could elicit several responses. Responses were recorded from the start of the signal until 20 s after the end of the signal. The table includes ambiguous signals, where the modality combinations were clear (e.g. facial-vocal signal), but at least one of the specific signal types could not be easily categorised given the signal repertoires used (Table 5). F: facial; V: vocal; G: gestural.

Variation in MM signal production rates – free versus fixed

As there is a key cognitive distinction between free MM signal combinations, where signals may be flexibly 'mixed and matched', and fixed MM signal combinations, which are necessarily combined, I investigated the individual and contextual factors which might influence the relative rates of these signals. I constructed a model to test whether variation in the mean MM signal production rate (signals/hour) could be explained by interactions between the following fixed factors: type of MM signalling (fixed, free) and (i) context of production, (ii) the mean number of individuals in the party, (iii) the age of the signaller and (iv) the sex of the signaller. The travel context was not included as most MM combinations included facial expressions, which could virtually never be captured during travel.

The full model comprised these interaction terms and the associated fixed factors. Individual identity was included as a random factor. The dependent variable was mean rate of MM signal production/hour. I included 156 data points from 26 individuals in the model. Overall, the full model (*N* = 26 individuals) did not explain a significant amount of variation in MM signal production rates, compared to a null model (X^2_{11} = 17.06, *P* = 0.106), indicating that these factors and interactions did not account for significant variation in the MM signal production rates.

As rank was only available for older individuals, I ran a separate model to assess the effects of rank, by adding rank as a fixed effect and the interaction between rank and signal type to the full model specified above (*N* = 114 data points from 19 individuals). This version of the model that included rank (*N* = 19) confirmed that the overall model did not explain a significant amount of variation in MM signal production rates (X^2_{13} = 6.70, *P* = 0.917).

Rates of the different types of free MM signal combinations were too low and lacked sufficient variability (e.g. the majority of individuals had rates of 0 signals/hour) to be subject to inferential statistics, however Figure 3 shows that there was interesting variation in the type of MM signals produced in rest, feed and groom contexts.

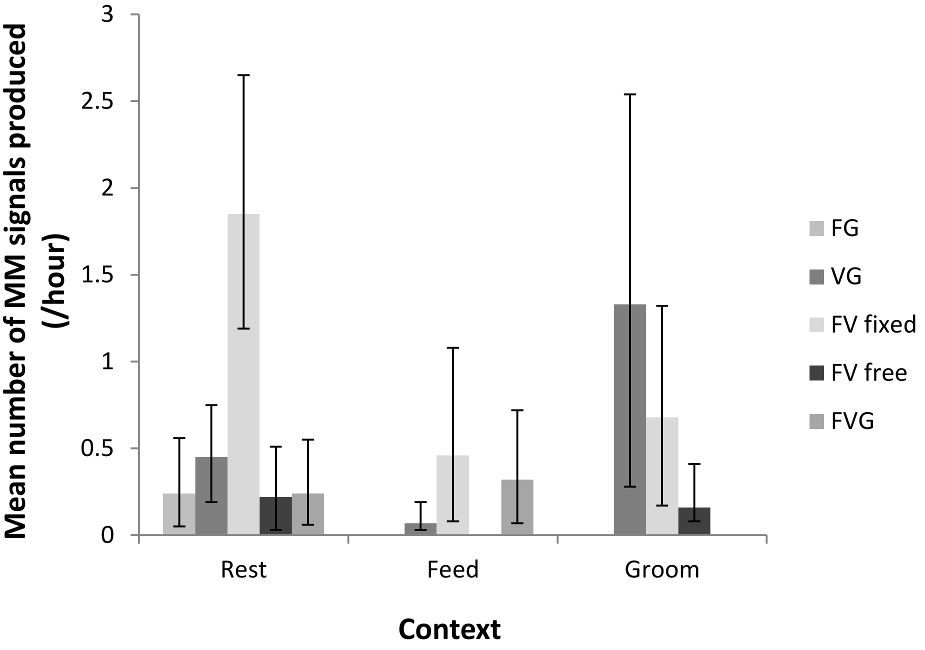


Figure 3. The MM signal production rate (per hour) of facial-gestural, vocal-gestural, fixed facial-vocal, free facial-vocal and facial-vocal-gestural combinations in the contexts rest, feed and groom. Error bars represent bootstrapped 95% confidence intervals, based on 1000 iterations. Error bars that do not overlap represent a significant difference. MM rate and confidence intervals derived from data of *N* = 25 (facial-gestural, fixed facial-vocal, free facial-vocal and facial-vocal-gestural rest), *N* = 26 (vocal-gestural rest, vocal-gestural, fixed facial-vocal, facial-vocal-gestural feed and vocal-gestural groom), *N* = 23 (fixed facial-vocal and free facial-vocal groom). Missing bars occur when the MM rate was zero.

Factors affecting UM and MM signal production

I constructed a model to test whether variation in the mean signal production rate (signals/hour) could be explained by interactions between the following fixed factors: type of signalling (UM, MM) and (i) context of production (rest, feed, groom), (ii) the mean number of individuals in the party, (iii) the age of the signaller and (iv) the sex of the signaller. The full model comprised of these interaction terms and the associated fixed factors. Individual identity was included as a random factor. The dependent variable was rate of signal production/hour. I included 117 data points from 26 individuals in the model. Note that for this model the travel context was excluded as no individuals had sufficient time for UM facial expressions or any MM combination involving facial expressions (i.e. facial-gestural, facial-vocal, facial-vocal-gestural) available in this context.

Overall, the full model (*N* = 26 individuals) explained a significant amount of variation in signal production rates, compared to a null model ($X^2_{11} = 147.06$, $P < 0.001$). Likelihood ratio tests revealed that there was a significant interaction between type of signal and context ($X^2_2 = 11.12$, $P = 0.004$; Figure 4). Figure 4 illustrates that signal production rates were significantly higher for UM signals, than MM signals in each context, but the difference between UM and MM rates was greatest in grooming and resting contexts, compared to the feed context. No significant interactions between signal type and age ($X^2_1 = 0.26$, $P = 0.613$), signal type and number of individuals in party ($X^2_1 = 2.15$, $P = 0.143$), or signal type and sex ($X^2_1 = 2.47$, $P = 0.116$) were found.

As rank was only available for older individuals, I ran a separate model to assess the effects of rank, by adding rank as a fixed effect and the interaction between rank and signal type to the full model specified above (*N* = 90 data points from 19 individuals). This version of the model that included rank (*N* = 19) confirmed that the overall model ($X^2_{13} = 138.61$, $P < 0.001$), and Context*UM/MM interaction ($X^2_3 = 19.51$, $P < 0.001$) were significant, however rank had no significant interaction with signal type ($X^2_1 = 0.08$, $P = 0.784$).

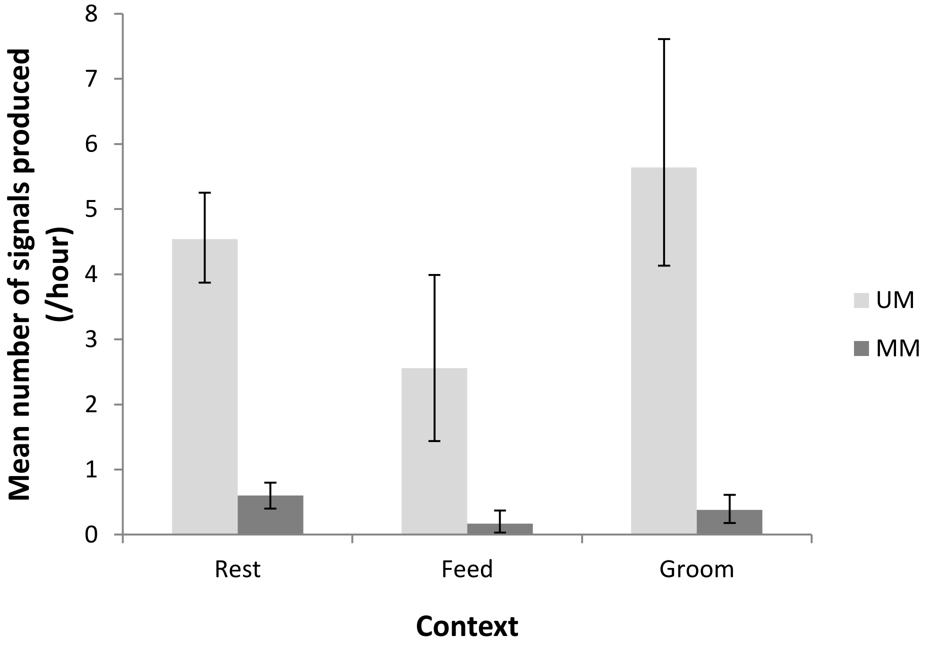


Figure 4. The mean signal production rate (per hour) of UM and MM signals in the contexts rest, feed and groom. Error bars represent bootstrapped 95% confidence intervals, based on 1000 iterations. Error bars that do not overlap represent a significant difference. Mean rate and confidence intervals derived from data of *N* = 23 (UM rest, MM groom), *N* = 25 (MM rest), *N* = 11 (UM feed), *N* = 26 (MM feed), *N* = 9 (UM groom).

Factors affecting unimodal signal production

As no individuals had sufficient time for UM facial expressions or any MM combination involving facial expressions available to calculate facial expression rates during the travel context, I ran two sets of models to examine (a) the effect of all contexts (including travel) on just vocal and gestural signals (facial expression excluded) and (b) the effect of a reduced set of context (excluding travel) on the full range of signals (facial expression included).

I first constructed a model to test whether variation in UM signal production rate (signals/hour) could be explained by interactions between the following fixed factors: type of UM signal (gestures, vocalisations) and (i) context of production (rest, feed, groom, travel), (ii) mean number of individuals in the party, (iii) the age of the signaller and (iv) the sex of the signaller. The full model comprised of the above interaction terms and the associated fixed factors. Individual identity was included as a random factor. The dependent variable was rate of UM signal production/hour. This model included the travel context, however excluded facial expressions. I included 184 data points from 26 individuals in the model.

Overall, the full model (*N* = 26 individuals) explained a significant amount of variation in signal production rates, compared to a null model ($X^2_{13} = 82.24$, $P < 0.001$). Likelihood ratio tests revealed that there was a significant interaction between type of UM signal and context ($X^2_3 = 57.87$, $P < 0.001$; Figure 5). Figure 5 illustrates that UM gestural signal production rates were significantly higher than UM vocal rates in rest and groom contexts. In contrast, in the travel context, UM vocal signal production rate was significantly higher than gestural production rates. In the feed context, although vocalisations were given at higher rates than gestures, there was not a significant difference between UM modality rates in this context. , No significant interactions between UM signal type and age (X^2_1 = 0.04, P = 0.843), UM signal type and the mean number of individuals in the party (X^2_1 = 0.01, P = 0.917), or UM signal type and sex (X^2_1 = 0.92, P = 0.338) were found.

As rank was only available for older individuals, I ran a separate model to assess the effects of rank, by adding rank as a fixed effect and the interaction between rank and UM signal type to the full model specified above (N = 139 data points from 19 individuals).This version of the model that included rank (N = 19) confirmed the overall model (X^2_{15} = 71.82, P < 0.001), and Context*Modality of UM signal interaction (X^2_3 = 46.52, P < 0.001) were significant, however rank had no significant interaction with Modality of UM signal (X^2_1 = 0.45 , P = 0.504).

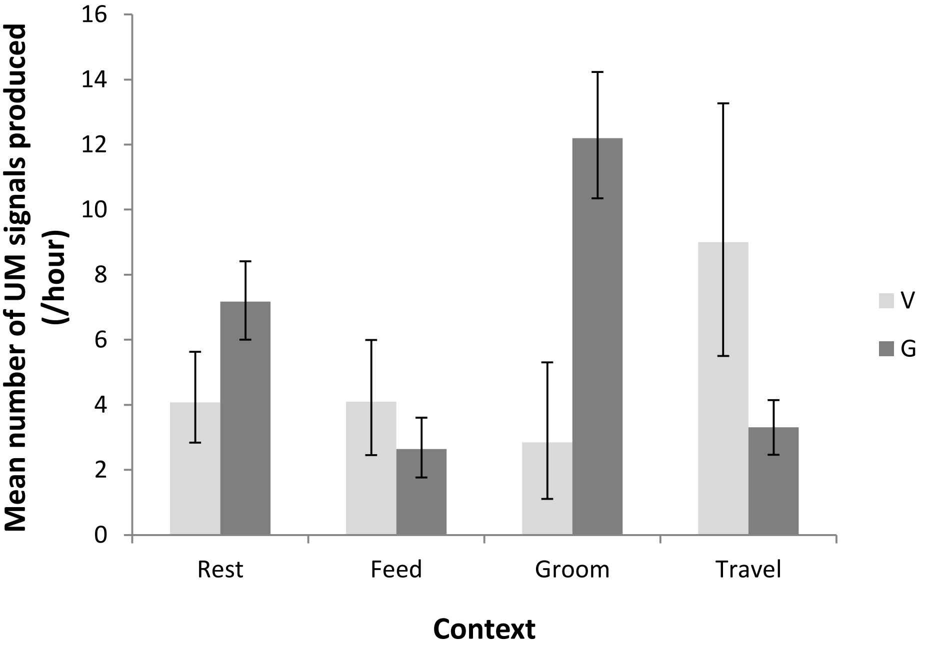


Figure 5. The UM signal production rate (per hour) of vocal and gestural signals in the contexts rest, feed, groom and travel. Error bars represent bootstrapped 95% confidence intervals, based on 1000 iterations. Error bars that do not overlap represent a significant difference. UM rate and confidence intervals derived from data of N = 25 (vocalisations and gestures rest), N = 26 (vocalisations and gestures feed), N = 23 (vocalisations and gestures groom), N = 20 (vocalisations travel), N = 16 (gestures travel).

Second, I constructed a model to test whether variation in UM signal production rate (signals/hour) could be explained by interactions between the modality/type of UM signal (facial, vocal, gestural) and (i) context of production (rest, feed, groom), (ii) mean number of individuals in the party, (ii) the age of the signaller and (iv) the sex of the signaller. This model excluded the travel context, however included facial expressions. The full model comprised of the above interaction terms and the associated fixed factors. Individual identity was included as a random factor. The dependent variable was rate of UM signal production/hour. I included 191 data points from 26 individuals in the model.

Overall, the full model (*N* = 26 individuals) explained a significant amount of variation in signal production rates, compared to a null model ($X^2_{17} = 144.98$, $P < 0.001$). Likelihood ratio tests revealed that there was a significant interaction between type of UM signal and context ($X^2_4 = 56.84$, $P < 0.001$; Figure 6). Figure 6 reveals a similar pattern of results as Figure 4, regarding vocalisations and gestures in rest, feed and groom, however it also illustrates that the rate of facial signal production is significantly below that for vocal and gestural signals in all of the three contexts. No significant interactions between UM signal type and age ($X^2_2 < 0.01$, $P = 0.998$), UM signal type and number of individuals in the party ($X^2_2 = 1.05$, $P = 0.591$), or UM signal type and sex ($X^2_2 = 2.78$, $P = 0.250$) were found.

As rank was only available for older individuals, I ran a separate model to assess the effects of rank, by adding rank as a fixed effect and the interaction between rank and UM signal type to the full model specified above (*N* = 146 data points from 19 individuals). This model that included rank (*N* = 19) confirmed the overall model ($X^2_{20} = 129.76$, $P < 0.001$), and Context*Modality of UM signal interaction ($X^2_4 = 40.26$, $P < 0.001$) remained significant, however rank had no significant interaction with Modality of UM signal ($X^2_2 = 0.90$, $P = 0.638$).

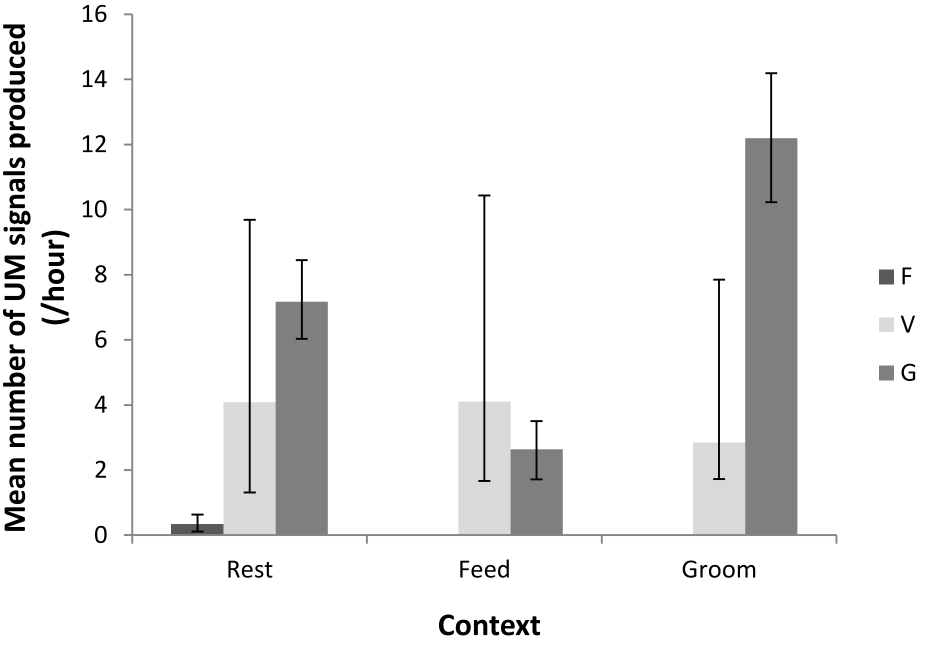


Figure 6. The UM signal production rate (per hour) of facial, vocal and gestural signals in the contexts rest, feed and groom. Error bars represent bootstrapped 95% confidence intervals, based on 1000 iterations. Error bars that do not overlap represent a significant difference. UM rate and confidence intervals derived from data of *N* = 23 (facial rest, vocal and gestural groom), *N* = 25 (vocal and gestural rest), *N* = 26 (vocal and gestural feed). Missing bars occurred when the facial rate was zero.

Recipient responses – MM signal vs UM components

I focused on examining the responses to the grunt + gesture MM signal and matched UM component grunts and gestures. I constructed a model to test if variation in whether or not the focal individual's signal elicited a response from individuals within 5 m could be explained by (i) the signal type produced (UM vocal, UM gestural, MM vocal-gestural), (ii) the number of individuals within 5 m (1-2, or 3+) or (iii) the rank of the signaller. The dependent variable was whether or not there had been any response (Y/N), fixed factors were the type of signal, the signaller's rank, and individuals within 5 m. Identity of the signaller and signal number, which denoted which UM and MM signals were matched together, were included as random factors. 104 data points from 7 individuals were included in the model.

Overall, the full model (*N* = 7 individuals) explained a significant amount of variation in whether or not the focal individual's signal elicited a response from recipients within 5 m, compared to a null model ($X^2_4 = 37.12$, $P < 0.001$). Likelihood ratio tests revealed that there was a significant main effect of signal type produced ($X^2_2 = 34.16$, $P < 0.001$; Figure 7). Figure 7 shows that UM vocal signals were significantly less likely to elicit a response from recipients, as compared to MM vocal-gestural signals or UM gestural signals. There was no significant difference in the proportion of MM vocal-gestural and UM gestural signals which elicited a response. A trend for lower ranking individuals to be more likely receive a response than higher ranking individuals was found, however this effect was not significant($X^2_1 = 2.85$, $P = 0.092$), nor was the effect of the number of individuals within 5 m of the focal individual ($X^2_1 = 2.61$, $P = 0.106$).

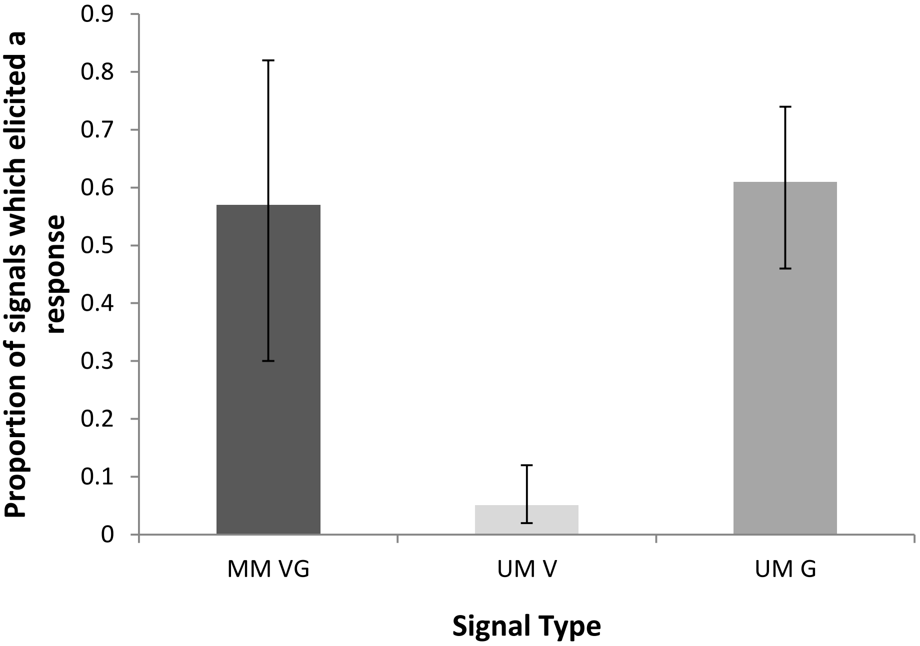


Figure 7. The proportion of focal individual MM vocal-gestural, UM vocal and UM gestural signals which elicited a response from recipients within 5 m. Error bars represent bootstrapped 95% confidence intervals, based on 1000 iterations. Error bars that do not overlap represent a significant difference. Data based on *N* = 7 individuals.

Do MM signals elicit the same responses as their UM components?

I investigated whether the main responses elicited by a MM vocal-gestural signal matched those elicited by either of its UM components. Main responses were defined as the most active response that was the closest to the final behavioural outcome. For instance, if in response to a focal individual signal, a recipient looked at the signaller, approached and groomed, the main response was taken to be grooming.

Of the seven individuals for which I compared MM signals and their UM components, Table 8 shows the four individuals for which the MM signal elicited a response, and thus the responses to the UM components could be compared to the response to the MM signal (see Appendix B for main responses elicited from all MM and matched UM signals, including those which did not elicit a response/were ignored). Whilst MM signals from two female individuals elicited responses that matched the majority of responses to their UM gestural, not UM vocal signals (dominance of gestural response), one male individual elicited different responses to his MM signal than either of the components (emergence). As this sample is very small, caution should be taken when drawing conclusions, as these findings are highly tentative.

Table 8. Instances where the main response of the UM vocal signal and UM gestural signal match the main response of the MM vocal-gestural signal for each individual

ID	Proportion (no.) of UM vocalisations whose main responses match MM signal	Proportion (no.) of UM gestures whose main responses match MM signal
AT (male)	0.57 (4/7)	0.13 (1/8)
PB (male)	0.00 (0/2)	0.00 (0/2)
PO (female)	0.13 (1/8)	0.8 (12/15)
WL (female)	0.00 (0/19)	0.82 (9/11)

Only individuals whose MM signals received a response were included in this table. See Appendix B for the type of responses elicited.

DISCUSSION

Although MM signals may not be as common as UM signals, this study has documented the production of 48 different free MM combinations. Whilst 22 of 26 individuals produced at least one free MM signal, each broad type of MM signal combination was observed to be produced by at least nine of the 26 focal individuals. This suggests that the vast majority of individuals have the capacity and motivation to flexibly and simultaneously combine signals from different modalities, albeit rarely. The number of UM signals produced per hour was found to be more than ten times higher than the number of MM signals in this study. This contrasts sharply with the two previous captive studies to compare proportions of UM and MM signals, which both found much higher relative rates of MM signals. Pollick and de Waal's (2007) chimpanzee signals consisted of 56% gestures, 22.5% facial/vocal signals, and 21.6% MM combinations of the two. Similarly, Taglialatela et al. (2015) found that approximately half of the vocalisations recorded were accompanied by another communicative signal/behaviour. Figure 1 provides a direct comparison to these previous findings from captive studies and clearly shows that here, from wild observations, relatively low levels of MM signals to UM signals were found. This could be attributable to several factors. First, I identified MM signals as ones with temporal overlap, whereas previous studies considered signals or behaviours produced within 2 s (Taglialatela et al., 2015) or even 10 s (Pollick & de Waal, 2007) of each other as MM signals. Second, I only considered vocal, gestural and facial signals, whereas Taglialatela et al. (2015) also included combinations of behaviours such as play or chase with vocalisations to be MM signals. Third, this study shows the importance of context in influencing the relative rate of UM and MM signals, whereas previous studies did not examine the same contexts as this study, nor did they specifically compare different contexts. For instance, Pollick & de Waal did not include rest, but importantly did include social play. Play is highly interactive, and it is common for individuals to show a range of MM signals in this context, such as play face, laughter, and various manual and non-manual gestures simultaneously, so this could also explain the higher proportion of MM signals recorded. Finally, these previous two studies were conducted in captivity, where the social and physical environment may favour higher rates of MM signalling. In an enclosed area individuals are not normally able to express fission-fusion behaviour and this may mean that individuals need to use more sophisticated signals to negotiate tense social interactions, where in the wild they could simply leave the party, or seek a greater distance from certain individuals. Furthermore, in a captive environment visibility is generally much higher than in the dense tropical rainforest, meaning that MM combinations including visual signals are more likely to be successfully received. Investigating MM communication in wild savannah chimpanzees could be an interesting avenue for future research to explore whether the differences between the levels of MM signals produced in the wild and captivity seen so far is due to strategies learnt to cope with the limited space in captivity and interactions with humans, or in fact the level of visibility.

The results partially supported the hypotheses that MM signals would be more likely to elicit a response than UM signals: the likelihood of a response was significantly higher with a MM grunt + gesture signal than a UM grunt signal, but similar to the matching UM gesture signal. This suggests that in the context of these specific signals, adding a vocal signal to a gesture does not change the likelihood of eliciting a response; in contrast, adding a gesture signal to a vocalisation significantly improves the chances of eliciting a response. This supports findings from Pollick & de Waal's (2007) study that indicated that MM signals of gestures combined with a vocalisation or facial expression were no more effective at eliciting responses than gestures alone. Although adding vocalisations to gestures may not increase the likelihood of obtaining a response, it may help disambiguate the signaller's intended meaning or convey more information than the UM signals in isolation. Indeed, in one individual the responses elicited to the MM signal were different to both the vocal and gestural components, indicating MM signals in chimpanzees have the potential to have emergent functions. Equally it could be the case here that vocalisations are used as attention-getting signals alongside gestures (similar to Leavens, Russell & Hopkins, 2010), for example when the recipient does not have their visual attention directed towards the signaller. In this case the gesture might be the signal to which the signaller actually wants the recipient to attend to. This could be analogous to gestures used by male chimpanzees in courtship, such as leaf-clipping and branch-shaking, which draw the female's attention to the male's penis (e.g. Nishida, 1980).

Descriptively, when examining MM signals that elicited a recipient response, in two of the four individuals the type of response elicited by the MM signal was more likely to match the response elicited by the gestural as opposed to the vocal components. Viewed in the framework of Partan and Marler (1999), this indicates that for these individuals this particular free MM signal may be best characterised as a non-redundant combination that retains a dominant gestural response. Whether similar findings would be obtained if a different type of vocalisation had been focused on remains unclear. The grunt vocalisation investigated here might be relatively ambiguous as it is frequently produced in a variety of contexts. In contrast, many of the gestures that were highly successful in eliciting responses (e.g. present groom) were highly specific to a groom context and had a clear and measurable recipient response. As the repertoire illustrates, wild chimpanzees produce a large array of free MM signals and further research needs to systematically investigate the recipient responses to these and their matched UM component signals in order to understand the range of functions free MM signals have in this species.

In contrast to my expectations, I found that the proportion of signals that elicited a response was not dependent on the rank of the individual who produced the signal, nor the number of individuals who were within 5 m of this individual. It could be that the likelihood of a response may be more influenced by the rank difference or relationship between signaller and recipient rather than the absolute rank of the signaller. I was not able to accurately calculate such relative dyadic measures, as for the majority of signals it was difficult to discern which individual was the recipient, and potentially there could have been several. In terms of the number of potential receivers, it could be the case that the majority of signals are in fact directed at a specific individual (e.g. Schel et al., 2013b), even if this might be difficult for human observers to detect, and thus the number of other individuals in the vicinity may not be an important predictor of a response. In the grunt + gesture MM signals that I investigated this is likely to be particularly true, as most signals occurred in a groom context, where the signals are likely to be directed at the grooming partner. In addition, I only considered grunts, which are an example of a ‘proximal’ vocalisation that Taglialatela et al (2009) showed were more likely to be directed towards specific individuals, and to be processed differently by recipients, compared to ‘broadcast’ vocalisations, such as pant hoots.

Relative rates of vocal, gestural and facial signal production varied as a function of context. It was predicted that wild chimpanzees might tailor their signalling to the recipient’s attentional state, as has been shown in captivity (Leavens et al., 2010), and there were indications of this in this wild population. The signal production rate of UM gestures was found to be significantly higher than UM vocalisations in rest and groom contexts. This could be because in these contexts the focal individual might be more likely to have the visual attention of the recipient (especially when in close proximity, such as during grooming), whereas during feed or travel recipients are less likely to have the visual attention of others. Conversely, during travel individuals appear to produce significantly higher rates of vocal signals, which are more likely to be received not only by members of their own party, but also by more distantly located individuals. Facial expressions were only observed in a rest context; for feed and groom contexts the 11 and 9 individuals that met the time criteria for calculation of a signalling rate had a facial signal production rate of zero. Thus UM facial expressions were recorded very rarely, and rates were significantly below those of vocal and gestural signals in rest, feed and groom contexts. It is also important to note that I only coded salient facial expressions (see Table 5), and had I applied full FACS coding (Vick, Waller, Parr, Pasqualini & Bard, 2007) to the videos, subtler facial movements may have been captured. Nevertheless, in the dense forest environment facial expressions alone may be difficult for receivers to detect, and they may be more effective when combined with other signals (as has also been suggested in crested macaques; Micheletta et al., 2013). Indeed Figure 3 shows that facial expressions are produced in all contexts in which I could measure them in combination with other signals. This highlights the importance of adopting a holistic MM approach to studying animal communication: facial expressions in wild chimpanzees are most commonly produced as part of MM signals and extracting facial expressions and analysing them in isolation from the composite signal is likely to lead to an incorrect understanding of signal function.

Contrary to my predictions, none of the individual factors I included in the models influenced the rate of UM and MM signal production. Age, sex and rank did not significantly interact with UM/MM signal rate. This indicates that learning to combine signals from different modalities and how to effectively use different types of signals may occur relatively early in development, before early adulthood. Previous research has shown that infant and juvenile chimpanzees may produce several different gestural signals in sequences as a ‘fail-safe’ strategy to elicit a response. In contrast, more mature individuals were found to produce fewer, but more successful signals (Hobaiter & Byrne, 2011b), and no differences in gesture signalling strategies were seen between sub-adults (10-14/15 years) and adults. In line with these findings, I found that age of the sub-adult and adult individuals I studied, did not influence the relative proportion of MM and UM signals produced. As Hobaiter & Byrne (2011b) found juveniles and infants often used rapid fire gesture sequences, likely to encourage recipients to respond, future research should investigate whether infants and juveniles adopt a similar strategy with signal combinations and produce a higher proportion of MM signals than adults.

By examining multiple modalities and their combinations simultaneously I have revealed free MM combinations and flexible usage of different types of UM signals across contexts. Facial expressions were rarely produced in isolation and instead were more commonly combined with other signals (see Figure 2): artificially extracting facial expressions from these composite signals could lead to misunderstanding of signal function. I advocate a MM approach to gain a full understanding not only of animal communication, but also of the evolutionary roots of human language. Human language is a multimodal communication system, with gestures and facial expressions accompanying and modifying the meaning of speech, and this study has shown that the ability and motivation to flexibly combine different signals is present in wild chimpanzees, and thus are likely to be present in our last common ancestor. Further research into the function of different free MM combinations may reveal the potential for generativity (emergent function, Partan & Marler, 2005) and social learning of MM signal combinations, which would have significant impact on our understanding of the evolution of these key facets of language.

In conclusion, the results reveal an impressive repertoire of free MM signals, but that these signals are used rarely compared to gestures and vocalisations in isolation. Interestingly facial expressions are more commonly produced as part of MM signals than in isolation in several contexts. Systematic investigation of the MM grunt + gesture signal and the UM component signals revealed MM signals were more likely to elicit a response than UM vocal signals, but not UM gestural signals, and several potential functions for this specific type of MM signal were identified. The relative rates of UM vocal, gestural and facial signals varied across contexts, indicating flexible use of different signalling modalities across contexts. The flexibility in communicative signalling this study has revealed, by adopting a MM approach, may represent an important cognitive foundation from which our own complex multimodal communication system could have evolved.

CHAPTER 3: The function of the Big Loud Scratch gesture during grooming

ABSTRACT

Determining the function of animal signals from both the signaller and recipient's perspective is crucial for an accurate understanding of animal communication and social interactions. One gesture which has been suggested to have a clear communicative function in chimpanzees is the 'big loud scratch' (BLS). Although researchers have previously suggested several different potential functions of the BLS, including acting as a referential signal to request grooming in a specific location, there has been little empirical investigation of this gesture. Here I collected observational data from 26 chimpanzees of the Kanyawara community, Uganda, on the production and reception of the BLS in one specific context; dyadic grooming. I used video data to test the following hypotheses: The BLS is used in dyadic grooming to (1) attract the visual attention of the partner; (2) initiate grooming; (3a) request grooming from the partner; (3b) request the partner to 'present groom', or (4) request grooming of a specific location. I found little support for the BLS functioning to gain the visual attention of the partner; the majority of BLSs were produced when the partner was already facing the signaller, and when this was not the case, the BLS did not seem effective at eliciting the partner to turn around. Equally, I found little evidence that BLSs were given to request grooming in a specific body area. BLSs were more often produced by 'groomers', rather than 'groomees'; when they were given by a groomee the groomer did not preferentially groom this location, and the groomee rarely appeared to pursue this goal. In contrast, groomers were significantly more likely to BLS in the 20 s prior to start of grooming than in the rest of the bout, indicating BLSs play a role in initiation of grooming. In addition, groomers were more likely to start to receive grooming immediately after a BLS. Whilst receiving grooming seems to satisfy the signaller, when the partner did not provide grooming, the signaller was significantly more likely to persist, elaborate or terminate the grooming bout. In contrast, although recipients often responded to groomer BLSs with a present groom gesture, this did not seem to satisfy the signaller. These findings suggest that this

signal has important functions in facilitating grooming interactions, and although it appears to be produced in a goal-directed manner, the BLS does not seem to be a referential signal, as was suggested by previous empirical work.

INTRODUCTION

Elucidating the function of specific signals is critical to understanding the communicative behaviour of any species. Here I discuss function both from the signaller and recipient's perspective, as these can differ. One method for investigating how a signal might be used from the signaller's side is by attempting to determine the 'goal' of the signaller, for instance by identifying the outcome that is satisfactory for the individual giving the signal (e.g. Hobaiter & Byrne, 2014; Roberts, Vick & Buchanan-Smith, 2012). Conversely, a signal's function can be explored from the recipient's perspective by looking at the frequency of different types of responses from the individuals that receive the signal; thus determining how others make use of the signal (e.g. Slocombe & Zuberbühler, 2005).

In order to determine the goal of the signaller, researchers have examined persistence in signalling and tried to identify 'stopping rules' to ascertain the circumstances or recipient responses that satisfy the signaller's goal and therefore lead to the cessation of persistent signalling. This approach has been used most extensively by gesture researchers, who have identified 'Apparently Satisfactory Outcomes' (ASOs) for a large portion of the wild chimpanzee gestural repertoire (Hobaiter & Byrne, 2014; Fröhlich, Wittig & Pika, 2016), wild bonobo repertoire (Graham, Furuichi & Byrne, 2016) and captive orangutan gestures (Cartmill & Byrne, 2010). As great ape gestures meet several behavioural markers for intentional production, these researchers often argue that these gestural ASOs reflect the intentional meaning of the signal. However, this same approach can be used to try and determine the goal of signaller and therefore the function of the signal from the signaller's perspective, without any assumptions about the nature of the cognitive processes underlying signal production. For instance, Thomas langur monkey males give predator alarm calls when detecting a tiger and they will continue calling until all group members have given at least one alarm call (Wich & de Vries, 2006). This experiment indicates that from the signaller's perspective the function of this call is to ensure that all group members acknowledge the predator threat, and calling therefore persists until this goal is achieved. Schel et al. (2013a) similarly found that chimpanzees persisted in producing alarm calls, until all party members were safe, indicating that the goal of the signaller may have been to warn others and encourage them to seek safety.

In order to understand the function of a signal from the recipient's perspective, research has focused on how individuals respond to, and use, certain signals. Most research has focused on the vocal domain, where playback experiments make it possible to test how receivers respond to the vocal signal alone, without other contextual and behavioural cues. The seminal studies of Seyfarth, Cheney and Marler (1980) showed that vervet monkeys respond to structurally distinct alarm calls for different predators, with the same adaptive anti-predator responses as they produce when detecting the predator themselves. This indicates that recipients can infer the type of predatory threat present from these alarm calls and use them to coordinate their predator response behaviour. Similar recipient responses to alarm calls in a diverse range of species have now been documented (e.g. chickens: Evans, Evans & Marler, 1993; meerkats: Manser, Bell & Fletcher, 2001; lemurs: Fichtel & Kappeler, 2002; Diana monkeys: Zuberbühler, 2000). In a feeding context, recipients may also infer the value or type of food being consumed by the caller and use the food-associated calls of conspecifics to influence their own foraging behaviour (e.g. where to look for food; what type of food is available in the vicinity; Slocombe & Zuberbühler, 2005). Whilst vocal signals often have important functions related to conveying information to receivers about external events in the world, great ape gestures are commonly used to request specific behaviour from recipients, particularly within dyadic interactions (e.g. Fröhlich et al., 2016; Hobaiter & Byrne, 2014).

In chimpanzees, one context where coordination and negotiation of behaviour between a signaller and recipient may be particularly necessary is in the critically important social interaction of grooming. The negotiation of this behaviour has more recently become the focus of research, with one oro-facial gesture shown to facilitate this cooperative behaviour being 'lip-smacking'; seen in wild chimpanzees. This gesture has been observed in several wild groups (e.g. Ngogo, Uganda: Watts, 2016; Mahale and Gombe, Tanzania: Nishida et al., 1999), and when produced at the beginning of a bout, may increase the grooming bout duration and grooming reciprocity (Budongo, Uganda: Fedurek et al., 2015). Related signals, such as ‘splutters’ and ‘teeth chomps’ have also been put forward as potentially having similar social functions during grooming in chimpanzees (Watts, 2016).

Aside from these oral signals, a further chimpanzee gesture, which captured the attention of Goodall (1986) as a signal with possible functions for coordinating involvement in grooming, was the big loud scratch (BLS). This was operationally defined by Hobaiter and Byrne (2011a) as a ‘loud, exaggerated scratching movement on the signaller’s own body’ (p. 753). Since Goodall’s first observations, several other researchers have reiterated the potential importance of this common signal in grooming, but also acknowledge its flexible use across a range of behavioural contexts (e.g. Hobaiter & Byrne, 2014). This flexibility suggests this signal is not a rigid stimulus-response to certain environmental triggers, and as there is indication that it seems to have different functions in different contexts, this gesture has the potential to provide insight into the cognitive complexities of the communication system of our closest living relatives.

Nevertheless there is debate as to the function of the BLS in a grooming context. Goodall (1986) first suggested that the scratch may function as an auditory attention getter, or that social grooming may be initiated with this signal, indicating that the signaller may be trying to elicit grooming. If the BLS is indeed an attention-getter this would be cognitively interesting as this might mean the signaller is manipulating the attentional state of the recipient, perhaps so they can then produce another signal once they have the recipient’s visual attention (demonstrating first-order intentionality; Liebal et al., 2013). A second study to advocate the role of the BLS in grooming initiation is that of Hobaiter and Byrne (2014); when recording the outcome of the BLS that the signaller is satisfied with, this often aligns with the meaning ‘groom me’, again suggesting the function is to elicit grooming. The BLS has, however, also been put forward as a referential signal in this context. Pika and Mitani (2006) carried out a systematic empirical investigation into this specific signal, to investigate whether the function of this ‘loud and exaggerated scratching movement’ was to elicit grooming in the specific location scratched. They found that this signal resulted in grooming of the scratched area in 64% of instances. They argued that the ‘directed scratch’ appeared to be a referential gesture, indicating the area of the body that the signaller wished to be groomed. However, in their study they only focused on male dyads, and did not test any alternate hypotheses to see whether these might better explain the findings. As this is the only evidence put forward to date, of a gesture which functions referentially in wild chimpanzees, it is important to try and replicate these findings in a different chimpanzee community, and also determine whether this signal has a similar function in females. If this gesture indeed functions referentially then this would have important implications for theories of language evolution, as this would suggest that spontaneous wild chimpanzee gestures share this crucial feature of human language.

The broad aim of the current study was to elucidate the function of the BLS during dyadic grooming, by testing the competing hypotheses outlined above (attention-getter, initiates grooming, requests grooming, referential). Furthermore, from my own observations, I was interested to explore whether the BLS might be used by the groomer to elicit a 'present groom' gesture from the partner (i.e. functions as a way of asking the partner to reposition so a different area can be groomed). Throughout, I focused only on grooming, as this requires coordination between individuals, and looked specifically at dyadic interactions as these make it easier to ascertain who the communicative partner is. I will be referring to the 'groomer' as the individual attending to the fur/body of a partner; combing through the fur or picking at the skin to remove dirt or parasites (grooming). 'Groomee' refers to the individual that is being groomed by the partner.

The four hypotheses and accompanying predictions were as follows:

(1) the BLS functions to attract the visual attention of the partner; it is predicted that a BLS is produced most often when the partner is not facing the signaller, that when this is the case the partner will then turn to face the signaller, then the signaller will produce another signal. If the partner does not turn around the signaller will persist (give more BLSs), elaborate (give another type of signal) or terminate the bout,

(2) the BLS functions to initiate grooming; it is predicted that BLS production rate is higher in the 20 s before dyadic grooming start, than during dyadic grooming. As Hobaiter and Byrne (2014) suggest the meaning of this signal is 'groom me', it is predicted that the rate of BLS production will be significantly higher for individuals that

will subsequently be groomed (groomees), compared to subsequent groomers. Conversely, if the BLS indicates willingness or intention to groom, it will be used more by groomers than groomees in initiation of a grooming bout, and may be associated with groomees switching roles to become the groomer during the bout,

(3a) when groomers produce BLSs they function to request grooming from the groomee (Hobaiter & Byrne, 2014: “groom me”); it is predicted that there will be a significantly higher rate of grooming direction switches, where the signaller is then subsequently groomed, in the 10 s following a BLS, than during the remainder of dyadic grooming, and the signaller will persist, elaborate, or terminate the grooming bout if they are not subsequently groomed,

(3b) when groomers produce BLSs they function to request the groomee to present groom; it is predicted that there will be a significantly higher rate of partner present grooms in the 10 s following a BLS, than during the remainder of dyadic grooming, and the signaller will persist, elaborate, or terminate the grooming bout if the partner does not subsequently present groom,

(4) when groomees produce BLSs they function to request the partner to groom in the specific location indicated by the scratch; it is predicted that within 10 s after the BLS, the partner will groom within 5 cm of the location of the scratch, and the signaller will persist, elaborate, or terminate the bout when the location of the scratch is not subsequently groomed.

METHODS

Study site and subjects

This study was carried out in Kibale National Park, Uganda, with the Kanyawara community of chimpanzees (please see Chapter 2 for details). The individuals included in this study were 13 males and 13 females; ages ranging 8 - 47 years (see Table 2, Chapter 2).

Equipment

All focal observational data were collected with a Panasonic HDC-SD90 camcorder, with a Sennheiser MKE 400 microphone attached. Videos were coded using Noldus Observer XT 10 event logging software (http://www.noldus.com/animal-behavior-research) for observational data.

Data collection

The data analysed for this chapter was extracted from the same observational video data collected for Chapter 2.

Video coding

Video coding with Observer XT 10 software was used to extract continuous information about the behaviours of the focal individual, as well as the point of specific behavioural events. Only those bouts where the grooming partner of the focal animal was over the age of four years were coded, as interactions with infants often involved less gestural grooming negotiation, and more physical positioning and movement of the infant by the older individual.

Table 9 shows the definitions of the key behaviours coded, which comprise the dataset used to address all hypotheses. If only one partner in the dyad is providing grooming, it is considered unidirectional, whereas ‘mutual’ refers to the situation where both individuals are simultaneously grooming one another.

Only data from dyadic grooming were analysed, and the 20 s before begin of dyadic grooming, for Hypothesis 2. The behaviours coded as continuous states, shown in Table 9, had to continue for >3 s in order to be coded. For instance, if the focal animal was the groomer for 15 s, then was the groomee for 2 s, and then the groomer again, this would all be coded as the focal animal being the groomer. This rule was adopted to ensure important behaviour changes were captured, and to make coding feasible. Point events were coded the moment that particular behaviour started, for example the point at which the partner started to turn around to face the focal individual.

Table 9. Descriptions of behaviours coded for the BLS analysis

Behaviour	**Coded for focal individual only, or also partner?**	**Coded as point event or continuous state?**	**Sub-behaviours**	**Description**
Dyadic grooming	Both*	Continuous state	-	Defined as grooming between two individuals aged over four years; this could be unidirectional or mutual. When another individual, over four years of age, joined the grooming bout by grooming with either one of the individuals in the dyad, this was no longer considered dyadic grooming. Grooming bouts involving infants younger than four years were not considered.
Grooming role	Both*	Continuous state	Groomer	The individual attending to the fur/body of the partner; combing through the fur or picking at the skin to remove dirt or parasites. The partner is not grooming the individual.
			Groomee	The individual having their fur/body attended to by the partner. The

				individual is not grooming the partner.
			Mutual	Both individuals in the dyad are attending to one another's fur/body simultaneously.
Partner facing or not facing	Focal individual only	Continuous state	Partner facing	The partner was 'facing' the focal individual when their head was positioned at such an angle that they would still be able to see a silent gesture given by the focal animal.
			Partner not facing	Coded when the partner had their face turned away to the extent that they would definitely not be able to see a silent gesture, or when the partner had their eyes closed (i.e. the focal animal did not have the visual attention of the partner).
Groomee turns around to face (focal) groomer	Focal individual only	Point event	-	This event was coded at the point that the groomee starts to turn their head towards the groomer. This is coded when the groomee goes from a state of not being able to see a silent gesture from the groomer, to turning in a deliberate motion to face towards the groomer; thus entering a state where a silent gesture could be seen.

Big loud scratch (BLS)	Both	Point event	-	This gesture was coded during, and in the 20 s before, dyadic grooming. It was defined as a ‘loud exaggerated scratching movement on the signaller’s own body’ (based on Hobaiter & Byrne, 2011a, p. 753). To aid reliable and systematic coding, I added several operational criteria: (1) the scratch must cover a minimum of approximately 15 cm distance on the body, (2) the scratching movement must involve the entire arm, rather than being from the fingers or wrist, (3) the scratching event must comprise two or more scratches (scratches within 10 s of one another were considered one BLS event), (4) the scratch must not be part of self-grooming, where an individual might scratch to lift up dirt or parasites so they can then pull these out of the fur and/or inspect them (I was only interested in mechanically ineffective gestures).
Present groom	Both	Point event	-	Defined as being when the ‘body is moved to deliberately expose an area to the recipients attention’ (based on Hobaiter & Byrne, 2011a, p. 756).

Body area groomed ◊	Both	Continuous state	Front of torso	Includes chest and belly.
			Back of torso	Includes upper and lower back.
			Arm	Includes hand and up to shoulder.
			Leg	Includes foot and up to hip.
			Face	Includes hairless area of the face, and ears.
			Head	Includes everything on the head except the face and ears.
			Ano-genital	Includes area around the anus and genitals.
Indicators of the signaller’s goal	Both	Point event	Persistence	Another BLS is given in the 30 s following the original BLS event.
			Elaboration	A different communicative signal is given in the 30 s following the original BLS event.

	Termination	The grooming bout is terminated by the signaller, within 30 s following the original BLS event.

*Coded for focal individual, but can infer behaviour of the partner from this. ◊ Only coded when grooming was unidirectional, not mutual.

Calculation of rates

Rates for the BLS produced in the 20 s before grooming start (Hypothesis 2) were calculated taking into account the time the individual was visible. When calculating rates during dyadic grooming (i.e. Hypotheses 2 and 3), it was assumed that both individuals in the dyad were visible for the entirety, as this was virtually always the case.

Statistical analysis

Individuals had multiple grooming bouts (range 8 - 34), so in order to avoid pseudoreplication (Waller et al., 2013), for each analysis, data from all available bouts for an individual were combined so each individual contributed a single data point to each analysis (for instance a rate would be calculated for an individual by summing all relevant signals and dividing these by all the available analysed time). For each analysis the distribution of the variables was plotted; for those where Q-Q plots and Shapiro-Wilk tests indicated non-normal distribution, non-parametric analyses were conducted (related-samples Wilcoxon signed rank tests), and the median and inter-quartile ranges (IQR) reported. When the data were normally distributed paired samples t-tests were used, and mean and standard deviation (SD) reported. All statistical tests were two-tailed. Cohen's r was calculated for non-parametric effect sizes, with 0.1 considered a small effect size, 0.3 medium and 0.5 large (Cohen, 1988). Cohen's d was calculated for parametric effect sizes, with 0.2 considered a small effect size, 0.5 medium and 0.8 large (Cohen, 1977).

RESULTS

Twenty-four hours and 25 min of dyadic grooming were coded from the total videos coded (see 'Data collection' section in Chapter 2). Within this time, 319 BLSs were given by the individuals in the grooming dyad, as well as 79 recorded in the 20 s before the start of dyadic grooming (from either individual of the subsequent dyad).

Hypothesis 1: The BLS is an attention-getter

Here only data from the focal individual were analysed, as whether or not the partner was facing was only coded from the focal animal's perspective.

Was a BLS produced more often when the partner was not facing the signaller?

Seventeen focal individuals had four or more BLS events (total BLS events = 146) during dyadic grooming, and entered into this analysis.

For these events the partner was significantly more likely to already be facing the focal individual (median = 83.33%, IQR = 32.50), than not facing (16.67%, IQR = 32.50), when the BLS is given (Wilcoxon, z = -3.45, $P < 0.001$), with a large effect size ($r = 0.59$).

When the partner was not facing the signaller at the time of the BLS, did they turn around to face them within 10 s after the BLS?

There were 12 focal individuals that produced at least one BLS when the partner was not facing them ($N = 29$ BLS events).

Of these, the partner only turned around to face the focal animal in 4/29 (14%) events.

When the partner was not facing, and they turned around in the 10 s after the BLS, did the signaller then give another, different, signal in the 10 s following?

This was investigated to explore whether the focal individual would produce a further signal, once they had their partner's visual attention. However, of the four BLS events ($N = 4$ individuals) where the partner turns around to face the focal individual within 10 s after the BLS, the focal animal did not produce another (same or different) signal in the 10 s following.

Hypothesis 2: The BLS initiates grooming

Was the BLS rate higher in the 20 s before the start of dyadic grooming, than during dyadic grooming?

Twenty-five individuals had a minimum of 60 s total time available from the 20 s before dyadic grooming periods, as well as a minimum of 900 s (15 min) during dyadic grooming (as a focal individual only).

For these individuals it was found that BLS production rate (/hour) was significantly higher during the 20 s before the start of a dyadic grooming bout, than during a dyadic grooming bout (Wilcoxon: z = 4.20, $P < 0.001$; see Figure 8), with a large effect size ($r = 0.59$).

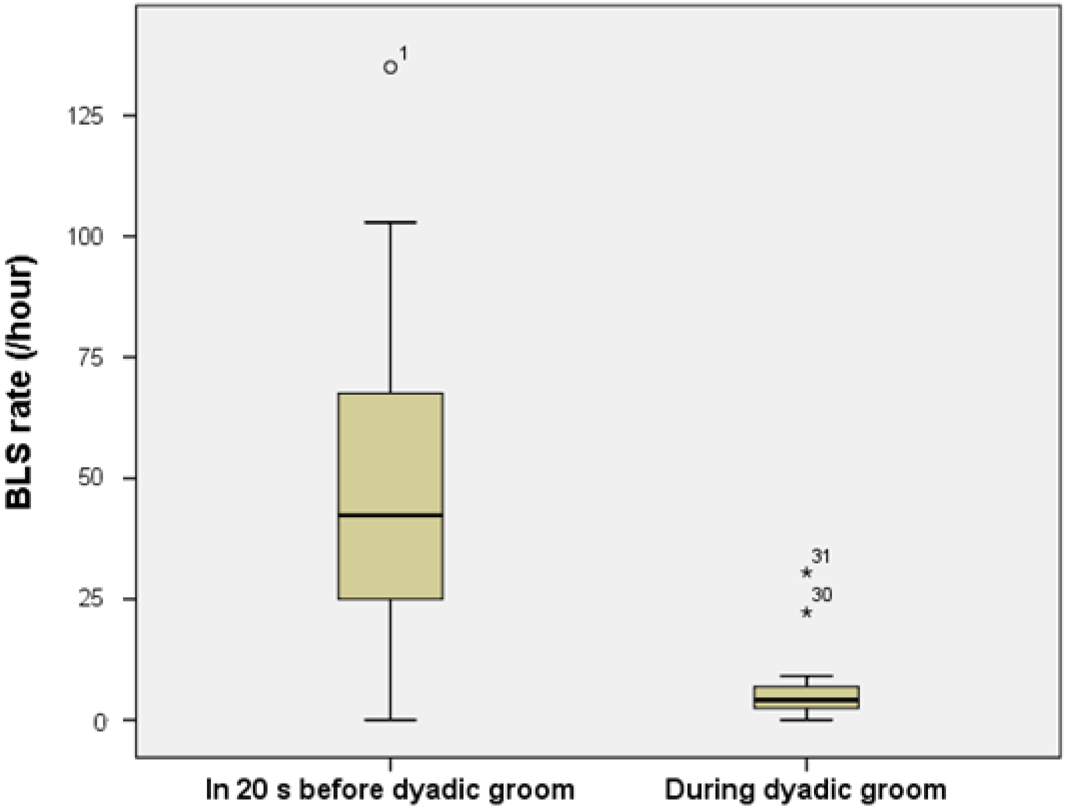


Figure 8. The median, IQR and range for BLS rate (BLS/hour), in the 20 s period before the start of dyadic grooming, and during dyadic grooming (*N* = 25). Small circles represent outliers, stars represent extreme outliers.

Were BLS rates in the initiation period higher for subsequent groomers or groomees?

Twenty-two individuals have a minimum of 30 s available from the 20 s before dyadic grooming periods when they then took the role of the groomer, and a minimum of 30 s available from the 20 s before dyadic grooming periods when they then took the role of the groomee (as either a focal individual or partner).

For these individuals it was found that BLS production rate was significantly higher in the 20 s period before the start of dyadic grooming for individuals who subsequently became groomers, than for subsequent groomees (Wilcoxon: z = 2.97, *P* = 0.003; see Figure 9), with a medium effect size (*r* = 0.45).

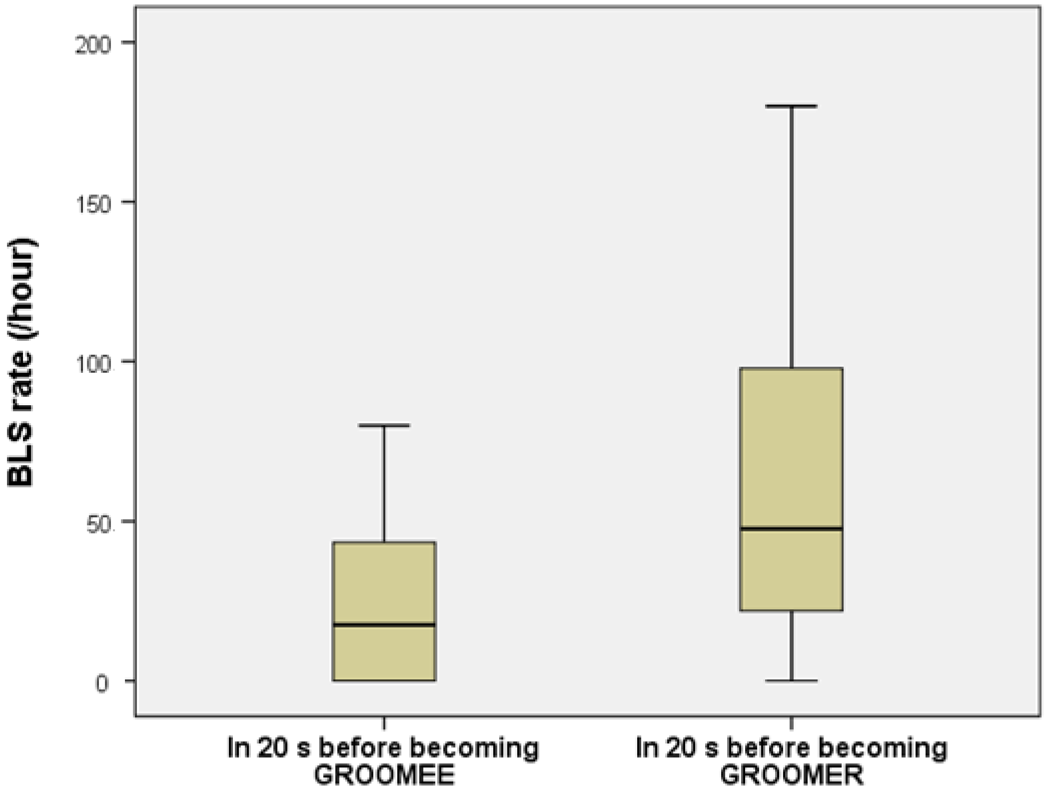


Figure 9. The median, IQR and range for BLS rate (BLS/hour), in the 20 s period before the individual became the groomee, or the groomer, in dyadic grooming (*N* = 22). Small circles represent outliers, stars represent extreme outliers.

Was the BLS given by the groomee to initiate grooming (switch to groomer role) during a dyadic bout?

Fourteen focal individuals gave a BLS as a groomee during dyadic grooming (*N* = 30 BLS events; range per individual 1 - 13). There were insufficient instances to calculate reliable rates of grooming direction switching in the 10 s after the BLS compared to the rest of the bout. However, descriptively, of the 30 BLSs given by a groomee, 16 (53%) were followed by a grooming direction switch in the 10 s following the end of the BLS, resulting in the groomee starting to groom the partner. Thus, there is some indication that BLSs predict the signaller starting to provide grooming to the partner during a bout.

Hypothesis 3a: The BLS is given by the groomer as a request for grooming during a dyadic bout

Was the rate of 'favourable' grooming direction switches higher in the 10 s following a groomer BLS, than at any other time when the individual is the groomer?

Fourteen focal individuals had four or more BLSs, given when they were the groomer (*N* = 101 BLS events), and a minimum of 900 s (15 min) of analysed time during which they were the groomer. For these I coded whether or not there was a 'favourable' grooming direction switch in the 10 s after the BLS signal, as well as at any other point during the time that the individual was the groomer. 'Favourable' was defined as switching from the role of a groomer to the role of groomee or mutual. Thus I could calculate for each individual the rate (/hour) of favourable switches occurring in (i) the 10 s periods after a groomer BLS and (ii) the remaining time as groomer (excluding all post-groomer BLS 10 s periods).

It was found that the rate of favourable direction switches, where the groomer then receives grooming, was higher in 10 s following a groomer BLS than in the remainder of time in the role of the groomer (t (13) = 5.52, *P* < 0.001), with a large effect size (*d* = 1.86). This finding is clearly seen in Figure 10 below.

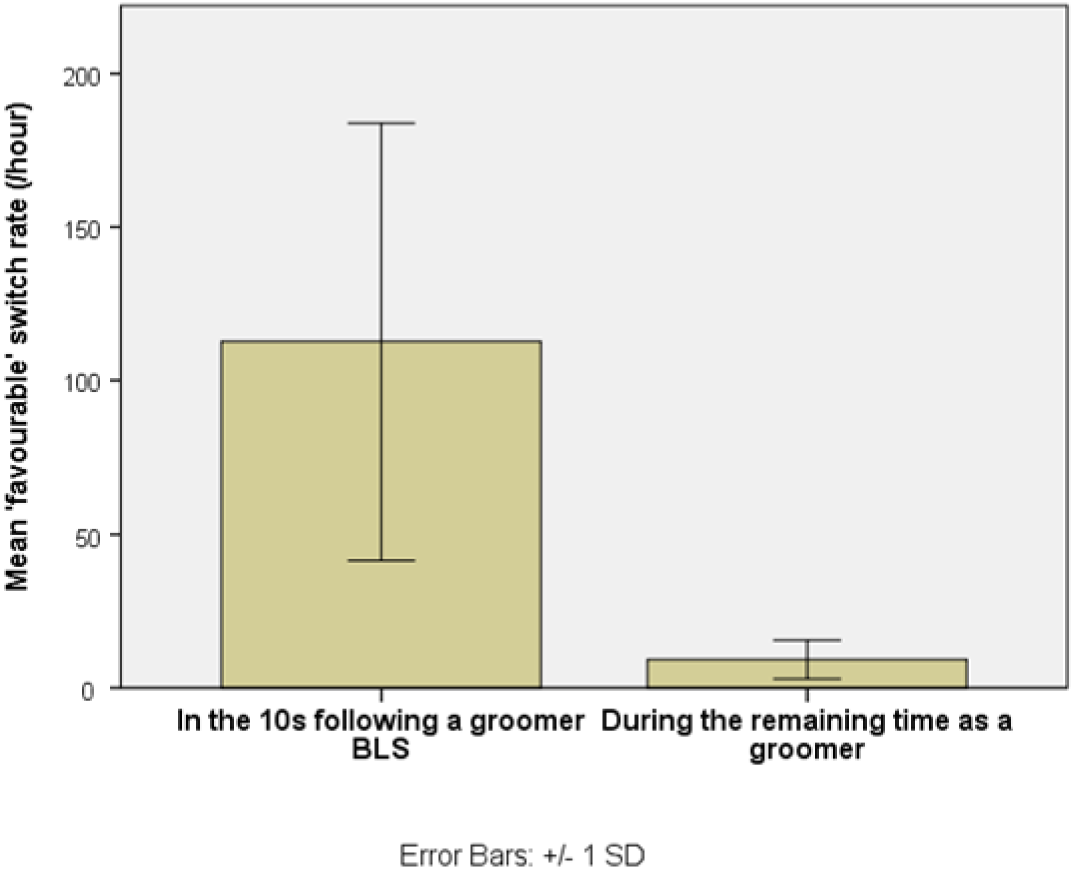


Figure 10. The mean (error bars represent 1 SD) of favourable grooming direction switches in the 10 s periods following a groomer BLS and in the remainder of all time as a groomer (*N* = 14).

If there was no favourable switch in the 10 s after the groomer BLS, did the groomer persist, elaborate, and/or terminate the bout?

All 14 individuals included in the analysis above, gave at least two BLSs that did not elicit grooming from the partner (*N* = 76 BLS events).

Of these, the groomer showed persistence after a mean of 15.14% (SD = 17.39) events, elaboration after 8.90% (SD = 17.98), and termination after 14.61% (SD = 23.86). Each mean was calculated by finding the percentage for each individual and then averaging across all individuals. Taking into account that following each signal there could be more than one of the above (e.g. persistence and then termination), still 27.27% of events where the groomer failed to elicit grooming from the partner, were followed by subsequent behaviour from the groomer that appeared to be in line with the goal of requesting to be groomed.

Conversely, when the groomer received grooming after the BLS (*N* = 25 BLS events) there were no cases of persistence, elaboration or termination. Thus, individuals were found to be significantly more likely to show persistence, elaboration or termination when they did not get groomed following the BLS, than when they did (Wilcoxon: z = 2.68, *P* = 0.007), with a large effect size (*r* = 0.51).

Hypothesis 3b: The BLS is given by the groomer as a request for the partner to ‘present groom’

Was the rate of presenting grooming by the partner higher in the 10 s following a groomer BLS, than at any other time when the individual is the groomer?

The fourteen individuals with four or more BLSs given in the role of groomer during were entered into this analysis (*N* = 101 BLS events); these all had a minimum of 900 s (15 min) of analysed time in the role of groomer. For these I coded whether or not there was a ‘present groom’ from the groomee in the 10 s after the BLS signal. Thus I could calculate the rate (/hour) of present grooms occurring in (i) the 10 s periods after a groomer BLS and (ii) in the remaining time as groomer (excluding all 10 s periods following a groomer BLS).

It was found that the rate of presenting grooming, was higher in 10 s following a groomer BLS than in the remainder of the time in the role of the groomer (Wilcoxon: z = 3.06, *P* = 0.002; Figure 11), with a large effect size (*r* = 0.58).

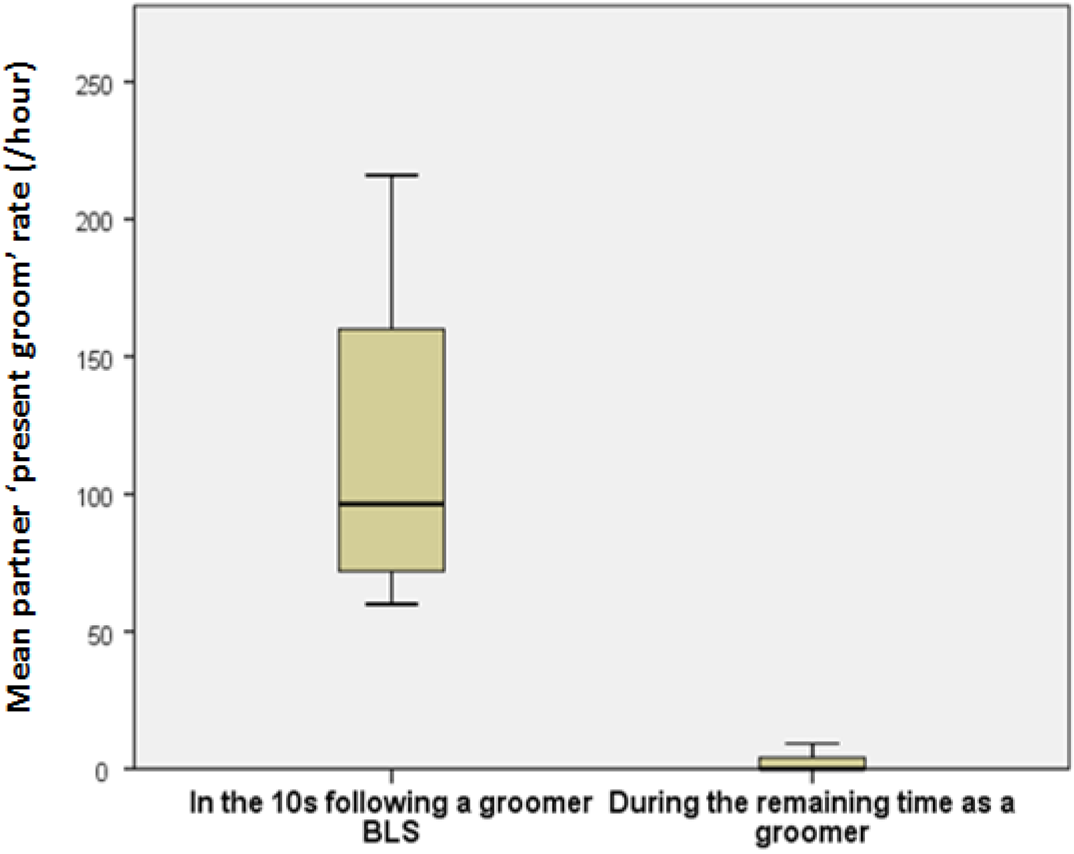


Figure 11. The median, IQR and range for presenting grooming rate (/hour), in the 10 s following a groomer BLS and in the remainder of all time as a groomer (*N* = 14).

If the partner did not present groom in the 10 s after the groomer BLS, did the groomer persist, elaborate, and/or terminate the bout?

All 14 individuals included in the analysis above, gave at least two groomer BLSs that did not elicit the partner to present groom (*N* = 73 BLS events).

Of these, the groomer showed persistence after a mean of 7.68% (SD = 12.89) events, elaboration after 7.74% (SD = 16.71), and termination after 8.87% (SD = 19.36). Overall, 18.45% of events where the signaller failed to elicit a present groom from the partner, were followed by subsequent behaviour from the groomer that appeared to be in line with the goal of requesting the partner to present groom.

Conversely, when the partner presented grooming after the groomer BLS (*N* = 28 BLS events), the groomer nevertheless showed persistence after a mean of 20.00% (SD = 33.15) events, elaboration after 5.00% (SD = 11.25), and termination after 15.00% (SD

= 33.75). Thus, in 21.67% of events, the groomer's behaviour is indicative of pursuing a goal that was not for the partner to present groom. This was also supported by the fact that there was no significant difference in the persistence, elaboration and termination shown when the partner did and did not present groom following the BLS (Wilcoxon: z = 0.09, *P* = 0.933).

Hypothesis 4: The BLS is a request by the groomee for grooming of a specific location ('directed scratch')

For this hypothesis it is important to highlight that the majority of BLSs during dyadic grooming are given by groomers (*N* = 202 BLS events), rather than groomees or mutual groomers (*N* = 117 BLS events). All BLSs produced by an individual who was the groomer before the BLS, and remained the groomer after the BLS, were excluded from this analysis. Thus the data set comprised 117 BLS events (*N* = 24 individuals), produced by an individual who was being groomed before and/or after the BLS (here referred to as 'groomee').

Of these 117, 12 BLS events (10%) were in a location within 5 cm of where the groomer was grooming at the time; these were also excluded from further analysis. At least for these 10% of scratches it seems unlikely that the function of the BLS was to redirect the grooming location.

Furthermore, a groomee BLS event covered on average of 1.5 (SD = 0.74) broad body areas, with almost one third (32%) of scratches covering more than one location. As these broad body areas could themselves encompass a relatively large area e.g. 'left arm', this makes it difficult to argue that the BLS conveys very specific location information.

When the groomee gave a BLS, did the groomer groom that location?

Eighty-six BLS events (*N* = 24 individuals), where the individual that scratched was subsequently groomed (i.e. was groomee or mutual groomer after the scratch) were examined.

Figure 12 shows that of the 24 events where subsequent grooming was within 5 cm of the BLS location, the majority of these BLSs were accompanied by a simultaneous present groom gesture, which indicated the same location as the BLS.

The 62 'non-matches' occurred when either a BLS was given alone, or accompanied by a present groom gesture which indicated a different area to the BLS gesture. Of the 15 instances where the simultaneous present groom gesture indicated a different location to the BLS gesture, the subsequent grooming matched the area indicated by the present groom gesture in 14 instances.

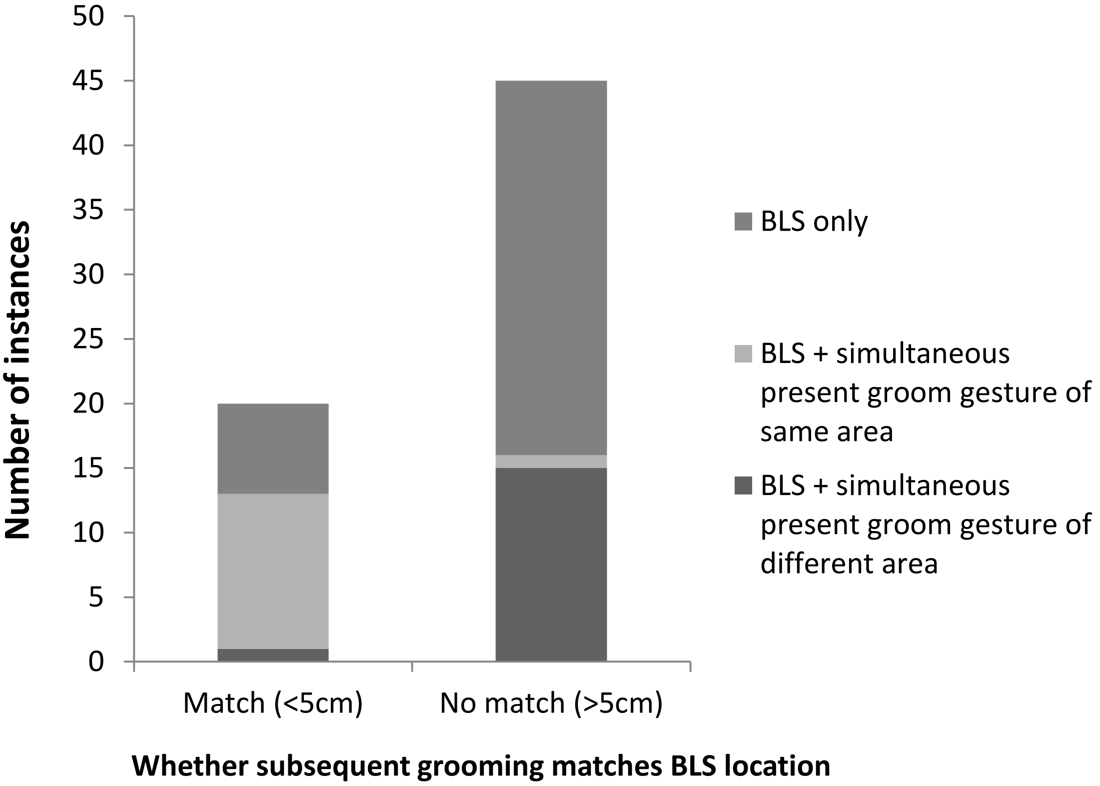


Figure 12. The number of instances where subsequent grooming did or did not match the BLS location (<5 cm), and the number of these where the BLS had been produced in isolation, alongside a simultaneous present groom gesture indicating the same area, or alongside a simultaneous present groom gesture indicating a different area (*N* = 24).

If the partner did not groom the scratched location after the BLS, did the signaller persist, elaborate, or terminate the bout?

This excluded the 12 events where the individual scratched within 5 cm of the location that was already being groomed, the 24 events where the subsequent grooming was within 5 cm of the BLS location, and the one event where the partner terminated (so the focal individual did not have opportunity to persist, elaborate or terminate); leaving 80 BLS events for analysis (*N* = 22 individuals).

In the 30 s after a BLS that did not elicit grooming within 5 cm of the location of the scratch there were three instances of persisting with another BLS of the same location (4%), and one instance of the signaller terminating the bout (1%). Thus in only approximately 5% of instances does the signaller seem to be pursuing the goal of being groomed in the location scratched.

Interestingly, in a further 10% of cases persistence or elaboration were shown by the signaller, however the subsequent signals indicated different body areas, thus these behaviours did not indicate that the signaller's goal was to receive grooming of the originally scratched location.

BLSs given in male-male dyads

Pika and Mitani (2006) included only males in their analyses, and investigated BLSs given between different dominance ranks of males (e.g. low, medium and high ranking). They found that BLSs occur most between high ranking males, and that positive responses (location matches) were also most likely to be seen in high ranking – high ranking male dyads. I wanted to explore whether I would also see a similar pattern of findings in the Kanyawara males.

Although sample sizes were too low to perform inferential statistics, Figure 13 shows descriptively that Kanyawara males do not seem to follow the pattern reported for Ngogo males. In Kanyawara BLSs were most often given by mid ranking males irrespective of the partner's rank and positive responses were not concentrated in the high ranking to high ranking dyads. In the male-male dyads, only 14% BLSs received grooming in the indicated location, compared to 64% reported in Ngogo (Pika & Mitani, 2006).

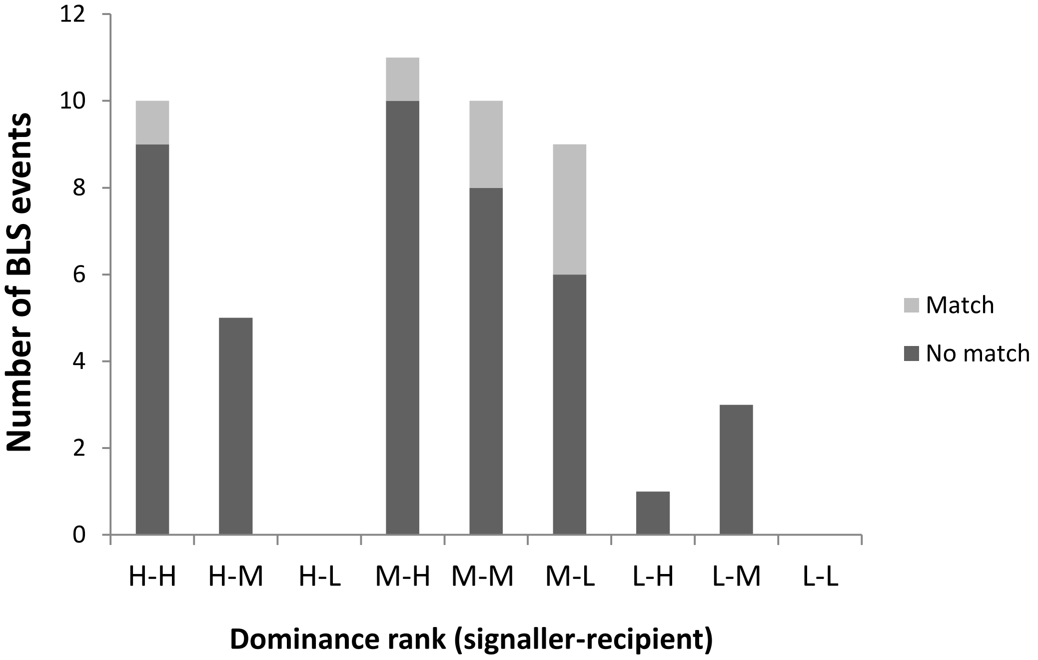


Figure 13. Distribution of BLSs across rank groups, focusing on the *N* = 49 BLS events given in male-male dyads (*N* = 14 males). The first letter on the x-axis label indicates the rank of the signaller, the second that of the partner.

DISCUSSION

The results of this study allow me to make several inferences as to the function of the BLS gesture in dyadic grooming in wild chimpanzees. First, the findings clearly suggest that despite the distinctive auditory component to this signal, the BLS does not appear to function to gain the visual attention of the partner during grooming (Goodall, 1986; Hypothesis 1). This was supported by the fact that the vast majority of scratches were produced when the partner was already facing the signaller, so they did not seem to be strategically given when the partner was not attending to the signaller. Additionally, for those instances where the BLS was given when the partner was indeed facing away, the partner was unlikely to turn around following the BLS and on the rare occasions when they did, no further signals were produced once the visual attention of the recipient was captured. Taken together, these findings indicate the signaller was not using the BLS to manipulate the visual attention of the partner.

Second, the results provide little support for BLSs functioning to refer to specific body locations that the signaller wanted to be groomed (Pika & Mitani, 2006; Hypothesis 4). I found that almost twice as many BLSs were given by individuals who were the groomer before and after the scratch, than individuals who were the groomees; Pika and Mitani unfortunately do not discuss the frequency of groomer scratches, so it is unclear if this pattern is also present in Ngogo. My data indicate that even if the BLS functions referentially when given by groomees, it likely has another function when given by groomers. As the average number of broad body areas covered by one BLS was 1.5, this lack of specificity in location also argues against the BLS referring to a particular 'spot' for grooming. Furthermore the fact that 10% of BLSs were produced by groomees within 5 cm of the location where the groomer was already grooming indicates that, at least for these cases, the signaller was not requesting grooming of a different location; although it could be contended that the groomee was encouraging the groomer to keep grooming the same location.

The most convincing evidence refuting the claim of the BLS as a referential signal is that when a groomee produced a BLS in isolation the location was three times as likely *not* to match the location of the scratch, than to match the location. The addition of a simultaneous 'present groom' gesture to the BLS which indicated the same location as the scratch drastically increased the likelihood of subsequent grooming matching that location, suggesting this gesture was much more successful at eliciting grooming of the presented area, than a BLS. Similarly, adding a simultaneous 'present groom' gesture to the BLS which indicated a *different* location to the scratch resulted in grooming of the area indicated by the 'present groom' in 14 of 15 cases, whereas in only one case did the subsequent grooming area match that of the BLS. This shows that the BLS likely has little influence on the location of subsequent grooming, however also that chimpanzees may already have an effective signal for requesting grooming in a specific location: the 'present groom' gesture. Further supporting this, the signaller showed relevant persistence, elaboration or termination behaviour in only approximately 5% of cases where grooming was not provided in the scratched location, showing that their goal in producing a BLS was unlikely to be to elicit grooming in the specific location scratched.

As groomees in Kanyawara do not seem to BLS to request grooming in a specific location, I tried to establish what function this signal may have when produced by a groomee during a grooming bout. I had insufficient instances to test this rigorously, however descriptively, around half groomee BLSs were followed by groomees switching roles and providing grooming to the partner. This mirrors the finding that BLSs prior to a grooming bout starting were given more often by individuals who then assumed the role of groomer, with the BLS possibly indicating their willingness or intention to initiate and provide grooming.

It is important to consider the implications of our failure to replicate Pika & Mitani's (2006) findings. One possibility is that the 'directed scratch' gesture observed in the Ngogo community potentially has a culturally learnt function and might be specific to this group. This community is known to be the largest in the world, and is certainly far larger than the Kanywara community (by approximately threefold); this huge number of potential communicative partners could mean that the individuals have honed their communication and grooming negotiation skills more so than other communities. Perhaps a single signal can be produced in subtly different ways or different contexts (e.g. between high ranking individuals), meaning that one signal can have several functions. It could be argued that the failure to replicate the findings of Pika and Mitani (2006) here, may be due to the smaller samples sizes I had (86 BLS events where the signaller was subsequently groomed; 49 in male-male dyads), compared to this previous study (186 BLS events). Whilst this is a concern and highlights the need for more data, the much lower rate of matching overall and in the male-male dyads (14% compared to 64% in Ngogo), and more distributed nature of these signals and positive responses across dominance classes (Figure 13), indicates even with a larger sample, the basic pattern of data from Kanyawara is likely to be very different from Ngogo. This indicates that the first claims of spontaneous referential gestures in chimpanzees, are certainly not representative of chimpanzees as a species and that this original claim needs contrasting with alternative hypotheses and data collecting on the goal of the signaller is required: intentional referential use of the signal was claimed, but not supported by data in the original study. In a broader sense it seems that although chimpanzees can produce intentional and referential pointing gestures in captivity, spontaneous referential gestures in the wild are certainly not universal, and this may have implications for theories concerning the origins of language.

In contrast to the lack of evidence we found for BLSs functioning to request grooming in a specific body location, I found good support for these signals playing a role in the initiation of grooming. BLS rates were significantly higher in the 20 s period before the start of dyadic grooming then during the grooming bout. To explore further the specific function of the pre-grooming BLS, I compared the rate of BLSs produced by the individuals that would become groomees to those that would become groomers. I found that production rate was significantly higher for those who would go on to be the groomer; this is also in line with groomee appearing to use this gesture before switching to a groomer role during dyadic grooming. Previous literature which suggested the role of the BLS in grooming initiation (Goodall, 1986; Hobaiter & Byrne, 2014), indicated that the to-be groomee would be more likely to BLS, as they report the signaller's goal to be requesting grooming. Contrary to these suggestions, the Kanyawara chimpanzees seem to use the BLS before grooming, and potentially by groomees within the bout to indicate a willingness to provide grooming.

The exploration of the BLS when produced by the groomer having a function to request a change in behaviour from the partner, either in the form of a favourable grooming direction switch (i.e. signaller receives grooming), or a present groom from the partner, showed that both of these occur at significantly higher rates in the 10 s following a BLS than during the rest of dyadic grooming. Thus, it seems likely that it is the BLS that is causing the partner to change their behaviour. Furthermore the groomer showed signs of pursuing the goal of receiving grooming in approximately one third of cases where a favourable grooming direction switch was not elicited in the 10 s after the BLS, and no signs of pursuing this objective when a favourable switch did occur after the BLS. In contrast, the signaller showed no signs of pursuing the goal of eliciting a present groom from the partner, showing no significant difference in frequency of persistence, elaboration and termination when the partner did and did not present groom following the BLS. Thus, although the partner often responded with a present groom gesture, the groomer did not appear to be striving for this response. This appears to suggest that the signaller may have been pursuing a different goal, and was not satisfied with the present groom of the partner; this refutes Hypothesis 3b. Moreover, this finding highlights the importance of focusing on the function of a signal from both the signaller and recipient's perspective, as in some situations the most frequent response given by the recipient may not be the one that satisfies the signaller. From this I would argue that the primary function of this signal, given by the groomer, is to elicit grooming from the partner, however occasionally an individual will produce a BLS and the partner may not be willing to reciprocate grooming, and so will make a counter demand, by producing a present groom gesture to encourage the partner to groom a while longer.

In future research it would be interesting to explore the effects of bond or relationship on the function of communicative signals; for instance testing whether function differs with different partners, to investigate whether there is flexibility in this respect. Similarly it would be important to compare different chimpanzee communities to elucidate how and why signal functions are established and passed on. In addition, there is much potential for the function of this common gestural signal (BLS) to be studied across many more behavioural contexts in wild chimpanzees, where it is likely to have different functions. Lastly, it would also be of value to test whether the proximate mechanism underpinning the production of these signals is stress or anxiety. Goodall (1968) originally described 'rough scratching', which she observed the chimpanzees to do during intense conflicts, social tension and other situations causing anxiety. This has similarly been reported in captivity (Aureli & de Waal, 1997), and is also noted in other primate species (reviewed by Maestripieri et al., 1992). Although the grooming context studied here may not appear to be a context involving intense anxiety, it could nevertheless be the case that individuals are nervous in these situations. To empirically test whether the BLS could be explained by anxiety one could investigate whether it is seen more often in subordinate individuals, than dominant, as lower-ranking individuals are more likely to fear aggression when approaching, or being near (e.g. grooming with), higher-ranking individuals.

In summary, the non-targeted use of BLSs to inattentive partners, the range of locations scratched within one event, and the failure of the partner to change their grooming towards the location scratched, clearly demonstrates that BLS gestures are not used as attention-getters or as referential signals in the Kanyawara community.

Conversely, strong support was found for the BLS functioning to initiate grooming when given before the start of grooming, and during grooming bouts by groomees, by potentially demonstrating a willingness to groom ('I want to groom'). Furthermore, during dyadic grooming I found convincing evidence that when given by the groomer, the BLS functioned to request grooming from the partner and thus elicit favourable grooming direction switches. Overall, this study shows that the BLS gesture likely functions to initiate, negotiate and coordinate grooming interactions.

CHAPTER 4: The relationship between communication and cooperation in wild chimpanzees

ABSTRACT

Humans have remarkable communicative and cooperative abilities, yet the evolutionary roots of these traits remains unclear. Whilst there seems to be theoretical consensus that language and cooperation have co-evolved, there is little empirical data on the relationship between communication and cooperation. Here I aimed to test whether individual variation in communicative behaviour is related to cooperative tendencies in our closest living relatives, through the examination of unimodal and multimodal communication and cooperative behaviour in wild chimpanzees. The communicative competence of individuals was assessed by measures extracted from focal video data capturing the rate and diversity of vocal, gestural, facial and multimodal signal production across contexts (cooperative: groom; non-cooperative: rest, feed, travel) and the rate and type of recipient responses elicited. Long-term Kibale Chimpanzee Project data were used to calculate the opportunities each focal animal took to engage in cooperative behaviours suggested to show reciprocal altruism: supporting others in agonistic interactions, and grooming. These data formed an index of cooperative tendency which was compared with the index of communicative competence for each individual. The critical finding was a significant negative relationship between composite communication and cooperation measures; indicating individuals that chose to cooperate in grooming and agonistic situations were those that were also less ‘communicative’. Exploring reasons for this unexpected finding, I found this effect was not likely due to individual variables such as sex, the specific contexts that communication is given in (cooperative vs non-cooperative) or whether cooperation is *received*, or *given*. Furthermore I tested if the negative relationship may have been due to more closely bonded individuals requiring less intense communication, and although this association was found to be in the predicted direction within dyadic grooming contexts, it was not significant. I discuss several possible reasons for these counter-intuitive findings, and suggest some important avenues for future empirical work on this topic.

INTRODUCTION

As hopefully evident from previous chapters, the linking theme throughout this research is the quest for evidence relevant to understanding the origins of human language. Here, I attempted to tackle this topic from a slightly different angle, and provide empirical data relevant to important theoretical accounts of the evolution of language.

As discussed in Chapter 1, altruistic acts are a widespread phenomenon in the cooperative human species (e.g. Bowles & Gintis, 2011). Cooperation, like our communication system, is highly complex and advanced, and several researchers have argued that there is interdependency between these two behavioural traits.

First, several theories suggest that some basic form of cooperation must already be in place in order for complex communication to evolve, as individuals must have an urge to share information and intentions with others, which could be argued to constitute a cooperative act (Grice, 1957; Nowak & Krakauer, 1999). Words are relatively "cheap signals" (Zahavi, 1993), and as such there must be another reason behind why individuals would believe each other's verbal utterances, if it is so easy to lie. An underlying cooperative foundation may be necessary for this to be the case, and in order for sharing of information to be an evolutionarily stable strategy. Thus, a cooperative society is likely to be prerequisite for the emergence and spread of a complex communication system, such as language.

On the other hand, it is also argued that more complex communication, which can refer to events and situations in the past, present and future, and thus be decoupled from the current surroundings or emotions of the signaller, is necessary for complex cooperation to be achievable (Brinck & Gaerdenfors, 2003). For instance, if aspiring to perform a novel cooperative act, at some point in the future (i.e. it is to some extent imaginary), one would need to have a structure in place to share this idea to others, and elicit their help and support; complex communication is an invaluable tool in this case. Without the help of symbolic communication, such as language, we may not be able to persuade others that a future goal is worth striving for, and be able to plan how this could be achieved (Gaerdenfors, 2004). Many evolutionary studies of human cooperation presuppose the existence of shared norms (e.g. Fehr, Fischbacher &

Gaechter, 2002), and complex communication may have been necessary for these to be established in the society. It has indeed been found that sending and receiving task-related messages increases cooperation by activating trust and fairness norms in humans (Cohen, Wildschut & Insko, 2009). Similarly, other researchers have suggested that language lowers the cost of finding and punishing free-riders in the group, thereby increasing cooperation, and even if some basic level of cooperation may be necessary for language to begin with, language then offers an enormous leap in coordination complexity (Smith, 2010).

Likewise, several researchers have proposed that the evolution of several distinctly human, highly advanced traits, including cooperation and communication, and others such as complex tool-use, occurred in concert (e.g. Pinker, 2010). In this case it is difficult to study and understand the evolution of these traits in isolation, as selection on one may have influenced and accelerated the evolution of “synergistic” traits (Szathmary & Szamado, 2008). Thus the study of links and relationships between traits is highly informative and important if we are to uncover the evolution of our extremely complex behaviour.

There have been surprisingly few attempts to empirically investigate the relationship between communication and cooperation, despite an abundance of theories acknowledging a possible evolutionary link between the two. As wild chimpanzees are known to communicate through a range of modalities, such as facial expressions, gestures and vocalisations (see Chapter 1), as well as exhibiting several behaviours with cooperative elements (e.g. hunting: Boesch, 2005; grooming: Gomes, Mundry & Boesch, 2009; forming coalitions and alliances: Watts, 2002), it is feasible to investigate these behaviours in this species.

The aim of the current study was to empirically investigate whether a positive association between communicative and cooperative ability, is found in chimpanzees. As it was outside of the scope of this thesis to explore this link across several different species, I endeavoured to look at this on an individual level. If inherent cooperation is truly necessary to develop more complex communication, or if more complex communication truly enables more cooperation, then, extrapolating from these theories to an individual level, one would expect more communicative individuals to be more cooperative. By exploring these behavioural traits in some of our closest living relatives, the chimpanzees, we can investigate whether this proposed relationship between the two was likely already present in our last common ancestors.

Thus, for this study, I aimed to construct a composite measure of communicativeness, comprising (1) the ‘quantity’ of communication, which included the rate of production of both unimodal (UM) and multimodal (MM) signals, (2) the ‘diversity’ of communication, which included the repertoire/diversity of different UM and MM signals produced, (3) the effectiveness in eliciting a response, to both UM and MM signals, and (4) the effectiveness in eliciting an appropriate response.

Alongside this measure of communicativeness I aimed to construct a measure of cooperativeness. Here I chose to look at behaviours that are costly for the actor and benefit the recipient, and will likely to reciprocated in the future (reciprocal altruism). There is often disagreement and general lack of consensus on the exact definition of ‘cooperation’; however the above definition is in line with much previous work (e.g. Nowak, 2006; Silk & Boyd, 2010; definitions discussed at length in West, Griffin & Gardner, 2007). I use the term ‘coordination’ to refer to the complementary execution of behaviours or roles from different individuals. Behaviours identified as mutualistic were not included here as it is often difficult to discern to what extent these are truly cooperative, rather than selfish; for instance differing levels of coordination and cooperation have been observed in hunting (e.g. Mitani & Watts, 2001; Hosaka et al, 2002; Boesch, 1994; Boesch, 2002). Thus, I included grooming; for which I recorded the number of times the individual groomed another individual, given the opportunities they had to do so, and support in aggressive interactions; for which I recorded the opportunities the individual took to perform conflict intervention (using vocal or non-vocal displays to interrupt or break up an aggressive interaction between third parties) or protection (actively supporting one individual involved in the aggressive interaction) when they witnessed an aggressive interaction between other individuals.

Given previous theories, I hypothesised that individuals showing a higher score on ‘communicativeness’ would also show a higher score on ‘cooperativeness’; thus that a positive relationship would be found between the two.

METHODS

Study site and subjects

This study was carried out in Kibale National Park, Uganda, with the Kanyawara community of chimpanzees (see Chapter 2 for details). The individuals included in this study were 13 males and 13 females; ages ranging 8 - 47 years (see Table 2, Chapter 2, which also shows dominance ranks).

Equipment

All focal observational data were collected with a Panasonic HDC-SD90 camcorder, with a Sennheiser MKE 400 microphone attached. Videos were coded using Noldus Observer XT 10 event logging software (http://www.noldus.com/animal-behavior-research) for observational data.

Communication data collection

The data analysed for this chapter was extracted from the same observational video data collected for Chapter 2.

Video coding of communication data

Video coding with Observer XT 10 software was used to extract continuous information about the communicative behaviours of the focal individual, as well as the point of specific behavioural events. Here only communication data extracted from the contexts rest, feed, groom and travel was used (see Chapter 2 for descriptions of these). Recipient response data was only extracted from the main study videos, as this was not systematically and reliably coded during the pilot study.

Criteria for, and calculation of, communicative sub-indices

The ‘composite’ communicative index was comprised of seven ‘sub-indices’. These are described in detail below. For each of the sub-indices, a single score was calculated for each individual that met the criteria for that sub-index. The mean and standard deviation score of the group of individuals that met the criteria for that sub-index was then determined. For each individual that met the criteria for that sub-index, a z-score was calculated by subtracting the group mean from the individual's score, and then dividing this by the group standard deviation.

The calculation of z-scores meant that the sub-indices were directly comparable (raw data were rates and numbers) and we could then combine them into a meaningful composite index. For each individual the composite index score was the mean of all sub-indices. An individual may not have met criterion for all seven sub-indices, but to have a composite index calculated they had to have a minimum of five sub-indices' scores available.

UM and fixed MM signal production rate

This sub-index was a measure of the quantity of UM (and fixed MM) signals produced by each focal individual. Rates (signals/hour) for the modalities: facial expressions, gestures, vocalisations and fixed facial-vocal signals were calculated for the contexts rest, feed, groom and travel. Fixed facial-vocal signals were included here, as these could not be freely decoupled, unlike the signals included in the free MM signal production rate.

The criteria to have rate calculated for a modality in a context was that the individual must have at least 30 min of coded time where that modality was available in that context (20 min for Travel; see Chapter 2 where this calculation is described in greater detail). This was 15 min (10 min Travel) for the fixed facial-vocal signal production rates.

A mean rate for each modality was calculated for an individual only when they met the above criteria for at least two of the four contexts, with those meeting criteria being averaged to give one rate for the modality. An overall mean UM rate was calculated for an individual only when they contributed at least three of the four mean modality rates.

Free MM signal production rate

This sub-index was a measure of the quantity of MM signals produced by each focal individual. Rates (signals/hour) for the free MM combinations: facial-vocal, facial-gestural, vocal-gestural, and facial-vocal-gestural, were calculated for the contexts rest, feed, groom and travel.

The criteria to have rate calculated for a MM combination in a context was that the individual must have at least 15 min of coded time where that MM modality combination was available in that context (10 min for Travel; see Chapter 2 where this calculation is described in greater detail).

A mean rate for each MM combination (e.g. vocal-gestural) across the available contexts was calculated for an individual only when they met the above criteria for at least two of the four contexts (e.g. had 15 min of vocalisations and gestures simultaneously available in rest, and 15 min available in feed). All individuals had MM rates for all four types of free MM combinations, and these were then averaged for an overall mean MM rate for each individual.

UM and fixed MM signal diversity

This sub-index was a measure of the number of different signal types each individual produced. For this sub-index it was necessary to allow identical time frames for each individual to have the opportunity to produce different signals, therefore only the following common context/modality combinations were included: vocalisations, gestures and fixed facial-vocal signals in rest, feed and groom, and facial expressions in rest only. The criteria for each of these modality/context combinations were based on the criteria used for the UM rate above i.e. for gestural and vocal signals 30 min of in rest, feed and groom, for facial signals 30 min in rest and for fixed facial-vocal signals 15 min in rest, feed and groom.

In order to sample the requisite time period for each individual in each context/modality combination, I first extracted from the videos a list of all time periods for which this context/modality combination was available. This list showed only the durations, so I was blind to the number or type of signals each period contained when selecting samples. For instance, for individual PB I would have a list of all durations for which gestures were available in rest. Using this list, I then summed the durations, starting from the shortest, until I reached the time criterion for that modality/context combination, i.e. 30 min for gestures in rest. As it was generally not possible to meet the criterion time exactly, the aim was to sum the durations so that these would be as close as possible to this time (the margin of error was max. +/-7% of the criterion duration). Then I recorded the number of different gesture types produced by PB across these durations. For each individual I then summed the number of signal types across all context/modality combinations, to produce one score for each individual, that represented the total number of different UM (and fixed MM) signal types produced across the above modality/context combinations.

This method was used as it was relatively random (only based on the durations that best made up the criterion time; I was blind to the signal production data at the point of sample choice), captured durations across several different focal days and party compositions (rather than simply signals produced during one or two focal observations), yet still allowed all individuals to have, as far as possible, the same opportunity to demonstrate their signal repertoires in each context/modality combination.

Free MM signal diversity

This sub-index was a measure of the number of different free MM signal combinations each individual produced. For this sub-index it was also necessary to allow identical time periods for each individual to have the opportunity to produce different signals, therefore only the following common context/modality combinations were included: facial-gestural, free facial-vocal, facial-vocal-gestural, vocal-gestural in rest, feed and groom, and vocal-gestural also in travel. The criterion for each modality/context combination was the same as for the free MM rate above i.e. 15 min of each MM modality combination in rest, feed and groom, and 10 min for travel.

The method for calculating a MM diversity score for each individual was essentially identical to that for calculating a UM score above, with the exception of different time criteria. Again, this resulted in one score for each individual, of the total number of different free MM signal combinations produced across the above modality/context combinations.

Recipient responses to UM and fixed MM signals

This sub-index was a measure of how often, after a UM signal or a fixed facial-vocal MM signal was produced by the focal individual, another individual within 5 m of the focal animal responded to this (see Methods of Chapter 2 for definitions and descriptions of responses). This was irrespective of the type of response (positive/negative/signal), and rather a measure of whether the signal had been received by others. Here I only included signals produced when there was at least one potential recipient within 5 m of the focal animal, and only those given in rest, feed, groom or travel. There could be several responses to one signal. For each signal produced by the focal individual the response time started at the start of the signal, and finished 20 s after the end of the signal, unless the focal individual gave another signal in this time, in which case the recipient response period of the first signal would be cut short.

In order to ensure that individual response rates were representative, a recipient response rate sub-index was only calculated for individuals who had a sufficient amount of recipient time available and thus met the following criterion:

$$\sum(analysed\ recipient\ response\ time * no.of\ recipients\ within\ 5\ m)i \ \geq 100$$

With *i* being each signal produced by the focal individual.

This ensured that each individual for whom this sub-index was calculated had produced at least the equivalent to one signal, with 20 s of analysed response time, with five recipients within 5 m, or five signals, each with 20 s analysed response time and one recipient within 5 m.

If individuals met this criterion for having sufficient opportunity for recipients to respond, then the recipient response rate was calculated using the following formula:

$$response\ rate = \frac{no.of\ responses}{\sum(analysed\ recipient\ response\ time * no.of\ recipients\ within\ 5\ m)i}$$

With *i* being each signal produced by the focal individual.

Thus the response rate took into account the time and number of recipients who had the opportunity to respond to the signal.

Recipient responses to free MM signals

This sub-index was a measure of how often, after a MM signal was produced by the focal individual, another individual within 5 m of the focal animal responded to this. The MM recipient response rate was calculated exactly as above for responses to UM and fixed MM signals, with the same criteria having to be met.

Appropriate recipient responses to UM signals

This sub-index was a measure of how often, after a UM signal was produced by the focal individual, another individual within 5 m of the focal animal responded to this in an appropriate or desired fashion. This measure was designed to establish how effective an individual was in achieving their goals, through changing the behaviour of others with communicative signals; in contrast to above, which simply shows how often an individual's signals are received and elicit any kind of response. This appropriate/inappropriate distinction was only possible to ascertain for a selection of signals, based on previous literature (see Table 10). Umbrella signals such as 'manual contact with another individual' were individually checked and the responses coded as appropriate or not depending on the specific signal. As there is no clear evidence for the likely desired responses to specific MM combinations of signals, this was only possible for UM signals.

Table 10. The signals coded for which there is literature to support identification of a potential appropriate response

Signal	**Likely desired/appropriate response**	**References**
FACIAL		
Bared teeth display	Affinitive behaviour, seeking contact and reassurance.	Van Hooff (1972) Waller & Dunbar (2005)

		Parr, Cohen & de Waal (2005)
Play face	Only seen during play. Seems to function to show benign intent – potentially prolonging the play bout.	Flack, Jeanotte & de Waal (2004) Parr, Cohen & de Waal (2005)
Scream face	Seen in the contexts of aggression and sexual encounters. In agonistic contexts, the likely appropriate response is cessation of aggression or gaining of support/assistance/reassurance from others.	Parr, Cohen & de Waal (2005)
Pout	Seeking contact and reassurance.	Parr, Cohen & de Waal (2005)
Whimper face	Affinitive behaviour, assistance/aid from others.	Van Hoof (1973) Parr, Cohen & de Waal (2005)
VOCAL		Submissive/non-submissive distinction, and context based on Goodall (1986) and Clark (1993).
Pant grunt	Submissive. Context = to dominant individual, reunion, greeting. Possible desired response = no aggression/being tolerated by the dominant individual.	Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Scream	Submissive. Context = during attack, post	Fedurek, Slocombe &

	aggression frustration, intense social excitement. Possible desired response = recruitment of aid in agonistic contexts.	Zuberbühler (2015), Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Waa bark	Non-submissive. Context = agonistic interactions, often given by bystanders or victims of aggression after aggression ceases. An aggressive threat. For victims the possible desired response = no retaliation by aggressor/aggressor retreats.	Fedurek, Slocombe & Zuberbühler (2015), Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Pant	Context = part of greeting or during grooming. Possible desired response = affiliative, positive responses.	Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Rough grunt	Non-submissive. Context = excited feeding, approaching preferred food. Possible desired response = reciprocation of rough grunts from others in close proximity.	Fedurek & Slocombe (2013), Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Cough	Non-submissive. Context = mild threat given to lower-ranking individuals. Possible desired response = termination of undesirable behaviour in the subordinate.	Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Laughter	Non-submissive. Context = play. Possible desired response = maintain or extend a play bout.	Matsusaka (2004), Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)

Whimper	Submissive. Context = distress. Possible desired response = reassurance/affiliative behaviour.	Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
Squeak	Submissive. Context = response to threat by dominant individual. Possible desired response = elicit reassurance behaviours from others/no further threats from dominant individual.	Slocombe & Zuberbühler (2010), Goodall (1986) and Clark (1993)
MANUAL GESTURES		
Brief manual contact with object or ground	Depends on specific signal. Can be "Stop that", "Move away", or "Sexual attention".	Hobaiter & Byrne (2014)
Manual contact with another individual	Depends on specific signal. Can be "Stop that", "Move away", "Contact", "Acquire object", "Move closer", "Climb on me", "Reposition body" or "Travel with me".	Hobaiter & Byrne (2014)
Manually displace object	Depends on specific signal. Can be "Move away", "Follow me", or "Sexual attention (to male)".	Hobaiter & Byrne (2014)
Arm raise	"Acquire object" (secondary outcome of arm raise is "Move away").	Hobaiter & Byrne (2014)
Arm swing	"Stop that", "Move away" (secondary outcome of arm swing is "Move closer").	Hobaiter & Byrne (2014)
Beckon	"Move closer" (secondary outcome of beckon is "Reposition body").	Hobaiter & Byrne (2014)

Big loud scratch	“Initiate grooming” (secondary outcome of BLS is “Travel with me”).	Hobaiter & Byrne (2014)
Embrace	“Contact” (secondary outcome of embrace is “Travel with me”).	Hobaiter & Byrne (2014)
Leaf clip	“Sexual attention” (to male, secondary to female).	Hobaiter & Byrne (2014)
Mouth stroke	“Acquire object” (secondary outcome of mouth stroke is “Move closer”).	Hobaiter & Byrne (2014)
Reach	“Acquire object” (secondary outcomes of reach are “Contact” and “Climb on you”).	Hobaiter & Byrne (2014)
Shake hands	“Contact” (secondary outcome of shake hands is “Stop that”).	Hobaiter & Byrne (2014)
NON-MANUAL GESTURES		
Bite	“Contact” (secondary outcomes of bite are “Stop that” and “Initiate grooming”).	Hobaiter & Byrne (2014)
Foot present	“Climb on me” (secondary outcomes of foot present are “Stop that” and “Follow me”).	Hobaiter & Byrne (2014)
Jump	“Stop that”, “Move away”, “Follow me”.	Hobaiter & Byrne (2014)
Present climb on me	“Climb on me”.	Hobaiter & Byrne (2014)
Present grooming	“Attend to specific location” (secondary outcome of present grooming is “Initiate grooming”).	Hobaiter & Byrne (2014)

Present sexual	"Sexual attention (to female)" (secondary outcome of present sexual is "Contact").	Hobaiter & Byrne (2014)
Rump rub	"Contact" (secondary outcome of rump rub is "Follow me").	Hobaiter & Byrne (2014)
Stomp	"Stop that", "Sexual attention (to male), (secondary outcomes to stomp are "Move away" and "Follow me").	Hobaiter & Byrne (2014)

In order to be considered for this sub-index, an individual had to have at least three signals where an appropriate outcome had been identified (see Table 10) and either an appropriate or inappropriate response recorded for each signal. Signals for which there was no response recorded were excluded as in these cases it was unclear whether the signal was not received or whether the recipient had received the signal but ignored it. The only signal for which 'ignore/no response' was considered appropriate was a pant grunt. These are only given by subordinate individuals to more dominant individuals. Dominant individuals accept the greeting and allow the subordinate to approach by not aggressing them/ignoring them; thus an 'ignore/no response' is a desired outcome in this case.

The following formula was used to calculate the proportion of signals eliciting an appropriate response:

$$Proportion\ of\ signals\ eliciting\ an\ appropriate\ response = \frac{no.of\ signals\ eliciting\ an\ appropriate\ response}{no.of\ signals\ eliciting\ a\ response\ (appropriate\ or\ not)}$$

Kibale Chimpanzee Project long-term data on cooperation

The 'composite' cooperative index was comprised of two sub-indices; grooming and aggression. For each, the calculated score for each individual was converted into a z-score. Again this was calculated by finding the mean and standard deviation for the group of individuals that met the criteria, and thus contributed a score; then subtracting the group mean from the individual's score, and dividing this by the group standard deviation, to determine the z-score for this measure for this individual.

The long-term data used for each of these sub-indices came from focal animal data collected by the KCP field assistants between February 2013 – March 2015 i.e. from the beginning of the pilot study until the end of the main study. Although some data were also available on meat-sharing, this was sparse and sporadic compared to the frequent observations of grooming and aggression, and thus was not included here.

Grooming

This sub-index was a measure of how often the focal individual provided grooming to another individual, given the opportunities they had to do so.

This was calculated by dividing the time an individual spent giving grooming (including mutual grooming) an individual over 10 years of age, by the number of (15 min) scan samples where the individual was resting or grooming in a party with at least one other individual over the age of 10 years. Grooming with individuals under 10 years old was excluded here, largely to exclude mothers grooming offspring, which is somewhat different from the reciprocal exchange of grooming between older individuals.

Criteria for the calculation of this sub-index were that the individual had to have at least 100 scans where they were resting or grooming in a party with at least one individual over 10 years.

Aggression

This sub-index was a measure of how often the focal individual took the opportunity to perform conflict intervention or protection when there was an aggressive event in the party.

I focused on aggressive events that met the following criteria: (1) the victim screamed, pant barked, or waa-barked (so it is highly likely that the majority of individuals in the party will have been aware of the aggression due to these loud vocalisations), (2) the duration of the aggression was 5 s or more (so that there was time for another individual to intervene in the aggression), and (3) the aggression involved individually directed chase or repeated aggressive contact (thus excluding low-intensity aggression consisting of threats, non-vocal or vocal displays, or very brief physical contact, e.g. a single hit). Conflict intervention (CI) was defined as performing a vocal or non-vocal display towards or near the aggressing individuals, disturbing the aggressive interaction or breaking this up completely (with no sign of supporting one individual specifically). Protection (PRO) was defined as actively supporting one of the individuals involved in the aggressive interaction, for example by threatening, chasing or charging one of the individuals, in aid of the other.

This sub-index was calculated by establishing the number of aggressive events that an individual was in the party for, and finding the proportion of these where that individual performed CI and/or PRO. Events where that individual was the aggressor or the victim were excluded, as they could not intervene in these. Equally, times when females intervened in aggressive events involving their offspring of less than 10 years were excluded.

Criteria for the calculation of this sub-index were that the individual had to have been in the party where an aggressive event occurred that met the above criteria, at least 150 times.

Criteria and construction of composite indices using z-scores

A composite communicative z-score was calculated for the individuals that had standardized score values for the following sub-indices: UM signal production, free MM signal production, UM and/or free MM signal diversity, UM and/or free MM recipient responses, and the appropriate recipient response score. For each individual who met this criterion, the composite communicative z-score was calculated as the mean of the standardised scores from the sub-indices available for that individual (minimum: 5; maximum: 7).

A composite cooperative z-score was only calculated for the individuals that had standardized score values for both the grooming and aggression sub-indices. For each individual who met this criterion, the composite communicative z-score was calculated as the mean of their grooming and aggression standardised scores.

Analyses could only be carried out with individuals that had both a composite communicative, and composite cooperative z-score, which meant that the four youngest individuals were excluded (AZ, OM, TS, UN), as well as two adult females (LN, UM; see Table 2, Chapter 2). AZ, OM and TS failed to meet the criteria associated with the calculation of the aggression and grooming sub-indices, comprising the composite cooperative index. LN, OM, UM and UN had less than the minimum of five communicative sub-indices available. Thus twenty individuals could be included in the overall comparison of the composite communicative and cooperative indices.

Statistical analysis

I constructed linear mixed models (LMMs) in order to test the relationship between communication and cooperation. These investigated the influence of continuous and categorical variables on the communication and cooperation sub-indices, and composites. When I had repeated sampling from the same individual, to control for pseudoreplication I fitted 'signaller' and 'partner' as random factors (Crawley, 2002) by conducting random intercepts models using the package lme4 (Bates & Maechler, 2009; https://cran.r-project.org/web/packages/lme4/index.html).

As I was running models with relatively small sample sizes (*N* = 17 - 25), I tried to limit the number of explanatory variables in each model in order to reduce the risks of destabilising the model or severely compromising statistical power. Thus the models presented each have a single explanatory variable. To assess if this variable explained a significant amount of variation in the dependent variable, I compared the full model to a null model containing just the intercept and any random effects, using a likelihood ratio test. All models were run in R v. 2.15 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org).

As some data were not available for all individuals (e.g. dominance rank), I sometimes constructed several models in order to test the hypotheses thoroughly, and to maintain a high number of individuals in each model.

Given the constraints the small sample size placed on the number of 'control' variables I could enter into the models, before running the main models I checked to see if the number of individuals available as potential recipients influenced the likelihood of signalling or initiating grooming.

First, it was found that variation in mean signal production z-score (of UM and MM), could not be explained by variation in the mean number of individuals in the party in the focal videos from which the UM and MM signal production rates were calculated; F (23,24) = 1.86, *P* = 0.186, *N* = 25 (the individuals meeting the criteria for the UM and MM signal production sub-indices). More details on how the number of individuals in the party for UM and MM was calculated can be found in Chapter 2. Second, the number of adult individuals in the party when an individual had the opportunity to groom and chose to do so (M = 6.48, SD = 1.87), was not significantly different from when they did not choose to groom another individual (M = 6.74, SD = 1.68); t (22) = 1.08, *P* = 0.294, *N* = 23 (the individuals meeting the criteria for the grooming sub-index).

These analyses show that the number of individuals in the focal party does not appear to influence the signal production rate or whether or not an individual chooses to groom, so were not further controlled in the main analyses.

RESULTS

Composite communication vs composite cooperation

Here the aim was to investigate whether composite cooperation was indeed positively related to composite communication, and whether individuals that scored highly on one also scored highly on the other. Twenty individuals entered into this analysis, each contributing both a communication and cooperation score.

Thus I constructed a model to test whether variation in the composite communication z-scores could be explained by variation in the composite cooperation z-scores. Contrary to predictions, a significant negative relationship between communication and cooperation z-score was found, indicating that individuals who scored highly on communication had a low score on cooperation, and vice versa (F (18,19) = 4.71, *P* = 0.044; Figure 14).

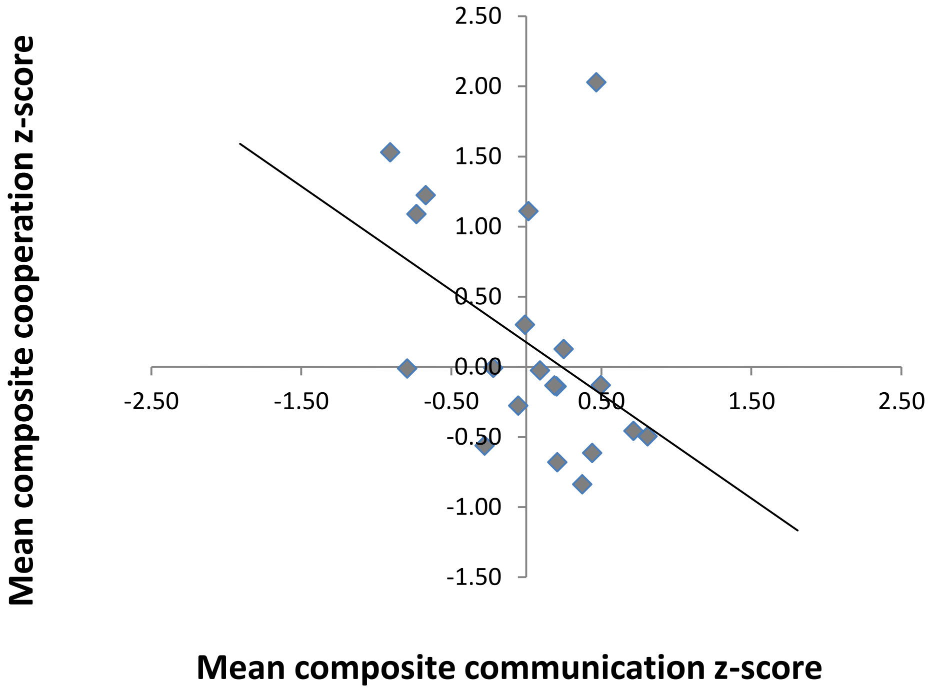


Figure 14. Scatterplot illustrating the significant negative relationship between composite communication and cooperation z-scores (*N* = 20).

From this it appears that individuals that have a high signal production rate and diversity, and often elicit responses, and appropriate responses, do not often take the opportunity to groom others, or aid others in aggressive events. Conversely, those that do tend to groom and help others, seem to produce fewer signals, demonstrate a smaller signal repertoire, and are less likely to elicit responses, or appropriate responses.

With a bigger sample size, the variables sex and rank would have been entered into this model, along with their interactions with cooperation. Unfortunately the sample size was too small to support the inclusion of so many explanatory variables, so I explored the effect of these variables separately.

First, sex, when entered as an explanatory variable (*N* = 20 individuals) had no effect on the composite communication index (F (18,19) = 1.52, *P* = 0.240). Equally, rank, when entered as an explanatory variable (*N* = 17 individuals), had no effect on the composite communication index (F (15,16) = 2.58, *P* = 0.129).

In order to explore whether an interaction between cooperation and sex might be present, I plotted the data for males and females separately to see if the same negative relationship between communication and cooperation was present for both groups. Figures 15 and 16 illustrate that males and females both demonstrate a negative relationship of similar magnitude, indicating that sex does not influence the nature of the relationship between communication and cooperation.

As division by sex is essentially the same as separating and comparing low and high ranking individuals (all males had a higher dominance rank than all females), no separate analysis was conducted for rank.

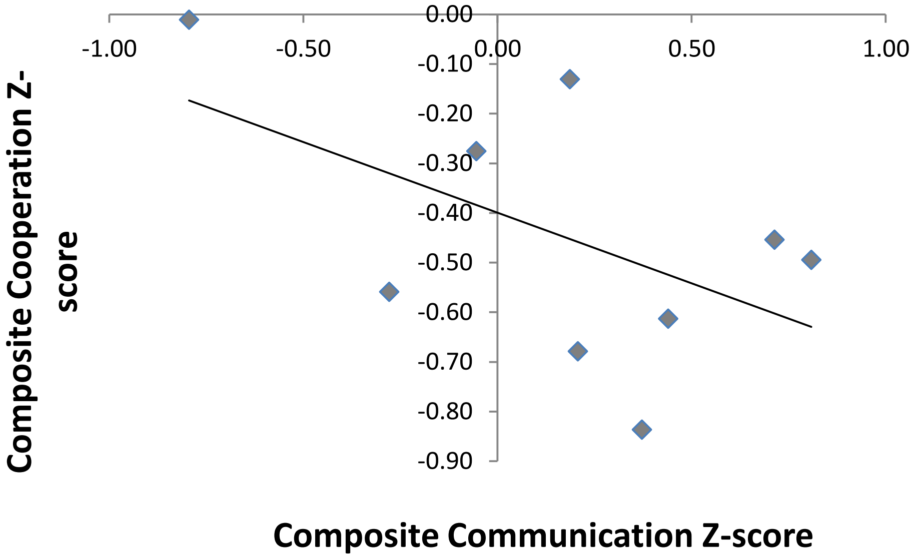


Figure 15. Scatterplot illustrating the negative relationship between composite communication and cooperation z-scores for females (*N* = 9).

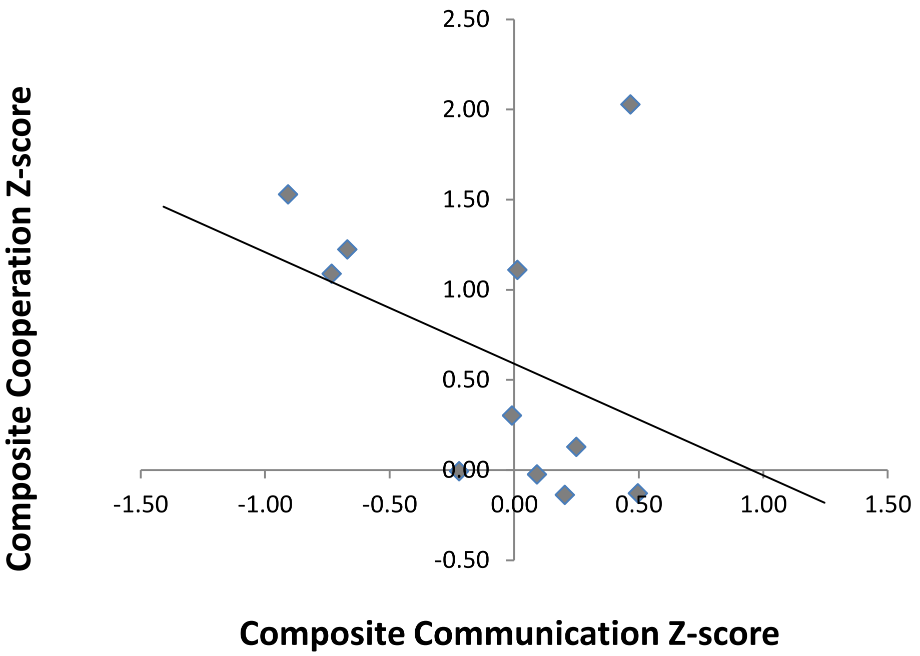


Figure 16. Scatterplot illustrating the negative relationship between composite communication and cooperation z-scores for males (*N* = 11).

Given the unexpected nature of finding a negative rather than positive relationship between communication and cooperation, I next endeavoured to explore what might be driving this relationship; first by checking the validity of the measures of cooperation.

Validity of measures of cooperation

One possible reason for the counterintuitive relationship between cooperation and communication found above could be that the composite cooperation index is not a valid measure of cooperation. I thus sought to assess if this measure followed patterns already established in the literature in terms of the expected associations between cooperation and sex and dominance.

Past research has established the connection between cooperation and sex, with male chimpanzees generally showing more cooperative behaviours in the wild (Gilby & Wrangham, 2008). On a related note, high-ranking individuals are usually the ones to show more cooperative behaviours, including policing in aggressive events (e.g. von Rohr et al., 2012; Boehm, 1994).

Thus, here I checked whether an effect of sex and rank would be found on the composite cooperative z-scores, as would be predicted from previous literature. To do this I first constructed a model to test whether variation in the composite cooperation z-scores could be explained by sex (rank was included in a separate model, below, in order to retain as many individuals as possible in both analyses). *N* = 20 individuals entered into this analysis.

Sex explained a signification amount of variation in the composite cooperation z-score, compared to a null model (F (18,19) = 16.51, *P* < 0.001), with males showing a higher score on cooperation (mean = 0.65, SD = 0.77) than females (mean = -0.45, SD = 0.27), as predicted from previous research.

Second, I constructed a model to test whether variation in the composite cooperation z-scores could be explained by rank. *N* = 17 individuals entered into this analysis.

Rank also explained a signification amount of variation in the composite cooperation z-score, compared to a null model (F (15,16) = 45.13, *P* < 0.001), with higher-ranking individuals demonstrating higher scores on composite cooperation (see Figure 17), as predicted from previous research.

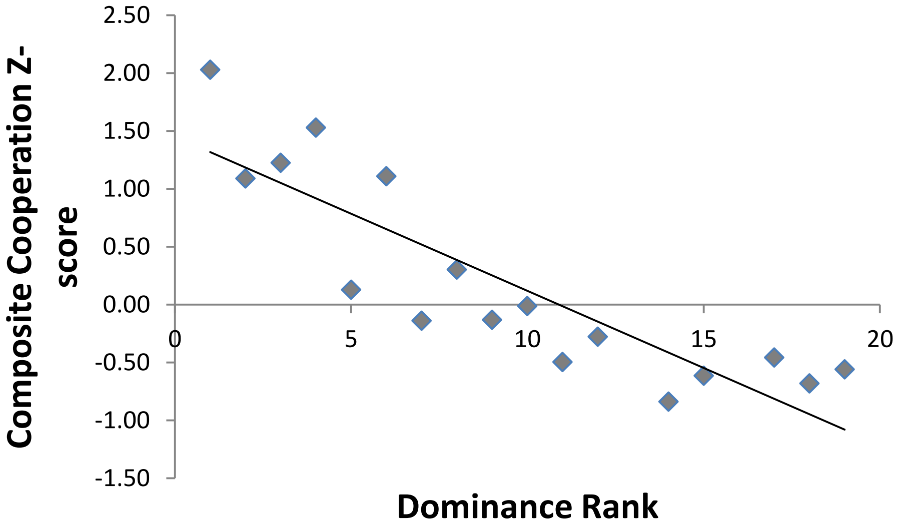


Figure 17. Scatterplot illustrating the significant negative relationship between dominance rank (1 = highest rank) and cooperation z-scores (*N* = 17).

Thus it appears likely that the composite cooperation index is measuring cooperation in a valid way.

Is the negative relationship driven by certain contexts or sub-indices?

As it seems that the significant negative relationship between communication and cooperation does not stem from an invalid measure of cooperativeness, it would be interesting to further investigate whether specific contexts or sub-indices are driving this relationship.

To explore whether this was driven by the fact that the composite communication index itself included communication in a cooperative context (groom), communication in grooming was separated. Thus I aimed to separately test whether (i) communication in a cooperative context (groom) could be predicted by composite cooperation, and (ii) communication in ‘non-cooperative’ contexts (rest, feed, travel) could be predicted by composite cooperation.

Thus I first constructed a model to test whether variation in the composite communication z-scores could be explained by variation in the composite cooperation z-scores, when only including communication in a grooming context. The same 20 individuals were included in the model. There was a non-significant trend towards individuals who scored highly on communication during the context of grooming to have a low score on cooperation, and vice versa (F (18,19) = 3.24, *P* = 0.089; Figure 18).

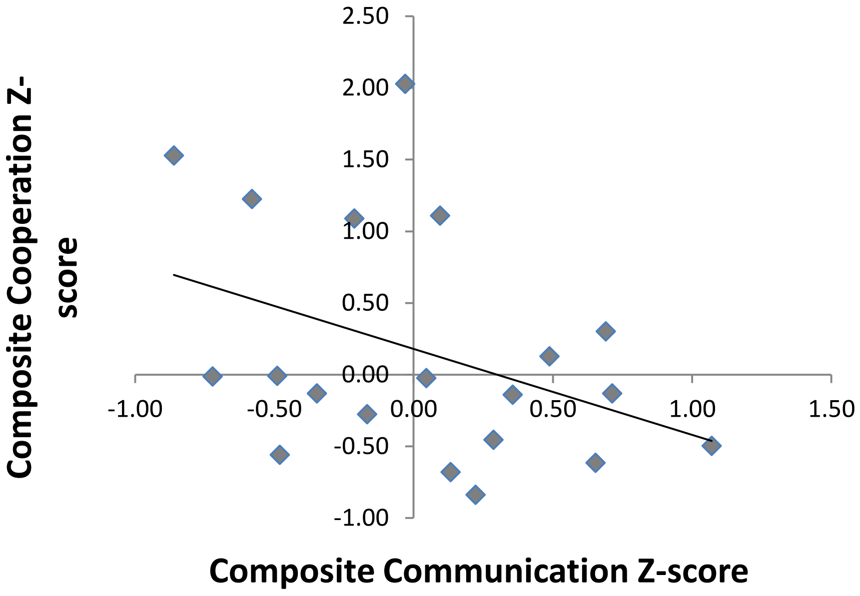


Figure 18. Scatterplot illustrating the negative relationship between communication in the cooperative context of grooming, and composite cooperation z-scores (*N* = 20).

Second, I constructed a model to test whether variation in the composite communication z-scores for 'non-cooperative' contexts could be explained by variation in the composite cooperation z-scores. Seventeen individuals were included in this analysis. Again, no significant relationship between communication in non-cooperative contexts and cooperation was found (F (15,16) = 0.72, *P* = 0.411), though the direction remained negative (Figure 19).

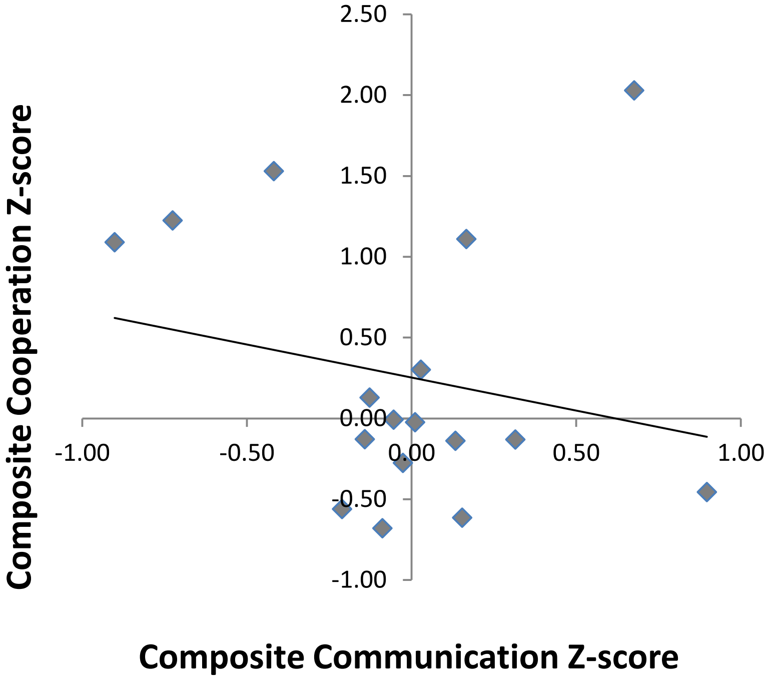


Figure 19. Scatterplot illustrating the negative relationship between composite communication and cooperation z-scores in the ‘non-cooperative’ contexts of rest, feed, and travel (*N* = 17).

Therefore, a negative relationship is found across cooperative and non-cooperative contexts, yet it requires the inclusion of both these contexts for the effect to reach significance. Thus, although a smaller association was found in the non-cooperative contexts, the overall relationship is not driven by communication a single type of context.

Next, I tested whether specific sub-indices were driving this key finding. In order to avoid excessive multiple testing, instead of running all possible comparisons, I was selective and focussed on the comparisons most likely to reveal important patterns, as explained below. I first separated the composite cooperation index into the two sub-indices: aggression and grooming, and the composite communication index into: signal production rate (mean of UM and MM), signal diversity (mean of UM and MM), and recipient responses elicited (mean of UM, MM, and appropriate responses). I then explored whether the communication composite index could be predicted by specific cooperation sub-indices and whether communication sub-indices could be predicted by composite cooperation; all statistical models of this are shown in Table 11 below.

Furthermore, as composite communication could be predicted by cooperation shown in grooming (see Model 1, Table 11), I also tested which specific sub-indices of communication could be best predicted by grooming cooperation (Models 6 - 8).

Table 11. Statistical models, testing whether variation in one composite index can be predicted by variation in the specific sub-indices of the other composite. The direction of the relationship between variables was determined by plotting the data and fitting a line of best fit.

Model	**Dependent variable**	**Independent variable**	**N**	**Result**	**Direction of relationship**
1	Composite communication	Grooming cooperation	*20*	**F(18,19)=24.83, *P* < 0.001**	Negative
2	Composite communication	Aggression cooperation	*22*	F(20,21)=0.039, *P* = 0.845	Positive
3	Signal production rate	Composite cooperation	*23*	F(21,22)=0.64, *P* = 0.433	Negative
4	Signal diversity	Composite cooperation	*18*	F(16,17)=0.45, *P* = 0.512	Negative
5	Recipient responses	Composite cooperation	*17*	*F(15,16)=3.65, P = 0.075*	Negative
6	Signal production rate	Grooming cooperation	*23*	F(21,22)=2.20, *P* = 0.153	Negative
7	Signal diversity	Grooming cooperation	*18*	**F(16,17)=7.00, *P* = 0.018**	Negative
8	Recipient responses	Grooming cooperation	*17*	**F(15,16)=5.91, *P* = 0.028**	Negative

Italics shows trend. **Bold shows significant effect.**

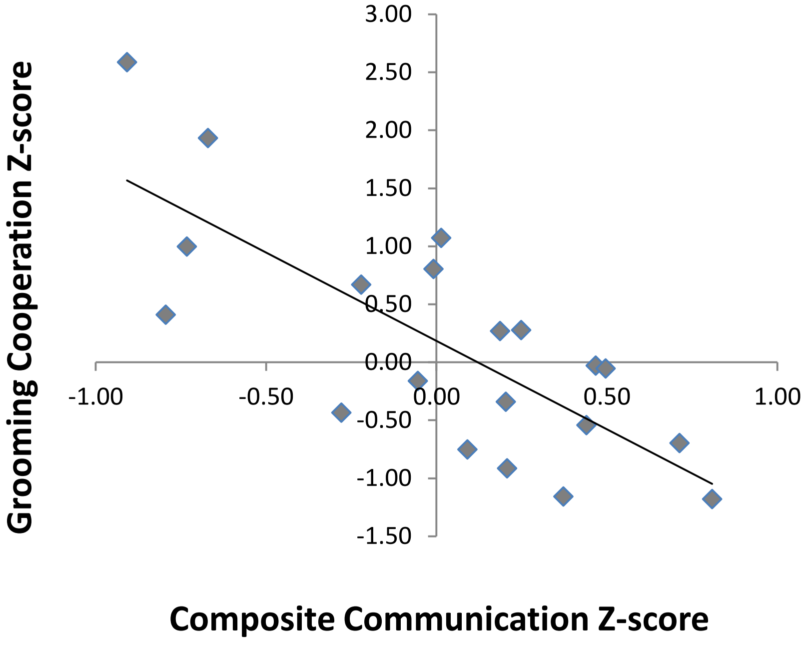


Figure 20. Scatterplot illustrating the significant negative relationship between composite communication z-scores and grooming cooperation z-scores (Model 1; *N* = 20).

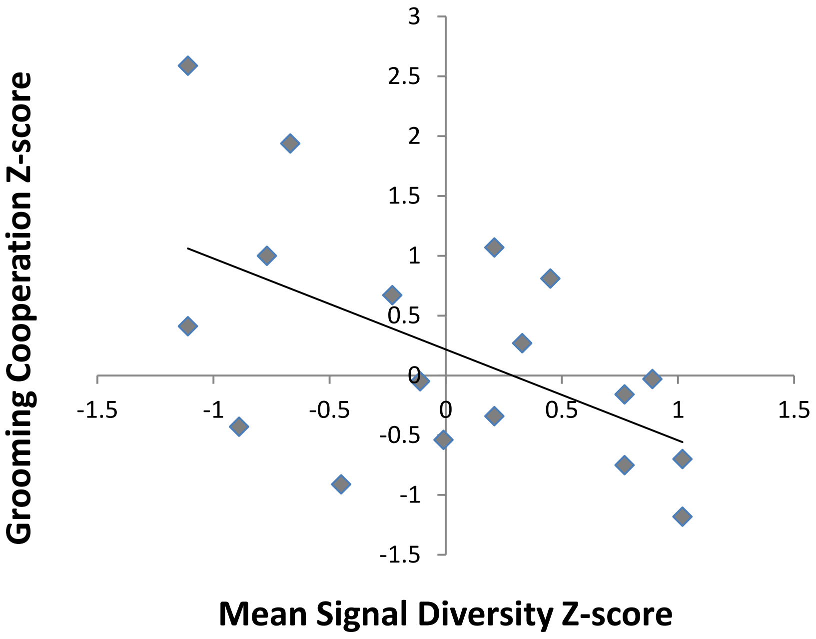


Figure 21. Scatterplot illustrating the significant negative relationship between the mean signal diversity z-scores and grooming cooperation z-scores (Model 7; *N* = 18).

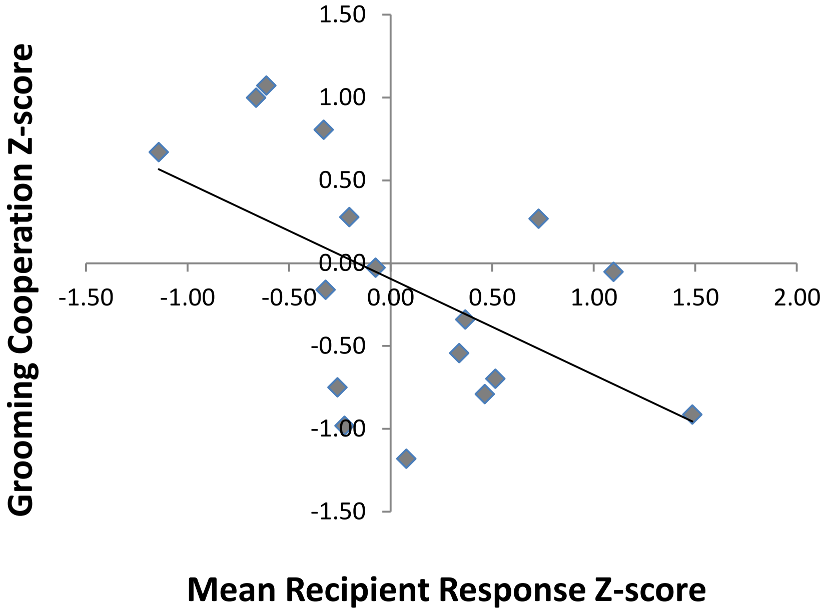


Figure 22. Scatterplot illustrating the significant negative relationship between the mean recipient response z-scores and grooming cooperation z-scores (Model 8; *N* = 17).

From Table 11 it can be seen that there is a trend for composite cooperation to predict recipient responses elicited (to UM, MM signals, and appropriate responses obtained). This was again a negative relationship, with those individuals that often elicited responses, and appropriate responses, being those that did not often groom others or police aggressive events. Similarly, it was found that variation in composite communication could be explained by variation in the number of opportunities an individual took to groom, with those individuals taking more opportunities to groom others, scoring significantly lower on composite communication (Figure 20).

Following on from this, it was found that variation in mean signal diversity and mean recipient response z-scores could be significantly explained by variation in grooming cooperation z-scores; again the relationship between these was negative (see Figure 21 and Figure 22).

Whilst cooperation during agonistic events alone was not a good predictor of communication, cooperation in the form of taking opportunities to groom was a good predictor of, and is more closely (negatively) linked to, overall communicativeness, and more specifically signal diversity and the rate of responses elicited.

Do individuals that RECEIVE more cooperation show higher scores on communicativeness?

It would make intuitive sense that individuals that produce more communication and receive more responses may also RECEIVE a lot of cooperation, in the form of grooming or aid in aggressive events. It could then be posed that more complex communication may have evolved to elicit cooperation from others, rather than individuals that are inherently motivated to be cooperative also being more communicative.

In order to test this I essentially reversed the cooperation sub-indices. For the aggression sub-index I was now interested in finding all events for which each focal individual was the victim, and the proportion of these where another individual showed PRO or CI. The criteria for ‘aggressive event’ were the same as described in the Methods. Only events where there was at least one other individual over the age of 10 years in the party were included, and for an ‘aggression support’ z-score to be calculated for an individual they had to have a minimum of 10 events for which they were the victim. In order to convert raw scores into z-scores the group mean and standard deviation of the proportion of events that elicited PRO/CI was established from all the individuals that met the criteria of being a victim in at least 10 events. For each individual a z-score was then calculated by subtracting the group mean from the individual’s proportion of victim events that elicited PRO/CI, and dividing this by the group standard deviation.

In a similar manner, for the grooming sub-index I was now interested in the time spent RECEIVING grooming, instead of GIVING. This was calculated by dividing the time an individual spent receiving grooming (including being groomed and mutual grooming) from an individual over 10 years of age, by the number of (15 min) scan samples where the focal individual was resting or grooming in a party with at least one other individual over 10 years. As before, criteria for the calculation of this sub-index were that the individual had to have at least 100 scans where they were resting or grooming in a party with at least one individual over 10 years. A standardised score was then calculated for each individual meeting this criterion.

For individuals who had standardised scores for both received agonistic support and received grooming, a 'received' composite cooperation index was calculated by taking the mean of the z-scores from these two sub-indices. I could then investigate the relationship between this 'received' composite cooperation, and composite communication.

Eighteen individuals entered into this analysis, each contributing both a communication and received cooperation score. I constructed a model to test whether variation in the composite communication z-scores could be explained by variation in the received composite cooperation z-scores. Again, a significant negative relationship between communication and received cooperation z-score was found, indicating that individuals who scored highly on communication had a low score on received cooperation, and vice versa (F (16,17) = 13.54, *P* = 0.002; Figure 23).

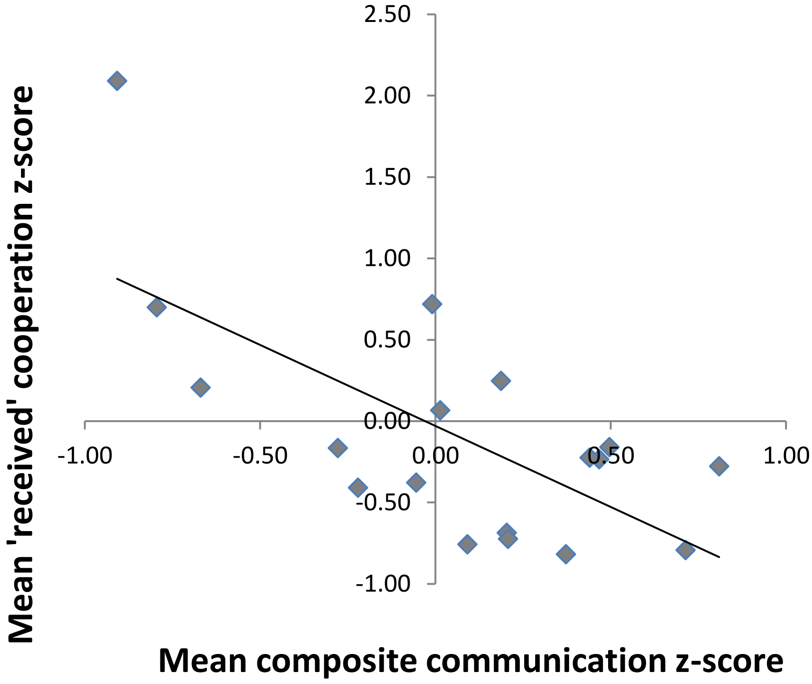


Figure 23. Scatterplot illustrating the negative relationship between composite communication and 'received' cooperation z-scores (*N* = 18).

From this it appears that individuals that score highly on communicativeness do not often receive grooming from others, or elicit more protection and conflict intervention when they are the victims in aggressive events. Conversely, those with low communicativeness are more likely to receive grooming, and aid during aggression. This seems to refute the idea that being highly communicative might help an individual elicit cooperative behaviours from others.

Do individuals who spend more time together require less communication?

The final avenue I explored was whether highly cooperative individuals, who have many well-developed bonds and alliances, may communicate often/preferentially with these individuals, where less communication may be necessary to ‘understand’ one another. In this case less communicative signals might be needed. Conversely, individuals that do not have many strong bonds with others (perhaps through lack of cooperative tendencies), may require more signals to meet their goals.

In order to test this I endeavoured to measure communicativeness between dyads, taking into account the composite association index (CAI) between the two individuals i.e. how often they spend time in proximity of one another. This way it was possible to analyse whether dyads with a stronger association show lower rates of signal production. I focused on communication during dyadic grooming as a test case, as it was possible to discern relatively clear communicative dyads during this context, where both individuals are solely or predominantly interacting with one another. Furthermore it was of special interest to look at the grooming context, which is considered cooperative in itself (by the definition used throughout this chapter), as the inclusion of this in the overall composite communication versus composite cooperation analysis showed that this context appeared to be making an important contribution to the original negative relationship.

The CAI, was calculated from three measures: (1) party level association; tendency to be in the same party, (2) 5 m association; frequency with which two individuals are within 5 m of one another, and (3) nearest neighbour association; frequency with which two individuals were seen as nearest neighbours. Scores for each measure were standardised against the community average, with any value above one being above the community average. The standardised scores for each of these three measures were averaged for each dyad to achieve the CAI for that pair of individuals (based on Gilby & Wrangham, 2008).

As a measure of communicativeness, here I focused on UM signal production during dyadic grooming (when in the role of groomer, groomee or mutual groomer). Signal production was only ever coded for one individual (the focal animal), in a dyad, thus each dyad could be represented by two data points, with the each individual being the potential signaller (if they met the time criteria explained below). I extracted all UM vocalisations and gestures produced by the focal individual (potential signaller) during each dyadic grooming event. Facial signals were not included, as there was variability in the time facial signals were available within the grooming bout, whereas vocal and gestural signals were always available. The UM signal production rate was calculated for each potential signaller with a specific partner, by dividing the number of signals produced by the signaller by the duration spent grooming with that partner. For instance, if AT produced five UM signals in 10 min of dyadic grooming recorded with LK, this was a rate of 30 signals/hour. Equally LK might produce three signals in 15 min of dyadic grooming with AT, resulting in a rate of 12 signals/hour. These would be entered into the model as two separate data points. The time criterion to be considered for this analysis was that the potential signaller must have at least five min of dyadic grooming with a specific partner.

I then constructed a model to test whether variation in the dependent variable: UM vocal and gestural signal production rate during dyadic grooming (signals/hour) could be explained by the potential signaller's CAI with their partner. Signaller ID and partner ID were included as random factors, to control for multiple sampling from each individual. Twenty-five potential signallers were included in this analysis and as each potential signaller could have several different partners, they generated a total of 69 data points for analysis.

Overall, the full model did not explain a significant amount of variation in UM signal production rate during dyadic grooming, compared to a null model ($X(1) = 2.41$, $P = 0.121$). This suggests that, although Figure 24 shows that individuals interacting with other individuals with whom they spend a lot of time with communicate with fewer signals, CAI does not significantly predict signal production in this context.

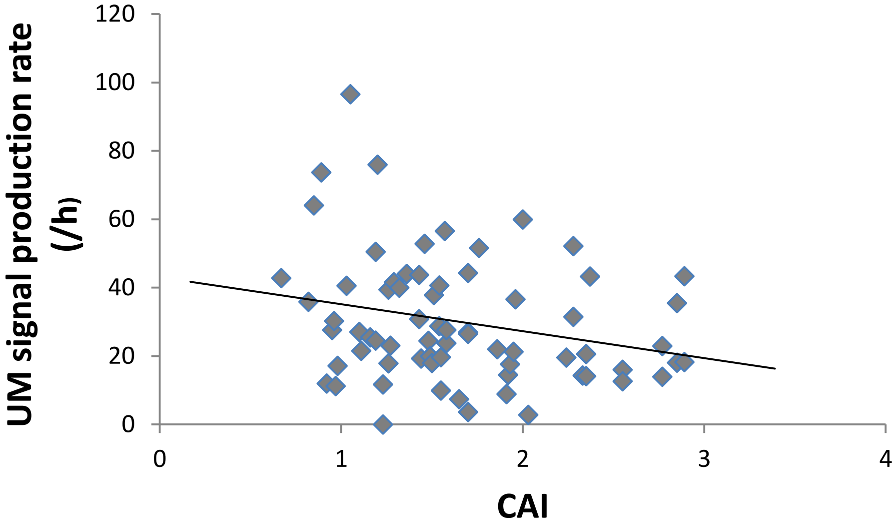


Figure 24. Scatterplot illustrating the relationship between the composite association index (CAI) and the rate of UM vocal and gestural production (*N* = 25 signallers, *N* = 69 data points). Higher CAI scores indicate a closer relationship within the dyad.

DISCUSSION

The key finding of this empirical investigation was a negative relationship between cooperative and communicative behaviour in chimpanzees; the opposite of that predicted by renowned theories of language evolution.

To explore possible explanations for this counter-intuitive relationship, I first established that this effect was not merely driven by certain groups of individuals in the sample, and that the same pattern held for males (high ranking) and females (low ranking) when examined separately. Second, I ensured that the composite cooperation measure was assessing cooperation in a valid way, and indeed cooperativeness varied as expected with sex and rank, in line with previous studies (e.g. Gilby & Wrangham, 2008; males/higher ranking individuals showing more cooperative tendencies). Following this, I focused on exploring the specific contexts or sub-indices that could be driving this finding. Separating communication in a cooperative context (groom), from communication in non-cooperative contexts (rest, feed, travel), likewise resulted in a negative relationship with composite cooperation for both contexts, though non-significant. Therefore the relationship does not appear to stem from communication exclusively in cooperative or non-cooperative contexts.

Nevertheless, it could be that a broader range of social contexts should have been included, alongside grooming, such as play and aggression, which are potentially more risky and require more negotiation. These might show different levels of communicativeness; in play, communication potentially occurs between many different (or frequently changing) partners and in agonistic interactions a victim might communicate to the aggressor, while simultaneously appealing to bystanders for assistance (Fedurek, Slocombe & Zuberbühler, 2015). Thus, the inclusion of other contexts requiring considerable social negotiation and coordination could potentially influence the relationship seen between communication and cooperation. Unfortunately it was outside the scope of this study to include these contexts, which were observed relatively rarely.

When determining whether composite communication (from all contexts), could be better explained by cooperation in grooming interactions or aggressive events, it was found that grooming cooperation could explain a significant amount of variation in composite communication, whereas cooperation in aggressive events could not. Further research is required to understand whether the types of cooperation identified in wild chimpanzees are truly equivalent in ‘cooperativeness’. This may not actually be the case, even when two behaviours are categorised as the same kind of cooperation e.g. reciprocal altruism. Further distinctions or sub-categories may be necessary. For instance, support of others in agonistic interactions could represent a relatively low cost opportunity for an individual to assert their dominance over an opponent. By joining a fight they did not initiate and joining forces with another individual they may increase the chances of winning the interaction and decrease the chances of retaliation. Therefore, what looks like cooperative behaviour on the surface, may be motivated by individualistic goals and thus agonistic support and provision of grooming may not be equivalent.

It was also found that grooming cooperation z-scores could explain a significant amount of variation in the communication sub-indices: signal diversity and recipient responses. This suggests that those individuals which give more grooming, are those individuals which use a more limited repertoire of signals, and are less likely to receive any kind of response (or appropriate response) from recipients.

I propose that this could be that due to the fact that individuals which provide (and receive) a lot of grooming may require a smaller repertoire of signals, as they require little or no elaboration to persuade others to provide a positive (grooming) response. Convincing another individual to groom you is an important and valuable skill, and some individuals may be able to initiate and maintain grooming bouts with little communicative effort. For instance if a high ranking male enters the party and is immediately groomed by another individual, this means he may not have to produce a 'present groom' gesture to request grooming. Such individuals may only require a relatively small set of additional signals for other goals that do not involve grooming (e.g. 'travel with me'). Others may not always respond to these, but perhaps the objective in these situations is not as urgent or important to warrant much elaboration. On the other hand, individuals who do not give or receive much grooming may require more elaboration in their signals; needing to use many different signal types or different MM combinations, especially when the goal is to elicit grooming. They may subsequently receive a good rate of responses to their elaborate signalling, but in order to achieve this they need to invest considerable communicative effort. Future research could empirically test this idea, by assessing whether more central individuals (identified by high eigenvector values in social network analyses; Newman, 2004), show less communication, as these individuals have more, and stronger, connections to others. As my example illustrates, high ranking males seem to be the individuals who it is easiest to envisage requiring little communication to initiate interactions, and as such it is surprising that neither rank nor sex predicted communicativeness. Future research should explore whether oestrus females are also able to initiate and maintain grooming with little communication, as they are already the focus of attention for males. If so, this may explain the lack of relationship between the composite communication measure and rank and sex. Consequently, it may be fruitful for future research to separate females' data into oestrus and nonoestrus periods to test whether their communication effort and efficacy varies systematically with oestrus.

Following this more detailed investigation into the influence of different contexts and sub-indices, I explored the idea that individuals who produce a high number and wide diversity of signals to elicit responses, may be doing so to elicit cooperative behaviour from others, and thus have a high rate of receiving rather than giving cooperative behaviour. This would circumvent the assumption that individuals must be inherently cooperative to also be more communicative. In this case the two would not be interdependent, but rather the relationship may be unidirectional, with communication eliciting more cooperation. It could be that the benefits of receiving cooperation then drive the evolution of more elaborate and complex ways to communicate, in order to receive more cooperative behaviour. However, contrary to these predictions, it was found that those individuals that were most communicative were least likely to receive cooperation from others, in the form of support in agonistic interactions or grooming received. This appears to refute the idea that being highly communicative might also function to elicit cooperation from others. One possible reason for ‘giving’ and ‘receiving’ cooperation to show a similar relationships with communication could be that often grooming and agonistic support are reciprocated (hence considered as reciprocal altruism; e.g. Mitani, 2006; Gomes, Mundry & Boesch, 2009; Koyama, Caws & Aureli, 2006), so it is perhaps unsurprising that levels of giving and receiving these types of cooperative behaviour are similar.

The final notion I aimed to test was whether highly cooperative individuals, who likely have stronger relationships and alliances, may communicate preferentially with the individuals with whom they spend a lot of time with, and with these individuals less communication may be necessary to ‘understand’ one another. Conversely, individuals that do not have many strong bonds with others (perhaps through lack of cooperative tendencies), may require more signals to meet their goals. I found that although the relationship was indeed in this direction, it was not significant, and strength of association could not explain a significant amount of variation in signal production rate within a dyadic grooming context. This does, however, highlight the potential importance of future research accounting for the identity of the audience and the focal animal’s relationship to audience members as another factor that may influence the amount and type of communication that occurs.

Taken together, this series of analyses and results indicate that when a relationship between aspects of communication and cooperation is found in chimpanzees, it is negative. I found no evidence of the predicted positive relationship between these two behaviours. I suggest that this negative relationship is most likely due to different individuals using different strategies to meet their social goals. Some may invest in forming reciprocal, cooperative bonds with others, gaining grooming and agonistic support without really having to ask for this, but may be less proficient in their general ‘communicativeness’ (e.g. the quiet, undemanding individuals that everyone happily does a favour for). Others invest in very elaborate communication to elicit responses from others, but must try harder to gain any grooming or agonistic support (e.g. the loud abrasive individuals who persuade you to pay attention to them, but you may not go out of your way to do them a favour).

In order to draw firm conclusions concerning the link between cooperation and communication in this species, however, future research needs to replicate this finding with larger samples. This would allow researchers to include more control variables in the models to test how robust and generalizable this finding is. In addition, future research should seek to address the following two issues that arise with this study. First, it is difficult to know whether the composite communication index is truly measuring overall ‘communicativeness’, as there is no previous literature to suggest what might comprise this. As logistically it was only possible in this study to focus on recipient responses from individuals within 5 m of the focal individual, I likely did not capture all recipient responses to signals directed at those further away, or even in different parties (e.g. long-distance vocal signals). With a larger team of researchers working together it might be possible in future studies to try and capture all responses from individuals inside the party and vocal responses from those outside it. Although I was comprehensive in including all modalities, an additional improvement for the future may be to focus on the psychological mechanisms underpinning signal production that have clear relevance for language. For instance, determining whether the signals produced showed signs of intentionality, functional referentiality, flexibility and signaller-recipient interchangeability, may be fruitful. Exploration of these signal facets would greatly benefit from controlled experiments in the wild, alongside detailed observations.

Second, a similar attempt to focus more on the psychological mechanisms underlying cooperative behaviour may also prove enlightening. For instance, researchers could try and establish the extent to which an individual assumes a specific role during mutualistic acts, whether there is any joint attention or intentionality seen during cooperative acts, and record how closely an individual keeps track of given and received cooperative behaviour. Unfortunately, investigation of these mechanisms involved in communicativeness and cooperativeness was not feasible in the timescale of this research project.

In addition to replicating this finding with a larger sample size, different chimpanzee communities should be compared to further our understanding in this area. Important behavioural differences have been found between the chimpanzees of East and West Africa, such as closer female-female social bonds and a more even spread of dominance between the sexes in Western chimpanzees (Gruber & Clay, 2016). Similarly, bonobos can also provide a valuable window into the behaviour of our last common ancestor, as this species has been suggested to be more tolerant and cooperative than chimpanzees (Hare et al, 2007), while also showing complex communicative signalling (Fröhlich et al, 2016). Thus, this species may be more likely to fit the cooperative theories of the evolution of communication than chimpanzees; indeed authors of recent studies pose that bonobos are perhaps a superior model for understanding the prerequisites of human communication (e.g. Rosanno, 2013). By honing in on the differences and similarities between these *Pan* species, and sub-species, it may be possible to identify the types of ecological and social pressures that lead to a specific relationship between communication and cooperation. This may help us understand some of the preliminary changes that facilitated the evolution of cooperation and language in humans.

Leading on from this, although the theorised positive relationship was not found on an individual level in chimpanzees, it may be that this relationship does exist at a broader species level, where selective pressures are more likely to act. A broad comparative study including several species would be necessary to investigate this. Whether correlations between cooperation and communication are found across species, will help us understand whether selective pressures tend to make the advancement of these traits, together, adaptive, or whether they are selected for independently. To complete such an extensive study comprising many different species, would require the establishment of a reliable and valid scale on which to measure their communicativeness and cooperativeness, and definitions of these terms that can be applied across target species. Moreover, it would be important to take into consideration that behaviours that look similar on the surface can be underpinned by very different psychological mechanisms, so it may be necessary to take into account the cognitive underpinnings of these domains. For instance, is the sophisticated ‘waggle-dance’ of honeybees, which refers to very specific, geographically distant, locations, a more cognitively and communicatively complex signal than the intentional, flexible and referential signals of a chimpanzee? Is cooperative breeding, as seen in many species, ranging from birds to marmosets, more or less cooperative than reciprocal altruism in chimpanzees? Defining and measuring the cognitive complexity of a behaviour is always going to be a challenge, but it is one that we should endeavour to confront.

Finally, it would be of great interest to focus on the complexity of communication during highly cooperative and coordinated behaviour (advancing the research here, which focused on communication in the cooperative context of grooming only). From this it would be possible to ascertain whether highly complex communication is truly necessary for more coordinated cooperation to be achieved in mutualistic acts in the wild (in captive paradigms with chimpanzees, cooperative communication in mutualistic tasks is minimal or non-existent, e.g. Bullinger, Melis & Tomasello, 2014).

If replicated, these results will have important theoretical implications for our understanding of human evolution. First, and most fundamentally, these findings may challenge theoretical assumptions that cooperation and communication co-evolved. Second, it could be that communication and cooperation are underpinned by different cognitive mechanisms in chimpanzees and humans; thus the expected positive relationship between cooperation and communication in early humans may not manifest itself in these great apes. Indeed Tomasello et al. (2005) argue that although chimpanzees are capable of mutualistic coordination of actions with others, the motivation to share intentions is a derived human characteristic that chimpanzees do not share. Therefore, although this species may demonstrate relatively complex communication, this noticeably lacks the cooperative nature of human language (Levinson, 1995) and chimpanzees show little impulse to communicate with informative or declarative intent (Tomasello et al., 2005). It could be that such a potential lack of inherent cooperative motivation in the individual, and in chimpanzee societies, means that more complex communication cannot evolve in this species. It may not be an evolutionarily stable strategy, as other individuals could merely exploit the information shared. This would indicate that these behaviours may not have been linked in our last common ancestor, with changes in cooperative motivations necessary once humans diverged, for language and extreme cooperation to then evolve in our lineage (Tomasello et al., 2005).

In summary, this is the first empirical investigation into the nature of the association between individual variation in communication and cooperation in some of our closest living relatives. Here I found no sign of a positive relationship between the two on an individual level, which was unexpected, given theories suggesting the interdependence of these domains. Perhaps more surprising, was the consistent finding of a *negative* relationship between cooperation and communication, indicating that more communicative individuals actually cooperate less (and also receive less cooperation from others), and vice versa. This intriguing finding provides the foundation for future research to explore this relationship in different contexts, across different chimpanzee communities, and a wide range of different species.

CHAPTER 5: General discussion

Here I will be focusing on the most pivotal and exciting findings from my research, and their wider implications. Comprehensive coverage of all results and discussion of each individual finding can be found in the respective empirical chapter, so will not be repeated here in full.

UM and MM signals

This study was the first to attempt to establish a repertoire of the types of signals that are freely combined by wild chimpanzees. From my observations, 48 different free MM signal combinations were documented, and the majority of focal individuals were observed to produce a subset of these signals. There is a high likelihood that both the community repertoire and individual repertoires would increase with further observations, as has been found with gestural repertoires (Hobaiter & Byrne, 2011a; Graham, 2016). This crucially shows that the majority of (if not all) adult and adolescent individuals have the ability and motivation to flexibly ‘mix and match’ signals of different modalities. The fact that the rates of different types of free MM combinations was not consistent across contexts suggests that MM signals (and specific combinations of modalities) may be more useful in some contexts, and less so in others.

Furthermore, the lower relative rates of MM to UM signals found here, compared to studies in captivity (e.g. Pollick & de Waal, 2007; though see important methodologically differences with their study in Chapter 2) can potentially inform us about the conditions in which MM signalling may be advantageous and effective. In a captive environment individuals may be in closer spatial proximity, have better visibility of one another, and frequently be in situations which call for greater social negotiation and coordination (as there is limited space to avoid and escape one another). Likewise, here I found that the highest rate of free MM signals were produced in the grooming context, where these factors also apply. Thus, it could be that MM communication is particularly valuable in close social situations, where more nuanced signals are required. This is perhaps unsurprising in light of theories that suggest that language replaced grooming as the social glue which cements primate societies (Dunbar, 1998). It could be the case that more sophisticated communication emerged in this context first, until eventually ‘vocal grooming’ (and language as a whole, comprising several modalities), replaced physical grooming as a relatively cheap and efficient method of reinforcing social bonds.

A further notable finding was that facial expressions were produced very rarely alone, and generally only observed as part of a MM combination. This gives empirical weight to the theoretical arguments regarding the importance of adopting a holistic multimodal approach (Slocombe, Waller & Liebal., 2011; Liebal et al., 2013). Had I taken a UM approach, and focused solely on facial expressions, I would most often have been merely recording a single component of a MM signal; if I had ignored the other component of the MM signal, I may have attributed the wrong function to this signal, or overestimated its flexibility (when the composite signal is in fact context specific). Supporting this claim, the preliminary evidence here suggests that free MM combinations produced by chimpanzees have the potential to elicit different responses than their UM component signals. This further reinforces the vital need for future research to take a MM approach to studying communication, which takes into consideration all communicative modalities, and the possibility of combinations of these. Only this way can we begin to fully understand signal functions, and the complete communication system of a species.

Overall, the findings of this investigation into UM and MM signalling suggest that in these chimpanzees, MM signal combinations were used flexibly across many different behavioural contexts. Although several scientists have emphasised the multimodal nature of animal communication, and specifically chimpanzee communication (e.g. Taglialatela et al., 2011), the current study has been the first in the wild to explore UM and MM signals in detail and in concert. Indeed, the findings here support the claims that MM signals are an important part of chimpanzee communication, and that our own multimodal language may have been built upon a multimodal foundation (Wacewicz & Zywiczynsk, 2016), already present in our last shared ancestor with chimpanzees.

Future research in MM communication

It remains a great scientific challenge to identify the selection pressures that have driven human communication to become the complex system we see in modern human language. Accordingly it can be beneficial to compare different communities of the same species, such as chimpanzees, to explore whether differences are found in communicative abilities in different environments and groups. As already mentioned in Chapter 2, it may be of interest to compare the communication of chimpanzees residing in dense forest to that of those residing in savannah habitats, to explore whether MM communication may be used more frequently in more open areas, where individuals are be more likely to be in sight of one another. This would reveal whether the relatively high levels of MM communication seen in captivity, compared to the wild, are due to increased visibility, or potentially other factors which come into play in a captive environment. Furthermore, as it has been proposed that we separated from our last common ancestor with great apes when our ancestors moved away from a forest habitat and began inhabiting more open savannahs and grasslands (e.g. Dart, 1925; Klein & Edgar, 2002), it would be intriguing to uncover whether this type of environment might have driven the increased use of MM signal combinations.

One could also compare different communities living in a similar habitat and try to elucidate mechanisms underpinning the production of MM signal combinations. These could include a biologically determined species-typical repertoire (as is now proposed for gestures; Byrne & Cochet, 2016), individual innovation, or social learning. It would be particularly interesting if group-specific signal combinations were found, indicating cultural variation in production of communicative signals. The definition of 'culture' in primate societies is a contentious term, however it has been described as "the way we do things" (McGrew, 2004, p. 25), or more formally as a social process by which something can be learned through observation of others, and thus passed to future generations (Whiten & Boesch, 2001). Although primate culture often focuses on material culture, such as foraging techniques, including tool use (e.g. Koops, McGrew & Matsuzawa, 2013), a comprehensive and collaborative study across seven long-running chimpanzee field sites identified a total of 39 behaviour patterns which were customary at some sites and absent at others, without obvious ecological reasons (Whiten et al., 1999). The behaviour patterns investigated comprised foraging tools, but also grooming, play and courtship behaviours. This study highlights the complex range of behaviours in which variation is found across chimpanzee communities, and also includes important examples of cultural variation in the communicative domain. One of these is ‘hand-clasp grooming’, or ‘grooming hand-clasp’ (McGrew & Tutin, 1978); a form of grooming behaviour, or gesture, that has been identified as a potentially cultural. Hand-clasp grooming occurs when two individuals are mutual grooming and they clasp one another’s raised hand, wrist or arm. This behaviour has been conspicuously observed in several chimpanzee communities (e.g. Kanyawara, Uganda: Wrangham et al., 2016; Mahale, Tanzania: McGrew & Tutin, 1978), however not others (e.g. Boussou, Guinea; Budongo, Uganda; Gombe, Tanzania: Webster, Hodson & Hunt, 2009, provide overview of site where hand-clasp grooming has and has not been observed). This might suggest a role of social learning in the communities where it is present, with evidence for variations in this custom being passed down along matrilines (Wrangham et al., 2016), though the specific function of this signal remains elusive.

Similarly, certain vocalisations are argued to be present in some communities of wild orangutan and absent in others (Wich et al., 2012), consistent with cultural variation in great apes in the vocal domain. Whilst the absence of a signal is hard to establish with certainty, group-specific modification of vocal structure has been documented in chimpanzees. So-called ‘dialects’, where male chimpanzees have been shown to have community-specific pant hoots, differing significantly in structure form those of neighbouring groups, have been most convincingly demonstrated by Crockford et al. (2004). They compared the pant hoots of three neighbouring communities in Tai forest, where differential genetic and ecological influences on call structure could be ruled out, and found that neighbour calls were maximally different, with less differences found between these groups and a distant strange community (70 km away). This suggests that acoustic differences in these vocalisations are learned from other group members, and due to active modification, rather than being genetically determined. By exploring the different MM signals produced in different communities, we have the opportunity to identify cultural variation in communication, and broaden our, thus far relatively limited, understanding of this area. Furthermore, group-specific signal combinations would be important for implicating social learning mechanisms in the emergence of free MM combinations, showing a key similarity with language.

Additionally, as I focused mainly on the production of signals, more detailed and experimental investigations of MM signals from the receiver's perspective are necessary to build a comprehensive understanding of these signals. My observations of recipient responses gave exciting indications that MM combinations may elicit different responses from recipients compared to the component signals given alone. Although due to the relatively rare occurrence of these signals, my observations are based on a very small sample of individuals and observations, they are important to indicate that 'emergent' (Partan & Marler, 1999) combinations may exist in the chimpanzee repertoire. From a language evolution perspective, emergent signals are crucial for understanding how a generative system such as language might have evolved. It may indicate that our last common ancestor had the beginnings of a flexible, open system, despite genetically constrained signal repertoires, that later hominin vocal learning abilities exploited to produce the generative communication system we see in modern humans, where infinite meanings can be produced from finite means (Chomsky & Miller, 1958).

Given the theoretical importance of emergent signals, it is vital that future research investigates this type of signalling through both observations and experiments. It is clear that the low production rate of MM signals in the wild means that in order to meaningfully analyse the function of MM signals, and compare their function to those of the UM components in the same context, much more observational data is necessary. It is unlikely that a single scientist will be able to collect sufficient data, and thus collaboration between chimpanzee communication researchers will be required to realise this goal. In a modern academic environment such collaboration is fraught with complications, but if data collection and video coding could be planned so comparable methods were used and subsequent data pooled, it will be possible to make much progress in this field.

Alongside these observational efforts, controlled experiments should also be carried out in captivity to focus on how UM and MM signals are perceived and responded to by recipients. One way to test this would be by using video playbacks of MM signals and their UM components to examine the outcomes associated with these, and thus possible functions from the recipients perspective. Specifically, this could be done by using a match-to-sample task in captivity (as used by Waller, Whitehouse & Micheletta, 2016), where the chimpanzees could be trained to match video sequences of behaviour with a corresponding outcome (e.g. ‘present groom’ with subsequent grooming), with this correct choice being reinforced. Then a novel behaviour/communicative signal could be presented, such as a MM signal (grunt and present groom), with the chimpanzee indicating which outcome they most likely associate with the MM signal. This choice could then be compared to the outcomes the individual matches with the UM components (e.g. grunt (no visual); silent present groom gesture). If the MM combination has an emergent function it should be matched to different outcomes compared to the UM components. These experiments would allow us to make more conclusive inferences on the types of outcomes that can be predicted from specific signals, as they would allow us to control for other contextual and behavioural cues that may also be influencing recipient responses in observational studies.

The function of the BLS

The results of this study support the view that the BLS facilitates negotiations in grooming interactions, first by potentially signalling the intent to groom (by the to-be groomer) before grooming initiation and during grooming itself, and equally as a request for the partner to groom the signaller during the bout. BLSs are not, however, the only signal used to coordinate grooming efforts. Recent research has shown that oro-facial gestures, including lipsmacks, given by the groomer at the start of a grooming bout, also increase the probability of the partner reciprocating grooming during the bout (Fedurek et al., 2015). Lipsmacks have also been shown to increase the duration of a grooming bout, but do not seem to be involved in initiation of grooming bouts; thus these two signals seem to play complementary roles in grooming coordination. Future research should examine how the combination of these signals influences grooming interactions.

Crucially, opposing previous suggestions (Goodall, 1986; Pika & Mitani, 2006), the BLS does not appear to function as an attention-getter, or as a referential signal. If found, these would have indicated potential intentional use (by manipulating the partner's visual attention), and referential use (by referring to a specific location to be groomed); two important facets of human language. My failure to replicate Pika and Mitani's findings casts considerable doubt over claims that wild chimpanzees use BLSs referentially, highlighting an intriguing contrast between the occurrence of referential gestures in wild and captive populations. In contrast to the wild, referential gestures have been documented to occur spontaneously in captivity (Leavens, Hopkins & Bard, 1996), where adult chimpanzees will point to objects and food they wish to acquire. This finding seems to show that chimpanzees are capable of performing a referential pointing gesture, without any kind of training to do this, although arguably this may be learned through passive observation of humans. Importantly, however, it also highlights the type of situation where a chimpanzee may be motivated to produce these types of signals; namely when they cannot reach the object and they can interact with 'helpful' human caregivers who respond positively to these signals. This unique set of circumstance (termed the 'referential problem space' by Leavens, Hopkins & Bard, 2005), is highly unusual in the wild (if it occurs at all). This neatly demonstrates how important it is to understand the demands and pressures of specific environments, in order to comprehend how a communicative signal is adaptive. Equally it shows how the lack of certain behaviours in the wild does not necessarily mean that chimpanzees do not possess the capacity for these behaviours, but perhaps only the motivation to produce them.

How we can progress in research in this field

The contrasting results obtained regarding the function of BLSs from two communities of chimpanzees residing in the same forest (Ngogo and Kanyawara), highlights the intriguing possibility that there may be cultural variation in the function of this signal. As discussed earlier in this chapter, investigating cultural variation in communicative signalling can make important contributions to our understanding of both communication and culture. In order to make progress in this domain, collaboration between researchers is necessary. At present I am in contact with researchers from Sonso and Ngogo (both Uganda), and we will be collaborating on a bigger project, looking at BLS function variation across these sites. From this we hope to achieve a stronger understanding of the types of factors influencing the production of this common gesture seen across all three groups, and the responses to this. Comparisons between these communities will be particularly interesting as two of these reside in the same forest (arguably in a more similar physical environment), while the third (Sonso) does not. Likewise the Ngogo community size is more than twice as big as either of the other two communities, which may then be considered to share a more similar social environment. As Pika and Mitani (2006) found evidence for the BLS to function as a referential signal in the Ngogo community, whereas in the Kanyawara community I did not, it will be crucial to align our methodologies exactly to eliminate methodological confounds. It is our hope that by working together, we will be able to bring to light some key findings on the mechanisms underlying variation in the use of this signal.

In addition to wild observations, experimental studies to test signal function should be conducted whenever feasible. In contrast to vocalisations, whose function from the recipient perspective has been thoroughly investigated for some time with playback experiments (e.g. Herbinger et al., 2009; Slocombe et al., 2010), recipient responses to gestural signals have never been tested in a comparable manner. Robotic models have been used successfully with other species to test responses to gesture-type signals (e.g. frogs: Laird et al., 2016; squirrels: Partan, Larco & Owens, 2009), however these are unlikely to be sufficiently realistic or robust to be practicably implemented with chimpanzees. Video playbacks and carefully designed experiments, possibly based around match-to-sample paradigms (see section above), could allow us to understand what contexts, other signals and outcomes recipients associate with different gestural signals. It would also be possible with video editing software to manipulate the level of contextual information surrounding signal production in order to see how the signal’s function or meaning may be modulated or reliant on contextual information. Such experiments, conducted in captivity, would add a valuable new perspective to our understanding of gestural signal function.

More communicative chimpanzees appear *less* cooperative

The fundamental finding of the investigation into the relationship between communication and cooperation was that it was in the opposite direction to that predicted; here, individuals scoring higher on measures of communication, scored lower on measures of cooperation. This did not seem to be driven exclusively by specific groups of individuals (males/females, high/low ranking), or specific communicative contexts; the negative relationship was seen in all permutations of these, thus seeming relatively robust. If replicated, this finding may indicate that cooperation and communication were not positively related in our last common ancestor. This means that the evolutionary time over which human cooperation and language likely co-evolved is limited, perhaps with a change in prosocial motivation required early in the human lineage, in order to lay the foundations for the co-evolution of these traits (Tomasello et al., 2005). The more radical alternative is a stronger challenge to these theoretical positions, and questioning whether cooperation and communication really were inter-dependent in human evolution. Further research is certainly needed before the potential theoretical ramifications of this initial finding can be fully understood, and to investigate whether it is really cooperation, or perhaps in fact competition, which requires more communicativeness.

Returning to the details of the negative relationship between the composite cooperative index and the communicative measures, further investigation found that this association was driven by provision of grooming, rather than provision of agonistic support. This may highlight important differences in the underlying mechanisms between these two behaviours that both appear to be reciprocally altruistic on the surface. Rather than being driven by a largely cooperative motivation, policing behaviours during aggression may often simply be an individual taking the opportunity to demonstrate and reinforce their own dominance in the group. This is unlikely to be the case with giving grooming; though this may also signal the strength of social bonds to others. While the negative relationship between communication and cooperation needs replication and further investigation, currently one feasible explanation for this pattern of results is that chimpanzees may be using one of two strategies to elicit positive behaviours from others. As outlined in Chapter 4, some may invest in producing a wide range of different signals, and show unsubtle, elaborate communication, which is often eventually successful (after some persuasion) at eliciting a response. However, these individuals may not readily engage in reciprocal cooperative acts. Conversely, other individuals may frequently perform these types of cooperative behaviours, such as grooming others, and thus other individuals are happy to pay them back in the form of reciprocated positive behaviours. If these positive actions are spontaneously provided or can be elicited by only very subtle signals (potentially not picked up by an observer), these individuals only have to produce a small number and a narrow range of other signals which might aid them in other contexts, for instance ‘move closer’ or ‘move away’, which are arguably less critical than grooming and social bonding. Although they may not always receive a response to these, the less important nature of these situations may not warrant elaboration.

To test this explanation, future researchers could separate cooperation given and received, into solicited and unsolicited sub-categories. This would allow direct testing of my idea that cooperation given and received by less communicative chimpanzees would be more frequently unsolicited. These ‘quiet’ cooperative individuals may be able to receive grooming and support, with little solicitation; and provide grooming with little negotiation. In addition to testing this explanation of the negative relationship between cooperation and communication, contrasting solicited and unsolicited cooperative acts, may also allow a better measure of cooperative tendencies. Perhaps providing grooming and support only when someone pleads for this, should also be considered a different level of cooperativeness to when an individual offers help with little request from the partner. Potentially the latter demonstrates more altruistic tendencies, as giving in to someone who is persistently harassing you for grooming or begging for aid in a conflict may simply just be a means of ending this irritation, rather than demonstrating cooperative motivations.

It is also possible that the personality of an individual may mediate the relationship between their communicative and cooperative behaviours. Thus future research could measure personality, including, for example, sociability, positive affect, grooming equity, anxiety and activity; five factors commonly identified in chimpanzees (e.g. Koski, 2011; Massen et al., 2013), and include these measures as explanatory variables in analyses.

The overall unexpected and counter-intuitive finding of a negative relationship between communication and cooperation may again highlight the general lacking cooperativeness in chimpanzees. This has been proposed from studies of both 'cooperative' behaviours, such as hunting; which in fact may simply be several groups members individually targeting the prey, and maximising their own chances of making a kill, given the behaviour of others in the group, in the absence of a joint or shared goal (e.g. Mitani & Watts, 1999), as well as communication, where chimpanzees show little motivation to communicate with informative or declarative intent, thus perhaps having no inherently cooperative urge to share information with others (e.g. Tomasello et al., 2005). Therefore chimpanzee communication, which may be argued to be relatively complex (e.g. in terms of audience effects, referentiality, intentionality, recipients taking context of signal into account etc.) may not be positively coupled with cooperation, as it may have evolved in different, perhaps competitive, situations in this species.

Future research on the relationship between communication and cooperation

The surprising results of this study pave the way for further explorations into the factors driving this negative relationship. Perhaps one of the first additional investigations which could prove enlightening, after replication of this study with a larger sample size, is to delve more specifically into the 'cognitive complexity' of communication and cooperation. This was unfortunately outside of the scope of the current work, but will hopefully capture the attention of future researchers. Measures of communication could include evidence for characteristics such as intentional and flexible signal production, and signaller-recipient interchangeability, which have clear relevance for language. Likewise, for cooperation, it may be fruitful to record the degree of variation in the intricacies of this behaviour, such as frequency of unsolicited cooperation and occurrence of joint attention during mutualistic acts. It could be the case that the level of cognitive complexity observed in communication is positively linked to that of cooperation; a reasonable assumption given that similar cognitive capacities may be involved (Pinker, 2010).

The next step towards a deeper understanding of this topic would be to focus on different sub-species of chimpanzees, whose behaviour may have been shaped by different ecological pressures. As noted in Chapter 4, there are marked differences between Eastern (studied here) and Western chimpanzees in terms of social bonds and dominance (Gruber & Clay, 2016). It would be intriguing to elucidate whether differences would be found in the relationship between communication and cooperation in these sub-species; helping us to understand what may have driven the evolution of these in relation to one another.

Finally, testing the original theories posing a positive connection between communication and cooperation in the human lineage, may ultimately be more productive on a species level, rather than at an individual level. Selection pressures are more likely to act and shape behaviour at this wider level, than an individual level. As suggested in Chapter 4, in future research it would be of great interest to attempt to establish the relationship between these two behaviours on a broader cross species level. Although theoretically important, such research would be incredibly challenging. Such a challenge can only be tackled with intense collaborative effort across researchers. In the past, only a few studies have managed comprehensive comparisons of behaviour across multiple different species; one of note being the investigation of self-control using problem-solving tasks, administered to 36 different species, ranging from great apes, to rodents, to birds (MacLean et al., 2014). Cross-species comparisons of the link between communication and cooperation would require, and warrant, a similar level of teamwork to this impressive study.

By now it is hopefully clear that a recurrent theme throughout the ideas in this discussion is the encouragement of closer collaboration between individual researchers and research groups, in order to make further progress in the areas of communication and cooperation. The collaboration seen between chimpanzee researchers in Whiten et al (1999) and Wilson et al (2014) were a great feat and a great success, and ideally such teamwork should be emulated in future research in this field. However, as outlined previously, such joint work is often hindered by several barriers in academia. These include the highly competitive environment surrounding grant money and pressure within the UK system for ‘high impact’ publications that are more likely when a paper is the first to document a novel finding or propose a novel idea. Frequently, researchers are thus unwilling to share such accomplishments, and will forego a bigger, more thorough and comprehensive research effort, or replication of a previous finding, in the quest for gaining a high impact first/last author paper. These issues can only be overcome with a certain level of compromise, and perhaps with scientific journals allowing more than one individual to be the first or last author, where this is appropriate, as well as stronger encouragement and support for joint, collaborative work. This would greatly improve future scientific output in terms of addressing research questions more comprehensively and efficiently.

Final conclusion

In summary, the findings in this thesis highlight the widespread ability of wild chimpanzees to combine a diverse range of signals from different modalities, and show the potential for signal combinations to have different functions than their constituent signals. My findings challenge previous claims that wild chimpanzees produce referential gestures in a grooming context and the unexpected, negative, relationship between communicativeness and cooperativeness provides important insights into the evolutionary timeline over which these capacities may have been positively associated. Thus, these findings advance our understanding of the complexity of chimpanzee communication, and its link with cooperation; hopefully adding a piece of the puzzle to the vast topic of the origins of language. Nevertheless, as is often the case, this research has generated many questions and avenues for subsequent studies, which will hopefully be pursued in the future.

As humans, we pride ourselves on our highly sophisticated communicative and cooperative tendencies; here I strongly advocate that we harness and utilise both of these capacities to push this field forward. To date we have made huge advancements in our understanding of our own communication system, as well as those of other species. However, to progress to the next level it will be necessary to break down traditional barriers between researchers and research groups (for instance in terms of modalities and species studied), which prevent them from collaborating and generating comparable data that can be shared. The scientific community should recognise the enormous benefits working together would have in terms of advancing our knowledge.

APPENDICES

Appendix A

Repertoire of specific MM signal combinations produced

	Across all eight contexts		Across rest, feed, groom and travel contexts Percentage of occurrences that elicited a response					
Signal	**No. of individuals to produce this signal**	**No. of occurrences observed**	**No. of occurrences with at least one recipient within 5 m**	**F, V, G or MM signal response**	**Movement response (%)**	**Positive response (%)**	**Negative response (%)**	**No response (%)**
FREE FACIAL-GESTURAL								
Play Face & Bite	7	8	NA	NA	NA	NA	NA	NA
Play Face & Brief Manual	1	2	NA	NA	NA	NA	NA	NA

Contact with Object or Ground								
Play Face & Kick	1	1	NA	NA	NA	NA	NA	NA
Play Face & Manual Contact with Another Individual & Bite	3	12	NA	NA	NA	NA	NA	NA
Play Face & Manual Contact with Another Individual	7	18	NA	NA	NA	NA	NA	NA
Play Face & Somersault	1	1	NA	NA	NA	NA	NA	NA
Scream Face & Mount Other Individual	1	1	1	0	0	0	0	100
Scream Face & Mount Other Individual & Bite	1	1	1	100	0	0	0	0
FREE FACIAL-VOCAL								
Bared Teeth Display & Whimper	1	2	2	50	0	0	00	50

Pant hoot Face & Soft Hoo	3	4	4	0	0	0	0	100
Play Face & Laughter	1	4	NA	NA	NA	NA	NA	NA
Play Face & Grunt	1	1	NA	NA	NA	NA	NA	NA
FREE VOCAL-GESTURAL								
Grunt & Arm-Raise	2	6	6	33	0	100	0	0
Grunt & Big Loud Scratch	4	6	4	25	25	0	25	75
Grunt & Bite	1	1	1	100	100	0	0	0
Grunt & Manual Contact with Another Individual	1	1	1	0	0	100	0	0
Grunt & Present Groom	4	9	9	0	0	67	0	33
Grunt & Present Sexual	1	1	1	0	0	0	0	100
Grunt & Puts Arm Around	1	1	1	0	100	0	0	0

Individual								
Grunt & Reach	1	1	1	0	0	100	0	0
Pant Grunt & Arm-Raise	1	3	3	67	0	67	0	0
Pant Grunt & Big Loud Scratch	3	4	3	33	33	33	0	0
Pant Grunt & Bite	1	1	1	0	0	0	0	100
Pant Grunt & Hand Fling	1	1	NA	NA	NA	NA	NA	NA
Pant Grunt & Present Groom	1	1	1	0	0	100	0	0
Pant Grunt & Present Sexual	2	2	2	0	0	0	0	100
Pant & Arm-Raise	1	1	1	100	0	100	0	0
Pant & Big Loud Scratch	1	2	2	0	0	0	0	100
Pant & Bite	2	2	2	0	0	50	0	50
Pant & Present Groom	1	1	1	0	0	100	0	0

Pant & Present Sexual	1	1	1	0	0	0	0	100
Rough Grunt & Big Loud Scratch	1	1	NA	NA	NA	NA	NA	NA
Soft Hoo & Big Loud Scratch	3	3	2	0	0	0	0	100
Soft Hoo & Brief Manual Contact with Object or Ground	1	1	1	0	100	0	100	0
Soft Hoo & Present Groom	1	1	1	100	0	0	0	0
FREE FACIAL-VOCAL-GESTURAL								
Bared Teeth Display & Whimper & Big Loud Scratch	1	1	1	0	0	0	0	100
Bared Teeth Display & Whimper & Rump Rub	1	1	1	0	0	0	0	100
Pant Hoot Face & Pant Hoot & Big Loud Scratch*	1	2	NA	NA	NA	NA	NA	NA

Pant hoot Face & Pant hoot & Brief Manual Contact with Object or Ground*	1	1	NA	NA	NA	NA	NA	NA
Pant Hoot Face & Pant hoot & Drum Feet*	4	6	1	0	0	0	0	100
Pant hoot Face & Pant hoot & Manually Displace Object & Drum Feet*	1	1	NA	NA	NA	NA	NA	NA
Pant Hoot Face & Pant hoot & Manually Displace Object*	3	10	3	0	33	0	0	67
Pant hoot Face & Pant hoot & Reach*	1	1	1	0	100	0	0	0
Play Face & Laughter & Bite	2	2	NA	NA	NA	NA	NA	NA
Play Face & Laughter & Manual	2	2	NA	NA	NA	NA	NA	NA

Contact with Another Individual								
Pout & Grunt & Big Loud Scratch	1	1	NA	NA	NA	NA	NA	NA
Scream Face & Scream & Brief Manual Contact with Object or Ground*	1	1	1	100	0	0	0	0
Scream Face & Scream & Reach*	1	1	1	0	0	0	0	100
Scream Face & Soft Hoo & Mount Other individual	1	1	1	0	0	0	0	100
Whimper Face & Whimper & Big Loud Scratch*	2	2	NA	NA	NA	NA	NA	NA
FIXED FACIAL-VOCAL								
Pant hoot Face & Pant hoot	13	58	35	43	3	6	6	57

Scream Face & Scream	9	14	10	30	10	10	40	50
Whimper Face & Whimper	5	10	3	0	0	0	0	100

The table shows the number of instances and number of individuals observed to produce different MM combinations, both free and fixed, across all eight behavioural contexts. It also shows the number of occurrences where the signal was produced in rest, feed, groom or travel contexts with at least one recipient within 5 m, and of these, the percentage of these occurrences that elicited each of the four recipient response types, or no response. One signal could elicit several responses. Responses were recorded from the start of the signal until 20 s after the end of the signal. This table only includes unambiguous signals that could be categorized based on previous literature. Any MM signals that contained ambiguous components were excluded. NA is reported when all signals of this type were produced outside of rest, feed, groom and travel contexts, or there were no signals produced in these four contexts with at least one individual within 5 m.

*MM signal contains fixed facial-vocal components, but addition of gesture permits categorization as free MM signal.

Appendix B

The types of main recipient responses elicited by each grunt + gesture MM signal and matching UM grunt and UM gesture signals

ID	Context	MM signal	MM main response	UM vocal signal	UM vocal main response	UM gestural signal	UM gestural main response
AT	Rest	Grunt + BLS	Fearful/submissive response	Grunt	Vocalisation (grunt)	BLS	Gesture (present groom)
				Grunt	Look response	BLS	Ignore
						BLS	Ignore
						BLS	Ignore

						BLS	Ignore
AT	Travel	Grunt + BLS	Ignore	**Grunt**	**Ignore**	BLS	Movement towards
				Grunt	**Ignore**	BLS	Look response
				Grunt	**Ignore**	**BLS**	**Ignore**
				Grunt	Vocalisation (soft hoo)		
				Grunt	**Ignore**		
BB	Groom	Grunt + BLS	Ignore	**Grunt**	**Ignore**	BLS	Groom response
				Grunt	**Ignore**	**BLS**	**Ignore**

						BLS	Gesture (brief touch of focal rump)
						BLS	**Ignore**
PB	Rest	Grunt + BLS	Look response	Grunt	Ignore	BLS	Gesture (BLS)
				Grunt	Ignore	BLS	Vocal-gestural (grunt and present groom)
PO	Groom	Grunt + Arm-raise	Groom response	**Grunt**	**Groom response**	**Arm-raise**	**Groom response**
				Grunt	Inspects swelling	**Arm-raise**	**Groom response**

				Grunt	Ignore	**Arm-raise**	**Groom response**
						Arm-raise	**Groom response**
						Arm-raise	**Groom response**
PO	Groom	Grunt + Present groom	Groom response	Grunt	Ignore	**Present groom**	**Groom response**
				Grunt	Ignore	**Present groom**	**Groom response**
				Grunt	Ignore	Present groom	Ignore
						Present groom	**Groom response**
						Present groom	Ignore

PO	Groom	Grunt + Present groom	Groom response	Grunt	Ignore	**Present groom**	**Groom response**
				Grunt	Ignore	**Present groom**	**Groom response**
						Present groom	**Groom response**
						Present groom	Look response
						Present groom	**Groom response**
WA	Travel	Grunt + Present sexual	Ignore	**Grunt**	**Ignore**	Present sexual	Look response

WL	Groom	Grunt + Arm-raise	Groom response	Grunt	Ignore	**Arm-raise**	**Groom response**
				Grunt	Ignore		
				Grunt	Ignore		
				Grunt	Ignore		
WL	Travel	Grunt + Manual contact with another individual	Climb on focal individual’s back	Grunt	Ignore	**Manual contact with another individual**	**Climbs on focal individual’s back**
				Grunt	Ignore	**Manual contact with another**	**Climbs on focal individual’s back**

						individual	
				Grunt	Gesture (drags branch on ground)	Manual contact with another individual	Starts walking after refusing to move
						Manual contact with another individual	Ignore
WL	Groom	Grunt + Present groom	Groom response	Grunt	Look response	**Present groom**	**Groom response**
				Grunt	Ignore	**Present groom**	**Groom response**
				Grunt	Ignore		

				Grunt	Ignore		
WL	Groom	Grunt + Present groom	Groom response	Grunt	Gesture (BLS)	**Present groom**	**Groom response**
				Grunt	Ignore	**Present groom**	**Groom response**
				Grunt	Ignore		
				Grunt	Ignore		
WL	Groom	Grunt + Present groom	Groom response	Grunt	Look response	**Present groom**	**Groom response**

				Grunt	Ignore	**Present Groom**	**Groom response**
				Grunt	Ignore		
				Grunt	Ignore		
YB	Groom	Grunt + Present groom	Ignore	**Grunt**	**Ignore**	Present groom	Groom response
				Grunt	**Ignore**	Present groom	Groom response
				Grunt	Vocalisation (grunt)	Present groom	Groom response
				Grunt	**Ignore**	Present groom	Groom response

	Grunt	**Ignore**		Present groom	Groom response

Up to five UM grunt and five UM gesture signals were matched to each MM grunt + gesture signal. Responses were recorded from the start of the signal until 20 s after the end of the signal. ‘Main’ response was defined as the most active response (Look<Signal produced<Behavioural). Bold typeface indicates that the UM main response matched at least one of the main responses to the matching MM signal.

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