EVOLUTIONARY AND DEVELOPMENTAL PERSPECTIVES ON ACCOMMODATION: A COMPARATIVE STUDY OF THE EARLY COMMUNICATIVE GESTURES IN HUMANS AND CHIMPANZEES

Evelina Daniela Rodrigues

Thesis supervised by

António José dos Santos, Ph.D.

Catherine Hobaiter,PhD

WJCR, Ispa-Instituto Universitário

Tese submetida como requisito parcial para obtenção do grau de

Doutoramento em Biologia do Comportamento

2024

2024

Tese apresentada para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia do Comportamento realizada sob a orientação de António José dos Santos e Catherine Hobaiter, apresentada no Ispa - Instituto Universitário no ano de 2023.

O presente trabalho foi financiado pela Fundação para a Ciência e Tecnologia (SFRH/BD/138406/2018 & COVID/BD/152944/2023).

Fundação
para a Ciência
e a Tecnologia

Nota prévia: A presente tese apresenta artigos científicos já publicados (capítulos 2 e 3), ou submetidos para publicação (capítulo 4) ou em preparação para submissão (capítulo 5). Ao longo da tese uso o pronome ‘we’ em vez de ‘I’ uma vez que estes trabalhos, embora liderados por mim, resultaram de frutuosas colaborações. Participei integralmente na conceção dos trabalhos, obtenção e análise dos dados, discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, 30 de Setembro de 2023

Evelina Rodrigues

ACKNOWLEDGMENTS

Carrying out this PhD project has been a challenging but beautiful adventure, and the list of people contributing to its success is anything but short. Many people gave their time to contribute to this thesis and for this I will always be grateful.

First and foremost, I am deeply grateful to my supervisors António José dos Santos, and Catherine Hobaiter, for their guidance and support during these last 5 years. Thank you, professor António, for believing in me and in this project since the very beginning . Thank you, Cat, for adopting me and for being such a great academic model and person. No matter where, in Portugal, Scotland, Uganda, or Japan, and even with a pandemic in the middle, you were always there for me.

I would like to thank my academic families in ISPA, and in St Andrews, the WildMinds group that made my times in St Andrews so worth it, and it has been a great pleasure to grow by their side. You are a reminder that science is much better when we do it together. I would like to thank FCT for the funding – it took a couple of years to get it but it was worth every second of wait and, without it, none of this would have been possible.

I want to thank all the human and nonhuman primates I had the pleasure to know better through the lens of my camera and extensive hours of coding behind the screen. Words can hardly describe how privileged I felt each moment the chimps shared the forest with me. It was a dream came truth and thank you Cat for that opportunity! I would like to thank the International Primatological Society that covered the costs of my fieldwork, and the Budongo Conservation field station staff that made everything going so smoothly. I would like to extend my sincere thanks to Monday who helped me collect my data in the forest and from whom I learned so much. This thesis would not have been possible without 60 little constellations, their parents and the amazing teachers and staff at Voz do Operário. I'm very thankful for everything I've learned with you and for your hospitality and kindness.

I'm deeply grateful to my partner, Ivo, who have always believed in me, in my potential as a researcher and as a person. Thank you for always encouraging me when I needed most. I could not do it without you, without our long conversations, laughter, crying, dances, celebrations and travels. I am forever grateful for your unconditional support and love.

I want to express my deep gratitude and inspiration for my family and my close friends outside academia and who stood by my side during the entire time of my PhD. I am really lucky to have a strong and supportive network of family and friends, who always believed in me. Thanks to my mother for representing a great role model, for keeping me grounded and being so patient with me. Thank you for all the support and for being always there, even when meant crossing the world by yourself and loosing connecting flights! Thank you also to my sister Dânia for being always a source of inspiration and support. She makes everything look easier and the world more cheerful and colourful.

There is one person, who really deserves a lot of gratitude but is unfortunately not around anymore. Pai, I hope you would be proud of this. Without your inspiration would have been difficult to overcome the most challenging moments. You'd have all the patience to listen and relisten to what I've been studying, and I know you'd have loved the sounds of the forest.

Palavras-chave:

Gestos, Acomodação, Chimpanzés, Crianças

Keywords:

Gestures, Accommodation, Chimpanzees, Toddlers

ABSTRACT

As we begin to interact within our social environment, it becomes crucial to learn the rules and skills to thrive, and accommodating the way we communicate is a key ability. Humans adjust their communication, consciously or subconsciously, at different levels by using different types of signals or adjusting a wide range of features in how they produce them. But whether the ability to accommodate is fully or partially derived from language raises important questions about which elements of communication are adjusted, and when different adjustments emerge during our individual developmental and in our evolutionary trajectory as a species. In this thesis we focus on gestures because of its importance in human ontogeny and in language evolution: young children spontaneously gesture before they start using language, and other great apes use a vast repertoire of gestures flexibly and intentionally. Comparing communicative interactions in humans and in our modern relatives, chimpanzees, can provide insight into shared features, and the communicative abilities of our last common ancestor, helping to elucidate the socio-cognitive foundations of language. To date, very few studies include both human and nonhuman primates: consequently, making comparisons often relies on comparing findings from different studies. However, we show that human and nonhuman gestural research has followed different approaches, making comparisons challenging. We describe and employ a similar methodology to explore how gestures are accommodated in two chimpanzee communities and four groups of humans (toddlers). Within this evolutionary framework we explore both the ability to accommodate communication from a broad perspective by looking at how chimpanzees communicate across different relationships during greetings and leave-takings, and the in-depth exploration of the gestural communication of chimpanzee mothers with their infants and other community members. We found that social aspects of relationships, such as kinship and rank, influence the likelihood of communication, and that kinship shapes more subtle features of the gestures produced, such as prominence and temporal patterns. We examined nuanced features of gestural communication in both chimpanzees and humans in the light of work on Child-Directed Communication (CDC) in language. Chimpanzee mothers accommodated their communication towards young individuals, but in different ways to CDC accommodation in adult use of language: they used shorter gesture units towards immature individuals and used more repetition towards older offspring. Taking a developmental perspective, we found that CDC emerged early in ontogeny, before language, with toddlers using a simpler gestural vocabulary and gesturing at a slower pace towards younger peers. We show that the ability to accommodate our communication, including to young individuals, is present in gestural communication of chimpanzees and pre-verbal children, suggesting that this ability is not a mere consequence of language but instead represents one of the foundational capacities on which language use is built. We share this ability to accommodating our communication with chimpanzees, and it was likely present in our last common ancestor, but different selective pressures may have shaped the expression of this ability in the two species.

RESUMO

À medida que começamos a interagir no nosso meio social, torna-se fulcral aprendermos as regras vigentes e as capacidades necessárias para prosperar, sendo a capacidade de ajustar a forma como comunicamos uma capacidade chave. Ajustamos a nossa comunicação, consciente ou subconscientemente, a diferentes níveis, podendo usar vários tipos de sinais ou ajustando uma ampla variedade de características na forma como os produzimos. Mas se a capacidade de acomodar é totalmente ou parcialmente derivada da linguagem levanta questões importantes sobre quais elementos e quando é que estes são ajustados durante o nosso desenvolvimento individual e na nossa trajetória evolutiva como espécie. Nesta tese, focamo-nos em gestos devido à sua importância na ontogenia humana e na evolução da linguagem: as crianças pequenas produzem gestos espontaneamente antes de começarem a usar a linguagem, e outros grandes primatas usam um vasto repertório de gestos de forma flexível e intencional. Ao compararmos as interações comunicativas em humanos e em chimpanzés, procuramos perceber que características e capacidades comunicativas estariam presentes no nosso ancestral comum, ajudando a elucidar as bases sociocognitivas da linguagem. Até ao momento, poucos estudos incluem primatas humanos e não humanos, e por este motivo, fazer comparações implica contrastarmos resultados de estudos diferentes que seguem abordagens distintas, tornando as comparações desafiantes. Recorremos a uma metodologia semelhante para explorar como os gestos são acomodados em duas comunidades de chimpanzés e quatro grupos de seres humanos (crianças pequenas). Dentro deste quadro evolutivo, exploramos quer a capacidade de acomodar a comunicação de uma perspetiva ampla, observando como os chimpanzés comunicam em diferentes relacionamentos durante encontros e partidas, assim como em mais detalhe exploramos os gestos das mães chimpanzés com os seus filhos e outros membros da comunidade. Descobrimos que aspetos sociais dos relacionamentos, como parentesco e posição hierárquica, influenciam a probabilidade de comunicação, e que o parentesco molda características mais subtis dos gestos produzidos, como proeminência e padrões temporais. Examinamos características detalhadas da comunicação gestual tanto em chimpanzés quanto em humanos à luz do trabalho realizado na área da Comunicação Dirigida às Crianças (CDC). As mães chimpanzés ajustaram a sua comunicação em relação aos indivíduos imaturos, mas de maneiras que diferem dos ajustes que adultos humanos fazem na sua CDC: direcionaram unidades gestuais mais curtas a indivíduos imaturos e usaram mais repetições quando comunicaram com filhos mais velhos. Numa perspetiva de desenvolvimento, descobrimos que a CDC surgiu precocemente antes da linguagem, com as crianças usando um vocabulário gestual mais simples e fazendo gestos a um ritmo mais lento quando interagindo com colegas mais novos. Mostramos que a capacidade de acomodar a nossa comunicação, inclusive em relação a crianças pequenas, está presente na comunicação gestual de chimpanzés e crianças pré-verbais, sugerindo que esta capacidade não é uma mera consequência da linguagem, mas representa uma das capacidades fundamentais sobre as quais a linguagem é construída. Partilhamos esta capacidade de acomodar a nossa comunicação com os chimpanzés, e é provável que esta estivesse presente no nosso ancestral comum, mas diferentes pressões seletivas podem ter moldado a expressão desta capacidade nas duas espécies.

TABLE OF CONTENTS

CHAPTER 1: General Introduction

CHAPTER 2: The Landscape of Gestural Research in Language Evolution: A Systematic Review

CHAPTER 3: Exploring greetings and leave-takings: communication during arrivals and departures by chimpanzees of the Bossou community, Guinea

CHAPTER 4: Chimpanzee 'babytalk': Gestural motherese in wild chimpanzees (*Pan troglodytes*)

CHAPTER 5: Toddler gestural accommodation in Portuguese nursery schools

TABLE INDEX

FIGURE INDEX

CHAPTER 1: General Introduction

1.1. The ability to accommodate in communication.

A fundamental element of developing social competence involves the skill of adjusting one's behaviour, including your communicative behaviour, in response to various subtleties present in the social environment (Brownell & Carriger, 1990). Although it may appear simple – we are rarely aware of the effort involved in even our own communication – accommodation as a process is quite cognitively complex, involving the compilation of information about past interpersonal and intergroup experiences and the incorporation of this information to adjust our own communication (Giles et al., 1987). In sociolinguistics, communicative accommodation is most frequently explored in the vocal domain. Accommodation can occur over the short-term (over seconds to hours) and long-term (over days to years; Ruch et al., 2018), and studies take into account the communicative registers of both the signaller and recipients, describing how communicative differences are reduced, maintain, or magnified when people interact (Giles & Powesland, 1975). In this dissertation, we focus on short-term accommodation and consider a broader perspective, exploring how individuals adjust their communication to their partners' characteristics and relationships, rather than the detailed alignment of communicative styles.

To accommodate successfully, signallers must be able to evaluate their partners' characteristics and interests and reconcile these with their own interests and communicative intentions (Giles et al., 1987). We can adjust our communication, consciously or subconsciously, at different levels by using different signal types or adjusting certain features of the signal. Let us take the example of greetings. We may greet a friend with a hug, but the intensity and duration of that hug may vary depending on which friend we are greeting, on how long we've known each other, on the closeness of our relationship, on the time since we last saw each other, or on a single event that happened to one of us earlier that day. In other circumstances a hug may not be appropriate at all. Within a professional context it might be more appropriate to shake hands instead. Across cultures, a relatively formal greeting might range from three kisses to a deep bow as a sign of respect, and we may choose to adapt the way we greet when greeting several people on the same occasion.

This variation raises an important point: the ability to accommodate our communication involves not only flexibility in using different signals according to specific situations and partners, but also the choice to not accommodate or to not use certain signals. Not accommodating – especially when we are able to – is equally informative of the social context or relationship. For example, not changing the way we greet when interacting with people from other cultures could indicate our resistance to adapt or integrate. If we meet a group of friends and we do not greet someone specifically, this absence of a targeted signal could indicate the quality of my relationship not only to that person, but also to the audience standing there. Therefore, not finding evidence of accommodation in instances of communication is not sufficient to make statements about the absence of this ability, as they may reflect a choice not to accommodate, or the existence of accommodation in under-explored or unrecognised areas of behaviour.

1.2. How can we study accommodation?

When we do detect accommodation, why do individuals accommodate the way they communicate, and how and what areas of their behaviour and signals do they accommodate? Which cognitive abilities and social conditions need to be in place to express this capacity? Our interest in the biological basis of this ability led us to investigate this topic at both the proximal and ultimate level, and we employed Tinbergen's famous framework as a valuable tool to structure this thesis. At the proximal level we can explore how accommodation occurs (as a mechanism) and how this ability arises in the individual (during ontogeny). At the ultimate level we have the possibility to explore why we accommodate our communication, in the sense of understanding its adaptive value (its function) and understanding the evolution (phylogeny) of this ability.

Once we start to navigate our social world, we need to learn the rules and acquire the tools to prosper, and accommodating the way we communicate is a key ability in this regard. There are numerous ways in which humans accommodate their communication – while this thesis will particularly focus on exploring its ontogenetic and phylogenetic roots, here we outline the ways in which it is fully expressed in human adults to set the context for these questions. There are two predominant models relating to accommodation: the Interactive Alignment Model (IAM, Pickering & Garrod, 2004); and the Communication Accommodation Theory (CAT, Giles et al., 1987). IAM comes from a cognitive-psychology and psycholinguistic tradition focusing on the proximate level of explanation (mechanism). This model assumes that speakers become more similar to, or converge on, each other as a by-product of the internal and automatic mechanisms of speech perception and comprehension. According to this model, accommodation is not seen as conversation strategy or even an intentional mechanism. CAT comes from a sociopsychological and sociolinguistic tradition that is more closely linked to ultimate (functional) aspects of communication. According to this theory, when interacting, individuals tend to decrease or accentuate communicative differences with their partner as a communicative strategy to express social closeness or distance, in ways that may or may not be voluntary (Giles et al., 1987; Ruch et al., 2018). Being able to signal social proximity serves two major cognitive and affective functions: to facilitate coherent interaction and to manage social distance between individuals as members of groups. By becoming more similar to the way other partners communicate, a signaller may gain the partner's liking – fostering closer bonding between them. On the other hand, becoming less similar is a way of expressing social distance, which could be used, for example, to assert a higher status (Zhang & Giles, 2018).

One challenge for developmental and comparative approaches is that when looking for accommodation in other communicative systems outside of fully developed human adult language, we may reach an overly hasty conclusion that these individuals are not able to accommodate. Indeed, even in adult communication, the expression of accommodation varies substantially across languages and cultures – and our biases in who and what is studied (Henrich et al., 2010) may influence the ways in which we recognise accommodation. Thus, to study the emergence of accommodation in a complex system of communication, such as language, it is useful to parse out individual features as starting points. Taking a systematic bottom-up approach, in which core behaviour – such as latency to respond, gaze direction, etc. – are described, rather than directly inferring cognitively complex constructs, such as theory of mind, is a useful approach to identifying accommodation in individuals or species who do not (yet) fully express language.

1.3. How can we study the evolution of accommodation?

The origins of language remain an unsolved puzzle in human evolution. Key anatomical structures involved in speech production, for example the brain and vocal apparatus, do not fossilize (Ghazanfar & Rendall, 2008). Although the emergence of language in its current form appears to be a relatively recent development in evolutionary terms, it is likely that this skill was built upon a foundation of existing cognitive and communicative competencies (Armstrong et al., 1994). To identify the evolutionary roots of language and, particularly, our ability to adjust it to our conversational partners, we must examine how other animals communicate. Although the communication systems and abilities of nonhuman species are important in their own right, patterns of similarity and distinction across their and our capacities may help us to explain the variation found in human social behaviour, communication, and language (Cairns, 1979; Tomasello & Call, 1997).

Communication systems evolve as a response to the adaptative pressures a species faces in its ecological niche and, as a result, each species possesses a communication system tailored to achieve its specific goals (Cheney & Seyfarth, 2018). Certain species, including humans, adjust their communication in response to alterations or disruptions in their surroundings, a phenomenon known as environmental adaptation. For example, captive common marmosets (*Callithrix jacchus*) increased their median sound level and call duration in response to increased background noise (Brumm et al., 2004). Similarly, in noisy conditions, it has been shown that we increase the pitch, amplitude, and duration of our utterances (Lombard effect; Junqua, 1996). The main function of environmental accommodation seems to be in optimizing signal transmission. A hypothesis put forth by Ruch et al. (2018) suggests that accommodation to social aspects, including to interactional partners, first occurred as a side-effect of environmental accommodation but was then exapted to serve independent social functions (for example, signalling social closeness).

Comparing communicative interactions in humans and in our modern phylogenetic relatives can reveal shared features and shed light on the communicative abilities of our shared, but now extinct, ancestors, helping to illuminate the social cognitive foundations of language (Hauser et al., 2002). If communicative traits and an ability to accommodate are present in our closest relatives, we may conclude that these emerged before language. On the other hand, the absence of similarities in close-related species but their presence in more distant-related species would suggest that they may have emerged via convergent evolution – to solve a similar communicative problem that these biologically distinct species share. Whether the ability to accommodate is fully, or at least partially, derived in humans raises the important question of which elements of communication have been adjusted and when they started being adjusted in the course of evolution.

1.4. Gestural communication

1.4.1. Why gestures

Focusing on gestural communication is promising for several reasons. Firstly, researchers have proposed ‘gesture’ as a potential precursor of language and the system in which key language abilities emerged in our evolutionary history, with a wide range of evidence showing that nonhuman great apes have more intentional control, flexibility, and interactional awareness of their gestures, than of their vocalisations or facial expressions (Armstrong et al., 1994; Call & Tomasello, 2007; Hewes, Andrew, Carini, Choe, Gardner, Kortlandt, Krantz, McBride, Nottebohm, & Pfeiffer, 1973).

Secondly, human communication is characterised by a tight integration between gesture and speech (Goldin-Meadow & McNeill, 1999). Adult speakers normally accompany their speech with expressive gestures (co-speech gestures; McNeill, 1992), and gesture plays an essential role during early childhood language acquisition, especially before children use spoken or signed language as their primary means of communication (e.g., Bates, 1979; Bates et al., 1975; Bruner, 1981).

In early human ontogeny, preverbal gesturing seems to be universal across cultures – and also shows key hallmarks of language capacities, such as intentional communication (Bates, 1979; Stivers et al., 2009). As a result, the study of gestural communication in young children is well suited for comparison with nonhuman primate gesture. In fact, several studies suggest that gestural communication in chimpanzees resembles that of human infants at a pre-linguistic stage (Pika, 2008; Pollick & Waal, 2007; Tomasello, George, Kruger, Jeffrey, & Evans, 1985). But to increase the validity of comparative studies and follow up on this work, researchers should use comparable data, following similar definitions and methodologies.

1.4.2. Gestures in humans

Humans gesture all the time and begin gesturing from a very early age. When people think about gestures, they are typically referring to movements of the limbs that help our speech, or cultural or iconic forms that convey a meaning on their own. Children use gestures for communicating before their first spoken words, and adult spoken language users use spontaneous manual gestures alongside their speech (co-speech gestures; Iverson & Goldin-Meadow, 1998; McNeill, 1992). It is still debated to what extent co-speech gestures are always communicative (directed to a recipient) and intentional (goal-directed and voluntarily produced): we often find ourselves gesturing, even when our audience cannot see us or when there is no audience at all. In these cases, co-speech gestures may serve as a cognitive tool to help the signaller work through tasks (Goldin-Meadow, 1993; McNeill, 1992).

Nevertheless, during ontogeny children learn to express communicative intent through gestures (Bruner, 1981; Butterworth, 2003). We cannot directly access intentions in non-linguistic communication, and preverbal children cannot yet communicate through linguistic means about their mental states. Therefore, developmental psychologists identified several behavioural markers as indicators of intentionality in preverbal communication. These markers included observable behaviour such as gaze alternation, persistence, and elaboration, which indicate that gestures produced from around 9-months of age are already communicative and intentionally produced (Bates, 1979; Bates et al., 1975). Moreover, infants seem also to be sensitive to the attentional state of their recipients, adapting the modality of their gestures accordingly. For example, children will use visual (silent) gestures more often when the recipient is looking (Bourjade et al., 2023; Rodrigues, Marôco, et al., 2021). Together, these behavioural markers suggest that a robust linguistic-like communication system is already in place before the infant is able to use language (Bates, 1979; Lock, 2004).

Traditionally, infants' gestural repertoires have been described in terms of their functions such as: 'comment', 'request', or 'protest' (e.g., Blake et al., 1992; Crais et al., 2009). From these descriptions, it becomes apparent that most of the gestures produced by children are referential (also called deictic gestures; establishing reference by calling attention to or indicating an object or event in the environment; Bates, 1979; Iverson & Goldin-Meadow, 1998). These gestures emerge at around 7-9 months and are usually triadic, in the sense they involve a third entity besides the signaller and the recipient, and dependent on context (Crais et al., 2009). They can be subdivided into: 'contact', if they include contact between the child and the object/ caregiver; or 'distal', if there is no contact with the caregiver/object, such as in pointing and reaching (Crais et al., 2009; Tomasello et al., 1997). Children use these deictic gestures with two main functions: imperative requests for actions or objects (Bates et al., 1975); and declarative purposes where gestures are used to draw another's attention to an object or entity for the sake of sharing attention (Liszkowski et al., 2004). Other types of gesture emerge later in ontogeny, for example representational gestures often appear at around 12-months. These include symbolic gestures that relate to an object or some feature of the object (e.g., cupped hand to mouth to represent 'drinking'), and conventionalized gestures that have their meaning socially defined and represent some action or concept rather than a specific object (e.g., waving good-bye, Crais et al., 2009). The focus on referential gestural communication – most frequently pointing – has limited the study of alternative functions and meaning; however, some recent studies show that a wider range of meanings may be present in child gesturing (Kersken et al., 2018).

1.4.3. Gestures in chimpanzees

Great ape gestures are of great interest because they appear to involve a higher level of intentionality (that is goal-directedness and voluntary control) as compared to their vocalizations and facial expressions. Primatologists applied the intentionality criteria developed to study the human infants preverbal communication described above (Bates, 1979; Bates et al., 1975) to illustrate that other apes also produce gestures intentionally (Leavens, Russell, et al., 2005; Plooij, 1978; Tomasello, George, Kruger, Jeffrey, & Evans, 1985). In fact, their communicative intent is often a prerequisite of the gestures included in great-ape research (Fröhlich, Kuchenbuch, et al., 2016; Hobaiter & Byrne, 2011b).

The first behavioural repertoires of chimpanzees included detailed descriptions of communicative behaviours in the wild (Van Lawick-Goodall, 1968). A focus on their gestural communication revealed their capacity for using gestures in different contexts (Goodall, 1986; Plooij, 1978). Since then, more detailed studies were conducted in captivity, and later again in the wild, providing further evidence for their intentional use and exploring their flexible use in different contexts (Call & Tomasello, 2007; Hobaiter & Byrne, 2011b).

The repertoires are usually based on the description of the forms of the gestures and categorized by the sensory channels used in their perception: silent visual gestures, contact gestures, and audible gestures (e.g., Hobaiter & Byrne, 2011; Tomasello et al., 1994). Despite form being described by observable objective features, a considerable amount of variation is present in the reported size of apes' gestural repertoires. For example, some researchers described repertoires containing around 25-35 gesture forms (e.g., Call & Tomasello, 2007; Tomasello et al., 1994), while others reported more than the double, with at least 66 gesture forms (e.g., Hobaiter & Byrne, 2011), or even over 100 (Genty et al., 2009). However, while the descriptions of the gestures were often similar, the difference in the number of 'types' included in the repertoires was sometimes due to level of granularity in the researchers' description of them, rather than variation in the apes' behaviour. For example, a 'stomp' performed with both feet ('stomp 2-feet') was considered by some researchers a different gesture type as compared to a 'stomp' performed with only one foot (Hobaiter & Byrne, 2011b); whereas others researchers would have considered it the same gesture action regardless of being performed by one or both feet (e.g., Fröhlich et al., 2017; Tomasello et al., 1985).

Understanding ape gestural meanings presented a comparable challenge to that of assessing their intentionality, as we cannot directly access mental states. Additional challenges arise because the same gesture can be employed in various contexts, or may have more than one possible meaning: individuals are able to use different gestures to achieve the same outcome, and a single gesture for several outcomes (so called, means-ends dissociation; Pika & Liebal, 2012; Plooij, 1978). Previous studies tackled the question of meaning by looking at the contexts in which gestures occur (Pollick & Waal, 2007; Tomasello & Call, 1997). More recent approaches focused on the interaction between the signaller and recipient to infer a gesture's meaning (Cartmill & Byrne, 2010; Genty et al., 2009); a system eventually described as the 'Apparently Satisfactory Outcome' (ASOs), which employs the reaction of the recipient that seems to satisfy the signaller (suggested by the cessation of the signalling, Hobaiter & Byrne, 2014). Aggregating the meaning of different instances of use and across individual signallers and signaller-recipient pairs, allows us to investigate the generalised meaning of a specific gesture form in a species or community (Graham et al., 2018).

1.4.4. Comparing gestural research in humans and other great apes

Gestures of human infants and other great apes, chimpanzees in particular, seem to share striking similarities in many different aspects: they are intentionally produced, as shown by distinct behavioural markers (e.g., Bates, 1979; Leavens et al., 2005); they are employed in different contexts, and may be used flexibly to express multiple meanings (e.g., Hobaiter & Byrne, 2014; Kersken et al., 2018). Furthermore, the descriptions of ape gestural repertoires indicate further similarities with human communication (Blake et al., 1992; Tomasello et al., 1994). A recent study using a descriptive methodology revealed an 89% overlap in the gestural repertoires of children and chimpanzees (Kersken et al., 2018), and naïve human adults appear able to intuitively interpret the meaning of other apes' gestures (Graham & Hobaiter, 2023).

Besides striking similarities, human and other apes' gestures do differ in some significant ways. Traditional research on human infants was biased towards 'empty-handed' gestures, with infants performing most of their gestures in space (Petito, 1988). However, when these same actions involve objects or include an object as a referent, they are frequently interpreted as functional object use play or meaningful action, rather than being categorized as gestures (Iverson & Goldin-Meadow, 2005). In contrast, research in nonhuman great apes always included gestures performed with objects (e.g., ‘object shake’) or that involved contact with objects (e.g., ‘stomp’) within gestural repertoires. This distinction could have resulted in an underestimation of the gestures produced by human infants, and an imbalance in comparisons with other great apes (Iverson et al., 1994; Pika, 2008).

One of the most important differences between human and nonhuman ape gestures, relates to their use as imperative or declarative signals. As opposed to gestures of human infants, most of the gestures used in interactions between other great apes can be defined as dyadic and imperative. Dyadic in the sense that they do not refer to an external entity, and imperative because they are used to get another individual to help in achieving a goal, and therefore a change in the recipient’s behaviour is expected. Humans, in addition to these types of gestures, also frequently use gestures to draw another’s attention to outside entities (triadic) for the sake of sharing attention (declarative; Bates, 1979). These referential gestures, declarative in their function, are rarely seen in other great apes – particularly in the wild. Nevertheless, referential gestures are not entirely absent from the repertoire of chimpanzees, especially when we consider that the third entity in a triadic interaction does not always have to be an external entity; but can include reference to areas on one's own body (Pika, 2008). For example, the ‘big loud scratch’ gestures in Ngogo chimpanzees apparently indicate a precise spot on the body where the signaller wants to be groomed (Pika & Mitani, 2006) although other chimpanzee communities do not seem to use it in this way (Wilke et al., 2022).

Ecologically-sensitive comparative designs and the use of similar definitions are crucial to demonstrate real individual, group, and species differences and to build valid conclusions and theories about the evolution of language (Bard & Leavens, 2014). As we have seen in previous sections, the study of gestures in human and nonhuman primate research developed under different approaches: human research has focused on the function of gestures and has been mainly conducted in experimental settings, whereas nonhuman research has focused on the form of gestures (i.e., descriptive repertoires) and has been largely conducted in observational settings (e.g., Graham et al., 2017; Pika, 2008). Methodological differences in comparative studies, including functional vs. descriptive approaches and confounds of experimental vs. observational settings, have limited the underlying conclusions made when describing patterns across studies or species. One potential solution involves employing similar approaches and aiming for settings that are as comparable as possible (Rodrigues, Santos, et al., 2021). For example, a recent study focused on the early communicative gestures in human and chimpanzee 1-year-olds observed across diverse socioecological settings and using a functional approach (Bard & Kishimoto, 2023). Although a functional approach to investigating gestures allows us to test our hypotheses about cognitive, social, and affective abilities, it is also important to take a step back and consolidate our knowledge about the fundamental capacities present in early communicative processes throughout more descriptive and detailed analyses.

1.5. The special case of child-directed communication

Within the many different ways that we accommodate in our communication, one well-recognised and wide-spread approach is used to engage with young children. This register is often referred to as 'motherese,' 'babytalk,' or 'infant/child-directed communication' (e.g., Falk, 2004; Schick et al., 2022). It is characterized by the use of a higher and more variable pitch, simplified vocabulary, more repetition, and a slower rate (Fernald et al., 1989; Snow, 1977). The input given to children in this register is not tied to the vocal modality, and similar patterns are found in sign languages and non-linguistic systems such as facial expression (Kim & Johnson, 2013; Reilly & Bellugi, 1996) and gesture (‘gesturese’). For instance, when adults communicate with infants, they tend to reduce their overall use of gestures, but increase their use of gestures that indicate an external referent (Bekken, 1989; Iverson et al., 1999).

This register is argued to facilitate language acquisition and promote social bonding across a wide variety of cultures. Widespread across cultures, child-directed communication represents an ideal candidate in which to investigate how and when our capacity for accommodation emerges both in our individual ontogeny and in our evolutionary past. Our cognitively sophisticated ability to accommodate our communication to our social partners was likely built on a set of precursor abilities already in place before acquiring language, and that are also shared with other species (e.g., the ability to remember previous interactions or to recognize different levels of social competence). Even young children seem to be sensitive to relatively small age differences in their peers, adjusting their behaviours accordingly (Brownell & Carriger, 1990; Franco et al., 2009), and they seem to adapt their speech following the patterns reported for child-directed communication (Dunn & Kendrick, 1982; Shatz & Gelman, 1973).

But when and how does our capacity to adjust our communication to young children emerge over the course of our lives and within an evolutionary context? Is it a by-product of language, or did it exist prior to language? We can explore these questions by analysing the early expression of human communication systems in preverbal children who have not yet fully developed language, and by examining the communication systems of other animals we can understand to what extent this ability might predate human communication (Schick et al., 2022).

1.6. The present thesis

In this thesis, we investigate how the ability to accommodate in our communication emerges and evolved. We focus on the early communicative gestures of young humans and chimpanzees applying the observational methods usually employed in studying nonhuman primates. In doing so, we can provide a direct comparison of the gestural behaviour in humans and chimpanzees – using the same methods and definitions. We use the *GesturalOrigins* framework recently published by Grund et al., (2023). This framework provides definitions, templates, and instructions relating to the data collection and coding process. The coding scheme was developed in ELAN, an open-source linguistic video annotation software (ELAN, 2022) and the coding protocol can be found in the materials made available by the authors. We use the same definitions and templates across the thesis to provide a robust and clear comparison of human and nonhuman communicative abilities. By following the *GesturalOrigins* framework, we also hope to provide sufficient detail to allow replicability and expansion of these studies, as well the exploration of new questions.

1.6.1. GesturalOrigins framework

Defining gestures. In all empirical chapters we use the same definitions and criteria to identify gestures in dyadic communicative interactions (interactions targeted to a single recipient). The current framework allows us to use different criteria to define gestures, or even to define them later based on the features coded. For example, the current coding scheme allows the coding of gestural actions that do not show evidence of being communicative (e.g., without any audience), or that are directed to a large general audience. Nevertheless, in this thesis we define all gestures *a priori* as directed and intentional, requiring that there was some behavioural evidence of intentional use to allow their inclusion in an analysis.

We define a gesture as a mechanically ineffective movement of the body or a specific body part, used voluntarily and intentionally to achieve a specific social goal (following: Hobaiter 2011, Grund et al., 2023). The voluntary part was specified to exclude automatic or reflexive automatic reactions to some external or internal cue. A gesture was considered intentional if at least one of the following criteria were met: i) audience checking, ii) response waiting, and/or iii) goal persistence. Audience checking refers to the signaller sensitivity to the recipient's attentional state and was detected via the gazing patterns of the signaller (towards the recipient) preceding gesture production, and appropriate adjustment of the signalling. For example, to increase the chances of a signal being perceived, silent gestures (if intentionally produced) are used when the recipient is looking or are performed after moving into the recipient's line of sight, whereas audible and tactile gestures are not. Response waiting refers to the period immediately after the gesture in which the signaller maintains visual monitoring of the recipient and/or holds their position, waiting for a response from the recipient without performing any other behaviour. Goal persistence refers to the use of further signals by the signaller until the goal is met.

A communication was only considered successful when the behavioural change from the recipient represented a plausible goal from the signaller's perspective (for example, being given an object, or moving closer, but not an aggressive act such as being hit). It is important to note that the goal is not always clear, as sometimes the gesture does not elicit a behavioural response from the recipient or elicits a behavioural outcome that is not likely to be a goal (e.g., a threat or attack). We used the ASO method to determine a gesture's goals: the changes in the recipient behaviour that apparently satisfied the signaller, suggested by the cessation of the signalling (Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014). The list of possible outcomes was based on recent studies conducted in other great apes (Graham et al., 2018; Hobaiter & Byrne, 2014) and slightly adapted for the study conducted with toddlers (also based on Kersken et al., 2018).

Gestural communication units. In the videos analysed in this thesis, we identify communicative events where the signaller produced one or more gesture tokens (instances). If the recipient gestures back in return, they are considered gestural exchanges (within the same communicative event). For each exchange we distinguish bouts and sequences of gestures based on the separation time between consecutively produced gestures (more than 1 second, and less than 1 second respectively; Figure 1).

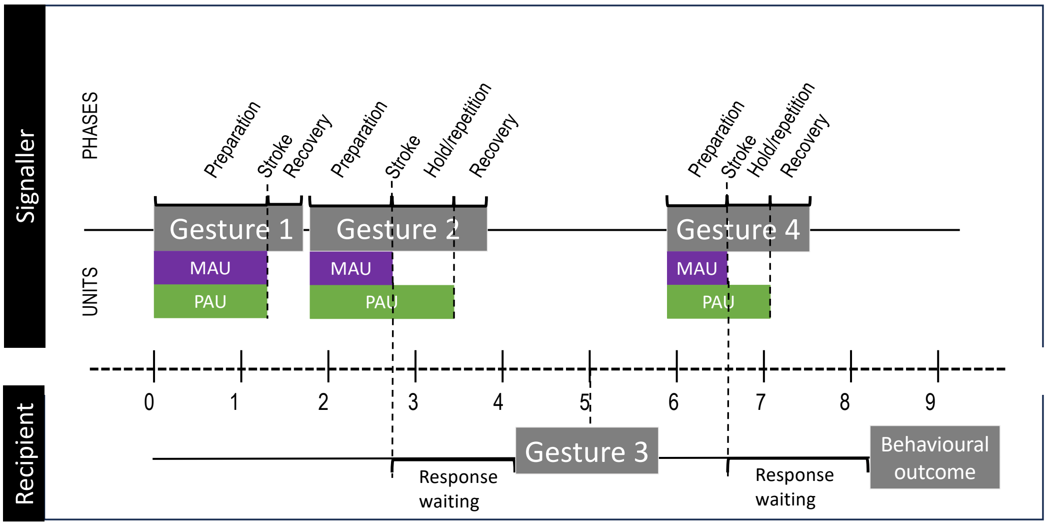


Figure 1. Visualisation of an example of gestural communication using the GesturalOrigins coding scheme. Includes with the phases (Preparation, Stroke, Hold/repetition, and Recovery) plus the gesture units (Minimum Action Unit, MAU; and Performed Action Unit, PAU) marked. Each communication is considered as a string of behaviours on a timeline that starts with the gesturing of one individual (the signaller) towards another (the recipient) and ends with a particular behavioural outcome (typically, either the goal of the signalling individual (ASO) or the failure of the communication. This example includes 2 exchanges from the signaller (exchange 1/3 with Gesture 1 and Gesture 2 , and exchange 3/3 including Gesture 4), and one exchange from the recipient (exchange 2/3 with Gesture 3). The first exchange includes two gestures in a sequence (Gesture 1 and 2) as they are separated by less than 1 second. Gesture 4 belongs to a different bout as it is more than 1 second apart.

Gestural units in this coding scheme are described in at two levels of resolution: the ‘gesture action’ and the ‘morph’. Gesture actions corresponding to the core bodily movement that describes the current gesture instance and differentiates it from all other actions. Additional characteristics, such as body part or repetition of the action, referred to as ‘modifiers’, are considered when describing variation in the production of those gesture actions (‘morphs’), and allow for a more fine-grained repertoire of units to be described. For example, the gesture action ‘hit’ may have two morphs when considering the modifier ‘repetition’: ‘hit’ when there is no rhythmic repetition and ‘hitting’ when there is rhythmic repetition. The level of granularity applied (gesture actions or morphs) depends on both the question being investigated and the size of the dataset available.

We code the precise duration of the gesture at different points in gesture production, from the moment the signaller initiates the gesture until the moment they return to the neutral position or move to produce a subsequent gesture in a sequence using the same body part. Based on the work of Kendon (2004), four stages in gesture production were considered: preparation (movement of the body into the position where the gesture can start to be expressed), action stroke (the section of the movement close to the gesture's apex in which the specific gesture is expressed), hold/repetition (optional phase where the position is sustained at the end of the stroke or the movement is rhythmically repeated), and recovery (movement of the body back to some position of rest/neutral position or into an action no longer considered part of the gesture expression).

In analysing the duration of gesture tokens, we focus on the relevant and informative section of the gesture, termed the Performed Action Unit (PAU). The PAU corresponds to the preparation, stroke, and hold/repetition phases. Grund et al., (2023) further distinguished the smallest possible section of the gesture movement in which the recipient can sufficiently distinguish the specific gesture action being produced (Minimum Action Unit, MAU), equivalent to the preparation and action stroke stages (Figure 1). Although we do not analyse MAU durations, we also analyse the hold/repetition phase duration, that starts where the MAU ends and lasts until the beginning of the recovery phase. Some gesture actions never include a hold/repetition phase (e.g., fling). In these situations, the MAU and PAU are the same duration. Other gesture actions do include an optional hold/repetition phase. For these types of gestures, the MAU and PAU may still be of the same length where a signaller chooses not to hold or repeat the gesture action in that instance of use. When the signaller does hold or repeat, the PAU will include the duration of the MAU plus the hold/repetition period (Figure 1).

1.6.2. Thesis outline

In Chapter 2, we address the importance of gestures in understanding language evolution in a systematic review of the literature. We apply this framework to the current landscape of data available from studies of gestural communication in human and nonhuman primates that make an explicit connection to language evolution. After a screening process of 923 papers, we extracted detailed information on 163 articles that allowed us to identify the areas of focus and apparent gaps within the field and discuss to what extent useful comparisons can be made across human and nonhuman studies at the present time.

In the following two chapters we investigate whether our closest phylogenetic relatives – chimpanzees – accommodate their communication at two different levels. In Chapter 3 we explore how communication in one chimpanzee community (Bossou) is shaped by the characteristics of the individuals present and other social features, specifically in greeting and leave-taking contexts. We analysed whether the probability of producing gestures was influenced by: i) individual factors of the interactants such as age, sex, or rank; ii) dyadic factures related to the quality of the relationship such as kinship, and the relative relationship in the social hierarchy; and iii) features of the immediate social group, such as the number of individuals present and the presence of adult males.

In Chapter 4, we take a more specific perspective and investigate how chimpanzee mothers in two different communities, one from Uganda and another from Guinea, accommodate specific features of their gesturing to the developmental stage of their offspring. We explore gestural features including: (a) the diversity of different gestures produced and their use in sequences (complexity); (b) the duration of gestures, and the gesture rate (tempo); and (c) the use of repetitions and objects in gestures (prominence). We frame this study within the child-directed communication literature. We first explore whether there is any evidence for gestural ‘motherese’ in chimpanzees by describing the communication that chimpanzee mothers direct to any individual of the community and compare whether and how this differs depending on the age, sex, and kinship of the recipient. We then focus on mother-offspring pairs to explore whether mothers also specifically accommodate their gestures to the age and sex of their own offspring.

Finally, in Chapter 5 we use the same methodology to explore the emergence of accommodation in human communication – specifically in toddlers’ gesturing. Children use gestures extensively before mastering speech. If the ability to accommodate in our communication emerges before language is fully developed, it might be expressed in the gestures produced by preverbal and early verbal children. We analyse the gestures produced by toddlers in three nursery schools in Portugal and explore communicative features such as: type/token ratio (complexity), gesture unit durations and gesture rate (tempo), and repetitions (prominence). We then test how these features vary depending on the age of their recipient.

We finish with a discussion and conclusion, integrating the findings across the different studies with each other and with the current state of the field. By applying a transparent and comparable approach under the same framework to humans and to our closest living relatives, we hope to provide insight into how and when our ability to accommodate in our communication emerged and shed new light on questions about the role gestures played in the evolution of human language.

CHAPTER 2: The Landscape of Gestural Research in Language Evolution: A Systematic Review

This chapter is based on Rodrigues, E. D., Santos, A. J., Veppo, F., Pereira, J., & Hobaiter, C. (2021). Connecting primate gesture to the evolutionary roots of language: a systematic review. *American journal of primatology*, *83*(9), e23313. Results were also presented at the Joint Conference on Language Evolution, Kanazawa, Japan (2022).

2.1. Abstract

Comparative psychology provides important contributions to our understanding of the origins of human language. The presence of common features in human and nonhuman primate communication can be used to suggest the evolutionary trajectories of potential precursors to language. However, to do so effectively, our findings must be comparable across diverse species. This systematic review describes the current landscape of data available from studies of gestural communication in human and nonhuman primates that make an explicit connection to language evolution. We found a similar number of studies on human and nonhuman primates, but that very few studies included data from more than one species. As a result, evolutionary inferences remain restricted to comparison across studies. We identify areas of focus, bias, and apparent gaps within the field. Different domains have been studied in human and nonhuman primates, with relatively few nonhuman primate studies of *ontogeny* and relatively few human studies of gesture *form*. Diversity in focus, methods, and socio-ecological context fill important gaps and provide nuanced understanding, but only where the source of any difference between studies is transparent. Many studies provide some definition for their use of gesture; but definitions of gesture, and in particular criteria for intentional use, are absent in the majority of human studies. We find systematic differences between human and nonhuman primate studies in the research scope, incorporation of other modalities, research setting, and study design. We highlight 8 particular areas in a call to action through which we can strengthen our ability to investigate gestural communication's contribution within the evolutionary roots of human language.

Keywords: gestures, language evolution, domains, humans, nonhuman primates

2.2. Introduction

Human language is a rich system of communication often argued to be qualitatively distinct from other animal species' communication (Christiansen & Chater, 2015; Hauser et al., 2002; Pinker & Jackendoff, 2005). The thousands of modern human languages are distinct in their expression, so much so that being a proficient language user in one language allows access to, at best, just a handful of others. Despite this, across the spectrum of modern human languages, each one contains a similar capacity for language-like communication. How and when language emerged remains under significant debate (e.g., Corballis 2002; Richerson et al. 2010; Bolhuis et al. 2014); but it was likely built on precursors, some of which may be detected in the communication of our modern primate relatives.

The availability of fossil evidence to resolve these debates is limited (Hsieh & Plotnick, 2020; although cf. Arensburg et al. 1989; MacLarnon and Hewitt 1999); and comparative studies of modern primate species' communication provide valuable insight. The presence and absence of features within human and nonhuman primate communication suggest potential precursors to modern systems of communication, and the pattern of presence across primate phylogeny can offer a potential timescale for their emergence. Comparisons within and across species typically rely on comparison across studies. Diversity in study methodology – from study species to socio-ecological context and more – is critical to properly exploring the full landscape of primate gestural expression. However, such diversity makes subsequent comparison across studies challenging, particularly where definitions and conceptual boundaries are opaque. In this systematic review we investigate those studies of spontaneous gestural communication in human and nonhuman primates that articulate an explicit connection between gesture and the evolutionary origins of modern human language. We incorporate a first use of Bourjade et al.'s conceptual framework for systematic comparison of gesture definitions (Bourjade et al., 2020) and investigate variation in different domains of research, in the study scope, in the inclusion of other signal sources (e.g., vocalizations), in the research setting, and in study design. We aim to provide an up-to-date description of the field, highlighting both what is understood and the areas in need of further research.

Language can be expressed in many forms, including spoken and signed: it is not the signal modality or channel of communication that defines human language so much as the way in which it is used. Many systems of communication across species encode sophisticated information, but nonhuman communication is typically broadcast irrespective of a recipient's attention, interest, or even presence (Rendall et al., 2009). Detecting language-like intentional communication is challenging because it depends not on the observable physical form of the signal but on the cognitive intention of the signaller. Imagine driving along a road and hearing another driver honking their horn as they approach you; there is no fixed information encoded in that signal. Unlike the acoustic structure of a monkey alarm-call (e.g., Seyfarth and Cheney 2003a, b), the uses of a car horn can mean very different things depending on what the signaller *intends* them to mean.

Intentional use, while a fundamental property of human language, remains apparently rare in communication of other species, including in many primate vocalizations (Rendall et al., 2009; Seyfarth & Cheney, 2003; Seyfarth & Cheney, 2003; although see Schel et al., 2013; Townsend et al., 2017). There is an exception: evidence for flexible intentional use is abundant in nonhuman ape (hereafter ape) gesture (Leavens, Russell, et al., 2005; Plooij, 1978; Tomasello, George, Kruger, Jeffrey, & Evans, 1985), driving interest in the evolutionary connections between ape gesture and human language, and 'gesture-first' hypotheses of language evolution (Corballis, 2002; Hewes, Andrew, Carini, Choe, Gardner, Kortlandt, Krantz, McBride, Nottebohm, Pfeiffer, et al., 1973; Rizzolatti & Arbib, 1998). More recent articulations recognise that language – like all animal systems of communication – is multimodal, and likely derived from multimodal systems (Gillespie-Lynch et al., 2014; Leavens, Russell, et al., 2010; Prieur et al., 2020; Taglialatela et al., 2011) but may have included a transition in the role of the different modalities, for example a shift in the vocal modality from supporting to carrying of information (e.g., Fröhlich et al. 2019).

Comparative studies seeking to draw specific comparisons between primate gesture and human language have been used to explore different aspects of primate species' gesturing including the physical *form* (as compared to linguistic lexicons; e.g., Brentari et al., 2012) and *meaning* (as compared to language-like semantics) of gestural signals (often through the study of message and context; e.g., Graham et al., 2018). The *structure* of gestural communication (in sequences of gestures; as compared to combinatorial structure and syntax in language; e.g., Hall et al., 2015), and the integration of gestural signals with other signal types, such as vocalizations and facial expression (*combination of sources;* e.g., Hobaiter et al., 2017a). From the perspective of the signaller and recipient, researchers have investigated how gesture develops behaviourally during *ontogeny* (e.g., Salo et al., 2018) and neurologically (*neural processes;* e.g., Biau et al., 2016), and similarities between how gesture and language are deployed (for example in brain or limb *laterality;* e.g., Meguerditchian et al., 2011).

One complication within gestural research, is that fact that researchers have no direct access to cognitive states (of either nonhuman or human subjects), and instead employ visible behavioural criteria to infer signaller intentions. These behavioural criteria were first developed in studies of pre-verbal human infants' ability to capture the attention of others and manipulate their behaviour (Bates et al., 1975, 1979). Today, criteria include behaviour such as whether the signaller shows sensitivity to the attentional state or composition of the audience, whether they pause (wait) for a response, and if they persist or elaborate when the recipient fails to respond (Leavens, Russell, et al., 2005; Liebal et al., 2004; Tomasello & Call, 1997). However, as the study of nonhuman primate gesture developed there has been variation in how these criteria have been operationalised and employed (Bourjade et al., 2020; Fröhlich et al., 2018; Leavens, Russell, et al., 2005).

Our ability to reliably detect patterns of similarity and distinction across modern primate species' communication is central to our ability to make inferences about the evolutionary trajectory of language. Variation in research settings, methods, or contexts can represent a strength, allowing for robust exploration of a particular finding. However, for this to be the case it is key that diverse methods are transparent about sources of variation (Bourjade et al., 2020; Fröhlich & Hobaiter, 2018). Characteristics of our study sample such as social background, responsiveness, or prior experience impact the generalizability of our findings (c.f. STRANGE framework, Webster & Rutz, 2020), and the over-representation of particular species or populations distort our ability to make phylogenetic comparisons (for example WEIRD – Western, Educated, Industrialized, Rich, and Democratic – humans, or BIZARRE – Barren Institutional Zoo And other Rare Rearing Environment – chimpanzees; Henrich et al., 2010; Leavens, Bard, et al., 2010). Previous studies have highlighted how systematic species-differences in individual history, tasks, and testing environments are confounded with apparent species-differences in communicative or other socio-cognitive abilities, such as their ability to follow gaze or produce pointing (Boesch, 2020; Leavens et al., 2019). Differences in methodology and context of study appear particularly profound when comparing human and nonhuman primate behaviour (Bard & Leavens, 2014; Leavens et al., 2019). Some of these differences may involve, for example, comparisons of institutionalized adult apes with non-institutionalized human children, or apes in caged environments with free-roaming human children (Bard & Hopkins, 2018; Leavens et al., 2019; Boesch, 2020). In some cases variation in our understanding across species is limited by what is both technologically feasible and/or ethical in nonhuman species, for example: the exploration of *neural processes* inside of living brains (c.f. Rizzolatti and Arbib 1998; Meguerditchian et al. 2010).

To explore meaningful patterns of similarity and distinction between human language and nonhuman gestural communication, we need to address apparent discrepancies in research approach and understanding. A crucial first step in this process is to better understand where any differences currently lie. A systematic assessment of the field allows us to better gauge the impact of any biases on our ability to develop clear hypotheses about the evolutionary trajectory of gesture and language. Bourjade and colleagues recently (2020) developed a framework to allow the systematic comparison of gestural definitions across primate studies – incorporating body parts, sensory modalities, social expression, and communicative and intentional properties. We include a first use of this tool, describing how primate species and study domains of gestural research vary in their concept of gesture, and then assessing how the species and study domains are differently represented in terms of study scope, the inclusion of additional sources such as vocalization or facial expression, and in research settings and study design. With this review we aim to 1) Identify both the areas of focus and apparent gaps within the field in studies that explore the connection between gestural communication and the evolution of human language, and 2) Identify to what extent useful comparison can be made across human and nonhuman studies at the present time and make recommendations for the future.

2.3. Methods

In March 2020, we conducted a search of peer-reviewed articles and book chapters in two search engines: Web of Science and PsycINFO. We used the SPIDER framework (Cooke et al., 2013) as the search tool to define our question scope and organize and list terms by the main concepts in the search question (Table 1).

Table 1. Search Tool SPIDER as applied to the current review.

Search categories	Potential search terms
Sample	Human and Nonhuman primates
Phenomenon of Interest	Language Evolution and Origins of Language
Design	Observational and Experimental studies
Evaluation	Gestural research domains of comparison
Research Type	Empirical Articles and Book Chapters

2.3.1. Search

We used the Phenomenon of Interest and the Evaluation categories from the SPIDER framework (Table 1) for our search string. We employed the largest time window allowed (1900 to 2019) and used both Web of Science and PsychInfo databases. While our search window extended back to 1900, more recent work is more thoroughly indexed in electronic databases, and as a result our search procedure may have failed to detect some earlier studies. Literature within Web of Science is systematically structured literature from the 1950s and both Web of Science and PsychInfo include books and other material within the Social Sciences and Humanities that are out of copyright. We did not apply search terms related to the sample (e.g., human, nonhuman, or even primates) at this stage, because research conducted on human (as compared to nonhuman) primates does not typically specify taxonomic terms to define the sample. Similarly, the type of study terms described in the design category (e.g., observational, experimental) is also often omitted in human work, so we removed this criterion in the first selection phase. Although no language restriction was applied at this stage, only studies with English abstracts or keywords were returned by the search because the search terms were in English. In PsychINFO the search term 'gestur*', AND 'evolutio*' OR 'origin*', AND 'languag*' or 'communicat*' was used as a filter in the title (TI), abstract (AB), or keyword (KW). In Web of Science, the same search terms were used as a topic (TS) filter (equivalent to title, abstract and keywords in PsychInfo). The final search string used in Web of Science was: (TS=gestur* AND TS= (languag* OR communicat*) AND TS= (evolutio* OR origin*)).

2.3.2. Inclusion and Exclusion criteria

We included publications in the review if they (a) included data from primates, (b) had gestures as a main focus, (c) make explicit the link between their study and language evolution;

and (d) relied on spontaneous communication. We included both journal articles and book chapters. Whole books (as a single 'unit') were not included because they typically include a range of differently structured studies, so considering them as their individual chapters was more compatible with the data extraction for journal articles. While all publications had to explore at least gestural signals, we also considered those employing a "multi-source" approach (extracting the information on data from other sources, such as vocalizations, for analysis).

We restricted our review of studies on primate gesture to publications that included an explicit reference to the evolution (or origin) of language (or communication). In order to assess the impact of this restriction on the literature returned we ran the same search excluding this requirement.

To be considered 'spontaneous' gestural communication, gestures must have been produced without explicit training. We excluded signed languages because they represent language in its full modern form and, like spoken languages, they are taught to some extent. In contrast, home-sign often develops spontaneously in an environment in which one person does not have easy access to the language modality of others around them. Home-sign studies can provide a unique opportunity to investigate the emergence of a combinatorial linguistic system (Goldin-Meadow & Yang, 2017). While home-sign becomes formalised over time, it can incorporate the use of a range of spontaneous gesticulation, gestures, pantomime, and symbols and we retained these studies in this review. Our primary exclusion criteria for the publications were (a) publications with abstract, or full text not available; (b) publications written in languages other than English; publications not focused on (c) primates, (d) neuro-typical subjects, (e) gestures, (f) spontaneous communication, (g) publications without empirical data (e.g., theoretical); and (h) not about language evolution. We checked publications according to these criteria in the order described above, and excluded a publication as soon as they failed to fulfil any criterion (although in practice there may have been further additional reasons for their exclusion).

2.3.3. Selection of material

Figure 2 shows the selection process of the articles through the FLOW diagram. Each manuscript was independently and randomly assessed by at least two researchers in the two main stages of material selection: abstract screening and full text screening. When two people disagreed or both were unsure about its inclusion, we solicited a third opinion (abstract screening: 127 of 963 publications; full text screening: 78 of 221 publications). We located 697 publications (692 articles and 5 book chapters) in Web of Science and 464 in PsychINFO (362 articles and 102 book chapters). We removed 198 duplicates, leaving 963 publications, including 862 articles and 101 book chapters (for a full list of all 963 publications see https://github.com/Wild-Minds/GestureStudies_SystematicReview); the oldest publication was published in 1975, and the most recent in 2019. Running the same searches but omitting the requirement for evolution/origin of language/communication from the string returned 6440 publications.

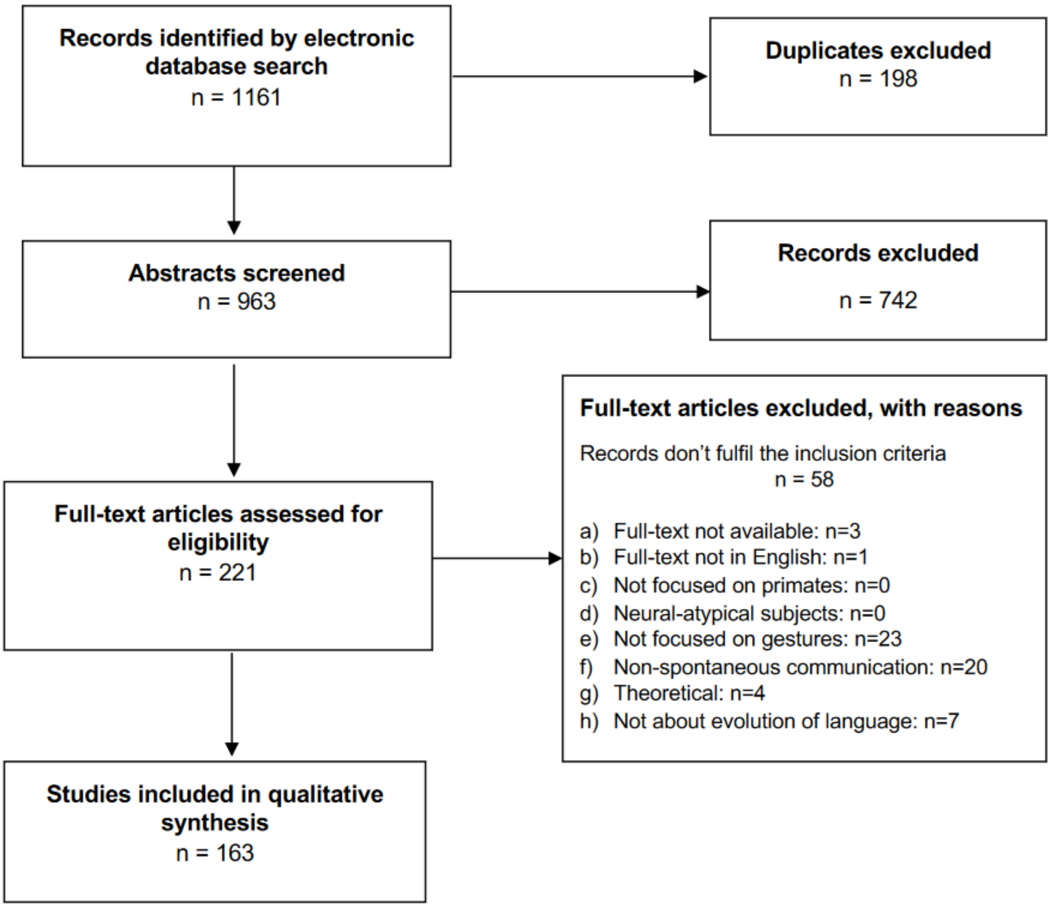


Figure 2. FLOW diagram. Number of studies identified, included and excluded and the reasons for exclusions through the different phases of the Systematic Review.

After abstract screening of the 963 publications, we removed a further 742 publications, leaving 221 publications for full text screening. In the full text screening phase, we excluded a further 58 publications because they did not fit the inclusion criteria (see detailed explanation in Figure 2). We excluded publications not focused on primates or focused on neuro atypical subjects during the abstract screening phase; however, the language evolution criterion was only applied at the full-text screening phase. Our final dataset included 163 publications (156 articles; 7 book chapters; for a full list of records see https://github.com/Wild-Minds/GestureStudies_SystematicReview).

2.3.4. Fields for data extraction

Fields for data extraction and their categories (Table 2) were developed following systematic assessment of a pilot search of the literature by EDR (n=383 studies) and were then discussed to consensus between co-authors before being applied to the data set from the full systematic review. Please note that through the methods and results of the manuscript, capitalized terms refer to these fields and categories of information extracted for analysis.

Table 2. Categories of each field extracted for analysis.

Field	Categories
Species	Humans Nonhuman primates: Great-apes (Chimpanzees, Bonobos, Gorillas, Orang-utans), Small-apes, Afro-Eurasian monkeys, monkeys of the Americas, and Strepsirrhines.
Socio-ecology Socio-economy	Nonhuman primates: Species-Typical (Wild non-anthropogenic); and Species-Atypical (Wild anthropogenic, Captive anthropogenic); Humans: WEIRD, Non-WEIRD industrialised, Small-scale non-industrialised.
Research domains of comparison	Combination of sources, Form, Laterality, Meaning, Neural processes, Ontogeny, and Structure
Gesture definition	Defined, Not defined Mechanical ineffectiveness: Mentioned, Not mentioned
Intentional communication criteria	Attention getting behaviour, Audience checking, Ceasing communication when goal is achieved, Change in recipient behaviour, Directed to recipient, Elaboration, Flexibility, Goal-directed, Initiating social interaction, Mechanically ineffective, Persistence, Response waiting, Sensitivity to the attentional state of the recipient
Body parts	Manual (hands, and upper limbs), Non-manual (head, orofacial, body), Both (manual and non-manual)

Gestural scope	Broad, Narrow
Multi-source	Vocalizations, Facial expressions, Lexigrams, None
Research setting	Familiar (Human: Home, Day-care centre; Nonhuman: Wild, Semi-Wild, Captivity); Unfamiliar (Laboratory); Both
Study Design	Experimental, Observational, Both

We recorded which Species of primate(s) was included in the study. Primate species were grouped into two categories: Human and Nonhuman primate categories, and within Nonhuman primates we further distinguished the following groups: Great-apes (Chimpanzees, Bonobos, Gorillas, Orang-utans), Small-apes, Afro-Eurasian monkeys (also referred to as Old World), Monkeys of the Americas (also referred to as New World), and Strepsirrhines.

We described the proximity of the environment in which data were collected to the socio-ecological environment of evolutionary adaptation (EEA) for Nonhuman primate species. Given the extent of recent rapid anthropogenic change this can be challenging to define for any modern species; however, for Nonhuman primates we provide a cautious description of the environment as either Species-Typical (Wild, non-anthropogenically modified) or Species-Atypical (Man-made, anthropogenically modified). All captive Nonhuman primates were considered to be in Species-Atypical environments, wild primates were only considered to be in Species-Atypical environments where data collection occurred in anthropogenically modified habitats (e.g., in crop-fields, human settlements).

We do not feel that any similar distinction can be made for modern Human populations, both because there is no solid evidence for what our human EEA looks like, and because all humans today – whether urban city or hunter-gatherer communities – live in habitats that are substantially anthropogenically modified from that EEA. However, we provide an indication of local socio-economic structure as being WEIRD (Henrich et al. 2010), Non-WEIRD industrial, or Small-scale non-industrial. Please note that the category of subjects covered by "Rich" is a global one, and likely includes a range of economic groups in Western Industrialised Countries. These socio-economic categories are not directly comparable to the Nonhuman primate ones of Species-Typical or Atypical.

We defined the Research Domain(s) explored, asking which area(s) of gestural communication were included in the study (for example: *form*, *structure*, or *ontogeny*; Table 3 for full list and definitions). We asked whether there was an explicit Definition included for Gesture (see Table 2). For the publications which provide an explicit definition of gesture, we used the conceptual tool proposed by Bourjade et al (2020) to analyse the requirements for a given behaviour to be categorized as a gesture. The authors provided 22 criteria covering 5 main areas: the body parts used to gesture, the sensory modalities mobilized by the gesture, the characteristics of its social expression, and its communicative and intentional properties.

Table 3. Descriptions of the research domains of comparison.

Research domains	Description
Combination of sources	Coexistence of two different signal categories (gesture, vocalization, and/or facial expression). Includes studies focused on the synchronization of the different sources.
Form	Physical form of the gesture(s). Includes studies that describe gestural repertoires.
Laterality	Predominance of one side of the body/brain involved in the execution of the communicative acts.
Meaning	Used in the broad sense without requirement for intentional use. Includes all informational and/or semantic content of gestures. Includes studies on iconicity, reference, and function.
Neural processes	Use of neuroimaging technology to study neural networks and their relation to communicative outputs.
Ontogeny	Development of communication and how it changes during the early stages of life.
Structure	Order and patterning of the communicative elements. Includes syntax.

Of those studies that provide an explicit definition of gesture, some include in this definition a requirement that they must fulfil certain intentionality criteria (captured by the 'communicative and intentional properties' aspect of Bourjade et al.'s framework). However, other studies test for the presence or absence of these behavioural markers, and do not include them within the definition of gesture (if provided). To capture these cases we further extracted whether or not there was a definition of or criteria for Intentional Communication, independently of their inclusion in any gesture definition. We also extracted information on the Body parts involved in gesturing even if they were not explicitly mentioned in the definition.

We did not include Body parts recorded as involved in non-gestural signals in this field, for example orofacial body parts used in facial expressions. We marked a study as Multi-source if it included information on Vocalizations, Facial expressions, and/or Lexigrams (arbitrary visual symbols representing words) used in addition to the Gestures.

In the majority of the animal communication literature, including some primate studies, the term 'multi-modal' has been employed to refer to the combination of information from different sensory channels (e.g. visual, auditory, tactile; Partan and Marler 1999; Partan 2002; Micheletta et al. 2013). However, within nonhuman ape communication this term is sometimes used to refer to the combination of different signal sources (e.g. gesture, vocalization, and/or facial expression; Pollick and de Waal 2007; Waller et al. 2013; Wilke et al. 2017). To avoid confusion, here we follow the wider use and employ the term 'multi-modal' to refer to the combination of sensory channels, and the term 'multi-source' to refer to the combination of signal types.

We took into account the Gestural scope of the study. Here, we defined studies that explored a specific context, or limited set of contexts (for example sexual solicitation and consortship), specific gestures, or limited types of gesture (for example tactile gestures, or specific gesture forms such as pointing) as Narrow. We defined studies that explored a question across contexts and gesture repertoires without further specification as Broad.

We then asked what Research setting data were collected from. We focused on an individual's familiarity with the environment in which the study data were collected. We defined two main categories: Familiar and Unfamiliar settings. These aimed to capture whether or not the communication studied took place in an environment which was similar to that in which the subjects spent their daily lives. In humans, Familiar settings corresponded to studies conducted in their Homes and Day-care centres, and in Nonhuman primates, corresponded to studies conducted in the areas of daily residence, whether in: Wild, Semi-wild, or Captive settings. In both Humans and Nonhuman primates, Unfamiliar settings corresponded to studies conducted in Laboratories (for example, specific research-only rooms). Even when Nonhuman primates visited research-only rooms most days, the setting was classified as Unfamiliar since individuals only spent a small portion of their day in these rooms.

We defined Study design as either Experimental or Observational. In Observational studies, researchers did not manipulate or interact with the subjects and/or their socio-ecological environment (beyond being present). We considered any kind of socio-ecological manipulation across Research Settings as an Experimental design.

2.3.5. Data extraction

'Research domain' was the only field involving a potentially subjective judgement, so in all cases two of the authors extracted this field, and any discrepancies were argued until consensus between the two original raters. A third independent opinion was solicited (38 of 221 publications) when the two original raters could not reach consensus, or when the initial disagreement between raters involved more than one domain.

2.3.6. Data analysis

We compared the number of studies focused on the different research domains and conducted in Human and Nonhuman primates using Chi-square tests. The relative contributions of each cell in the computation of chi-square tests are reported through standardised residuals (Std. res.). For changes in the number of studies conducted in each domain over time (response variable) we used a Generalized Linear Model with a Poisson error distribution and log link function. Test predictors included the interaction between domain and year. As an overall test of the effect of the year in the number of studies conducted in the different domains, we compared the full model's deviance with that of a null model comprising only the intercept, and the control predictor (domains). To test the differences across domains we compared the full model's deviance with that of a reduced model lacking the interactions (between domains and year). All statistical tests were two-tailed and run in R version 4.0.2.

2.4. Results

2.4.1. Primate species

Which primate species are represented in the review? Within the studies of primate gesture that make an explicit connection to understanding the evolution of language we found a similar number included data on Human (N=80) or Nonhuman (N=87) primates, but only a small set (N=4) included empirical data on both Human and Nonhuman primates. Fifteen of the Nonhuman primate studies included more than one species. Of the Nonhuman primate species studied, the majority focused on Great apes (N=75/87, 86%) with a strong bias towards Chimpanzees (N=56/87, 64%; see Figure 3). We found no studies of gesture that made an explicit connection to the evolution of language in Small apes, Monkeys of the Americas, or Strepsirrhines.

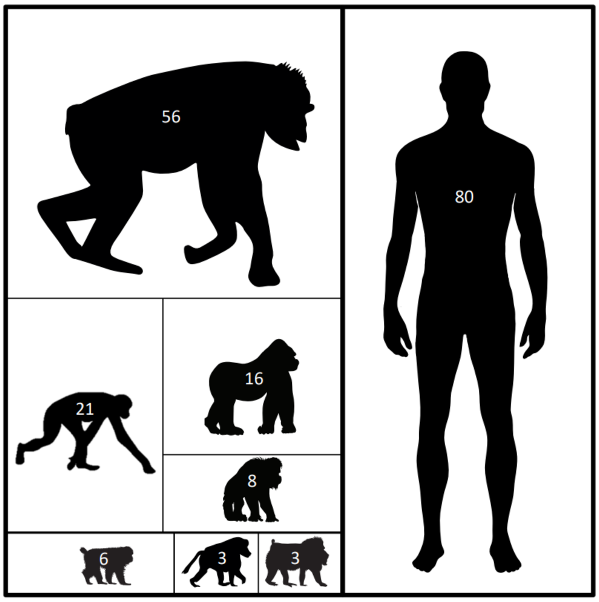


Figure 3. Primate species represented in the review. Area represents the number of studies in the review including that species. Nonhuman primates (on the left) include Great apes (chimpanzees, bonobos, gorillas, and orang-utans), and Afro-Eurasian monkeys (macaques, baboons, and mandrills).

How does Socio-ecological environment vary within Nonhuman primates? Of the 87 studies of Nonhuman primates, 57 (66%) were conducted in Captive anthropogenic Species-Atypical environments, and 30 (35%) were conducted within Wild non-anthropogenic Species-Typical environments. No studies included data from Wild primates in anthropogenic Species-Atypical environments.

How does socio-economic culture vary within Humans? The majority of Human participants were from WEIRD societies (N=68/80, 85%); ten studies included Human participants from Non-WEIRD industrial societies (N=10/80, 13%), and two studies included Human participants living in Small-scale non-industrial societies (N=2/80, 3%).

2.4.2. *Research domains*

Which research domains are studied and how does this change over time? The majority of studies (N=153/163, 94%) included work on several of the seven research domains (total number of research domains recorded N=429; Table 4). The number of studies varied across these domains (Chi-square test: X2= 161.4, df=6, P<0.001). *Meaning* represented the most prolific domain of study (Std. res.=10.722; N=139/163, 85%), followed by *form* (Std. res.=2.582; N=80/163, 49%). Studies focused on *laterality*, *neural processes* and *structure* were less frequent (Std. res.=-3.213, -5.972, -3.765 respectively) and with *neural processes* being the least explored domain (N=18/163, 11%; Table 4).

Table 4. Number of studies in each domain according to the Gesture definition, Intentional criteria, Gestural scope, Source, Research setting, and Study design. N = number publications. Combination of sources (Comb), form (Form), laterality (Lat), meaning (Mean), neural processes (Neur), ontogeny (Ont) and structure (Struct). The sum of the studies specified by domain for each field differs from the total of studies considered in this analysis because a single study could include more than one domain of gestural research.

		N	**Comb**	**Form**	**Lat**	**Mean**	**Neur**	**Ont**	**Struct**
	Total	163	73	80	38	139	18	47	34
Gesture definition	Defined	106	44	63	24	93	7	32	16
	Not defined	57	29	17	14	46	11	15	18
Intentional criteria	Considered	52	17	39	8	47	0	10	10
	Not considered	111	56	41	30	92	18	37	24
Body parts	Manual	88	46	39	26	72	15	29	13
	Non-manual	7	4	2	2	4	2	2	1
	Both	56	21	36	9	52	0	14	12
Gestural scope	Broad	51	17	30	14	46	0	11	11
	Narrow	112	56	50	24	93	18	36	23
Sources	Gesture	76	0	44	22	67	5	15	18
	Multi-source	87	73	36	16	72	13	32	16
Research setting	Familiar	96	37	58	24	87	0	24	17
	Unfamiliar	60	31	19	9	47	11	21	16
	Both	7	5	3	5	5	7	2	1
Study design	Experimental	79	43	24	19	64	18	27	16
	Observational	79	27	54	17	71	0	19	17
	Both	5	3	2	2	4	0	1	1

The oldest study retained was published in 1975 (note that electronic databases used contain a limited number of publications prior to the 1950s and only 9 publications dated pre-2000 were retained following the abstract and full-text screening phases). Research domains were recorded with increasing frequency year-on-year (full-null model comparison: χ^2=257.109, df=7, P<0.001), however the increasing rate didn't significantly vary across domains (full-reduced model comparison: χ^2=7.224, df=6, P=0.301; Table 5).

Table 5. Results of the model (estimates, together with standard errors, confidence intervals, and significant tests). Domains were dummy coded with Combination of Sources being the reference category.

Terms	Estimate	SE	lower CI	upper CI	z-value	*P*
(Intercept)	-209.357	52.542	-324.425	-116.015		[1]
Domains Form	-100.185	80.641	-263.923	57.334		[1]
Domains Laterality	-61.053	77.288	-216.596	91.426		[1]
Domains Meaning	-39.745	69.151	-174.244	100.741		[1]
Domains Neural processes	-5.944	82.719	-176.749	154.343		[1]
Domains Ontogeny	3.194	69.615	-132.627	144.387		[1]
Domains Structure	-239.809	124.467	-514.930	-18.625		[1]
Year	0.104	0.026	0.058	0.161	3.981	<0.001
Domains Form : Year	0.050	0.040	-0.028	0.131	1.246	0.213
Domains Laterality : Year	0.030	0.038	-0.045	0.108	0.793	0.428
Domains Meaning : Year	0.020	0.034	-0.050	0.087	0.583	0.560
Domains Neural processes : Year	0.003	0.041	-0.077	0.088	0.068	0.946
Domains Ontogeny : Year	-0.001	0.035	-0.072	0.066	-0.042	0.966
Domains Structure : Year	0.119	0.062	0.009	0.256	1.926	0.054

[1] not shown because of having a very limited interpretation.

Which research domains are studied in Human and Nonhuman primates? Research effort across research domains was differently distributed in Human and Nonhuman primates (Chi-square test: χ^2=27.204, df=6, P<0.001; Figure 4). *Meaning* was the most frequently recorded domain in both Human (N=70/80, 88%) and Nonhuman primate (N=73/87, 84%) publications and was similarly represented. *Ontogeny* was most strongly biased towards Humans (Std. res.=3.051), and *form* was most strongly biased towards Nonhuman primates when compared to Humans (Std. res.= 3.548, Figure 4).

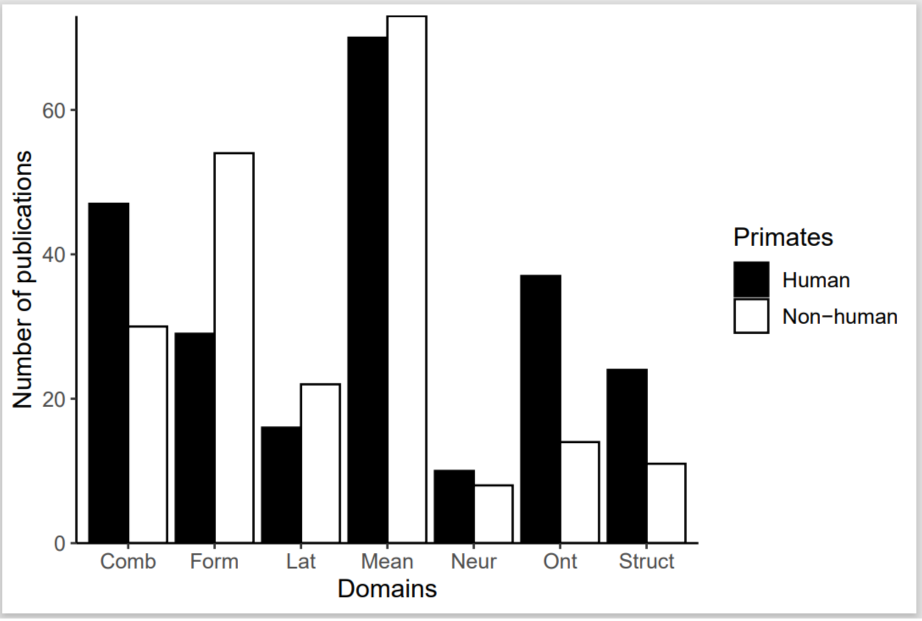


Figure 4. Number of studies in Humans and Nonhuman primates across different research domains. Black bars indicate human subjects, white bars nonhuman subjects. Combination of sources (Comb), Form (Form), Laterality (Lat), Meaning (Mean), Neural processes (Neur), Ontogeny (Ont) and Structure (Struct). Note that some studies included more than one research domain.

2.4.3. Defining gesture and intentional communication

Do studies include an explicit definition for Gesture and how does it vary with species and domain? Although all publications had gesture as their main focus, over a third of the studies (N=57/163, 35%) did not provide a formal definition for their use of Gesture (or any of the specific forms of Gestures used). A definition of Gesture was more likely to be absent in studies of Humans (N=41/80, 51%) than in studies of Nonhuman primates (N=16/87, 18%; Chi-square test: χ^2=18.581, df=1, P<0.001). Only 42 studies explicitly included mechanically ineffectiveness in their definitions of gesture. Studies of Nonhuman primates included reference to mechanical ineffectiveness in their definitions of Gestures (N= 37/87, 43%) more so than studies of Humans (N=5/80, 6%; Chi-square test: χ^2=27.243, df=1, P<0.001).

Of the 106 publications that included a definition of Gesture(s), approximately half (N=52) defined only the specific gesture form considered in their studies (e.g. clap, defined as "One hand is brought forcefully downwards, palm facing down, to strike other hand, palm facing upwards; upper hand is recorded as dominant" in Fletcher, 2006) but provided no specific definition of what makes a Gestural signal. The proportion of studies defining gesture differed across domains (Chi-square test: χ^2=18.054, df=6, P=0.006; Table 4). Studies focused on gesture *form* were the most likely to define Gesture or subtypes of gestures used, and studies focused on *neural processes* were the least likely to include any definition of Gesture (Std. res.=2.852 and -2.376 respectively).

Of the 54 studies that provided an explicit definition of gesture, all gestures necessarily included a visual component in their Sensory Modality. Gestures were also defined as compounds that, in addition to visual information, also included an auditory or tactile component in the majority of studies (N=37/54, 69% and N=40/54, 74% respectively, Table 6). In terms of their Social Expression, gestures were defined as produced in the presence of an audience in 89% of studies (N=48/54); and as addressed to specific recipient(s) in 82% of studies (N=44/54); however, gestures were defined as produced while looking at the recipient in only 6 of the 54 studies (11%; Table 6). For gestures' Communicative Property, the majority of studies (N=51/54, 94%) defined gestures as a subcategory of communicative signals, while only three studies (6%) defined them as encompassing all communicative signals. Gestures were defined as mechanically ineffective in 69% of studies (N=37/54), and gesture was defined as being followed by a change in the recipient's behaviour in most cases (N=34/54, 63%; Table 6).

Table 6. Number of studies using the criteria proposed by Bourjade et al. 2020 for defining 'gesture'.

Category of criteria	Specific criteria for defining Communicative gesture (CG)	Number of studies
Body part	Any body part including face	5
	Any body part excluding face	36
	Exclusively manual	13
	Exclusively facial	0
Sensory modality	CG has necessarily a visual component	53
	CG is visual or visual and auditory	37
	CG is visual or visual and vocal (mobilizing the vocal chords)	0
	CG is visual or visual and tactile	40
Social expression	CG is produced in the presence of an audience	48
	CG is addressed to specific recipient(s)	44
	CG is produced while looking at the recipient	6
Communicative property	CG encompasses all communicative signals	3
	CG is a subcategory of communicative signals	51
	CG is mechanically ineffective	37
	CG is followed by a change in the recipient's behaviour in most cases	34

Intentional property	CG is necessarily an intentional communicative signal	33
	CG is produced towards a visually attentive recipient	2
	CG is followed by response waiting (a pause in the gesturer's actions)	24
	CG is repeated, combined or replaced by other CGs if no response comes	28
	CG is not consistently triggered by specific environmental conditions	0
	CG is expressed in various functional contexts	0
	CG is associated with an Apparently Satisfactory Outcome (ASO)	5

Do studies include a specific definition of and criteria for intentional communication? How does it vary with species and domain? Specific criteria for intentional communication were only provided in 52 of 163 articles (32%; Table 4). Of the 54 studies that provided an explicit definition of gesture, 33 (61%) included a requirement that gestures were necessarily an intentional communicative signal. Response waiting and persistence or elaboration were included in approximately half of the studies with a definition of gesture (N=24/54, 44%; and N=28/54, 52% respectively). A more recent criterion (Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014), gestures were defined in association with an Apparently Satisfactory Outcome in only 9% (N=5/54) of the studies. No studies specified that gestures should not be consistently triggered by specific environmental conditions, and while information on functional context was included in studies, no study required in their definition that gestures be flexible across functions contexts (Table 6).

Across all studies, including those with no explicit definition of gesture, only a very small proportion of publications with Human data provided explicit intentionality criteria (n=5/80, 6%), while more than half of publications with Nonhuman primate data did so (N= 48/87, 55%; Chi-square test: χ^2=43.812 df=1, P<0.001). Of the studies that included intentionality criteria, persistence was the most common criteria provided (N=34/52, 65%; see Table 7). The proportion of studies using intentional criteria differed across domains (Chi-square test: χ^2=26.468, df=6, P<0.001). Research focused on *form* was more likely to contain explicit intentional criteria than research focused on other Domains (Std. res.= 3.921). No study focused on *neural processes* provided intentionality criteria in their research (Std. res =-2.873; Table 4).

Table 7. Different criteria used by the studies to define intentional gestural communication. Authors often used multiple criteria to define intentional communication. One of the studies using multiple intentional criteria was conducted in both Human and Nonhuman primates; as a result, the sum of the studies with humans and nonhumans may exceed the total number of studies that considered each criterion.

Criteria for Intentional Gesture	Human	Nonhuman	Total
Persistence	2	33	34
Response waiting	1	29	30
Directed to recipient	3	24	27
Audience checking	2	23	24
Sensitivity to the attentional state of the recipient	1	23	24
Goal-directed	1	14	15
Elaboration	0	10	10
Change in recipient behaviour	0	7	7
Mechanically ineffective	1	5	6
Ceasing communication when the goal is achieved	0	5	5
Attention getting behaviour	1	3	3
Initiating social interaction	0	3	3
Flexibility	0	2	2

Which Body Parts are taken into account to produce Gestures? How does it vary with species and domain? Across all studies we found a particular focus on Manual gestures: 54% of the publications (N=88/163) considered only Manual gestures, 4% considered only Non-manual gestures (N=7/163), 34% considered both Manual and Non-manual gestures (N=56/163), and 7% (N=12/163) did not specify the body part. However, within those studies with an explicit definition of gesture, 76% included movements of any body part (N=41/54; 5 of these definitions considered any body part including the face, and 36 of these definitions considered any body part but excluded the face; Table 6).

Across the full dataset, studies of Humans included more manual gestures than studies of Nonhuman primates (χ^2=10.774, df=2, P=0.005). Studies differed on the body parts included across all domains (χ^2 =21.432, df=12, P=0.044;Table 4). Studies on *form* were more likely to include both manual and Non-manual gestures, and studies on *neural processes* were more likely to include manual gestures (Std. res.=2.206 and 2.440 respectively).

2.4.4. Scope

Which type of Scope is represented in the studies included in the review? How does the Scope of the studies vary with species and domain? Most studies were focused on specific gesture types or specific contexts and were classed as having a Narrow scope (N=112/163, 69%). Studies with a Broad scope were found less often in Human than in Nonhuman primate research (χ^2=18.914, df=1, P<0.001). Although all the domains were explored more often using a Narrow scope, the extent of this bias varied across domains (χ^2=13.948, df=6, P=0.030) with *form* and *laterality* least biased (Std. res.=-1.606 and -0.954 respectively), as compared to *neural processes* which were exclusive studied with a Narrow scope (Std. res.= 2.842;Table 4).

2.4.5. Sources

Do studies incorporate additional Sources as well as Gesture? How does Source vary with species and domain? Approximately half of the studies (N=87/163) considered additional sources to gesture. Vocalizations were considered in almost all multi-source studies (N=81/87, 93%), whereas Facial expressions and Lexigrams were described in 17% of multi-source studies (N=15/87). Nine articles considered two or more sources in addition to Gesture. Studies conducted in Humans (N= 53/80, 66%), as compared to Nonhuman Primates (N=37/87, 43%), were more likely to include a multi-source approach (χ^2=8.507, df=1, P=0.004). Studies of gesture in Humans including data on Vocalizations (N=51/80; 64%) more often than studies conducted in Nonhuman primates (N=33/87, 38%). The proportion of studies considering multiple sources varied across research domains (χ^2=69.984, df=6, P<0.001), with a multi-source approach always occurring in studies focused on *combination of sources* (Std. res.=7.635), and less frequently on studies focused on *form*, *laterality,* and *meaning* (Std. res.= -3.066, -2.378, and -2.443 respectively).

2.4.6. Research setting

Which Research settings are represented, and how does these vary with species and domain? Most of the studies were conducted in Familiar settings (N=96/163, 59%). The frequency with which different Research settings were used varied across Human and Nonhuman primates (χ^2=61.578, df=2, P<0.001). Studies of Nonhuman primates were conducted more often in Familiar settings (N=71/87, 82%), and studies with Humans were conducted more often in Unfamiliar settings (N=53/80, 68%;Table 8).

Table 8. Number of studies discriminated by Research setting.

Research setting	Human	Nonhuman
Familiar		
Daycare	5	-
Home	19	-
Daycare + Home	1	-
Captivity	-	35
Wild	-	30
Captivity + Wild	-	1
Sanctuaries	-	5
Unfamiliar		
Laboratory	53	7
Both		
Captivity + Laboratory	-	7
Home (H)+ Laboratory (NH)	2	2

Research settings used also varied across Research domains (Chi-square test: χ^2=62.12, df=12, P<0.001). *Form* was studied most often in Familiar settings and *neural processes* were usually studied in Unfamiliar settings (Std. res. = 2.995, and 2.278 respectively, Table 4).

2.4.7. Study design

Which Study designs are represented and how does the Study design vary with species and domain? Both Observational (n=79/163, 49%) and Experimental (n=79/163, 49%) designs were employed equally frequently in these studies; 5 studies incorporated both designs (3%). Studies with Humans applied Experimental designs more often (n= 58/80, 73%), and studies with Nonhuman primates applied Observational designs more often (n=61/87, 70%; Chi-square test: χ^2= 35.846, df=2, P<0.001).

The relative use of Observational and Experimental designs varied significantly across domains (Chi square test: χ^2=37.317, df=12, P<0.001). Studies analysing *form* used

Observational designs most often, whereas studies focused on *neural processes* were always Experimental (Std. res.= 3.914 and 4.406 respectively; Table 4).

2.5. Discussion

Studies of gestural communication that make an explicit connection to the evolutionary origins of language exist in similar numbers for both human and nonhuman primates; however, only four of the 163 studies included in this review incorporated data from both human and nonhuman primates, and only 15 included more than one nonhuman primate species. As a result, our ability to investigate species' similarities and distinctions across primate taxa and infer an evolutionary trajectory for language from this field, is almost entirely dependent on comparison across studies. By conducting a systematic review, we are able to describe to what extent current methods allow us to do so reliably. We find substantial variation in the conceptual and methodological approaches used. While variation allows for a diverse and robust examination of gesture in this context, it presents particular challenges for the effective comparison across studies and species on which the evolutionary approach depends.

There were limitations to the literature returned in our search process, for example, older material (particularly pre-1950) is not systematically indexed in electronic databases. However, perhaps the most important one was in our requirement for an explicit reference to the evolution or origins of language or communication. We were initially surprised that, in employing this restriction, we excluded work we regularly cite as relevant to the evolutionary origins of human language, including our own studies. Removing the requirement for the 'evolutionary' terms from our search returned around 6,500 results; whereas with them, our structured search returned around a thousand items (with just over a sixth of that retained once the systematic selection criteria had been applied). One explanation for the extent of these exclusions is that many of the empirical studies on nonhuman primate gesture (including our own) avoid explicit discussion of their potential connection to the evolution of human language – and in particular do not do so in the title, keywords, or abstract; the fields most commonly indexed across databases. In some cases, not doing so may be because the primary focus of the paper was a description of the species communication – nonhuman primate gesture is of interest in its own right, not just as a means of comparison to human communication. Nevertheless, these studies may usefully inform our understanding of the evolutionary trajectory of linguistic features. For example: some studies that explore the combination of gestures into sequences (e.g., Tempelmann and Liebal 2012; McCarthy et al. 2013), relevant to understanding similarities and differences to human language *structure,* or studies on *neural processes* of homologous brain area activation in human and nonhuman primate signalling (e.g., Hopkins et al. 2007, 2008) were excluded because they did not make an explicit connection to the evolution of language. Similarly, some studies of human gesture discussed its relationship to individual *ontogeny* of language, but did not explicitly consider the relevance of the work to the evolution of language (e.g., Bates et al. 1979; Iverson et al. 1994).

While widening our search to more broadly encompass primate gestural research would successfully retain these studies, it would also add a very large literature that provides limited insight into the evolution of language (for example, work on leaf-clipping as a sexual solicitation in chimpanzees; Nishida 1980; or work on big loud scratch as grooming solicitation; Nakamura et al. 2000) and such a large corpus risks diluting our ability to provide a clear over-view of the field. There may also be a justifiable reluctance to engage in 'just-so story-telling' in research that does not explicitly test evolutionary hypotheses. Spurious statements about the relevance of any nonhuman primate behaviour to human behaviour unhelpfully reinforce human-centric approaches to the study of nonhuman behaviour, which risk us overlooking extraordinary nonhuman species-specific capacities. Whereas carefully considered discussions can be helpful, they require a substantial investment that may distract from the main aim of research that did not set out to explicitly further a comparative approach. Nevertheless, our theoretical papers often use the findings from these same empirical studies of primate gesture as the foundation for the hypotheses we develop on the evolution of human language. While it is certainly the case that studies of nonhuman primate gesture contribute to a much wider range of questions beyond the possible evolutionary origins of human language, it may be worth reflecting on the apparent scope in our field to more explicitly test evolutionary hypotheses in a wider range of our empirical work. For example: by establishing multi-species primate datasets that employ a coherent study methodology, or allow for the extraction of like-with-like features for comparison, we can test hypotheses that address how aspects of gesture are adapted to a particular species socio-ecology (c.f. Prieur et al., 2020).

Developing hypotheses on the evolution of behaviour within primate history requires that we have sufficient rich data across, and within, primate taxa. However, we found that studies of nonhuman primate gestural communication were largely limited to chimpanzees and bonobos. A number of studies in monkeys were excluded because they involved training them to produce a particular gesture (e.g., Meunier et al. 2013; Defolie et al. 2015) leaving only a handful of studies in Afro-Eurasian monkeys, and no studies on monkeys of the Americas, small apes, or Strepsirrhines. While chimpanzees and bonobos represent our closest living relatives, and these studies allow us to ask whether or not a particular feature of language is uniquely human, they provide a more limited scope for exploring the possible evolutionary trajectory of language over a longer period. In addition, implicit hierarchies exist between species in their relevance to human origins that may obscure the deeper roots of some features (Bourjade et al., 2020). We see this illustrated in our data in the very limited number of human studies that explicitly test whether the gestures explored meet criteria for intentional use – there is an assumption that human behaviour always does. Our findings similarly highlight that there is often an implicit assumption of the importance of ape behaviour for understanding human evolution, whereas studies of monkey behaviour are required to more thoroughly establish the grounds for comparison (Bourjade et al., 2020). Data on the spontaneous gestural communication from a more diverse range of species – including direct comparisons between nonhuman primates – are necessary for a deeper and more nuanced understanding of how and when the capacities that underpin language evolved.

Our understanding of gestural signals' contribution to the evolutionary origins of human language may also be compromised by the use of specific human and nonhuman primate populations to represent species-specific characteristics. Every species' system of communication – including primate gesturing – is in some way adapted to a species' specific and distinct socio-ecological niche (Cheney & Seyfarth, 2018). The majority of studies of nonhuman primate gesture in our review were conducted on groups living in man-made anthropogenic environments that do not reflect the socio-ecological environments to which their communication is adapted. Even among studies of wild primates, a focus on a few specific groups or populations (e.g., Pika and Mitani 2006; Hobaiter and Byrne 2011a; Roberts et al. 2012), likely impacts our understanding of species-typical behaviour. Similarly, in human studies there was also a focus on specific groups: as in many fields of study (Henrich, Heine, Nature, et al., 2010), there was a strong bias towards studies of human gesture in WEIRD socio-economic cultures. Our understanding of the links between primate gesture and human language can be strengthened by more direct testing of the impact of species socio-ecology and individual life-history characteristics on gestural expression (e.g. Prieur et al., 2020), although doing so will take substantial large-scale datasets.

Different environments may promote the use of certain gestures that are not expressed in other environments (see Leavens et al. 2005 for the example of pointing). The frequency and quality (context, interaction partner, and group membership) of interactions seem to influence the frequency of gesture use and the size of gestural repertoires, for example: higher interaction rates with non-maternal conspecifics and a larger number of previous interaction partners are both related to more frequent gesturing and the use of more gesture types (Fröhlich et al., 2017, 2018). Thus, it is particularly important to complement the detailed data from captive settings with more diverse data from primates living in their naturally structured social units (Cheney & Seyfarth, 2018; Fröhlich & Hobaiter, 2018). Given the well-established presence of rich cultural variation in behaviour (Boesch et al., 1994; McGrew et al., 1997; Whiten et al., 1999) a richer understanding of the communicative abilities in diverse populations, in a range of environments (Hobaiter & Byrne, 2011, 2014), in other great apes (gorillas, bonobos and orang-utans; Bard 1992; Genty et al. 2009; Schamberg et al. 2016; Knox et al. 2019), and in other primate species (e.g., Japanese macaques, mandrills, pygmy marmosets, capuchin monkeys, bonnet macaques; Itani 1963; Kudo 1987; De La Torre and Snowdon 2002; Wheeler 2010; Gupta and Sinha 2016) is necessary to better understand the evolutionary trajectory of primate gestural communication and its relationship with language.

The steady increase across most domains highlights the increasing interest in, and relevance of gesture to, questions related to language evolution; however, research efforts remain unequally distributed across domains and between species within domains. *Meaning* was the most popular domain and was similarly explored in both Human and Nonhuman primates. Studies of *form* were most biased towards Nonhuman primates and *ontogeny* were most biased towards studied in humans.

Studies of *meaning* in gestural communication are now the most common focus. Gestural research has sometimes employed the signaller's behaviour or the context of the signal use as a proxy for 'meaning' (Bard and Leavens 2014; Tomasello et al., 1994). Reflecting gesture's intentional use, recent studies employ a combination of signaller and recipient behaviour in order to take a cognitive-linguistic perspective and infer the signaller's intended meaning (e.g., Genty et al. 2009; Cartmill and Byrne 2010; Hobaiter and Byrne 2014; Graham et al. 2017). The large number of studies of signal *form* in other primates is likely because this domain includes the description of communicative repertoires, a common focus when exploring the communication of any nonhuman species (e.g., Berg 1983; Conner 1985; Edds-Walton and Edds-Walton 1997). However, the lack of similar systematic descriptive studies of human gesture forms again makes comparison with nonhuman primate research challenging (Kersken et al., 2018; Müller, 2005). Gestural *ontogeny* has been explored in humans for decades in the context of its relevance for language development; however, it is only more recently that researchers started to frame their results within the evolutionary puzzle or explore this domain in nonhuman primates.

Both within and between human and nonhuman primates, studies used different definitions of which movements and body parts constitute a gesture, and different criteria to define their intentional use. Some studies defined gesture broadly to include body postures, while other studies employed more restrictive definitions including specific criteria, or specific body parts. Over half of the studies were restricted to manual gestures, but a considerable number of studies (~40%) were more flexible, including movements from the whole body or other body parts. None of this variation is necessarily problematic; however, a significant cause for concern, given this variation in definition, is that more than a third of the studies in this review didn't provide a definition for their use of gesture at all. These differences in the fundamental basis of what 'a gesture' is may have significant consequences for the study of comparative communication: particularly where different studies across different species are directly compared. It would be unnecessarily limiting to require a single definition of gesture, and, for example, there is no particular problem with considering only manual gestures. However, given the variation across the field, to allow effective comparison across species and populations, it is imperative that studies define their specific usage.

One aspect of gesture *form* we did not directly compare were gestural repertoires. Composed of graded movements (for example from shake to swing or reach to fling), the identification of distinct gesture forms is typically done from the subjective and anthropocentric-centric perspective of the researcher(s) (c.f. Hobaiter & Byrne, 2017b). Even within a research group there may be variation between studies; for example, where more data become available or new species comparisons suggest previously undetected similarities or differences of *form* (c.f. Byrne et al., 2017; Genty et al., 2009; Graham et al., 2017; Hobaiter & Byrne, 2011b; Knox et al., 2019). Descriptions of repertoires take substantial study effort (Byrne et al., 2017; Hobaiter & Byrne, 2011), and are vulnerable to under-sampling (Knox et al., 2019) – making comparison across studies particularly valuable. However, our current ability to do so remains very limited: under a third of the studies we analysed provided any description of their specific gesture form(s). Even where written descriptions are available these can be difficult to interpret. As open-access online data-archiving becomes increasingly accessible, the use of video examples (e.g. www.greatapedictionary.com) highlighting both the archetypical form and variation around it, will make a substantial contribution to our ability to systematically compare like-with-like within gesture *form*, without necessitating the use of universal – and potentially restrictive – agreed repertoires.

The use of a clear framework for comparison allows us to highlight not only the variation in the frequency with which criteria for intentional gesture use are applied, but also differences in the types of criteria used between human and nonhuman primates (Bourjade et al., 2020). Once again, across studies and across human and nonhuman primates, we find substantial variation. Where definitions were available, Persistence was the most popular criterion, with gestures considered intentional when the signaller persists in producing further gestures if a response is not obtained from the recipient. The criteria for defining intentional communication were originally developed in order to explore the development of prelinguistic communication in human infants (Bates et al., 1975, 1979), but their explicit use seems now largely restricted to nonhuman primate studies. Over half of the nonhuman primate studies reviewed provided some criteria for defining intentional gesture. However, while many required gesture cases to meet one or more criteria for intentional use from a set, they typically did not specify which were met (Genty et al., 2009; Hobaiter & Byrne, 2011b; c.f. Leavens et al., 2005). No one criterion is a panacea for the challenge of identifying mental states from observable behaviour. Audience-checking could simply reflect a shift in attention between objects of interest. Response-waiting could reflect a brief rest in activity. Providing more detail on the frequency and distribution of the different criteria within a study would allow for more direct comparison of intentional gesture use across studies and species of nonhuman primates and improve our ability to assess the extent to which particular criteria provide robust, reliable, measures (e.g., Prieur et al., 2018).

In contrast to the relatively widespread use of criteria to define intentional gesture in nonhuman primates, just four studies in humans and one on both human and nonhuman primates, provided any criteria for intentional gesture use. While humans are clearly capable of intentional communication, we are equally capable of producing fixed non-intentional signals (for example an involuntary yelp, smile, or laugh; Provine 1992; Kawakami et al. 2007). Moreover, mechanically ineffectiveness seems to be a criterion often applied in nonhuman primate research to define gesture, but rarely seen in human gestural research. Including all human gesture-like movements, irrespective of the objective evidence for their communicative and intentional use, while limiting nonhuman primate data to only those gestures used with evidence for intentional use, again, impacts our ability to make meaningful comparisons between human and nonhuman gesture. Doing so furthers the double standard too often applied in comparative research, which sees systematic species-differences in testing conditions or criteria mistaken for species-differences in cognition (Bard & Leavens, 2014; Leavens et al., 2019).

The majority of the studies reviewed employed a narrow scope of focus, investigating specific gesture types or specific contexts. However, studies in nonhuman primates were more likely to have a broad scope than studies with humans; for example: they more often included descriptions of gestural repertoires rather than a specific *form* such as pointing. Again, there is no intrinsic benefit to employing a narrow or broad scope, but both are needed across species in order to compare like with like.

Almost half the studies in this review included other signal *sources* with their gesture data; however, the integration of gestures, vocalizations, and facial expressions remains under-studied in nonhumans relative to humans, despite recent calls to investigate it (e.g., Slocombe et al. 2011; Waller et al. 2013). Where signal sources are combined in communication, for example gesture and facial expression, studying one in the absence of the other may limit our interpretation of signal function (Wilke et al., 2017). However, studying different signal types and sources in combination can be methodologically challenging. For example, studies of gesture often focus on visual information, and the signaller and recipient's visual attention; neither of which may be as relevant to the production or receipt of vocal signals (Schel et al., 2013). The development of methodologies that can be applied across sources will allow for more widespread multi-source comparisons (Müller, 2005; Slocombe et al., 2011).

Ape cognitive and social development, including in their communicative repertoires (Boesch, 2007; Leavens et al., 2019), is sensitive to a wide range of social and environmental factors, and interactional experience has been shown to impact the development of gestural use (e.g., Bard et al. 2014; Fröhlich and Hobaiter 2018). We found that nonhuman primates were more often studied in environments that were familiar to them and used observational research designs. In contrast, human research was mainly conducted in unfamiliar environments, such as research laboratories, and used experiment designs. Collecting data within a laboratory setting allows nuanced control of specific variables; however, these methods are typically challenging to replicate in an ethical manner with nonhuman primates. Slocombe et al. (2011) previously highlighted the lack of nonhuman primate gestural work in the wild (although see now for example: Hobaiter and Byrne 2011a,b; Roberts et al. 2012; Graham et al. 2018), but it is similarly noteworthy that very little gestural work on humans is done outside of unfamiliar laboratory settings (c.f. Kersken et al. 2018).

Diversity in definitions and methods allows for robust testing of a particular line of research, with different perspectives and findings contributing to a deeper and more nuanced understanding of the question. As a result, it is critical that we allow researchers' sufficient flexibility in their definition of and exploration of primate gesture. Without this we would only stifle comparison – potentially missing crucial similarities and differences. However, where diversity is present, the absence of definitions and transparent descriptions of methods are a problem – particularly so as our ability to make explicit points about the evolution of a particular aspect of language often depends on comparison across species and studies.

We can summarise our findings in the following 8-point call to action for researchers interested in how gestural communication may inform our understanding of language evolution.

1. There is substantial scope in the wider gestural field to more explicitly test evolutionary hypotheses in our empirical work.
2. Data are needed on spontaneous gestural communication from a more diverse range of species, in particular outside of *Pan* ape species, and including direct comparisons between nonhuman primates.
3. Data are needed from more diverse populations in diverse environments that consider the impact of socio-ecology and socio-economy on the use of gesture.
4. There is particular scope for studies of gesture *forms* in humans, and studies of gesture *ontogeny* in nonhuman primates.
5. Given the variation across the field it is imperative that studies define their specific usage of gesture.
6. Providing more detail on the frequency and distribution of the different criteria for intentional use, in particular in humans, will improve our ability to assess the extent to which particular criteria provide robust, reliable, measures.
7. The development of methodologies that can be applied across sources will allow for more widespread multi-source comparisons.
8. In addition to studies of human gesture outside WEIRD populations, there is also substantial scope for studies of natural human gesture in familiar, non-laboratory, environments.

We hope that this review serves to highlight not only the challenges, but also the areas of particular promise for future research. A detailed understanding of human and nonhuman primate gesture will take more than one researcher's or research group's lifetime of study. Diversity in our study subjects and approach will provide a more nuanced understanding, but transparency and replicability in our methods are equally crucial to our ability to draw meaningful conclusions about gestural communication's role in the evolution of human language.

CHAPTER 3: Exploring greetings and leave-takings: communication during arrivals and departures by chimpanzees of the Bossou community, Guinea

This chapter is based on Rodrigues, E. D., Santos, A. J., Hayashi, M., Matsuzawa, T., & Hobaiter, C. (2022). Exploring greetings and leave-takings: communication during arrivals and departures by chimpanzees of the Bossou community, Guinea. *Primates*, *63*(5), 443-461. Results were also presented at the VIth Protolang Series Conference, Lisbon, Portugal (2019) and at the VIIth Iberian Primatological Conference, Lisbon, Portugal (2019).

3.1. Abstract

In humans' fission-fusion societies, ritualized non-linguistic signal exchanges that include gestures, vocalizations, and facial expressions are regularly observed at both arrivals (greetings) and departures (leave-takings). These communicative events play an important role in the formation and maintenance of social relationships. Wild chimpanzees also form large communities that split into smaller fluid parties during daily activities, with individuals moving freely between them. However, in chimpanzees only greetings have been reported. This study explores signal exchanges in the Bossou chimpanzee community during fissions (departures) and fusions (arrivals) given an individual's social rank, kinship, position as traveller or party member, the level of potential threat, and the party size and presence of mature males. We analysed three time periods (1993-1994; 2003-2004; 2013-2014) during which the composition and social hierarchy of the community varied. We show that the occurrence and form of communication during fission and fusion events are mediated by social factors, including rank, kinship, and party size and composition. Individuals were more likely to communicate during fusions than during fissions, communication was more likely to be produced towards a higher ranking individual and to non-kin individuals, but the tendency to communicate in general increased with an increase in social rank. The presence of more individuals, and in particular mature males, decreased the likelihood of communication. Communication during fusions supported patterns reported in previous studies on greetings; and our results support the argument that, if present, leave-takings are not a common feature of chimpanzee social interactions. Current methodological difficulties regarding the function of declarative signals hinder our ability to discriminate potential parting rituals within communication before departures. Given similar methodological difficulties, we also provide a note of caution in the interpretation of all signals produced during fusions as 'greetings'.

Keywords: *Pan troglodytes,* communication, greetings, leave-takings, fission-fusion

3.2. Introduction

In species with fission-fusion social systems, over the course of a typical day an individual will leave and re-join others multiple times. The individuals they fission from or fuse together with vary, but across these interactions there remains a coherent community or social group. These social dynamics sound familiar because humans are a fission-fusion species. We often disperse from our living partners in the morning and re-join them later. In the meantime, we meet other people from within and outside of our different social groups. These comings and goings are often accompanied by ritualised communications – greetings and leave-takings – that play an important role in validating access to and managing continuity in social relationships (Goffman, 1967). These rituals vary in form according to particular features of the people we meet and our relationship with them, such as: their familiarity, age, gender, social status, etc. as well with some contextual features such as the individual's role: indicating who is traveling and who remains, the length of time elapsed since the previous encounter, the distance between interactants, and the number of individuals present (Ferguson, 1976; Morita, 2011; Youssouf et al., 1976). Despite rich cultural variation in the form of these rituals across humans as a species, they often share common elements, especially in the form of non-linguistic signals. The use of greetings and leave-takings in the appropriate context seems to be a human universal, likely evolutionary ancient in humankind (Firth, 1972).

Could greeting and leave-taking behaviour be evolutionary older and precede the emergence of the linguistic communication that characterizes our human lineage? Or be a widespread feature of highly-social fission-fusion animal species? To investigate these questions, we must look outside of the human species and explore patterns of similarity and distinction in the communication that occurs during fission and fusion events in other species, in particular primates. Many social species produce signals when approaching other individuals from within their social group (Smith et al., 2011; Sogabe & Yanagisawa, 2007; Whitehead & Rendell, 2014). In primates, signals produced when approaching or being approached by others in the same party (e.g., Smuts and Watanabe 1990; Fedurek et al. 2019) or when joining a party have been widely reported in various modalities (e.g., Aureli and Schaffner 2007; Scheumann et al. 2017). For example, some species use tactile signals such as "embraces" to reduce tension (spider monkeys: Aureli and Schaffner 2007), and vocal "greeting calls" are produced by many primate species when meeting . Primates also combine signals of different modalities during encounters (Alfaro, 2008; Luef & Pika, 2019). For example, baboons use multi-modal combinations that include visual signals (such as facial expressions, e.g., ear-flattening, and gestures, e.g., crouching), audible signals (e.g., grunt vocalizations), and tactile signals that include contact with vulnerable body parts (e.g., genital touching; Smuts and Watanabe 1990; Whitham and Maestripieri 2003).

A number of studies have explored 'greetings' in one of our closest living relatives: chimpanzees (Fedurek et al., 2021; Laporte & Zuberbühler, 2010; Luef & Pika, 2017). Chimpanzees (*Pan troglodytes*) are highly social, living in large stable communities within which smaller parties and individuals interact with highly-fluid fission-fusion dynamics (Goodall, 1986; Nishida, 1968). They live in philopatric societies with a relatively strong hierarchy in which mature males typically outrank mature females (Goodall, 1986; Newton-Fisher, 2004). Chimpanzees form long-term alliances with both kin and non-kin group members, and these relationships have an important impact on individual fitness (Gilby et al., 2013; Pusey et al., 1997; Wroblewski et al., 2009). In these highly dynamic societies, individuals may not see others from within their social group for days, or even months. During time apart, interactions with and between others may have impacted relative rank or the strength of a social bond (Laporte & Zuberbühler, 2010). Greetings offer the opportunity to clearly signal dyadic rank-relationships or social bonds after a separation, both within the dyad and to others in the vicinity (Luef & Pika, 2019), and without the need for more costly strategies such as physical aggression (Fedurek et al., 2021; McGrew & Baehren, 2016).

During chimpanzee fusion events, the most frequently observed and widely studied communicative behaviour is the *pant-grunt* vocalization, which varies along a gradient that includes *pants* up to *pant-barks,* and, occasionally, is combined into *pant-hoots* (Goodall 1986; Crockford and Boesch 2005; Laporte and Zuberbühler 2010; Fedurek et al. 2021). Pant-grunts are typically associated with showing subordination by a lower-ranking individual towards a higher-ranking individual (Bygott, 1979; Laporte & Zuberbühler, 2010). Between males their use is largely dictated by the dyadic relationship of the two individuals approaching each other (Fedurek et al., 2019); and changes in the direction of their use between mature males are used as a behavioural indication of changes in social relationship or rank (Neumann et al., 2011; Newton-Fisher, 2004). However, particularly outside of male-male interactions, pant-grunts can be used more flexibly, and their production also depends on the size and composition of the audience (Laporte & Zuberbühler, 2010). Reciprocal exchange of greetings within a dyad may include pants and pant-grunts, as well as other signals and behaviour, depending on the nature and strength of the social relationship or the presence of others near-by (Luef & Pika, 2017, 2019).

Pant-grunts (like many signals) have typically been studied in isolation; however, chimpanzees, like humans and many other species (Acquistapace et al., 2011; Genty, 2019; Grafe et al., 2012), exchange a wide variety of vocal, gestural, and other signals in their greetings. The use of gestures by chimpanzees when greeting is less well studied, but includes: *bobbing*, *crouching*, and *presenting* (De Waal, 2007), or *nibble cheek*, *nibble ear*, and *embrace*, among others (see Luef and Pika 2017). Greetings incorporating gestures are more likely to elicit responses than vocal-only greetings (Luef & Pika, 2017), but the impact of individual and socio-ecological features on the use of gestures and signal combinations during greetings remains unclear.

While the occurrence and importance of greetings across primate species is well established, there is no similar body of work on leave-taking outside of humans (McGrew & Baehren, 2016). Even in the very well-studied chimpanzee, there are only anecdotal descriptions (De Waal, 2016). A recent survey of researchers across 10 chimpanzee field-sites on the occurrence of any leave-taking behaviour preceding a fission concluded it was likely absent (McGrew and Baehren 2016; but cf Heesen et al. 2021). Given the ease with which greetings are detected in social species, the apparent absence of leave-taking outside of humans appears to represent a striking divergence. If leave-taking is absent outside of humans, it suggests that there was selection for this type of signalling in humans. A number of potential functions for leave-taking in humans have been suggested (for example: signalling inaccessibility, supportiveness, or summarising recent interaction; Knapp et al. 1973). Alternatively, the ability to take-leave may depend on other cognitive capacities, such as the ability to imagine (Saito et al., 2014) or plan for future interactions and events (Suddendorf and Corballis 2010), which may be specific to humans (but cf Janmaat et al. 2014). Nevertheless, without systematic exploration, their presence, or absence, in other primate species remains unclear.

A particular problem in studying both potential leave-taking and greeting in nonhuman species is in differentiating these from other communications produced in proximity to a fission or fusion event, for example: a failed solicitation to travel together prior to departure, or a request to groom on arrival. A recent study of chimpanzee and bonobo interactions described the use of signals in an ‘exit phase’, arguing that here both partners are signalling the mutual intention to stop the interaction, and compare this to taking leave (Heesen et al., 2021). The use of imperative requests to ‘Stop behaviour’ have been previously described in great ape gesturing (e.g. Genty et al. 2009; Hobaiter and Byrne 2014); but requests to terminate a specific behaviour followed by one individual leaving are not necessarily leave-taking, in the same way that requests to initiate a behaviour on arrival are not necessarily greeting. While context has been used as a proxy for meaning in many studies of nonhuman communication (Call & Tomasello, 2007; Pollick & de Waal, 2007), context and meaning do not necessarily map. A negation gesture that means ‘Stop that’ can be used across many behavioural contexts, but its meaning is highly specific (Hobaiter & Byrne, 2014). The pant-grunt vocalizations that are frequently a focus in studies of chimpanzee ‘greeting’ are also used to signal submission towards higher-ranking individuals even where the signaller and recipient have been in the same party for an extended period (Fedurek et al., 2019; Laporte & Zuberbühler, 2010), but potential greetings include the exchange of a wide-range of signals outside of those associated with dominance and submission (e.g. Luef and Pika 2017). One approach to differentiating signals that function as greetings or leave-taking from within the signals that are produced in the context of arrival or departure is to compare communication in these cases to that produced across other contexts. A large body of evidence for signals that appear specific to meeting or leaving other individuals would provide a stronger case for the presence of greetings or leave-taking within these contexts.

In this study we explore the apparent behavioural asymmetry related to potential greeting and leave-taking behaviour in chimpanzees. We take a systematic multimodal approach and describe the frequency and form of signals produced when fissioning from or fusing with other individuals, given the number of opportunities to do so. We then investigate how individual, dyadic, and group-level features shape communication during these events.

At the individual level we examined how social rank, level of threat, and relative position (as traveller or party member) influence the likelihood of communication occurring at a fission or fusion event. Emotional arousal has been argued to represent an underlying cause for the production of ‘greeting’ calls (Fedurek et al., 2021; Goodall, 1986; Luef & Pika, 2019), and we predicted communication would be more likely to occur when the level of potential threat of physical aggression is high. Previous studies on *pant-grunts* suggest that low ranking individuals are more likely to greet than higher ranking individuals, possibly to reduce the likelihood of receiving aggression when approaching others (Fedurek et al., 2019; Laporte & Zuberbühler, 2010). As well as producing a higher number of calls, low-ranking individuals produce more complex calls in the presence of high-ranking individuals, possibly related to high levels of excitement and to the increasing chances of receiving aggression when a call is not produced . As a result, low-ranking individuals may be more likely to communicate and may do so more often in events with a higher level of potential physical risk (threat). We further investigated the impact of the individual’s relative position to the party (as traveller or party-member) on the probability of communication. In addition to signalling the nature of the relationship, greeting and leave-taking rituals may function to inform partners and the wider audience about an individual’s decision to travel. Once the decision to travel is made, both the traveller and the party-member may communicate; however, the party-member may only become aware of the traveller’s decision to travel after some behavioural indication of traveling, and for that reason, we predicted that travellers may be more likely to communicate.

At the dyadic level we looked at whether communication during a fission or fusion event was mediated by kinship. Kinship appears to influence cooperation and affiliation rates among wild chimpanzees (Fedurek et al., 2021; Gilby & Wrangham, 2008; Langergraber et al., 2009; Luef & Pika, 2019). However, to our knowledge, the impact of kinship on communication during fission-fusion events has not been directly explored. Previous research shows that greetings are less likely to occur and are less elaborate between closely affiliated dyads (Luef & Pika, 2019). Building on these findings, we predicted that kin-related individuals would be less likely to communicate. We further investigated if communication varied with the relative difference in social rank of the two individuals. *Pant-grunts* and vocal combinations are most often given by low-ranking individuals towards high-ranking individuals (Fedurek et al., 2019; Luef & Pika, 2019). As greeting calls are often associated with visual signals linked to submission (Fedurek et al., 2021), we predicted that communication would be more likely to occur from lower-ranking individuals towards higher-ranking individuals.

At the group level, we examined the influence of the composition of the audience on the probability of communication occurring. Specifically, we investigated whether communication depended whether mature males were present, and on the total party size. The presence of the alpha male and an increasing number of bystanders, in particular mature males, appears to have an inhibitory effect on the probability of females producing *pant-grunts* (Laporte & Zuberbühler, 2010). As a result, we predicted that communication would be less likely to occur in the presence of mature males and in larger parties.

Finally, we describe the types of signals produced, and explored the impact of social relationship on the channel of communication used (gestural, vocal, facial, multi-channel).

To summarize, the goal of our study was to understand how social features influence the probability of communication occurring and the types of signals used during fission or fusion events. For this purpose, we studied the opportunities to communicate during fissions and fusions and analysed the influence of social factors at different levels (individual, dyadic and group level).

3.3. Material and Methods

3.3.1. Study site and subjects

The dataset contains data from 22 wild chimpanzees (12 females and 10 males) during three field seasons (1993-1994, 2003-2004, and 2013-2014) at the long-term field site of Bossou, Guinea (7°39′N, 8°30′W). The Bossou chimpanzee community (*P.t. verus*) is quite unusual as chimpanzees are both habituated to humans and coexist both closely and largely peacefully alongside local human communities (Matsuzawa et al., 2011; Sugiyama & Koman, 1979). We evaluated the scope for sampling bias in our study using the STRANGE framework (Rutz & Webster, 2021; Webster & Rutz, 2020). The community size ranged from 9-18 individuals, which is relatively small. Chimpanzee communities are more typically around 30-70 individuals (ranging from 7-144 with a median 42 in a recent comparison across 18 groups in three subspecies: *P.t.schweinfurthii*, *P.t.troglodytes, P.t.verus*; Wilson et al., 2014; although note that within these data the West African sub-species (*P.t.verus*) range is 7-43 with a median 34). Aspects of chimpanzee behaviour at any one time may be impacted by individual differences (for example, the identity of the alpha-male, the presence of particular kin and non-kin relationships, the group demography). The impact of individual differences may be particularly strong in Bossou, where, for example, there were only ever a maximum of three adult males. As a result, it may be challenging to disentangle the effects of age-class and rank. Similarly, the effects of kinship and social-bonding may be difficult to discriminate in Bossou, as there are very limited numbers of dyadic relationships, and smaller communities of chimpanzees and communities of the West African subspecies appear to be generally more cohesive (Lehmann & Boesch, 2004). We addressed these biases in part by including data from three different periods (at 10-year intervals), allowing us to increase the number of individuals present in the data and the diversity of other socio-demographic factors.

In the first period (1993-1994), the community consisted of 18 individuals: 8 adults (males: 16+ years, females: 15+ years), 1 subadult (males: 10 to 15 years, females: 10 to 14 years), 3 juveniles (5 to 9 years), and 6 infants (0 to 4 years). In subsequent years, the overall community size decreased (n=15 in 2003-2004, and n=9 in 2013-2014) as individuals disappeared (including probable emigrations) or died, and no immigration occurred (see Table 9). Our data were highly representative of the Bossou community over the 20-year time period, including 22 of the 25 individuals present Table 9.

Table 9. Characteristics of the study subjects, including ID, sex, age and rank during the three periods analysed in the current study. * subject was present in the community but did not contribute data (no observations available or age < 1 year).

ID	**Sex**	**1993-1994**		**2003-2004**		**2013-2014**	
		Age	**Rank**	**Age**	**Rank**	**Age**	**Rank**
Tua	M	43	Alpha	53	Gama	-	-
Kai	F	43	Alpha female	-	-	-	-
Nina	F	39	High-ranking F	-	-	-	-
Na	M	8	Immature – 1	-	-	-	-
Nto	F	0	Immature – 2*	-	-	-	-
Fana	F	37	High-ranking F	47	High-ranking F	57	High-ranking F
Foaf	M	13	Beta	23	Beta	33	Beta
Fotaiu	F	2	Immature – 2	12	Low-ranking F	-	-
Fanle	F	-	-	6	Immature – 1	16	Low-ranking F
Fokaiye	M	-	-	2	Immature – 2	-	-
Flanle	M	-	-	-	-	6	Immature – 1
Fanwa	M	-	-	-	-	2	Immature – 2
Jire	F	35	High-ranking F	45	High-ranking F	55	Alpha female
Juru	F	0	Immature – 2*	-	-	-	-
Jeje	M	-	-	6	Immature – 1	16	Alpha
Velu	F	34	High-ranking F	44	High-ranking F	54	High-ranking F
Vui	M	7	Immature – 1	-	-	-	-
Vuavua	F	2	Immature – 2	12	Low-ranking F	-	-
Veve	F	-	-	2	Immature – 2	-	-
Yo	F	32	High-ranking F	42	Alpha female	52	High-ranking F
Yolo	M	2	Immature –2	12	Alpha	-	-
Pama	F	26	High-ranking F	36	High-ranking F	46	-
Pili	F	6	Immature – 1	-	-	-	-
Poni	M	0	Immature – 2*	-	-	-	-
Peley	M	-	-	5	Immature – 1	15	-

Video data in the Bossou Archive were collected at two natural outdoor ‘laboratories’ that were originally established in the Bossou chimpanzee home-range to study their tool use: ‘Bureau’ located on the top of Mont Gban in the first two periods: 1993-1994 and 2003-2004; and ‘Salon’ located in the middle of Mont Ghein in the last period of data collection: 2013-2014 (Figure 5; Matsuzawa 1994, 2011; Biro et al. 2003). By crossing the roads between the two forests (Hockings et al., 2007), both sites were regularly used by the chimpanzees for cracking palm-nuts with stone tools. During the dry season the quantity of palm-nuts and water available in the outdoor laboratories were controlled by the research team (Hayashi & Inoue-Nakamura, 2011; Inoue-Nakamura & Matsuzawa, 1997; Sousa et al., 2009), so all data collection occurred during periods in which food resources were consistently available. The presence of a specific food resource, even where reliably available, may lead to increased arousal (Kalan et al., 2015; Muller & Wrangham, 2004), which in turn may impact the way in which communication is expressed. However, high-pitched food-calls were rarely observed upon arrival to the outdoor laboratories, in contrasts to the chimpanzees' arrival at a high-value food resource, such as a large fruiting tree (Hayashi, personal communication). Moreover, nuts, which requires additional cracking skill, appear less preferred when fruit is available nearby. Consumption of nuts increases in dry season, which has lower fruit availability (Yamakoshi, 1998), but some fruits remain available year round, and chimpanzees also crop-raid in the village for high calorie cultivars when other food resources are limited (Hockings et al., 2009). Competition between individuals may also be mitigated by individual preferences for particular tools (Carvalho et al., 2009), as well as the reliable availability of nuts (Inoue-Nakamura & Matsuzawa, 1997). The Bossou chimpanzees spend extended periods of time at these locations, typically visiting once or more per day, and spending over a total of 20-30 hours each year (within the natural nut season, which lasts ~1-3 months; Biro et al. 2006; Sousa et al. 2009). As a result, in addition to tool using, the videos in the Bossou Archive contain abundant data on the community's social interactions (e.g. Schofield et al. 2019). The area is flat and clear, so filming conditions are ideal, allowing continuous recording of all individuals arriving and leaving the party, their interactions, and the communicative signals produced.

Figure 5. A group of chimpanzees feeding in the outdoor laboratory, 'Salon' (photograph by Catherine Hobaiter)

3.3.2. Data coding

Data were coded into a bespoke Filemaker Pro database, which was set up so that each opportunity to communicate corresponded to a record (for full details on the variables coded see **Appendix A 1**). We coded data on interactions that occurred immediately before a fission event (the last interaction before someone left the party) or after a fusion event (the first interaction after someone joined the party) between any two individuals. Where two individuals left the party (fission events) with less than 5min between their individual departures and traveling in the same direction, we considered them to be potentially travelling together (joint-travel) and distinguished these from other fusion events. Similarly, where two individuals joined the party by arriving from the same direction with less than 5min between their fusion events, we considered them to be in a potential joint-travel.

All interactions that occurred immediately before a fission event were considered potential leave-takings, and those that occurred immediately after a fusion event were considered potential greetings. A signal's meaning or function (for example: as a greeting) does not necessarily map onto the context in which it is used (for example: on arrival). It is possible to produce communication in both arrival and departure contexts that are not greetings or leave-takings, for example: a failed request to 'travel together' immediately before fissioning would be difficult to distinguish from a leave-taking communication, and a request to 'groom me' immediately after arrival is not necessarily a greeting. As a result, we label the communication produced in these two contexts as *potential* greetings, and *potential* leave-takings. We compare the most common signals produced during each of these events to those produced in other contexts (for example: traveling, grooming, affiliation etc.) to determine whether we could identify signals specific to a fission or fusion context.

In addition to recording the communications that occurred, we assessed the opportunities to communicate for each fission and fusion. For example: in a fusion event where a single individual arrives to join a group (traveller) of three others (party-members) there are three potential opportunities for that individual to produce a potential greeting communication. We investigated each dyadic interaction from the perspective of the traveller as the focal, and from the perspective of the party-member as the focal. Within 393 video clips (28 days of observations across the 3 different periods) we recorded 253 fission and 215 fusion events (Table 10).

Table 10 - Data available for analysis in each period of data collection : number of Clips, number of Days, Duration of video footage (in minutes), number of Fission events, number of Fusion events, and number of Opportunities to communicate during Fission and Fusion events.

Period	# Clips	# Days	**Duration** (min)	Fissions	Fusions	Opp. in Fissions	Opp. in Fusions
1993-1994	34	6	359	47	36	344	270
6am-10am	9	3	118	18	12	122	76
10am-2pm	22	5	153	19	15	116	118
2pm-6pm	5	3	88	10	9	106	76
2003-2004	147	11	1471	137	115	1064	934
6am-10am	59	8	551	68	61	432	486
10am-2pm	29	6	363	51	31	318	300
2pm-6pm	60	7	531	18	23	314	148
2013-2014	210	11	722	69	64	354	334
6am-10am	82	6	203	14	7	66	32
10am-2pm	57	5	219	36	33	114	190
2pm-6pm	72	6	300	19	24	172	112

3.3.3. Individual, Dyadic, and Group features

For each individual, we recorded their individual identity, relative position (traveller or party-member), the level of potential threat experienced, and social rank. Following Laporte and Zuberbühler (2010), we used the behavioural context prior to the interaction as a proxy for the level of potential threat interactions in that behavioural context typically represent, and grouped these into three categories. Low threat-level contexts: affiliation, grooming, social play; Neutral threat-level contexts: no visible social interaction such as feeding, resting, travelling, solitary play, moving in the trees, moving up/ down trees; and High threat-level contexts: agonism, display, displace or sexual contexts. Social ranks are typically classified using pant-grunt vocalizations (e.g., Newton-Fisher 2004; Fedurek et al. 2021); however, doing so here, where we explore the impact of social rank on the use of signals that include pant-grunts, would be circular. Instead, rank was classified by an experienced observer of these chimpanzees for each period, based on a suite of behaviour that included displacements and agonistic interactions as well as rank. While the assessment of rank in this way can be challenging in a typical-sized community, there were never more than three adult male chimpanzees, and adult female social rank is typically stable across the lifetime (Foerster et al. 2016). Male chimpanzees were classified as having a social rank of: Alpha, Beta, or Gamma on the basis of age and social interactions (such as *pant-grunts*). All mature male chimpanzees were considered to rank above all mature female chimpanzees. Mature female chimpanzees were categorised as having a social rank of: Alpha female, High-ranking (all other adult females), or Low-ranking (all subadult females). The distinction between Alpha female and High-ranking female was made on the basis of behavioural interactions, for example displacement at preferred feeding and nut cracking sites. All mature females were considered to rank above all immature individuals. We included all juveniles (male and female) in the social-rank category Immature-juvenile, and all infants (male and female) in the social-rank category Immature-infant. Individual rank was assigned per period, and the ranks were then scaled between 0-1 with Immature-infant individuals at the bottom of the scale (0) and Alpha male at the top of the scale (1).

For each dyad we considered kinship and rank relationships. Within kinship, only maternal bonds were considered so mother-infant, maternal-grandmother-infant, and maternal-sibling relationships were labelled as Kin, and all others as non-Kin. Data on the independence status of immature individuals were not available, thus mother-infant relationships include all mother-offspring pairs. Using the social rank categories described above, we then classed the focal individual as having one of: lower, same, or higher rank as their partner in the dyad. Finally, we recorded the group-size (number of individuals in the party) and the presence of males in the party (present, absent).

3.3.4. Signals

For each opportunity to communicate, we recorded whether any communicative signal was produced by the focal (yes, no). Where signals were produced, we distinguished gestures, vocalizations, facial expressions, and combinations of two or more of these channels (multi-channel). Gestures were defined (following Hobaiter and Byrne 2011) as a "discrete, mechanically ineffective physical movements of the body observed during periods of intentional communication" by the focal. These movements included movements of the whole body, limbs, and head, but not facial expressions or static body postures. In order to be considered a gesture, one of the following criteria for intentionality had to be observed in conjunction with the gesture: audience checking (the signaller shows signs of being visually aware of the potential recipients and their state of attention), response waiting (the signaller pauses at the end of the communication and maintains some visual contact) or, persistence or elaboration (the production of further gestures, after response waiting and in the absence of a response that in other cases is taken as satisfactory). Gestures were based on the classification used in Hobaiter and Byrne (2017) and contained a total of 93 types (see Appendix A 2 for a full repertoire). The chimpanzee gestural repertoire includes gestures with only visual information (for example an arm-raise) and which are limited by lines of sight between the signaller and recipient; gestures that include tactile information, for which the signaller must be within reach of the recipient; and gestures that include auditory information – including signals that can be detected by out-of-sight individuals over medium distances (e.g. up to 100m; Hobaiter and Byrne 2012) and in the case of drumming at over a kilometre (Arcadi et al., 1998). Vocalizations were single (single element or a series of elements of the same call type) or combined calls (series of elements of different call types) emitted by the focal. Vocalizations all include both visual and acoustic information, and the chimpanzee repertoire varies from extremely soft calls such as pants and hoots (Crockford et al., 2018), to, again, those that can travel over a kilometer (Arcadi et al., 1998). Facial Expressions were recorded when focal produced a visual-silent signal facial display, and transmission of these are limited by lines of sight between the signaller and recipient. As movements of the face often occur along with vocalizations, in order to be considered as a facial expression they needed to be independent of any recent vocalization (at least 2 seconds separation). We included 12 vocalizations (adapted from Crockford and Boesch 2005) and 9 facial expressions (adapted from Parr et al. 2005) in the communicative repertoire (see Appendix A 2 for repertoires). There is substantial grading across the categories in any vocal repertoire, so we followed previous literature in employing a broad definition of pant-grunts as pants with a voiced element, which includes acoustic variants that range from noisy pants to pant-barks.

3.3.5. Data reliability

Gestures, unlike vocal signals, show overlap in their physical form with non-communicative actions and non-intentional cues, and are discriminated by accompanying indications of their intentional use. In particular, we followed previous work in distinguishing the frequently used gesture type – Big Loud Scratch – from non-communicative scratches (scratching for hygiene or as a result of arousal; Goodall, 1968; Plooij, 1978; Pika and Mitani, 2009; Hobaiter and Byrne, 2011). We excluded all scratches that were small and/or rapid in movement (as being potentially associated with stress or displacement activity), or followed by any self-directed hygiene behaviour. We only considered scratches produced in an exaggerated manner (here a long, slow movement, with a clearly audible component) and that were accompanied by additional behavioural indications of intentional use: audience checking, response waiting, and/or persistence. We carefully checked all Big Loud Scratch candidate gestures for indications of intentional use and applied a very strict assessment for audience checking that excluded cases where visual checking by the signaller was potentially peripheral (in doing so we excluded an additional n = 12 potential Big Loud Scratch gestures).

We conducted inter-observer reliability between the primary coder (EDR) and another experienced coder (CH) on 5% of the dataset (142 opportunities to communicate within 23 events). Inter-observer reliability was conducted on the three core variables 1) whether a communication had occurred, 2) where there was communication which channel it was in, gestural, vocal, facial or combination, and 3) the signal types recorded in a communication. A good level of agreement was achieved on all three variables (Cohen’s Kappa: communication K= 0.78, channel K=0.75, signal type K=0.71.

3.3.6. Statistical analysis

All models were implemented with R v4.0.2 (R Development Core Team & R Core Team, 2020) using the packages ‘brms’ and ‘rstan’ (Bürkner, 2017; Stan Development Team, 2020). The package ‘brms’ allows users to fit Bayesian generalized multivariate multilevel models using Stan. The package ‘rstan’ provides R functions to parse, compile test, estimate, and analyse Stan models. In all our analyses, one data point represented an opportunity for an individual to communicate within a dyad made up of the traveller (the individual fissioning from or fusing with the party) and the party-member. Each dyad was considered twice, once from the perspective of the traveller (and their opportunity to communicate) and once from the perspective of the party-member (and their opportunity to communicate). Before fitting models, we rescaled each numeric input to have mean of 0 and standard deviation of 1 to have comparable estimated coefficients (Schielzeth, 2010). Multicollinearity between variables was assessed by Variance Inflation Factors (Field et al., 2012) using the R package 'car' (Fox & Weisberg, 2019). We used weakly informative Cauchy-distributed priors on all logistic regression coefficients, each centred at 0 and with scale parameter 10 for the intercept and 2.5 for all other coefficients (Gelman et al., 2008). Posterior estimates were generated using the Hamiltonian Monte Carlo algorithm. We used 3000 iterations for two chains in the first two models and 7000 iterations for two chains in the third model. Chain convergence and influential cases were assessed by visual inspection of traceplots and Pareto Smoothed Importance Sampling plots (PSIS) respectively (McElreath, 2020; Vehtari et al., 2019). For all models, we present the 95% credible interval.

Model 1: How does communication vary between fission and fusion events? We tested whether individuals were more likely to communicate during fission or fusion events. To do so, we examined the influence of the type of event (fission or fusion) and whether or not these were associated with joint-travel on the likelihood of communication. From the 468 events and 3302 opportunities to communicate that were coded, we excluded from analysis opportunities in which we could not determine from the videos whether or not communication occurred due to limited visibility (1 fusion event and 105 opportunities to communicate). We included 467 fission or fusion events comprising 3197 opportunities to communicate (1749 during fissions and 1448 during fusions) were included for analysis. We fitted a Bayesian generalized linear multilevel model with a binomial response variable (communication occurred = yes or no). Where individuals fissioned or fused within 5 min of each other and travelled to/from the same direction they were marked as a possible joint-travel. Test predictors in this model included type of event (fission or fusion), possibility of joint travel (yes or no), and the interaction between both. We controlled for the period (1: 1993-1994, 2: 2003-2004, 3: 2013-2014) and for individual, dyadic, and group features. Individual features comprised focal position (traveller, party-member), focal rank (z-transformed), and level of threat experienced (low, neutral, high); dyadic features included kinship (kin, non-kin), and rank relationship (rank of the focal as: higher than, equal to, or lower than the partner); and group features included group size (z-transformed), and presence of males (yes, no). As random factors we included the identity of the focal, the identity of the partner, and the event number (given there was variation in the number of opportunities to communicate per event). We included a maximal random slope structure for the test predictors.

Model 2: Which social features affect the probability of communicating during fission and fusion events? We were interested in understanding how social features impacted the probability of communication when individuals joined or left their conspecifics (fusion and fission events respectively) without being involved in any possible joint-travel. Excluding any events that might have been joint travels left a total of 202 fission or fusion events and 1221 opportunities to communicate. We again fitted a Bayesian generalized linear multilevel model with a binomial response variable (communication occurred = yes or no). As fixed effects we included the type of event (fission or fusion) and the social features: focal position, focal rank, level of threat experienced by the focal, kinship, rank relationship, presence of males, and group size. Because social features could have different impacts on potential greetings and leave-takings, we included the interaction between these features and the type of event. As random factors we included the identity of the focal, the identity of the partner, and the event number. Given the smaller dataset following the exclusion of possible joint-travels, we were unable to include a maximal random slope structure for the test predictors.

Model 3: What determines the channel of communication during fissions and fusions? Individuals can communicate through gestures, vocalizations, facial expressions, or by combining these different channels of communication. Of the 221 communications in a fission or fusion event, we excluded 30 where we were not sure if signals in one or more channels occurred. We fitted a multinomial logistic regression, again using the ‘brms’ and ‘rstan’ packages, using each of the three signal channels plus their combination as a possible response (gestures, vocalizations, facial expressions, and multi-channel combinations). We tested if the type of event, level of threat experienced by the focal, kinship, and rank relationship influenced the channel chosen to communicate. We controlled for presence of males and group size as fixed effects. As a random effect we included the identity of the focal. Given the small sample size, we were unable to include a maximal random slope structure for the test predictors. We further restricted model complexity by excluding recipient and event number as random effects, as their inclusion increased the number of influential cases 50-fold. We interpret the outcome of this model with this limitation in mind.

3.4. Results

Communication occurred in 21% (n=54/253) of fission events and in 41% (n=88/215) of fusion events. Most events provided multiple opportunities to communicate, individuals communicated in 4% (n=75/1749) of opportunities during fissions, and in 11% (n=155/1448) of opportunities during fusions. Excluding possible joint travels, individuals communicated in 4% (n= 23/620) of opportunities during fissions and in 14% (n= 81/601) of opportunities during fusions.

3.4.1. Model 1: How does communication vary between fission and fusion events?

There was a main effect of the type of event (fission, fusion), and of apparently travelling together (joint-travel) on the likelihood of communication occurring (Table 11).

Table 11. Results for Model 1, testing when communication occurred across fissions and fusions taking into account possible joint travel. Factors in italics were controlled for. Posterior estimates and 95% credible interval for all fixed effects, and Odds Ratio for the estimates. Significant effects are reported in bold and control variables in italic.

	Estimate	Est.Error	Q5	Q95	Odds
Intercept	**-3.173**	**0.666**	**-4.517**	**-1.921**	**0.042**
Type of Event [Fission]	**0.825**	**0.574**	**-0.332**	**1.948**	**0.257**
Possibility of joint travel [Yes]	**0.825**	**0.574**	**-0.332**	**1.948**	**0.417**
Type of event* Possibility of joint travel	0.825	0.574	-0.332	1.948	2.282
Period [2]	*-0.309*	*0.415*	*-1.102*	*0.519*	*0.734*
Period [3]	*0.218*	*0.515*	*-0.749*	*1.263*	*1.243*
Level of threat [High]	*2.406*	*0.382*	*1.682*	*3.176*	*11.085*
Level of threat [Low]	*2.195*	*0.274*	*1.679*	*2.755*	*8.983*
Focal rank	*0.592*	*0.165*	*0.269*	*0.912*	*1.807*
Focal position [Traveller]	*0.320*	*0.208*	*-0.087*	*0.732*	*1.378*
Kinship [Kin]	*-0.215*	*0.300*	*-0.802*	*0.361*	*0.807*
Rank relation [Focal > Partner]	*-1.272*	*0.455*	*-2.164*	*-0.387*	*0.280*
Rank relation [Partner > Focal]	*0.078*	*0.432*	*-0.749*	*0.921*	*1.081*

Presence of males [Yes]	*-0.688*	*0.313*	*-1.310*	*-0.094*	*0.503*
Group size	*-0.947*	*0.188*	*-1.324*	*-0.593*	*0.388*

Individuals were less likely to communicate during fissions as compared to fusions (OR=0.257, Figure 6a), and were less likely to communicate when apparently travelling together (OR=0.417, Figure 6b). The full model explained a moderate portion of the variance in incidence of communication (R2=0.309).

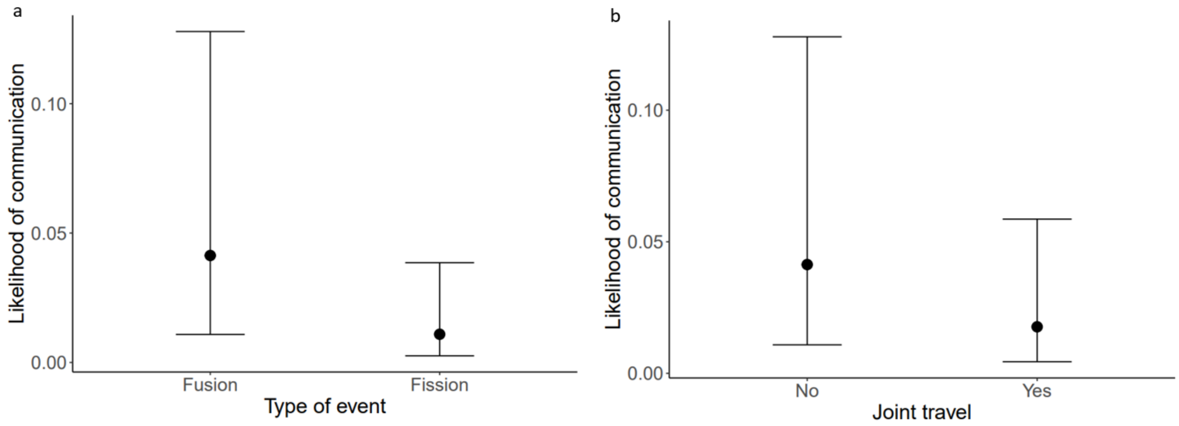


Figure 6. Impact of the type of event (a), and possibility of joint travel (b) on the likelihood of communication occurring in a fission or fusion event.

3.4.2. Model 2: Which social features affect the probability of communicating during fission-fusion events?

Several test predictors strongly influenced the probability of communication occurring during fission-fusion events (excluding potential joint-travels), but only low levels of threat had a differential impact on the likelihood of communication during fissions and fusions (Table 12). At low (but not neutral, or high) levels of threat individuals were 88% less likely to communicate in fissions as compared to fusions (OR=0.124, Figure 7a). Focal rank impacted the likelihood of communication: one standard deviation increase in focal rank increased the odds of communicating during a fission-fusion event by a factor of 2.507 (Figure 7b). There was weak evidence that kin-related individuals were less likely to communicate (OR=0.321, Figure 7c). Communication was 88% less likely to occur towards lower ranking individuals (OR=0.120, Figure 7d). Audience composition impacted the odds of communication: when males were present the odds of communication by the focal in a fission-fusion event decreased by 70% (OR=0.296, Figure 7e); and one standard deviation increase in group size, decreased the odds of communication by the focal by 56% (OR=0.443, Figure 7f). There was no evidence for the effect of focal position (as traveller or party member) on the likelihood of communication. The full model explained a moderate portion of the variance in incidence of communication (R2=0.397).

Table 12. Results for Model 2, testing which features affected the probability of communicating during fission or fusion events. Posterior estimates and 95% credible interval for all fixed effects, and Odds Ratio for the estimates. Significant effects are reported in bold and control variables in italic.

	Estimate	Est.Error	Q5	Q95	Odds
Intercept	**-4.296**	**1.049**	**-6.444**	**-2.344**	**0.014**
Period [2]	*0.644*	*0.686*	*-0.604*	*2.056*	*1.905*
Period [3]	*0.450*	*0.774*	*-0.984*	*2.046*	*1.568*
Type of Event [Fission]	0.952	1.020	-0.966	2.975	2.590
Level of threat [Low]	**3.794**	**0.545**	**2.813**	**4.940**	**44.450**
Level of threat [High]	**3.019**	**0.607**	**1.848**	**4.255**	**20.463**
Focal rank	**0.919**	**0.288**	**0.363**	**1.505**	**2.507**
Focal position [Traveller]	0.415	0.372	-0.313	1.143	1.515
Kinship [Kin]	**-1.137**	**0.597**	**-2.354**	**-0.017**	**0.321**
Rank relation [Partner>Focal]	0.733	0.705	-0.618	2.135	2.082
Rank relation [Focal>Partner]	**-2.121**	**0.806**	**-3.744**	**-0.576**	**0.120**
Presence of males [Yes]	**-1.219**	**0.528**	**-2.288**	**-0.190**	**0.296**
Group size	**-0.814**	**0.268**	**-1.39**	**-0.322**	**0.443**
Type of event * Level of threat [Low]	**-2.088**	**0.794**	**-3.716**	**-0.574**	**0.124**
Type of event * Level of threat [High]	-1.986	1.386	-5.025	0.469	0.137
Type of event * Focal rank	0.080	0.434	-0.766	0.956	1.084
Type of event * Focal position	-0.558	0.630	-1.770	0.667	0.573
Type of event * Kinship	-0.146	1.236	-2.965	2.047	0.864
Type of event * Rank relation [Partner > Focal]	**-1.633**	**0.915**	**-3.446**	**0.089**	**0.195**
Type of event * Rank relation [Focal > Partner]	-0.323	1.089	-2.509	1.757	0.724
Type of event * Presence of males	0.169	0.754	-1.303	1.647	1.184
Type of event * Group size	0.346	0.401	-0.446	1.121	1.414

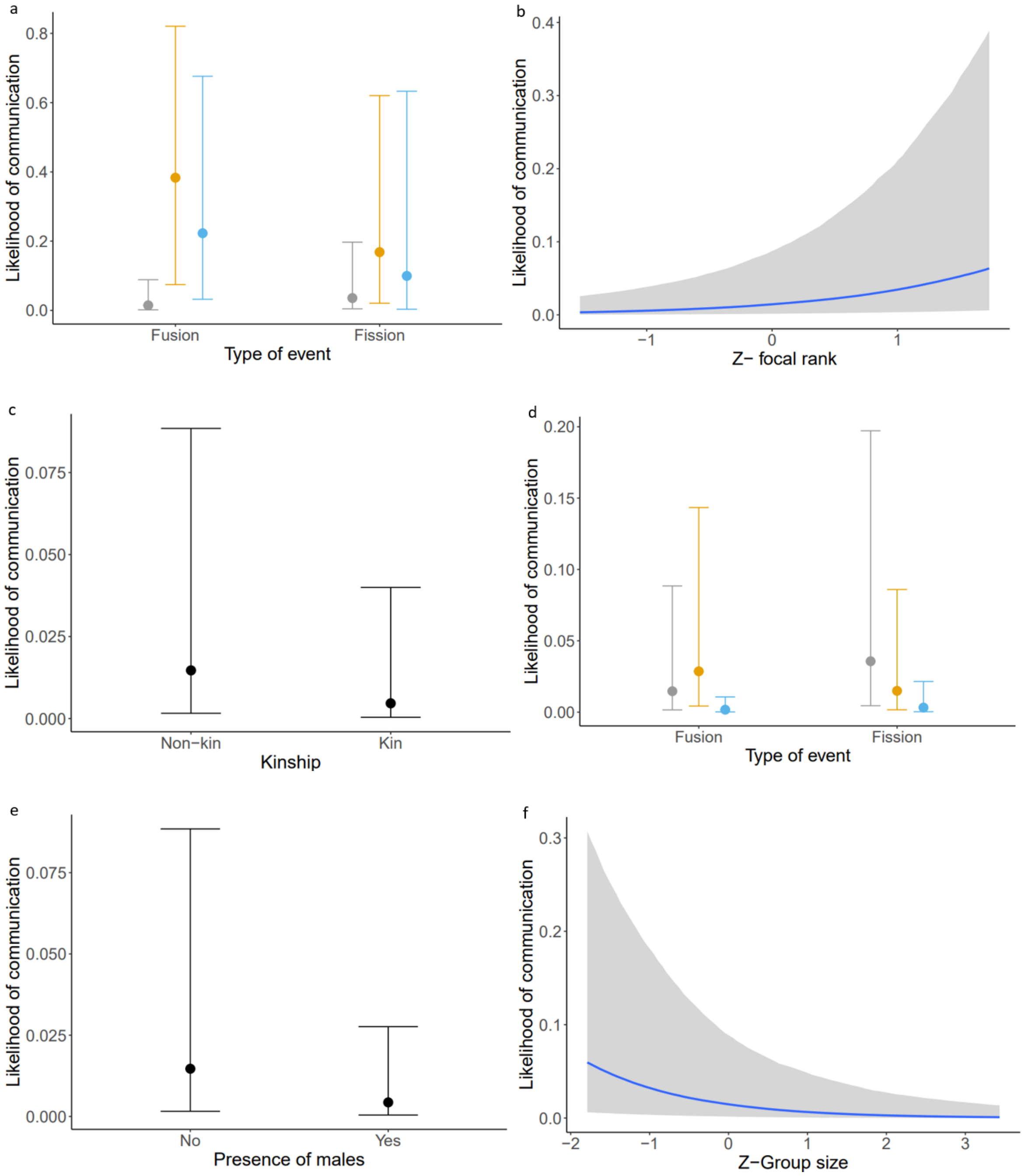
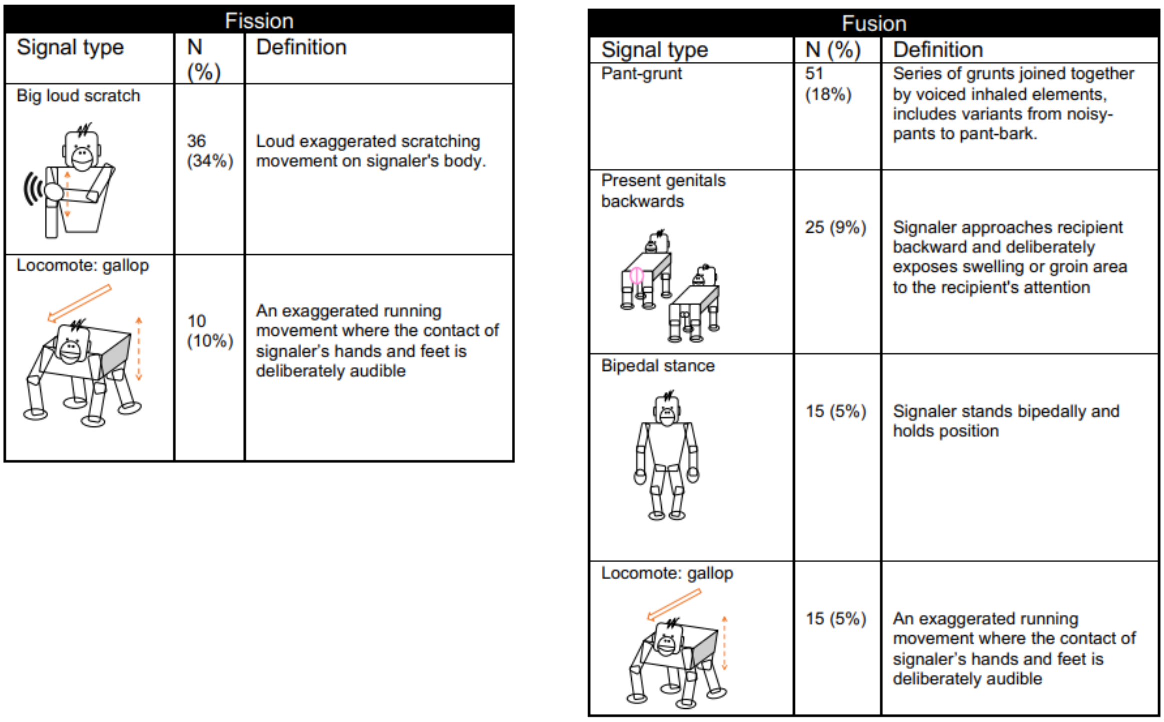


Figure 7. Impact of social features on the probability of communication in fission and fusion events. (a) levels of threat experienced during fission and fusion events, with neutral level of threat represented in grey, low level of threat represented in orange, and high level of threat represented in light blue, (b) z-transformed focal rank, (c) kinship, (d) rank relationship F=P focal and partner have same rank; P>F: partner rank higher than focal; F>P: focal rank higher than partner, (e) presence of males, (f) and z-transformed party size.

3.4.3. Which signal types are used in fission or fusion events?

Within the 221 communications we recorded 383 signals: 102 signals (86 gestures, 13 vocalizations, 3 facial expressions) during 66 fissions, and 281 signals (178 gestures, 84 vocalizations, 19 facial expressions) during 153 fusions (see Appendix A 2 for more detail). The most common signals produced during fissions were the *big loud scratch* gesture (n=36, 35%), followed by the *locomote: gallop* gesture (n=10, 10%), which together represented approximately half of the signals produced when an individual fissioned (Figure 8). The most common signals produced during fusions were the *pant-grunt* vocalization (n=51, 18%), followed by the *present-genitals backwards* gesture (n=25, 9%). Together with the *bipedal stance* gesture (n=15, 5%) and the *locomote: gallop* gesture (n=15, 5%), these 4 signals represent over 40% of the signals produced in fusions.



Fission		
Signal type	N (%)	Definition
Big loud scratch	36 (34%)	Loud exaggerated scratching movement on signaler's body.
Locomote: gallop	10 (10%)	An exaggerated running movement where the contact of signaler's hands and feet is deliberately audible

Fusion		
Signal type	N (%)	Definition
Pant-grunt	51 (18%)	Series of grunts joined together by voiced inhaled elements, includes variants from noisy-pants to pant-bark.
Present genitals backwards	25 (9%)	Signaler approaches recipient backward and deliberately exposes swelling or groin area to the recipient's attention
Bipedal stance	15 (5%)	Signaler stands bipedally and holds position
Locomote: gallop	15 (5%)	An exaggerated running movement where the contact of signaler's hands and feet is deliberately audible

Figure 8. The signal types used most often during fissions (on the left) and fusions (on the right). The number of occurrences and definitions for all signals can be found in the Appendix A 2. Signal types are accompanied by BonoboBOT 1.0. illustrations ki kindly provided by Kirsty E. Graham.

3.4.4. Which channels of communication are used in fission or fusion events?

We recorded 191 communications in which we were able to record the presence or absence of signals in all three channels of communication. Gesture-only communications occurred most often (in 110 events) and these were similarly distributed across fissions and fusions (46 during fissions and 54 during fusions). Vocalization-only communications occurred less often (in 36 events) and were less likely to occur during fissions than fusions (6 during fissions and 30 during fusions). Facial-expression-only communication only occurred once (during a fusion). Multi-channel communication occurred in 44 events and was recorded more often during fusions (10 during fissions and 34 during fusions).

Across all social features of the interaction we explored, gesture-only communication was observed more often than communication in other channels or multi-channel communication (≥58% of communications; Figure 9), with the exception of situations involving high levels of threat, in which individuals employed gestural, vocal, and multi-channel communication to a similar extent (36%, 36%, and 29% respectively).

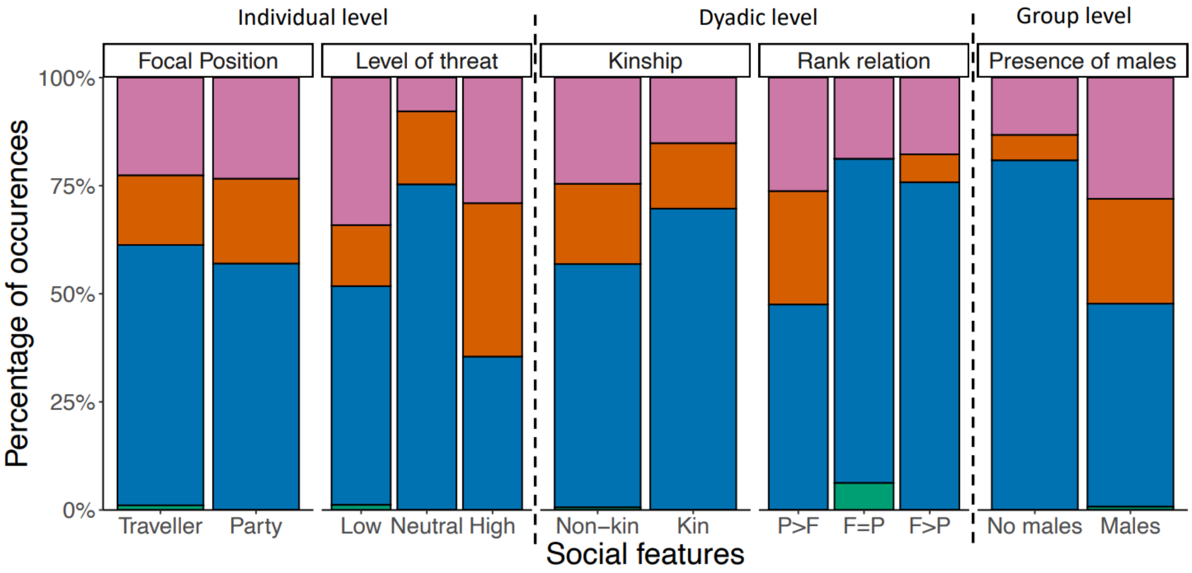


Figure 9. Proportion of communications produced in each channel across different social features at the individual, dyadic, and group level. Green bars represent facial expression-only communications; blue represent gesture-only; orange represent vocal-only, and pink represent multi-channel combinations. Rank relationship is categorised as F=P focal and partner have same rank; P>F: partner rank higher than focal; F>P: focal rank higher than partner.

3.4.5. Model 3: What impacts the channel of communication in fission or fusion events?

We included the 191 instances of communication in which we were able to record the presence or absence of signals in all three channels of communication. The channel of communication varied according to the type of event, the relative rank relationship within the dyad, and the presence of males (Table 13). Gesture was the most commonly employed channel of communication, and individuals used gesture more often during fissions, as compared to fusions (OR=5.667, Figure 10a). Lower ranking individuals were less likely to use gestures, as compared to individuals with similar ranks, towards higher-ranking individuals (OR=0.105, Figure 10b). Individuals were more likely to combine signals of different channels when experiencing low levels of threat when compared to neutral levels of threat (OR=4.808: Figure 10c). Finally, there was no evidence that kinship influenced the signal channel used.

Table 13. Results for Model 3, testing which features influenced the channel of communication during arrivals and departures. Posterior estimates and 95% credible interval for all fixed effects, and Odds Ratio for the estimates. The Vocal modality was set as the reference level. Significant effects are reported in bold and control variables in italic.

	Estimate	Est.Error	l-95% CI	u-95% CI	Odds
Modality: Facial Expression					
Intercept	-9.938	10.432	-38.410	1.047	<0.001
Type of Event [Fission]	-2.169	6.845	-19.977	4.280	0.114
Level of threat [Low]	3.640	7.363	-2.544	22.069	38.085
Level of threat [High]	-2.197	6.221	-18.043	4.612	0.111
Kinship [Kin]	-2.286	6.314	-17.502	3.939	0.102
Rank relation [Partner > Focal]	-8.189	10.236	-33.566	0.250	<0.001
Rank relation [Focal > Partner]	-4.885	9.351	-26.225	2.265	0.008
Presence of males [Yes]	*2.811*	*6.530*	*-3.201*	*21.007*	*16.62*
Group size	*0.245*	*1.441*	*-2.666*	*3.064*	*1.278*
Modality: Gesture					
Intercept	**3.460**	**1.272**	**1.171**	**6.184**	**31.808**
Type of Event [Fission]	**1.735**	**0.684**	**0.469**	**3.180**	**5.667**
Level of threat [Low]	0.695	0.569	-0.399	1.823	2.003
Level of threat [High]	-0.371	0.658	-1.684	0.896	0.690
Kinship [Kin]	-0.336	0.728	-1.771	1.099	0.715
Rank relation [Partner > Focal]	**-2.252**	**1.060**	**-4.601**	**-0.378**	**0.105**
Rank relation [Focal > Partner]	-0.038	1.082	-2.343	1.986	0.963
Presence of males [Yes]	*-1.560*	*0.645*	*-2.894*	*-0.351*	*0.210*
Group size	*0.155*	*0.257*	*-0.348*	*0.659*	*1.168*
Modality: Multichannel					
Intercept	0.629	1.308	-1.865	3.363	1.876
Type of Event [Fission]	-0.038	0.804	-1.619	1.540	0.962
Level of threat [Low]	**1.570**	**0.649**	**0.354**	**2.885**	**4.808**
Level of threat [High]	0.572	0.72	-0.828	1.998	1.772
Kinship [Kin]	-0.374	0.764	-1.919	1.084	0.688
Rank relation [Partner > Focal]	-1.014	1.052	-3.288	0.906	0.363
Rank relation [Focal > Partner]	0.283	1.101	-1.951	2.407	1.327
Presence of males [Yes]	*-0.695*	*0.689*	*-2.084*	*0.615*	*0.499*
Group size	*0.123*	*0.255*	*-0.382*	*0.616*	*1.131*

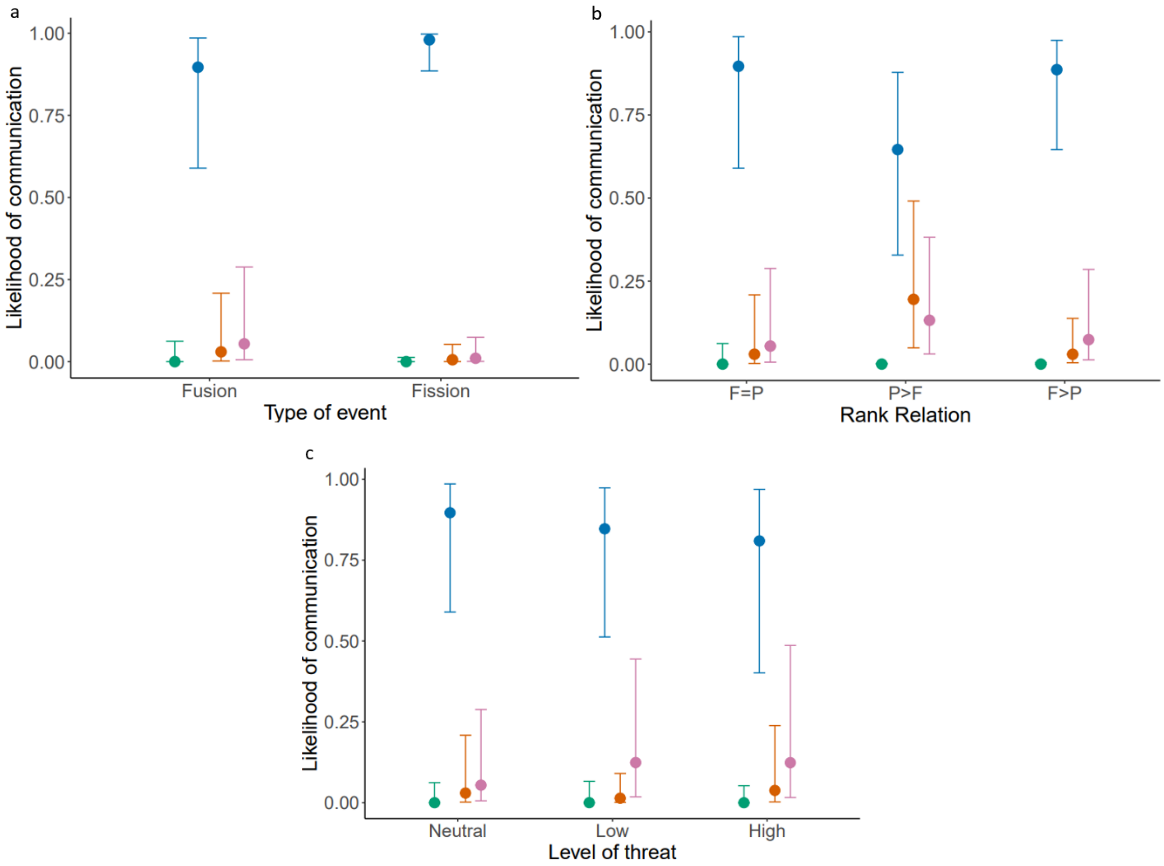


Figure 10. Impact of social features on the channel of communication used in fission and fusion events. (a) type of event, (b) rank relationship, and (c) level of threat; with facial expression, gestural, vocal and multi-channel events represented in green, blue, red, and pink respectively. Rank relationship is categorised as F=P focal and partner have same rank; P>F: partner rank higher than focal; F>P: focal rank higher than partner.

3.5. Discussion

We show that the occurrence and form of communication during fission and fusion events is mediated by social factors. Communication occurred in both contexts, but more than twice as often during fusions than during fissions. In addition, communication during these events was selective, with only a small portion of the number of opportunities to communicate acted on.

Chimpanzees were more likely to communicate to particular individuals. More communication occurred towards higher-ranking individuals and between non-kin individuals, and there was an inhibitory effect of the presence of bystanders (increased party size), particularly where these included males. As well as being more likely to be communicated to, higher-ranking individuals were themselves, in general, more likely to communicate than individuals of lower rank. Behavioural contexts that represented either high or low potential-threat levels resulted in higher levels of communication than neutral ones, although this pattern appeared driven by fusions; individuals experiencing low levels of potential threat were particularly unlikely to communicate during departures (fissions). In signal form, gesture-only communications were the most commonly employed and were similarly produced across both fissions and fusions. Gesture-only communication was less likely to be used when the communication partner was of higher rank, particularly during fissions. Vocal-only and multi-channel combinations were employed to a similar extent and relatively less often, but chimpanzees were more likely to combine signals from different channels when experiencing lower levels of potential threat.

Chimpanzees employed almost three times as many different gestural signal types as vocal signal types in these contexts. As a result, while vocalizations were in general recorded less often, *pant-grunt* vocalizations remained the most frequent signal type recorded in fusion events, more than twice as frequent as the next signal (the *present-genitals backwards* gesture). As communication during fusion events was more common than in fissions, and *pant-grunt* vocalizations are closely associated with social rank in chimpanzees (Bygott, 1979; Laporte & Zuberbühler, 2010), our findings that communication in these contexts was more likely to be produced towards higher-ranking individuals may have been driven, in part, by the prevalence of *pant-grunts.*

Our findings largely support those previously described in specific studies of chimpanzee 'greetings'. For example, *pant-grunt* greetings are more likely to be given when approaching higher-ranking individuals (Laporte & Zuberbühler, 2010; Luef & Pika, 2017), and across contexts higher-ranking males tended to employ more gestures than other mature individuals (Hobaiter & Byrne, 2017). However, the Bossou chimpanzee community is unusually small (2-3 adult males across our study periods), and rank in our study is largely described by sex and age, so an apparent rank effect may also have been driven by a tendency for younger individuals to be less likely to communicate in these contexts.

Our finding that individuals in potentially high threat situations (for example shortly before or after an aggressive attack, a display, or sexual behaviour), were more likely to communicate than those in apparently neutral situations (e.g. feeding or resting) is similar to the findings that greetings (Luef & Pika, 2019) and more specifically *pant-grunt* vocalizations (Fedurek et al., 2021; Wittig & Boesch, 2003) provide a relatively low-cost opportunity to mitigate the need to engage in physical contests by signalling the current status of dyadic rank-relationships (Fedurek et al., 2019; Newton-Fisher, 2004). However, we also found that individuals were as likely to communicate during apparently very low threat interactions (for example, communication shortly before or after grooming or play), showing that chimpanzees are more likely to communicate when engaging in diverse social activities independently of their valence. This pattern of communication suggests that signalling the current status of the relationship shortly before or after a period of separation may be important in affiliative, as well as competitive, relationships. Signaling relationship status may be less important where these are kin-based. The small and cohesive nature of the community may make it difficult to discriminate social-bonds on the basis of kinship, from the strong non-kin social bonds that are a feature of chimpanzee behaviour (Crockford et al., 2013; Samuni et al., 2018) – perhaps particularly so in smaller communities (Lehmann & Boesch, 2004). Despite this, we continue to find a small effect of kinship: maternal kin appear to be less likely to communicate during fissions and fusions, even once possible joint travels were controlled for. As well as functioning to reassert the (postive or hierachical) nature of chimpanzees' relationships, communication in these contexts may be particularly important in relationships in which the nature or quality of the pair-bond may vary: you choose whether or not to keep your friends, but not your family.

Being a traveller or a party-members did not affect the likelihood of communicating. In other words, these communications do not appear to be limited to signalling your intention to join or travel, and if communication in these contexts represents greetings or leave-takings, there is no clear pattern to who employs these – it is as likely to be the individual being left behind or being joined, as the individual who is leaving or joining. While the choice to arrive or depart is made by the individual travelling, both the traveller and party-member can make a choice to communicate in this context, and in doing so perhaps inform the other individual or wider audience of the nature of their relationship. Fedurek et al. (2019) reported a higher frequency of *pant-grunts* for individuals who were being approached within a party. However, the decision to approach already indicates a decision to engage with a specific individual. As we see from the relatively low proportion of opportunities to communicate in fusions (and very low proportion in fissions), chimpanzees are highly selective in who – among the individuals present – they communicate with in these contexts. This pattern could represent a choice to communicate with particular individuals, and/or a choice *not* to communicate with specific others. In other words, the decision to communicate may include both the relationship between the two individuals (potential signaller and recipient), and the relationship between these two individuals and others who are present. Supporting this hypothesis, we found that chimpanzees were less likely to communicate in the presence of larger numbers of other individuals, in particular where these included other males. Chimpanzee bystander effects are well documented (e.g., Slocombe and Zuberbuhler 2007; Townsend et al. 2008; Laporte and Zuberbühler 2010; Mielke et al. 2017), and greeting an individual in the presence of other higher-ranking individuals may, for example, lead to aggression (Fedurek et al. 2021) - a strong disincentive for greeting indiscriminately or based only on the nature of your relationship with the potential recipient.

Our findings support the broad pattern that shows little evidence for parting rituals in chimpanzees. While individuals were more likely to communicate during fusions, communication did occur during fissions; however, whether or not these communications represent 'leave-taking' to the chimpanzees using them remains unclear. As McGrew and Baehren's (2016) survey highlighted there is no agreed definition for leave-taking. If we base our expectations of function or form on human rituals, we will likely miss chimpanzee-specific uses; nevertheless, we need a definition that would allow us to distinguish leave-taking from other types of communication that might occur in fission events. We can say several things: if present, explicit signals of leave-taking appear to be rare. Fewer than 5% of opportunities to do so involved any communication during fissions, and none of the signals produced were specific to this context. As a result, we are very cautious about assigning the signals produced during departures as leave-taking. The most common signal, the *big loud scratch* gesture, which represented almost half of all the signals produced, is produced during requests to 'Travel with me' by adult chimpanzees (Fröhlich, Wittig, et al., 2016b; Hobaiter & Byrne, 2014; Wilke et al., 2017) and is used for the same function by orang-utans (Fröhlich, Lee, et al., 2019), indicating that at least some of these communications were likely failed requests to travel. Similarly, it is difficult to distinguish interrupted communication. For example, if a juvenile invites another individual to play, but then sees their mother is leaving, they may interrupt the play interaction to follow their mother. Distinguishing this from them having said 'good-bye' to their play partner is difficult.

Importantly, we can make the same argument for the potential greeting signals produced during fusions – *pant-grunt* vocalizations and *present-genital* gestures are also made between individuals in other contexts (Hobaiter and Byrne 2011, 2014) – and pant-grunts in particular are used when two individuals approach each other, even where they are already in the same party (Fedurek et al., 2019). The unidirectional use of *pant-grunt* vocalizations between adult males, including when already within the same party, suggests that these signals function to indicate hierarchical relationships – which, as found in human greetings (Firth, 1972), are often important to establish or reinforce when meeting. The physical similarity between chimpanzee gesture forms during arrivals and those produced in human greeting-rituals (e.g. *kiss, bow*) is at first compelling, but – to date – evidence for similarity in their meaning remains limited. Great ape signals, and in particular their gestures, are flexible in function and meaning (Graham et al., 2018; Hobaiter & Byrne, 2014). The definition of the context of 'greeting' in chimpanzees varies between studies (for example fusions following separations of 5 min up to those of several hours), and there has been a tendency to employ wider context, rather than the specific exchange of behaviour, to define function in nonhuman primate communication (Call & Tomasello, 2007; Laporte & Zuberbühler, 2010; Luef & Pika, 2017; Ouattara et al., 2009). Thus, we also urge greater caution in assuming that all signals given in a potential greeting context function as greetings.

The study of greeting and leave-taking highlights the constraints underlying the detection of meaning in nonhuman communication. The broader patterns of use provide a compelling case that communication during fusions serves to demonstrate the nature and strength of social bonds, and so – perhaps irrespective of specific meaning – functions similarly to human greetings. However, there is – so far – no similar case for the pattern of communication prior to fissions and leave-taking. If leave-taking is absent in chimpanzees, it may be because there is no similar social need for it. That may be because chimpanzees do not engage in the imaginative future-tracking required to promote the need for leave-taking: we do not say good-bye every time someone steps out of the room for a moment, only when we imagine or predict that we will not see them for a longer period. Similarly, for the individual leaving, the highly fission-fusion nature of their sociality may make it difficult to predict whether they will be absent for a longer period. It may be more effective to invest in a clear signal of the relationship on arrival, when the parameters of the need to communicate are more clearly defined (I have been away for X-time, the other individuals present are A,B,C, etc.). Finally, when a human leaves their immediate social party, doing so essentially prohibits social contact with them (without technology), while chimpanzees have at least two long-distance (>1km) regularly produced social signals: *pant-hoots* and *drums*, both of which appear to encode aspects of signaller identity and activity (Babiszewska et al. 2015; Fedurek et al. 2016; Fitzgerald et al. in revision), allowing them a possible means to 'touch base' with other individuals, even when split across parties.

If leave-taking is present in chimpanzees, it may be particularly rare in the Bossou community during the nut-cracking season. West African chimpanzees, and smaller communities of chimpanzees, are relatively cohesive (Lehmann & Boesch, 2004; Sugiyama, 2004) and most individuals meet most days. In addition, the presence of a valuable and consistently available food resource at the nut-cracking site during the dry season may further reduce any uncertainty about the likelihood of re-encountering another individual in the near-future. In contrast in the highly fission-fusion communities of East African chimpanzees, individuals – and in particularly the more rarely studied females – may not meet for weeks or months (Goodall, 1986; Nishida, 1968).

We show that chimpanzees are selective about their use of communication during fission and fusion events, which is mediated by both individual and social factors including rank, kinship, and audience size and composition. Our data largely support and extend the findings in studies of greeting in other chimpanzee communities. By taking a broad approach across opportunities to communicate and signal channels, we show the importance of considering the full range of signals employed in these contexts, as well as the specific individual and community level socio-ecological context of their use. Our use of systematic video-coding allows us to provide a thorough description across signalling channels, including subtle visual signals that can be missed or neglected. Further research is needed across different chimpanzee communities – in particularly on the highly fission-fusion East African females – and with larger datasets that allow us to better explore the infrequent use of communication during departures. For example: investigating the impact of how far apart individuals are (within or outside of the range of long-distance conspecific signals – such as pant-hoot calls or buttress drumming in chimpanzees) and for how long, as well as exploring changes in the behaviour of individuals before and after some-one arrives or leaves, could provide crucial new understanding of the function of communication in these contexts for fission-fusion species. We particularly highlight the methodological challenges in detecting signals that are functionally equivalent to leave-taking and we urge caution in interpreting communications during fusion events as functionally equivalent to greetings. While great ape communication, and in particular their gestures (Hobaiter & Byrne, 2011b; Leavens & Hopkins, 1998; Tomasello, George, Kruger, Jeffrey, Farrar, et al., 1985), has been showed to be clearly intentional; there remains limited exploration of the sharing of different types of intentions outside of human communication. While a *big loud scratch* gesture may not function to signal 'good-bye', there is a distinction between the imperative 'travel with me' and the declarative

‘I’m leaving’. Exploring the intention sharing of other apes in greater detail may deepen our ability to detect the evolutionary origins of human leave-taking – and greeting – behaviour.

Declarations

Conflict of interest: The authors declare that they have no conflict of interest.

Data and Code Availability: Data, scripts, and online resources available in https://github.com/Wild-Minds/Bossou_HelloGoodbye

CHAPTER 4: Chimpanzee ‘babytalk’: Gestural motherese in wild chimpanzees (*Pan troglodytes*)

This chapter is based on Rodrigues, E.D., Santos, A.S., Safryghin, A, Hayashi M., & Hobaiter C. Chimpanzee ‘babytalk’: Gestural motherese in wild chimpanzees (*Pan troglodytes*) Manuscript in preparation for publication. Results were also presented at the VIIIth Protolang Series Conference, Rome, Italy (2023).

4.1. Abstract

The way in which humans modify their communication when interacting with young children (child-directed communication, CDC), while not universal, is often expressed in very similar ways across different cultures. Its widespread use suggests that it may be a species-typical capacity within human communication, and could potentially be evolutionarily older than modern humans. The study of child-directed communication in other great apes allows us to gain insights into its evolutionary roots. From the different type of communicative signals employed by chimpanzees, gestures are a promising modality, as they are already employed in highly flexible ways that appear sensitive to characteristics of the recipient. In humans, child-directed communication is centered on features that remain unexplored in other apes: complexity, tempo, and prominence. We explored these features in the gestural communication of chimpanzee mothers with offspring from two different communities. We first investigated whether these females adjusted their gestural communication based on the age, sex, and kinship of any recipient that they interacted with. We then focused on mother-offspring pairs to analyse whether they adjusted their gestural communication to the developmental stage and sex of their offspring. Our findings revealed that chimpanzee mothers do tailor their gesturing to their recipient's age and kinship relationship, but not to their sex. Mother chimpanzees used shorter units towards immature individuals and used more diverse gesture repertoires towards subadults (trends that hold when analysing the subset with their offspring). Mothers employed shorter gestures, communicated at a faster pace, with a more diverse set of gesture forms, and were less prone to use repetitions in gesturing towards non-kin individuals. When communicating specifically with their offspring, they were more likely to use repetitions towards older offspring. The majority of the patterns found in the analysis of mother chimpanzees' communication to any member of the community were not found in the mother-offspring subset of communications, suggesting that kinship and recipient age may interact. Chimpanzees do accommodate their communicative features to immature individuals, suggesting that this ability likely has deep evolutionary roots and may have been a trait of our common ancestor. However, the variation from the child-directed communication patterns of accommodation suggest that these adjustments may have developed by prioritizing different functions from the ones observed in human communication.

Keywords: child-directed communication, immature-directed communication, gestures, chimpanzees, accommodation

4.2. Introduction

Humans regularly adapt how they communicate in order to accommodate who they are communicating with (Giles et al., 1987; Hayes et al., 1987). Primarily investigated within speech, researchers have documented adjustments in features such as accent, pronunciation, speech rate, utterance length, and the complexity of vocabulary and grammatical structures (e.g., Biersack et al. 2005; Kemper 1994). Analogous non-verbal adjustments have been also reported, including in sign languages (e.g., Stamp et al. 2016) and gestures (e.g., Iverson et al. 1999). Through these adjustments, humans may, consciously or subconsciously, shift their communicative style – tailoring their communication based on specific attributes of their conversational partner, such as age, status, or type of relationship. For example, we may adapt the complexity of our vocabulary and the pace of our communication when talking to young children or elderly people. Similarly, our communication style with friends, colleagues, or strangers differs based on the nature of our relationship and on the level of common ground we share.

A particular type of accommodation occurs when communicating with young individuals: child-directed communication (also known by many different names including: 'motherese', 'parentese', 'babytalk', and 'infant-directed communication'). In humans, characteristics of this special communicative register include the use of simplified vocabulary, slower tempo, exaggeration of certain communicative features, and a higher rate of repetitions. Although not universal, and with considerable variability in how it is expressed between cultures (including in the number and type of communicative features that are adjusted), this special register is found all over the globe, and given the evidence that it appears to be species-typical – and thus, likely biologically inherited – may be evolutionary older (Falk, 2004). To trace the evolution of this ability to accommodate our communication to infants and children, we need to explore the plasticity of other communicative systems in other animal species – particularly when communicating to immature individuals, and particularly in closely related species, such as the other great apes. By doing so, we can distinguish between alternative evolutionary scenarios: i) the ability to accommodate communication to young individuals arose after our split with a last common ancestor, and is not present in the communication of our closest modern relatives; ii) it is shared with other great apes, suggesting the presence of this ability is evolutionarily older, and was present in a last common ancestor; or iii) this ability arose independently several times as a result of adaptive benefits for communication in a particular socio-ecological niche, and can be fully or partially shared with more distantly related taxa (convergent evolution; Schick et al., 2022). To properly explore all three scenarios requires data from across a wide range of species, including those that are phylogenetically distant but have other socio-cognitive features in common with humans, such as elephants (Bates et al., 2008). Here, we make a start towards investigating this question with a comparative study of communication in wild chimpanzees.

Immature-directed communication – communication specifically directed at an immature individual and accompanied by changes in structural or acoustic features (Schick et al., 2022) – has been observed in the vocal domain across various taxonomic groups, including: bats (e.g., Fernandez and Knörnschild 2020), cetaceans (e.g., Sayigh et al. 2023), birds (e.g., Chen et al. 2016) and nonhuman primates (e.g., Whitham et al. 2007). However, there are very few studies describing immature-directed vocalizations in great apes (but see: Fröhlich et al. 2016; Wich et al. 2012) and no evidence, to date, for variation in the acoustic features usually adjusted in immature-directed communication. This pattern of results across phylogenetically distant taxa would suggest that child-directed communication patterns may have emerged in humans via convergent evolution. Nevertheless, it remains an open question whether this emerged in only humans, or in all apes.

Moreover, human language is not limited to speech – it includes spoken and signed forms, and signed-language also shows evidence of child-directed communication patterns (e.g., Masataka 1992). Non-vocal communication also plays an important role in other apes, and adaptations for immature-directed communication may have occurred in other channels. Great apes also communicate through facial expressions and through large repertoires of gestures (Cartmill, 2008; Genty et al., 2009; Parr & Waller, 2006). Some evidence for immature-directed gestures has been reported in great apes (e.g., wild chimpanzees: Fröhlich et al. 2016; wild orang-utans: Knox et al. 2019; captive gorillas: Luef and Liebal 2012), and parallels can be drawn between the structural adjustments observed in immature-directed vocal communication and those present in gestural communication. For example: repetition, a structural feature commonly found in child-directed communication, has been identified in the gesturing of gorillas, where the frequency of repetitions and sequences composed by tactile elements was higher when addressing infants (e.g., Luef and Liebal 2012).

In this study, we were interested in exploring how wild chimpanzees adapt their gestural communication to the sex and age of immature individuals. As animals flexibly adapt their behaviour to fluctuations in their physical and social environment, studying their behaviour in the wild allows us to account for selective pressures that act on the development of specific forms of communication, such as immature-directed communication, within their natural environment. Certain environmental contexts that promote the use of specific gestures may be absent, or be expressed differently in captivity. Moreover, differences in time budgets between captive and wild settings can lead to variations in the frequency of particular gestures or certain contexts, as captive individuals spend less time on activities like foraging and feeding and more time in play (Graham et al., 2022; Pruetz & McGrew, 2001).

Chimpanzees, like all great apes, experience an extended period of immaturity resulting in a long-lasting and intense relationship between mother and infant (Goodall 1986; Hayashi and Matsuzawa 2017). Chimpanzee mothers adapt their behaviour to their offspring's social development by employing different socialization strategies based on the offspring's sex. Specifically, mothers with male offspring tend to be more gregarious as males will need to integrate into the adult male hierarchy and can start to invest early in long-term social bonds, whereas females typically migrate between communities at maturity (Murray et al. 2014). In light of the developmental needs of the growing infant and of the social dynamics inherent to fission-fusion societies, chimpanzees (and chimpanzee mothers in particular) may also adapt their communicative behaviour to the age and sex of their offspring.

Chimpanzees used diverse vocalizations, and some calls (e.g., 'hoos', 'soft barks') are frequently employed between mothers and offspring during travel and foraging (Fröhlich, Wittig, and Pika 2016; Goodall 1986). However, as infants spend most of the time in close proximity to their mother, and early mother-infant communication in chimpanzees is frequently contact-based (Plooij 1978), much mother-infant communication occurs in gestures, which offer opportunity to communicate through the visual, auditory, and tactile modalities. Young individuals often start with a bias towards tactile gestures (Fröhlich, Wittig, et al., 2016a), perhaps as a reflection of their tendency to remain in very closely proximity to their mother; but, with increasing age the physical distance between mothers and their infants increases, and visual gestural communication plays an increasingly important role in mother–infant coordination (Bard et al. 2005; Fröhlich, Wittig, and Pika 2016). Some adjustments described in chimpanzee mothers' communicative behaviour specifically relate to their use of gesture modalities depending on offspring age: chimpanzee mothers are less likely to produce tactile gestures, when compared with visual gestures, as their infants get older (Fröhlich, Wittig, et al., 2016b). However, to date, only broader aspects of gestural communication, such as the modality used, have been investigated and finer-grained features of accommodation in gestural communication, such as communicative unit durations and rates, remain unexplored.

The aim of this study is to investigate whether wild chimpanzees accommodate their gestural communication to immature individuals. For this purpose, we focused on chimpanzee mothers with offspring, and we first investigated whether they adjusted their gestural communication to a recipient's age, sex and kinship when interacting with any individual in the community. We then focused on mother-offspring pairs to analyse whether they adjusted their gestural communication to the age and sex of their offspring. The focus on mother-offspring interactions will allow us to explore adaptations to more subtle age differences. We particularly explored: vocabulary complexity, temporal patterns, and prominence of their communication.

If chimpanzee mothers accommodate their communication following the patterns found in human child-directed communication, we predict that when communicating with immature and younger individuals, chimpanzees will use simpler gestural 'vocabulary', gesture at a slower pace, and use more prominent gestural units.

4.3. Method

4.3.1. Study site and subjects

The dataset contains communicative gestures produced by 25 mothers from two wild and habituated chimpanzee communities: 15 females from Sonso (East African Chimpanzees; *Pan troglodytes schweinfurthii*) and 10 females from Bossou (West African chimpanzees; *Pan troglodytes verus*). To be included in our study, females had to be subadult or adult (older than 9 years-old) with at least one dependent offspring present in the group during the study period (Table 14). Following Reynolds (2005), we defined age groups as follows: infants (0–4 years), juveniles (5–9 years), subadults (males: 10–15 years, females: 10–14 years), and adults (males: 16+ years, females: 15+ years). As this project focused on gestures produced by specific females, and the Sonso archive was more recent than the Bossou archive, we collected additional data on Sonso females from November 2022 until January 2023.

The Sonso community (~70 individuals) is a forest edge community of the Budongo Forest Reserve in Uganda (1°350 and 1°550 N and 31°080 and 31°420 E). This chimpanzee community has been followed daily since 1992, between 7.30 and 16.30, by a team of experienced field assistants who conduct daily focal follows within the community. We followed a focal behaviour sampling approach (Altmann 1974), in which all social interactions that were judged to have any potential for gestural communication were recorded. The videos were catalogued and stored at the University of St Andrews Wild Minds Lab database (Hobaiter et al., 2021), which has now 17-years of data from the Sonso chimpanzee community.

Table 14. Focal females and respective offspring during the study period.

Community	Female ID	Year of Birth	Study Period	Offspring (year of birth)
Bossou	FL	1997	18/12/2007-18/12/2017	FE (2007); FW (2011)
	FN	1956	07/01/1992-18/12/2017	FF (1980); FT (1991); FL (1997)
	FT	1991	12/01/2002-31/12/2003	FK (2001)
	JR	1958	08/01/1992-18/12/2017	JK (1989); JU (1993), JJ (1997); JD (2000); JY (2004)
	NN	1954	12/01/1992-30/12/1996	NA (1985); NTO (1993)
	PL	1987	15/02/1998-13/01/2000	PK (1996)
	PM	1967	09/01/1992-18/12/2010	PL (1987); PO (1993); PE (1998)
	VL	1959	14/01/1992-27/12/2013	VI (1986), VV (1991)
	VV	1991	17/12/2003-31/12/2003	VE (2001)
	YO	1961	08/01/1992-28/12/2015	YU (1984); YL (1991)
Sonso	DL	2002	25/11/2022-14/01/2023	DL (2018)
	HT	1978	08/09/2008-15/01/2023	HW (1993); HL (2001); HY (2005); HR (2009); HM (2013); HD (2017)
	JL	1990	05/12/2007-24/01/2023	JB (2011); JA (2018)
	JN	1984	06/02/2008-21/12/2022	JT (1999); JS (2006)
	KA	1998	21/02/2008-27/01/2023	KQ (2016); KA3 (2022)
	KL	1979	15/12/2007-23/01/2023	BH (1994); KM (1998); KC (2006); KO (2014); KM2 (2020)
	KU	1979	05/09/2008-27/01/2023	KT (1993); KN (1998); KS (2003); KH (2008); KF (2014); KI2 (2020)
	KW	1981	12/11/2007-21/07/2012	KZ (1995); KR (2001); KB (2007); KJ (2013)
	KY	1983	25/02/2008-09/01/2023	KA (1998); KX (2013); KV (2014)
	MK	1980	15/12/2007-07/06/2009	MD (2002); MI (2007)
	NB	1962	21/11/2007-02/08/2012	MS (1992); NR (1996); NT (2003)
	RH	1965	05/08/2008-27/07/2009	NK (1982); RS (1997); RM (2002); RF (2007)
	RM	2002	19/06/2008-27/07/2009	RA (2020)
	RS	1997	25/02/2008-30/06/2011	RK (2013)
	ZM	1968	20/01/2008-15/02/2011	KY (1983); ZG (1997); ZK (2011)

The Bossou community lives in the forests of South-Eastern Guinea (7° 39′ N, 8° 30′ W). During the study period (1992-2017) the community size ranged from 9 to 22 individuals.

Two natural outdoor ‘laboratories’ were originally established in their home range to study tool use: ‘Bureau’, located on the top of Mont Gban; and ‘Salon’, located in the middle of Mont Ghein (Matsuzawa 1994, 2011; Biro et al. 2003). In these outdoor laboratories, a small quantity of palm nuts and water were made available and controlled by the research team (Inoue-Nakamura and Matsuzawa 1997; Sousa et al. 2009; Hayashi and Inoue-Nakamura 2011). The Bossou chimpanzees visit these locations, once or more per day, during the dry season, which lasts ~1–3 months, typically from around December until February (Biro et al. 2006; Sousa et al. 2009). Video of all individuals arriving and leaving the outdoor laboratories, and their social interactions, including the communicative signals produced by each individual, was continuously recorded by researchers since 1988. The videos were catalogued and stored at the Primate Research Institute at Kyoto University, with over 35-years of video footage archived to date.

We considered the specific biases in our sample using the STRANGE framework (Webster and Rutz 2020; Rutz and Webster 2021). While the Sonso community represents a typically sized East African community (ranging around 30-70 individuals), the Bossou community is small even for West African chimpanzee community standards (West African communities are typically smaller in comparison to East African communities, typically ranging from 7-43; Wilson et al. 2014) and contained a maximum of three adult males at any one time. Furthermore, over recent decades, this community has experienced a strong decline due to a combination of respiratory infections that hit the community in 2003 and very limited immigration. The reduced number of individuals limits the diversity of dyadic interactions and types of relationships, and certain aspects of their behaviour might be strongly impacted by individual factors (for example the identity of the alpha male or the group demography). We addressed these biases in part by including data from across a wide range of years in this community. In doing so, we increased the number of individuals present in the data, and the diversity of other socio-demographic factors. The inclusion of these two groups from two sub-species provided important further diversity of individuals, generations, and local sociology-ecology within the sample.

4.3.2. Coding Procedure

Coding scheme. We extracted archival video data from Sonso and Bossou that were included in the wider *GesturalOrigins* project. Videos were labelled and catalogued in a Filemaker Pro database containing the clip directories for each field site. The gestures identified in these clips were coded by EDR, AS, and CH using the software ELAN. A specific coding scheme and the definitions of the fields and categories used were based on the protocol published by Grund et al., (2023).

For this study, we focused on the following individual and relational features: signaller and recipient ID and age; recipient sex; their kinship relation (mother-offspring, offspring-mother, grandmother-grandchild, siblings, non-maternal kin related). For each communicative event, we extracted information about the goal (e.g., give me affiliation, groom me, etc.), gesture actions (e.g., Raise, Push, etc.), their sequential use (relative position in the sequence), and evidence for emphasis, persistence, and number of repetitions in gesture actions that allow repetition in their structure (e.g.: Hitting, Stomping). Our coding scheme allowed us to extract detailed information about the timings of different communicative elements such as the sequence duration, Minimum Action Unit (MAU), Performed Action Unit (PAU), and Hold/ Repetition phase (see Figure 11 and next section for further details).

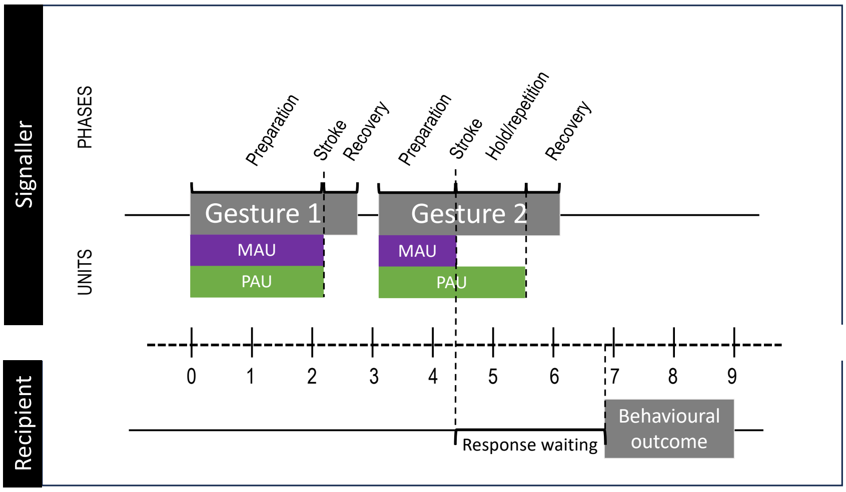


Figure 11. Visualisation of an example of gestural communication including 2 gestures in a sequence, using the GesturalOrigins coding scheme. Each communication is considered as a string of behaviours on a timeline that starts with the gesturing of one individual (the signaller) towards another (the recipient) and ends with a particular behavioural outcome (typically, either the goal of the signalling individual (ASO) or the failure of the communication).

Definitions and Key terminology employed in the study. We defined a gesture as a discrete, mechanically ineffective physical movement of the body observed during periods of intentional communication (Hobaiter & Byrne 2011). In order to be considered intentional, potential gestures needed to be targeted to a particular recipient with the goal of influencing their behaviour in a specific way and had to be accompanied by one or more of the following criteria: audience checking, response waiting, and goal persistence (Bates et al., 1975; Grund et al., 2023; Leavens et al., 2005; Tomasello et al., 1985).

By following the *GesturalOrigins* protocol, each category included in the repertoire (‘gesture form’) was based on the ‘gesture action’ level. Gesture actions correspond to the bodily movements at the core of gesture forms that distinguish every gesture instance. These gesture actions are considered together with additional characteristics that are considered relevant for the study (‘modifiers’), to produce more fine-grained repertoire of units (‘morphs’). For example, considering the modifier ‘repetition’ for the gesture action ‘Stomp’ will result on to the inclusion of two gesture morphs: ‘Stomp’ for gesture instances that do not contain rhythmic repetition, and ‘Stomping’ for the ones that do contain rhythmic repetition. In this study we identified ‘repetition’ and ‘directedness’ as relevant modifiers. From the initial set of 83 gesture actions and according to the selected modifiers (repetition and directedness), we observed 18 gesture actions with gesture morphs, resulting on a repertoire of 101 specific gesture forms. Definitions of the gesture forms included in the repertoire are available in Supplementary materials (Appendix B 1).

The goals were determined based on the Apparently Satisfactory Outcome (ASO, Cartmill & Byrne, 2010; Hobaiter and Byrne, 2014). ASOs correspond to the behavioural reaction of the recipient that seem to satisfy the signaller, in that they represent a plausible desire for the signaller and led to the cessation of communication. We only coded the goals for communications that were associated with changes in the recipient behaviour that were considered successful (i.e., changes that seems to satisfy the signaller). Definitions of the goals included in this study are also available in the supplementary materials (Appendix B 2).

In the dynamic movement that constitutes a gesture, it is possible to identify different stages. Kendon (2004), in his work on co-speech gestures, discriminated four stages in gesture production: preparation, action stoke, hold, and recovery. Taking these stages into account, Grund et al., (2023) identified the: Minimum Action Unit (MAU) that starts at the point the signaller initiates their gesture and corresponds to the smallest possible section of the gesture movement in which the recipient can sufficiently distinguish the specific gesture action being produced (equivalent to the preparation and action stroke stages). Some gesture actions have the option of then being held in place or rhythmically repeated (hold/repetition phase, equivalent to the hold stage). We term the combination of the MAU and the optional hold/repetition phase the: Performed Action Unit (PAU). The PAU ends when the signaller begins to return into a neutral position (recovery stage) or starts a subsequent gesture in a sequence using the same body part.

Data reliability. Inter-observed reliability was conducted on 5 % of the coded gestures. Each gesture form was sampled a proportionate number of times based on how frequently the gesture form was represented in the full dataset. We set a maximum threshold of 7 gesture instances per gesture form, to provide balance across a wide range of gesture actions, and at least one example of every gesture form that was observed more than 10 times. We excluded from the IOR coding gesture forms that were coded fewer than 10 times overall; these ‘rare’ gesture forms were discussed by the coders to ensure that they were coded in a similar way. In order to prioritize clear cases for the IOR coding in which all the variables of interest could be detected, a proportionate sample of 15% of the data for each gesture form was first created, and then clear cases were included from this to make up the 5% sample. A second coder coded the following variables: Gesture action, MAU end point, and PAU end point, Directedness (is the gesture directed to another individual?), Emphasis, Repetition count, and Goal. Perfect agreement was obtained for MAU and PAU durations (ICC=1) (Inter-class correlation coefficient; McGraw and Wong 1996). Agreement was almost perfect for Goal (Kappa=0.874), substantial/almost perfect for Directedness and Gesture record (Kappa=0.799 and Kappa=0.801 respectively), substantial for Repetition count (Kappa=0.699), and fair for Emphasis (Kappa=0.318; Cohen’s Kappa; Cohen 1960).

4.3.3. Models and statistical analysis

Our study explored five gestural features within three different dimensions (complexity, tempo, and prominence) at three levels of potential gestural accommodation (gesture, sequence, and individual; Table 15).

At the gestural level we were interested in the duration of particular phases of the gesture production (gesture units). We focused on (1) the *PAU* and on (2) the *hold/repetition phase*. The PAU corresponds to the section of the gesture that provides information to the recipient (Figure 11). The hold/repetition phase is only possible for some gesture actions and corresponds to a decision to continue the action and may provide information on willingness to wait or persist (e.g., keeping a Reach gesture action in place, or rhythmically repeating a Hit(ting) gesture action). For each gesture we marked whether it was considered to involve *repetition* as a form of emphasis, either because a) there was repetition of the gesture action within an instance of gesturing (e.g., Hitting), or b) because there was repetition of the same gesture form in the sequence of gestures (e.g., Hit, Hit, Hit).

At the sequence level we calculated the *gesture rate* corresponding to the number of gestures per sequence divided by the total sequence duration. Finally at the individual level we calculated the *type/token ratio* that consisted of the number of gesture forms performed by the individual (individual repertoire size) divided by the number of gesture instances (Table 15).

Table 15. Analysis structure. Models (Mod) for each gestural feature with respective datasets and sample sizes (N) for Mother-all and Mother-offspring comparisons.

Dimension	**Level of analysis**	**Gestural feature**	**Mother-all (a)**			**Mother-offspring (b)**		
		Response variable	*Mod*	*Dataset*	*N*	*Mod*	*Dataset*	*N*
Tempo	Gesture	(1) PAU duration	1a	gest.data.a	1206	1b	gest.data.b	535
Tempo/ Prominence	Gesture	(2) Hold/Rep phase duration	2a	gest.data.a	1206	2b	gest.data.b	535
Prominence	Gesture	(3) Use of repetitions	3a	gest.data.a	1206	3b	gest.data.b	535
Tempo	Sequence	(4) Gesture rate	4a	seq.data.a	1035	4b	seq.data.b	346
Complexity	Individual	(5) Type/token ratio	5a	ind.data.a	400	5b	ind.data.b	175

4.3.4. Model specifications

We fitted multiple models to test to what extent predictor variables, such as: recipient age, recipient sex, and kin relationship between the signaller and the recipient influenced the features of the gestural communication. The features included: gesture units' duration (models 1 and 2), use of repetitions (models 3), rate (models 4), and type/token ratio (models 5;Table 15). We used generalised linear mixed models (GLMM; Baayen 2008) with gaussian error structure and identity link function for models 1 and 2, binomial error structure and logit link function for models 3 and 5, and Gamma error structure and log link function for models 4. All models were performed in R version 4.0.2 (R Development Core Team, 2020) using the package lme4 (Bates, 2015).

In the first set of analyses (a) we included all gestures produced by the females to any individual of the community and considered recipient age as a categorical variable with four levels: infant, juvenile, subadult, and adult. For the subset of data used in the second set of analyses (b) including only the gestures that the mothers produced towards their offspring, we included recipient age as continuous variable in years. An exception was made when analysing the type/token ratio used towards their offspring (5b) where relative proportions were required. For this analysis we again considered recipient age as categorical.

In all models, to control for confounding effects, we included social unit as fixed effect into the model. In models 1-4 we also controlled for signaller age. As random effects (intercepts) we included the identity of the signaller, the identity of the recipient, and the goal of the communication. An exception was made for Models 2b and 3b in which we excluded the recipient identity from the random structure because its inclusion explained only very little variance and prevented the models from converging.

Prior to running the models, we z-transformed signaller and recipient age to aid in interpretability (Schielzeth 2010). To control for collinearity, we determined variance inflation factors (VIF; Field 2005; Quinn and Keough 2002) from a model including only the fixed main effects using the function vif of the Rpackage ‘car’ (Fox & Weisberg, 2011). Collinearity was not an issue (maximum VIF = 1.30). To test the overall significance of our key predictor (recipient age; Forstmeier & Schielzeth, 2011) we compared full models with reduced models lacking the key predictor using a likelihood ratio test (Dobson & Barnett, 2018). Tests of the individual fixed effects were derived using likelihood ratio tests (R function drop1 with argument ‘test’ set to ‘Chisq’).

4.4. Results

In total we included 1206 gesture tokens produced by chimpanzee mothers towards any individual of the community, of which 550 were directed to their offspring (Table 16). From the repertoire defined in our coding scheme, females used approximately half of the gesture forms available (n=53/101). Sonso mothers produced 735 tokens in 43 gesture forms, of which 407 tokens in 28 gesture forms were directed towards their offspring. After inspecting the cumulative frequency of gesture forms produced by the Sonso mothers, our sample repertoire had reached asymptote within our observed contexts (overall gestures: 613; gestures towards offspring: 307;Appendix B 3;Appendix B 4). Bossou mothers produced 471 tokens in 42 gesture forms, of which 143 tokens in 26 gesture forms were directed towards their offspring. Our sample repertoire for the Bossou mothers did not reach the asymptote within our observed contexts for the gestures produced to any individual in the community (n=577); but reached asymptote in the subset of gestures directed towards their offspring (n=109;Appendix B 5;Appendix B 6). Results regarding full models (estimates, standard errors, significant tests and confidence intervals) are available in the supplementary materials (Appendix B 7-Appendix B 12).

Table 16. Number of gesture actions and tokens produced by each focal female. The number of tokens is indicated per category of the recipient attributes (recipient age and sex) and kin relationship analysed. Recipient age includes the following categories: infant (Inf), juvenile (Juv), subadult (SubAd), and adult (Ad). For kin relationship we indicated the number of tokens for non-kin and kin individuals, specifying the tokens directed towards offspring in brackets.

Focal	**Gesture forms**	**Tokens**	**Recipient age**				**Sex**		**Kin**	
			Inf	**Juv**	**SubAd**	**Ad**	**Females**	**Males**	**Non-kin**	**Kin (Offspring)**
DL	8	44	26	4	0	14	39	5	15	29 (29)
FL	19	47	11	12	1	23	5	42	5	42 (23)
FN	20	59	14	15	5	25	26	33	29	30 (20)
FT	23	61	22	23	0	16	20	41	26	35 (22)
HT	17	68	17	44	1	6	44	24	15	53 (37)
JL	14	51	0	30	5	16	29	22	22	29 (0)
JN	12	32	8	16	1	7	9	23	7	25 (25)
JR	26	136	36	56	12	32	61	75	97	39 (39)
KA	25	84	33	22	12	17	47	37	42	42 (32)
KL	20	96	42	29	8	17	33	63	23	73 (73)
KU	13	79	25	40	2	12	8	71	19	60 (60)
KW	13	56	18	13	12	13	32	24	18	38 (38)
KY	8	18	10	1	0	7	13	5	5	13 (12)
MK	8	25	1	2	9	13	10	15	24	1 (1)
NB	21	100	7	56	5	32	66	34	33	67 (67)
NN	10	31	14	0	3	14	17	14	25	6 (6)
PL	3	3	1	2	0	0	2	1	2	1 (1)
PM	11	28	6	7	0	15	12	16	25	3 (3)
RH	5	11	1	4	0	6	5	6	4	7 (7)
RM	11	22	17	1	0	4	21	1	5	17 (15)
RS	18	36	3	10	10	13	26	10	27	9 (0)
VL	9	18	6	4	1	7	6	12	16	2 (2)
VV	9	24	13	7	2	2	16	8	11	13 (12)
YO	17	64	25	23	2	14	30	34	64	0 (0)
ZM	4	13	0	5	6	2	0	13	2	11 (11)

4.4.1. Mother-all individuals

Chimpanzee mothers adjusted the duration of the Performed Action Unit (mean PAU duration=2.48 seconds, sd=2.71, and range=0.15-34.77) to their recipient (full-null model comparison: χ^2=25.557, df= 5, p<0.001). We found a significant effect of recipient age (F=4.917, df=3, p=0.002) with chimpanzee mothers using shorter PAUs towards juveniles as compared to adults (estimate=-0.335, z=-3.761, p=0.001,Figure 12), and longer PAUs towards kin, as compared to non-kin, individuals (F=14.686, df=1, p<0.001;Figure 13). Recipient sex did not influence the duration of PAUs (F=1.542, df=1, p=0.218).

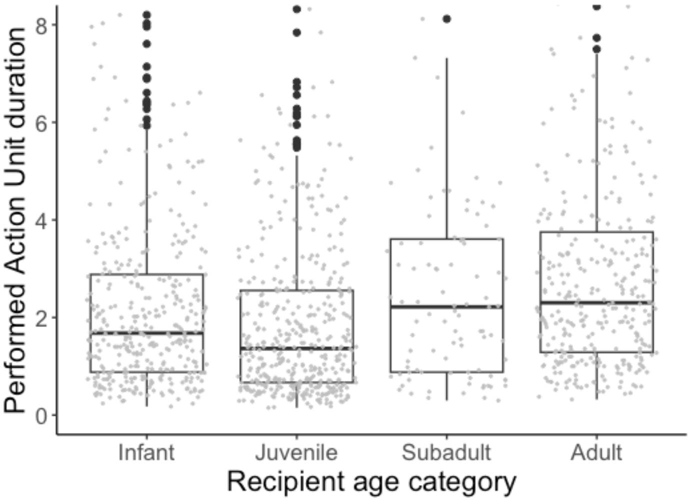


Figure 12. The duration of the Performed Action Units separately for each recipient's age category. Some outliers were cut to improve readability in the main section of the plot.

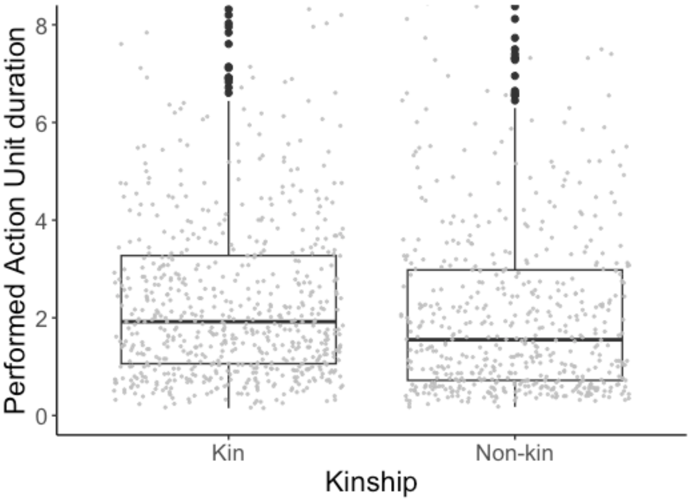


Figure 13. The duration of the Performed Action Units towards kin and non-kin individuals. Some outliers were cut to improve readability in the main section of the plot.

Of the 1206 gesture tokens included in this study, 894 had a hold/repetition phase (mean duration=1.41 seconds, sd=2.45 and range=0-32.22). Chimpanzee mothers also showed accommodation of the duration of the hold/ repetition phase depending on their recipient (model 2a: full-null model comparison: χ^2=15.502 df=5 p=0.008), in particular with recipient age (F=5.335, df=3, p=0.001, Figure 14). Signallers used gestures with shorter hold/repetition phases towards infants and juveniles as compared to adults (estimate=-0.39336, z=-3.195, p=0.008, and estimate=-0.37433, z=-3.204 p=0.008 respectively) and subadults (estimate=0.44820, z=2.858, p=0.017, and estimate=0.429 z=2.828, p=0.017, respectively). Recipient sex and kinship did not influence the duration of the hold/repetition phase (F=0.831, df=1, p=0.366, and F=3.998, df=1, p=0.046, respectively).

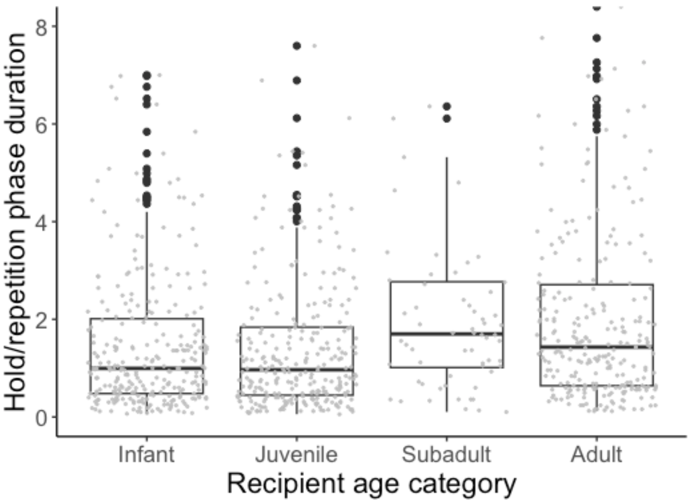


Figure 14. The duration of the hold/repetition phase separately for each recipient age category. Some outliers were cut to improve readability in the main section of the plot.

The use of repetitions varied with the recipient (full-null model comparison: χ^2=25.28615, df=6, p<0.001). Mothers were less likely to use repetitions when gesturing towards non-kin individuals (χ^2=5.572 df=1, p=0.018; Figure 15).

Chimpanzee mothers produced a mean = 1.27 gestures per sequence (sd=0.68, range=1-9) and their sequences lasted a mean=3.36 seconds (sd=3.50, range=0.33-39.76). Chimpanzee mothers adjusted their gesturing rate (number of gestures per sequence divided by the sequence duration) towards their recipients (χ^2=13.949, df=5, p=0.016), gesturing faster towards non-kin individuals when compared to kin-individuals (χ^2=10.905, df= 1, p<0.001; Figure 16). Recipient age and sex did not influence mothers' gesturing rate (χ^2=2.931, df=3, p=0.402 and χ^2=0.622, df=1, p=0.430 respectively).

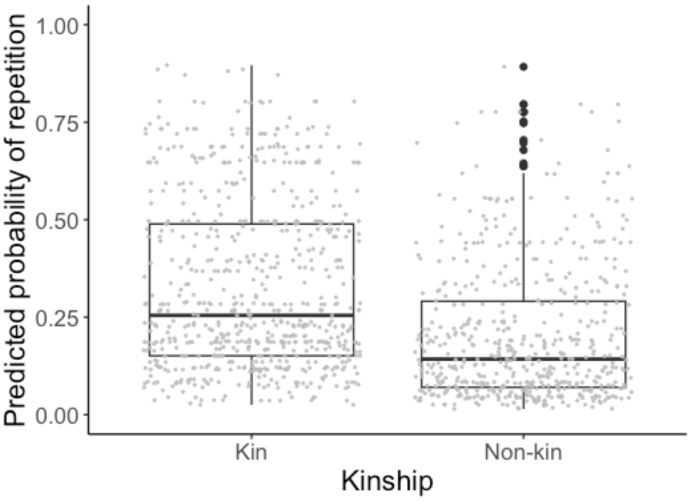


Figure 15. Predicted probability of using repetitions towards kin and non-kin individuals. Some outliers were cut to improve readability in the main section of the plot.

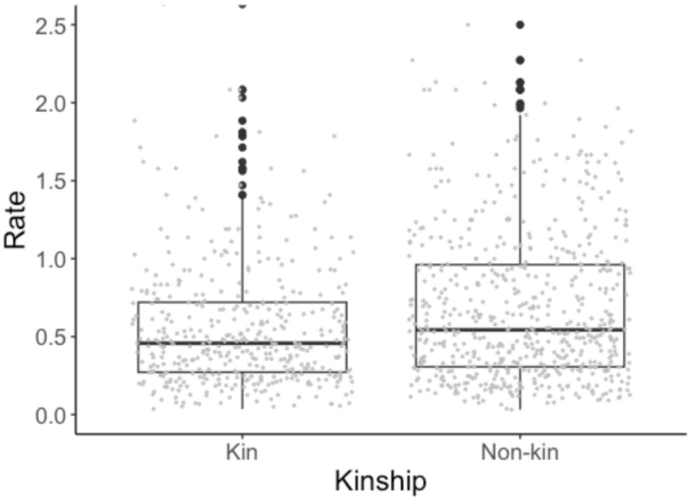


Figure 16. Rate of the mothers' gestural communication (number of gestures per sequence divided by the sequence duration) towards kin and non-kin individuals. Some outliers were cut to improve readability in the main section of the plot.

Mothers also adjusted their type/token ratios to their recipient (full-null model comparison: χ^2=31.586, df= 5, p<0.001), including to both their age (χ^2=11.299, df=3, p=0.010, Figure 17) and their kin relationship (Figure 18). Mothers used a more diverse set of gesture forms when gesturing towards subadults as compared to adults (estimate=0.6699, z-value=2.655, p=0.0476), and in communication directed towards non-kin individuals as compared to kin individuals (χ^2=17.134m df=1, p<0.001).

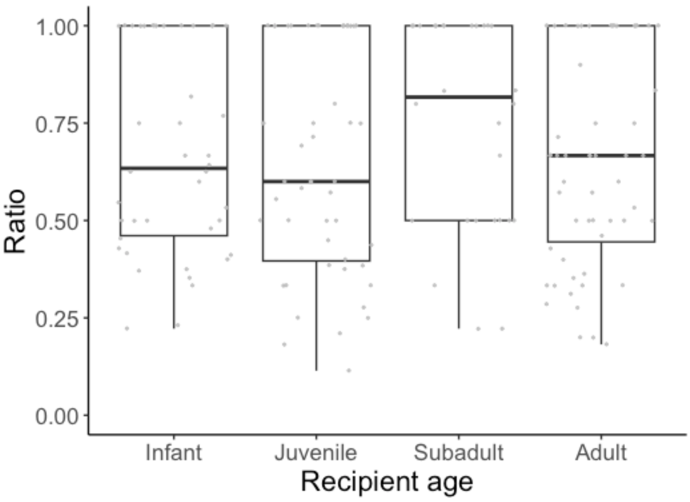


Figure 17. Ratio of distinct gesture actions used towards recipients of different age categories.

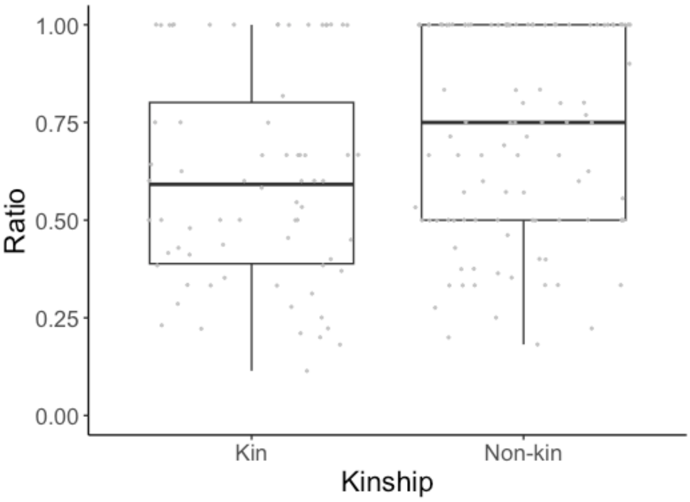


Figure 18. Ratio of distinct gesture actions used towards kin and non-kin individuals.

4.4.2. Mother-offspring pairs:

Of the 1206 gestures included in this study, 550 were directed by chimpanzee mothers towards their offspring. Mothers did not adjust the PAU duration, nor the hold/ repetition phase duration to the sex or the age of their offspring (full-null model´s comparisons: χ^2=0.821, df= 2, p=0.663 and χ^2=1.933, df= 2, p=0.38 respectively). However, the use of repetitions did vary (full-null model comparison: χ^2=10.036, df=2 , p=0.007), with increasing use of repetitions with the increasing offspring age (χ^2= 5.648, df=1, p=0.017, Figure 19).

We analysed 360 sequences produced by mothers towards their offspring. The gesturing rate did not vary with the offspring attributes (full-null model comparison: χ^2=0.261, df=2, p=0.878).

Mothers adapted the type/token ratio, to their recipient attributes (full-null model comparison: χ^2=14.451, df= 4, p=0.006), namely to their age (χ^2=12.170, df=3, p=0.007, Figure 20). Mothers used a more diverse set of gesture actions towards subadults when compared to juveniles (estimate=0.823, z-value=3.397, p=0.005).

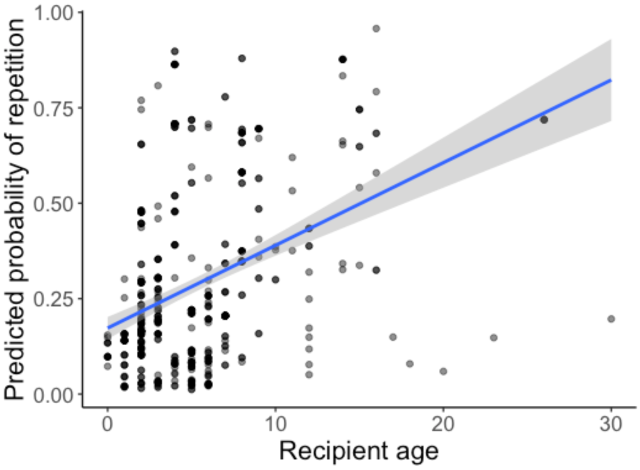


Figure 19. Predicted probability of using repetitions with the increasing age of the offspring.

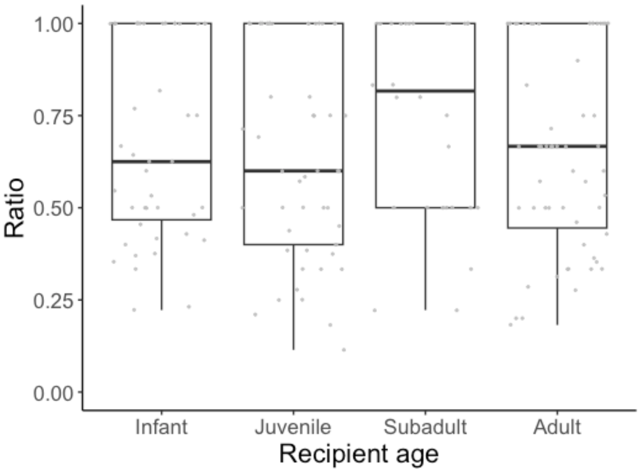


Figure 20. Ratio of distinct gesture forms used towards offspring of different age categories.

4.5. Discussion

Chimpanzee mothers adjusted the expression of their gestural communication to the age of their recipient and with their kinship relationship, but not to the sex of their recipient. Across recipients, mothers used shorter units towards immature individuals, and used more diverse gesture repertoires towards subadults as compared to adults. Their kinship relationship with the recipient impacted a range of features: mothers used shorter PAUs, communicated at a faster pace with a more diverse set of gesture forms, and were less likely to use repetitions towards non-kin individuals. When focusing on the subset of communication directed towards their offspring, chimpanzee mothers were more likely to use repetitions towards older offspring and used a more diverse set of gesture forms towards their subadult offspring (as compared to juveniles).

The lack of any effect of recipient's sex on gestural expression suggests that this may not be a particularly salient feature for mothers to adapt the expression of gestural communication. It may, instead, be more critical to adapt other social behaviour in which communication occurs – such as gregariousness. A mother might have more prominent impact on their offspring’s development by changing the number and range of available social partners through selective subgrouping (Murray et al., 2014). A recent study focusing on gesturing through development analysed broader aspects of the communication and found that immature males tend to employ a larger repertoire as compared to immature females (Fröhlich et al., 2017). These communicative differences might be a consequence of mothers’ behavioural adjustments to the social dynamics impacting the opportunities immature individuals have to communicate. By socialising more, immature males may have more opportunities to interact with a range of different social partners and may be deploying a wider range of their repertoire as a result.

The age of the recipient influenced some of the gestural features analysed in this study, but in the opposite direction to that predicted from the use of child-directed communication in human languages, for example: mothers produced shorter gestural units towards immature individuals. They produced shorter Performed Action Units (the full duration of the gesture, excluding the recovery phase) and, within this, shorter hold/repetition phases towards infants and juveniles as compared to towards adults and subadults. In combination, this suggests that mothers were shortening the optional aspects of gesture production (holds and repetitions).

A possible explanation for this counter-CDC pattern, may relate to gestural complexity. We used gesture unit durations as a proxy for temporal patterns, predicting that – as in child-directed communication – mothers would use longer units towards younger individuals. However, the dimensions usually explored in child-directed communication (and in immature-directed communication in other animals) such as the ones investigated in this study (complexity, tempo, and prominence) are likely intertwined. For example, hold/repetition phases may be a measure of tempo but also of prominence (gestures with a long hold/repetition phase are likely to be more prominent). Similarly, hold/repetition phases may also encode complexity, but here with the opposite logic that longer gestures including hold/ repetition phases might be more complex, encoding information in addition to the core meaning of the gesture action. There may be subtle differences between rhythmic repetition within a single gesture instance (Hitting), and the repetition of a simple unit (Hit) several times in a sequence. The choice of using a gesture action with repetition is made *a priori* by the signaller, while repeating a gesture action afterwards (outside the rhythmic pattern) may be an *a posteriori* decision – perhaps the result of persistence when the recipient doesn't change their behaviour in a satisfactory way. Mothers may opt for these more complex variants when interacting with older individuals but prefer to use simpler structures (in the form of shorter gestures) towards immature individuals to avoid misunderstanding.

Interestingly, when analysing the subset of communication between mothers and their offspring we did not find any effect of the recipient age on these temporal aspects. It is possible that this trend only emerges in larger datasets or that it might be driven by non-kin individuals with whom the mother is likely less familiar and interacts with less frequency. Despite the secure and tolerant environment provided by the mother that encourages their offspring to explore and develop various skills, individuals beyond the mother-offspring pair can represent a significant risk – up to and including infanticide (Lowe et al., 2020) – that may have a significant impact on their communication. In fact, researchers found higher interaction rates with nonmaternal individuals were associated with an increase in gesture frequency and repertoire size of immature chimpanzees, while interaction rates with the mother had no effect (Fröhlich et al., 2017). In rhesus macaques, it was observed that females employed distinct vocalizations to communicate with the infants of other females, but not with their own offspring (Whitham et al., 2007). The authors proposed that these vocalizations might serve as a signal of 'friendly intent' before engaging in social interactions with the infants, and clear communication of this intent might be more important from non-kin related individuals. Similar pressures may be acting on the chimpanzee mothers, who incorporate a diverse set of short gestures at a faster pace without repetitions when communicating with non-kin individuals, perhaps for clarity or efficiency.

The use of shorter gestures towards younger individuals may also relate to efficiency: mothers may prefer to be more efficient when communicating with immature individuals. They may also employ less response waiting and move to simply achieving a goal through effective means – for example: picking up an infant, or pushing a persistent juvenile out of the way. Similarly, the lack of an effect of recipient age within the subset of offspring could be attributed to the close physical proximity females have with their own offspring, again, allowing them to carry out actions directly. The finding that mothers employ shorter gestures with immature individuals and longer gestures with kin individuals, suggests that an interaction between kinship and recipient age might also counterbalance the effect of these features in mother-offspring communication, as compared with mothers' communication to partners in the community in general.

Chimpanzee mothers communicated with a more diverse set of gesture forms and were less likely to use repetitions towards non-kin individuals. Here mothers may be opting for more efficient communication towards non-kin individuals, not only by using short units but also at a faster pace. Gestural repertoires of great apes are currently far larger than the set of identified goals (e.g., Cartmill and Byrne 2010; Genty et al. 2009) and contain substantial redundancy (Graham et al., 2018; Hobaiter & Byrne, 2014). The use of a smaller set of gestures with kin may suggests that the use of something like a within-family 'dialect' in which the same forms are used with individuals with whom they have more familiarity or shared common ground.

Chimpanzee mothers used a particularly diverse set of gesture forms towards subadults, a trend that held even with their own offspring. Sub-adulthood corresponds to a potentially stressful period in chimpanzees during which they become independent from their mothers and cannot count on their mothers' constant support. New challenges emerge with the need to adapt to different social dynamics within their group. Males are forming new relationships and taking on new roles in the social hierarchy (Goodall, 1986; Newton-Fisher, 2004), and females will be starting to consider emigration to other communities. Both sexes will be involved in novel contexts as a result, including a wider range of sexual and social behaviour. In these circumstances, new goals for communication emerge, creating the opportunity and the need for different gesture types, both for the subadult signallers, and for the other community members that communicate with them.

Finally, and perhaps a little surprisingly, chimpanzee mothers were more likely to use repetitions when communicating with older offspring. Here, again, an interaction between kinship and recipient age may exist, as we did not find this trend in communication with older individuals in general. The repetitive patterns usually found in child-directed communication (more repetition towards younger individuals) have been described in other great apes (Luef and Liebal 2012). However, repetition is a broad term that may include repetitions within the gesture action (e.g., Hitting), with the same sequence; and after response waiting in different bouts. In humans, repetitions may have different purposes, for example: repetition may be related to word learning and vocabulary in children, but also to a lack of comprehension by the recipient (Schwab & Lew-Williams, 2016). In the current study, we included all types of repetitions, and it may be helpful in the future to discriminate the different types of repetitions in case they serve distinct functions or convey different information.

This study shows that chimpanzees do accommodate their communication when interacting with immature individuals, suggesting that this ability is evolutionarily older, and was likely present in a last common ancestor. However, the way in which chimpanzees accommodate their communication differs from what has been described in human languages (and in the child-directed communication register in particular). This difference might be the result of accommodation being shaped by different evolutionary pressures. One potential function of accommodating your communication is to signal social closeness or distance to a partner. For example, neighbouring groups of wild chimpanzees seem to have more distinct pant-hoots, compared to more distant groups that differed only randomly. This pattern suggests that demarcation of group distinctiveness may be more important for neighbours, than for complete strangers (Crockford et al., 2004).

Adding to the social function of accommodation, there are other social pressures known to impact chimpanzee communication, such as dominance relationships not only among those directly involved in the communication, but also among individuals in the audience nearby. For example, the higher rank of a partner or the presence of higher-ranking individuals in the audience can influence the likelihood of communication taking place (Laporte & Zuberbühler, 2010; Rodrigues et al., 2022). Within chimpanzee societies, the function of signalling social distance or other aspects of hierarchical relationships may be even more prevalent than other functions of accommodation and, in this particular case, more important than one of the most commonly described function for child-directed communication: facilitating learning (Ruch et al., 2018).

Finally, it is likely that the different features of individuals analysed here (their age, sex, and kinship) and the relative relationship between mothers and the individuals they communicate with represent different social contexts for communication in chimpanzees as compared to humans. In chimpanzees, the kinship and age of your recipient clearly plays an important role in the expression of gesturing. Future studies may help disentangle the contribution of the different communicative attributes and relationships here by including their interactions in larger datasets. There remain many other aspects of gestural communication (and other co-occurring modalities) in which accommodation could be fruitfully explored. By showing that accommodation can manifest at a more detailed level, we hope to encourage future research to explore additional communicative features.

CHAPTER 5: Toddler gestural accommodation in Portuguese nursery schools

This chapter is based on Rodrigues, E. D., Hobaiter, C., Henderson, M., Grund, C., & Santos, A. J. Toddler gestural accommodation in Portuguese nursery schools. Manuscript submitted for publication. Results were also presented at Scottish Primate Research Group meeting, Edzell, Scotland (2023).

5.1. Abstract

This study investigated whether toddlers accommodate their gestures to partners of different ages. Video data from 53 toddlers (410-1080days, 27boys) were collected during free play time in 3 Portuguese nursery schools. Toddlers adjusted their vocabulary complexity and the temporal patterns of their gestures to the recipient's age, but did not change their prominence. Toddlers communicated with younger peers at a slower pace and using a simpler vocabulary, following child-directed communication patterns. However, when comparing adult-directed with peer-directed communication, toddlers used a more diverse set of gestures and shorter gestures. This study suggests that our ability to accommodate our communication emerges before language is fully developed, and that accommodation is flexibly expressed as a result of intersecting features of social partners.

Keywords: Child-directed communication, Gestural accommodation, Toddlers

5.2. Introduction

A central aspect of developing social competence is the ability to adjust one's behaviour to myriad nuances within the social environment, including to features of our social partners' identity and behaviour (Brownell & Carriger, 1990). Communicative behaviour is no exception: we accommodate speech and gestures to our partners' characteristics and relationships (Giles et al., 1987). Adults do so at a broad level by employing different signals: for example, we may greet a friend with a hug or a kiss, but with a stranger, we might shake hands; and, in some circumstances and cultures, people bow or kneel before a powerful person as a sign of respect. We can also modify more subtle features of our communication such as complexity (degree of elaboration), tempo (speed), and prominence (notability; Biersack et al., 2005; Snow, 1977). These adjustments can be almost imperceptible at times and may be processed at a subconscious level. For example, when we communicate with speakers who do not share our first-language (so called: 'foreigner-directed speech'), we tend to speak more slowly, and to articulate our words more clearly (Biersack et al., 2005; DePaulo & Coleman, 1986).

Another well-known example of linguistic accommodation in our daily life is the special register (communicative style) we use when talking to young children, often referred to as infant-directed speech, child-directed speech, babytalk, or motherese (Ferguson, 1964; Snow, 1977). Infant-directed speech is typically characterized by the use of a higher and more variable pitch, simpler vocabulary, more repetition, and a slower rate (Fernald et al., 1989; Snow, 1977). Argued to facilitate language acquisition and to promote social bonding, these adjustments have been reported across a wide variety of different cultures and languages (Fernald et al., 1989; Kitamura et al., 2001; Masataka, 1992). However, which features are present, as well as the nature and quantity of input given to children varies across cultures (e.g., Loukatou et al., 2022; Soderstrom, 2007). In some cultures, children are rarely directly addressed and yet they rapidly acquire language, suggesting that while infant-directed speech is important in many cultures, it is not essential for language development (Lieven, 1994; Ochs & Schieffelin, 1984). Infant-directed speech is not the primary (let alone exclusive) source of linguistic input for young children (Soderstrom, 2007) and investigating the influence of other environmental aspects that affect language development is crucial in furthering our understanding (Hoff, 2006; Oshima-Takane et al., 1996; Schick et al., 2022).

The use of a special linguistic register towards young children is found in both spoken and signed languages. When signing with young infants, adults tend to repeat utterances, use more exaggerated signs, and sign at a slower tempo, including the use of longer signs (Holzrichter & Meier, 2000; Masataka, 1992). Infant-directed language – both spoken and signed – is also accompanied by other non-linguistic adjustments, such as more exaggerated facial expressions (Kim & Johnson, 2013; Reilly & Bellugi, 1996) and modified patterns of body motion ("motionese") that involve using movements that are larger in scale but reduced in complexity (i.e., with small and simple action units, Brand et al., 2002). In addition, adults tend to modify their use of para-linguistic gestures in infant-directed communication ("gesturese"): when communicating with infants, as opposed to other adults, adults reduce their use of gesture overall (in particular using fewer beat gestures: non-meaningful movements, typically biphasic and produced with the hands or head accompanying the rhythm of the speech); but do increase the use of gestures indicating an external referent (deictic gestures; Bekken, 1989; Iverson et al., 1999; O'Neill et al., 2005).

But when and how does the ability to accommodate our communication emerge? Our cognitively sophisticated ability to accommodate our behaviour according to our social relationships was likely built on a set of ontogenetic precursor abilities already in place, such as the ability to distinguish different partners, to remember the result of previous interactions, and to use different signals to achieve the same goal. These abilities seem to emerge early in infancy, for example, toddlers (1-3 year-olds) can remember previous interactions with different partners (Hawley, 1999; Hinde, 1976) and adapt their behaviour according to the partner's social characteristics, including age, gender, interaction style, and expertise (Brownell & Carriger, 1990; Kachel et al., 2021). Toddlers' ability to use different signals to achieve the same goal is another indicator of communicative flexibility (Bates et al., 1975; Kersken et al., 2018). Early in ontogeny they seem broadly sensitive to both their partners' age and differences in their 'social competence' (here defined as: the ability to evaluate social situations and determine what is expected or required in a given context; APA Dictionary of Psychology, 2023). Fourteen-month-old children already demonstrate an impressive set of skills to seek, elicit, and employ information from individuals with differing levels of competence (Chow et al., 2008; Zmyj et al., 2010). As these interactions are shaped by different expectations of different partners who have different motivations, the way toddlers respond to peers and adults also differs, for example: giving them back different things in response to the same request (Franco et al., 2009; Kachel et al., 2021). Moreover, toddlers seem to be sensitive to relatively small differences in age, already ascribing different interpersonal qualities and competences to peers of different ages, and adjusting their behaviour accordingly (Brownell & Carriger, 1990;

Franco et al., 2009). In sum, young children seem already able to adapt their communication in similar ways to the patterns described in adult use of infant-directed speech. Preschool children use shorter utterances, less complex structures, and more repetition when communicating with younger partners (Sachs & Devin, 1976; Shatz & Gelman, 1973), and take their listeners' linguistic capacity into account, making adjustments when communicating with younger peers (Shatz & Gelman, 1973). Dunn & Kendrick (1982) found similar patterns in even younger infants. When communicating with infant siblings, children as young as two-years old increased their use of attention getting utterances, made their speech shorter in duration, and used fewer exchanges and more repetition. Some infant-directed speech features used by adults have not, yet, been observed in children, for example: 4-year old children spoke more slowly and used shorter words, but did not modify their pitch (Weppelman et al., 2003).

As young children are still learning to master language, there may be limits on the way in which they can adjust their speech and sign. But, as shown in adults, adjustments may also be present in communicative behaviour outside of language. Given that children remain predominantly nonverbal until well into their third year (Eckerman et al., 2001) it is important to consider adjustment across non-linguistic communicative expression. One prominent form of communication in toddlers is gesture use, and its role in linguistic development prior to and accompanying speech is well described (Bates et al., 1975). As a result, early spontaneous gestures represent an ideal – and to date untested – system in which to explore the emergence of accommodation skills in early ontogeny.

The goal of the present study was to make a first attempt to investigate the emergence of accommodation and child-directed communication within the naturalistic gesturing of toddlers. We opted for the term 'child-directed communication' for two main reasons: the word 'communication' aims to capture the multichannel nature of the diverse modifications beyond spoken language use; and we use the word 'child' to include the communication directed towards toddlers (as opposed to only infants younger than 1-year old). We examined whether toddlers adjust their gesturing to their recipients' age, suggesting the use of a child-directed communicative register. To do so, we compared toddlers' adult-directed and peer-directed gestures during periods of free play. We then focused on gestures directed to peers and explored whether toddlers were sensitive to more fine-grained age differences in their communication towards younger and older peers. We explore three dimensions frequently studied in child-directed communication: vocabulary complexity, temporal patterns, and prominence. To measure vocabulary complexity, we focused on the diversity of gesture forms and on the use of gesture sequences. To explore variations in tempo we analysed changes in gesture duration and gesture rate (number of gestures per sequence divided by the sequence duration). Finally, to assess prominence, we looked at the likelihood of using repetition and incorporating objects in gesturing. We predict that toddlers will use simpler vocabulary, will gesture more slowly, and will use more prominent gestures when directing their gestures towards younger individuals (towards peers as compared to adults, and towards younger, as compared to older, peers).

5.3. Methods

5.3.1. Participants

Formal collaborations were established with three nursery schools, comprising four groups of toddlers (Table 17), from the wider Lisbon area. The parents of these toddlers received information on the project and were asked for written permission for their child to participate in the study. Informed consent was obtained for all the toddlers from the four groups (n=63). To be included in the study, toddlers had to meet the following criteria: they had to be typically developing children aged between 367 days (12 months) and 1101 days (36 months) at the beginning of the observational period. In addition, they had to be present on at least two of the days in which observations took place. In the end, a total of 53 toddlers (27 boys; 26 girls) between the ages of 410 days and 1080 days were included in the current study (Appendix C 1).

Table 17. Characteristics of the study groups (sample size, gender, and age range in days) and observation time (period of data collection). Each group was identified by the nursery school in which data were collected, and for the two groups from the same nursery school (Voz do Operário da Graça), the room was also specified (s3 and s4). As some toddlers were not included in the study, the size of the whole group (N group) and the number of toddlers included in the study (N this study) are indicated.

Nursery school/ group	N group	N (this study)	Number of boys (this study)	Age range (days)	Period of data collection
Voz do Operário da Ajuda	12	11	6	410-912	06-14/12/2021
Voz do Operário da Graça – s3	16	14	6	499-841	02-10/05/2022
Voz do Operário da Graça – s4	18	12	6	846-1052	14-24/02/2022
Voz do Operário do Laranjeiro	17	16	9	472-1080	17-25/01/2022

5.3.2. Data collection

Data collection occurred between December 2021 and May 2022 (Table 17). In each nursery school the period of data collection (approximately two weeks) was preceded by a week of habituation in which the researcher collecting the data (EDR) was present for the daily routines and collected ad libitum videos so that the toddlers could become accustomed to her presence and that of the camera. Interactions between the researcher and the toddlers were avoided wherever possible in order to minimise any interference with the toddlers' typical behaviour and the daily routines of the nursery school. The toddlers were free to move around the playground, which contained a range of toys located on the floor or in specific containers, as well as play-structures. In addition to the researcher, there were always one to three adults known to the toddlers in the play area (one teacher and two classroom assistants).

Video-footage was collected during playtime (mostly indoor) throughout the day using 5-min focal sampling (Altmann, 1974; Hawley & Little, 1999). We included 30 minutes of video per child (six 5-min focal periods), providing a total of 1590 minutes of observation.

5.3.3. Data coding and definitions

We coded each child's gesture use from the video data following a bottom-up approach that minimises a priori structural choices and inferences about gesture form and function (*GesturalOrigins*; Grund et al., 2023). The framework is implemented in the linguistic coding software ELAN 6.4 (*ELAN*, 2022) and the protocol and definitions are described in detail in Grund et al. (2023). Gestures were defined as discrete, mechanically ineffective physical movements of the body (including the whole body, limbs, or head) observed during periods of intentional communication (Hobaiter & Byrne, 2011b). Intentional communication was defined as communication deliberately targeted to a particular recipient, with the aim of influencing their behaviour in a specific way. In order to be considered intentional, potential gestures needed to be accompanied by one or more of the following criteria: audience checking, response waiting, or goal persistence (Bates et al., 1975; Grund et al., 2023; Leavens et al., 2005; Tomasello et al., 1985; Table 18).

We employed the following features in analyses: the signaller and recipient ID, age, and gender; gesture actions (e.g., Embrace, Grab, etc.) and their morphological aspects including emphasis, object contact, and object use, their structural aspects including the number of gestures per sequence and persistence; and finally, their temporal aspects including durations for individual gesture tokens (Performed Action Unit duration) and of sequences of gesture tokens (Table 18 for full definitions). We first considered gestures at the level of Gesture Actions (Table 18). The 52 Gesture Actions we observed were then further refined to more specific Gesture Morphs through the inclusion of two modifiers – repetition (e.g., Stomp vs Stomping) and directedness (e.g., Present vs Present directed); resulting in a repertoire of 67 gesture forms (Table 19). A wide range of modifiers can be considered in the description of specific gesture forms, resulting in finer and finer grained splitting. The decision of which level of granularity to consider was driven by both the available data density (if every possible modifier is applied very few cases of each morph are available, limiting analyses) and by the relevance of specific modifiers. Here we selected rhythmic repetition and directedness as both have been shown to be salient in children's gesturing (Kersken et al., 2018; Liszkowski, 2010; Murillo et al., 2021).

Table 18. Definition of key terms and coded features. Terms employed follow the GesturalOrigins framework (Grund et al., 2023).

Term	Definition
Gesture action	Bodily movement that describes the current gesture instance. Each gesture form has an action movement at its core that distinguishes every gesture instance. These gesture actions are considered together with additional modifiers to produce more fine-grained gesture morphs. For example, the gesture form 'Present directed' corresponds to the gesture morph that results from the gesture action 'present' with the modifier 'directedness'.
Modifiers	Additional characteristics considered with the gesture actions that can be used as building blocks to further specify the observed behaviour, allowing for flexibility in constructing repertoires of gesture forms at different levels of granularity. In this study two modifiers were considered: rhythmic repetition and directedness.
Performed action unit (PAU)	The relevant and informative section of the gesture that includes the Minimum Action Unit (MAU) plus an optional hold or repetition phase. The PAU starts with the body part performing the gesture moving from its neutral state (or a previous gesture in a sequence) to perform the gestural movement and ends as soon as the signaller starts to return it into a neutral position (or, alternatively, starts a subsequent gesture in a sequence using the same body part). This means the PAU does not include the recovery phase that corresponds to the body part performing the gesture returning into its neutral position.
Minimum Action Unit (MAU)	The smallest possible section of the gesture movement in which the recipient can sufficiently distinguish the specific gesture action being produced. The MAU starts at the point when the signaller starts moving from neutral position (or a previous gesture in a sequence) and ends when the gesture action is fully in place.
Neutral position	When the body part involved in gesturing is at rest or used in non-communicative behaviour before and after its employment in gesturing.

Repetition gestures	In addition to the MAU, these gestures (e.g., Hitting, Stomping) include a rhythmic repetition phase in their gesture production. These gestures are distinguished from multiple single gestures (e.g., Hit, Stomp) by the rhythmic nature of the repeated movement.
Repetition count	Where gesture actions could be rhythmically repeated, we counted the number of repetitions.
Emphasis	Where two gestures of the same form are used with a communication, we indicate whether a gesture is produced with more or less energy invested into it (for example in terms of the size or speed of the movement) as compared to the previous examples.
Object contact	Indicates whether the signaller made contact with an object during the gesture.
Object use	Indicates whether an object was manipulated in order to produce the gesture.
Sequence	All gestures produced with less than 1-second between them. The 1 second is measured from the end of the MAU. Sequence duration is measured from the start of the first gesture to the end of the last gesture of that sequence, and thus includes both the gestures and any brief pauses in the sequence.
Audience checking	The signaller checks the recipient's state of visual attention before the production of the signal
Gaze before	The signaller looks in the direction of the recipient before starting a sequence of gestures
Gaze during	The signaller looks in the direction of the recipient while producing a sequence of gestures
Response waiting	The signaller pauses and waits for the recipient to respond to signaller's request. Pauses indicating response waiting must last for at least 1-second from the end of the last MAU in a sequence.
Persistence	The signaller continues to signal after response waiting and persists (same gesture forms) or elaborates (novel gesture forms) with more gesturing when the recipient does not respond or responds in a way that does not appear to satisfy them.

Table 19. Gesture action definitions and the frequency with which they were directed towards Adult and Peer recipients, distinguishing between older and younger peers. Forty-five gestures were directed to peers that could not be identified and are not included in the older/younger totals.

Gesture action	**Definition**	**Adult**	**Peer**	**Peer**	
				Older	**Younger**
Beckon	A scooping movement from one or more of the signaller's joints (e.g., fingers, wrist, elbow)	1	5	3	0
Bite	Signaller's mouth/teeth close on the recipient's body	0	5	3	1
Bite: Kiss	Gentle contact with the signaller's mouth that doesn't hold the recipient's body (see 'Bite')	0	2	0	2
Bounce	Rhythmic vertical up-down movement of the signaller's body.	16	13	6	6

Bow	Signaller bends forward from the waist.	4	1	1	0
Clap	Signaller moves both palms towards each other which are brought together with audible contact (may be repeated).	6	5	3	2
Crouch	Signaller lowers body by bending knees	1	5	3	1
Embrace	Signaller wraps one or both arms around recipient	4	6	2	4
Fling	Rapid movement of hand or arm away from the signaller's body, typically towards recipient	0	19	8	11
Grab	The signaller's hand is firmly closed over part of the recipient's body	2	19	6	11
Grab Hold	Same as 'Grab' but hand of signaller stays closed around recipient's body for at least 2 seconds	0	4	3	0
Hit(ting) Object/Ground [1]	Signaller makes a short hard contact with the ground/object	3 (3)	5 (6)	2 (2)	3 (2)
Hit(ting) Object/Ground with Object [1]	An object is brought into short hard contact with another object or ground	2 (1)	4 (3)	0 (1)	4 (2)
Hit(ting) Other with Object [1]	Same as 'Hit other', but the hand holds an object which is brought into contact with the recipient’s body	5(0)	9(6)	4(3)	5(3)
Hit(ting) Object/Ground Soft [1]	Same as 'Hit object/ground' but contact is gentle (as in tap, pat etc.)	2 (13)	6 (7)	0(5)	6(2)
Hit(ting) Other [1]	Same as 'Hit object/ground', but signaller makes deliberate contact with recipient as part of action	1(1)	16 (6)	11 (4)	5(2)
Hit(ting) Other Soft[1]	See 'Hit object/ground soft' but contact is deliberately made with recipient's body	4(11)	12(14)	8(7)	4(7)
Hit(ting) Self [1]	Same as 'Hit object/ground', but signaller makes deliberate contact with own body as part of action	3(0)	5(1)	4(0)	0(1)
Hit(ting) Self Soft[1]	Same as 'Hit object/ground soft' but contact is deliberately made with signaller's body	19(5)	4(1)	3(0)	1(1)
Hit(ting) Bystander[1]	Same as 'Hit other' but contact is made with third party (not the recipient)	2(0)	0(0)	0(0)	0(0)
Hit(ting) Bystander Soft [1]	Same as ‘Hit other soft' but contact is made with third party (not the recipient)	1(0)	0(0)	0(0)	0(0)
Jump	Both feet leave the ground simultaneously, accompanied by horizontal displacement	5	6	1	5
Locomote Gallop	An exaggerated running movement where the leg movements are typically stiff (straightened)	2	1	1	0
Lunge	Signaller's body is rapidly thrust towards recipient. No contact is made	0	3	3	0
Object Head	Signaller places detached object on their head and leaves it in place.	1	1	0	1
Object Mouth Unattached	Signaller holds an object in mouth. Hands should not normally be involved	0	1	0	1
Object Move Attached	Same as 'Object move unattached' but object remains attached to the environment	3	2	0	2

Object Move Unattached	Object is displaced, contact is maintained through movement. Object is free to move and not attached to environment	4	29	22	6
Object Shake	Repeated back and forth movement of an object (typically one still attached in the environment)	7	20	12	8
Out	Signaller's arm is extended out from the shoulder to the side of the body, elbow and hand are held in line	9	12	6	6
Over Stance	Signaller pauses while standing with at least one arm that has been moved into position and held over the recipient's body. In full form signaller's body forms a bridge over the recipient	0	3	1	2
Pot Human-Specific	Conventionalized gestures corresponding to the gestures whose form and function are culturally shared. No variation seen in the form and never occurring detached from its meaning	41	62	37	22
Present (directed)[2]	Signaller moves body or body part to deliberately expose an area to the recipient's attention	22(23)	10(8)	6(1)	4(6)
Pull (directed)[2]	Same as 'Push' but the contact between the signaller's hand and the recipient's body part happens usually in a grab position	1(1)	40(6)	15(1)	24(5)
Push (directed)[2]	Signaller contacts recipient's body (typically hand) and force is exerted into the recipient's body as if to displace recipient	6(0)	87(17)	46(9)	40(8)
Raise	Signaller raises body part (typically hand or arm) in a generally vertical movement	35	36	18	15
Reach	Signaller's body part (typically hand or arm) extended towards the recipient with no contact	241	243	142	83
Rocking Sit	Signaller moves body back and forth, or side to side, while sitting	0	1	0	1
Rub	Signaller push/rubs body part up and down against body of recipient (typically with hands)	0	3	3	0
Rub Self	Signaller push/rubs body part against part of their own body (typically with hands)	4	3	0	3
Shake	Signaller moves part of their body quickly and repeatedly back and forth (typically hand/arm or head)	58	69	44	24
Shake Other	Signaller holds body part of other individual and moves it quickly and repeatedly back and forth	0	1	1	0
Spin Pirouette	Signaller stands and turns around their bodies vertical axis while also displacing along the ground	1	0	0	0
Stance Bipedal	Signaller stands stiff in front of the recipient and holds position	0	1	0	1
Stomp(ing) Object[1]	The signaller's foot (or sometimes hand) is lifted vertically and brought into short hard contact with the ground (or object)	9(4)	8(7)	5(3)	3(2)
Stroke	Active gentle movements of the signaller's palm or fingers (rarely other) on the recipient's body	2	0	0	0
Swing (directed)[2]	Smooth continuous motion of signaller's body part (normally arm of leg) back and forth	4(2)	0(0)	0(0)	0(0)

Throw Object	Object is moved and released so that there is displacement of the object through the air after moment of release	0	5	2	3
Throw Threat	Object is lifted into position to throw it but is held in that position (typically raised above shoulder) without release	0	3	2	1
Touch	Light contact (typically of the signaller's fingers, knuckles, hand, or foot, rarely other) on the body of the recipient, contact under 2 seconds	25	27	14	12
Touch Long Other	Same as 'Touch' but contact is held for under 2 seconds	8	3	1	2
Touch Object	Same as 'Touch' but contact is made with a specific object/ground in a location between the signaller and recipient	44	16	11	3

[1] Distinct gesture forms considered based on regular rhythmic repetition, with the respective frequencies indicated in parenthesis.

[2] Distinct gesture forms considered based on the consistency of the recipient's behavioural reaction and the movement/location suggested by the signaller gesture action, with the respective frequencies indicated in parenthesis.

5.3.4. Data analysis

We examined how the gestural communication of toddlers was affected by the recipient's age. We focused on six different gestural features and fitted one model for each feature (Table 20). To explore vocabulary complexity, we calculated (1) the diversity of gestures and (2) the use of sequences. The diversity of gestures corresponded to the number of distinct gesture forms used by each child. To explore temporal patterns, we analysed (3) the gesture duration and (4) the gestural rate. The gesture duration corresponded to the relevant section of the gesture (PAU; see Table 18). The gesture rate was calculated as the number of gestures per sequence divided by the total sequence duration. To explore prominence of the gestural communication we analysed (5) the presence of repetition and (6) the use of objects. Within repetition we included examples of repetition by the signaller that occurred at both the gestural level (i.e., repetition of the gesture action within an instance of gesturing, e.g., Hitting, or Stomping), at the sequence level (the addition of further gestures of the same form) and at the bout level (persistence or elaboration, i.e. the addition of further gestures separated by more than 1 second; see Table 18). In considering the use of objects, we included gestures in which an object was used to produce them either as an object manipulation gesture (e.g., Object shake), or one that contacted an object or surface (e.g., Hit object; see Table 18).

We ran each model on two sets of data: (a) a first dataset including all gesture tokens produced by the focal, in order to compare the communication directed towards adults with that directed towards peers (n=1595); and (b) a second dataset including only the communications occurring between peers, in order to explore how the same gestural features varied with recipient age at a more nuanced level (n=878). Our analyses explored three different levels of gestural accommodation (Individual, Sequence, and Gesture), resulting in six different datasets (Table 20). Of the 923 gestures directed towards peers, 45 gestures were discarded from the subset of analyses focusing on peer communication due to a lack of relevant information about the recipient. One of the toddlers was never observed to communicate with other peers and for that reason was not included in the second set of analysis (b). For a repository containing the data and analyses see https://github.com/EDanielaRodrigues/ToddlersAccommodation.

Table 20. Analysis structure. Models (Mod) for each gestural feature with respective datasets and sample sizes (N) for Adult-Peer and Peer-Peer comparisons.

Dimension	**Level of analysis**	**Gestural feature**	**Adult-Peer (a)**			**Peer-Peer (b)**		
		Response variable	*Mod*	*Dataset*	*N*	*Mod*	*Dataset*	*N*
Vocabulary complexity	Individual	(1) Diversity of gestures	1a	ind.data.a	106	1b	ind.data.b	104
	Sequence	(2) Use of sequences	2a	seq.data.a	923	2b	seq.data.b	538
Tempo	Sequence	(3) Gesture rate	3a	seq.data.a	923	3b	seq.data.b	538
	Gesture	(4) Gesture duration	4a	gest.data.a	1595	4b	gest.data.b	878
Prominence	Gesture	(5) Repetition	5a	gest.data.a	1595	5b	gest.data.b	878
	Gesture	(6) Use of objects	6a	gest.data.a	1595	6b	gest.data.b	878

5.3.5. *Model specifications*

We fitted models to test the impact of the recipient age on the different gestural features mentioned above (1-6). All models were Generalized Linear Mixed Models (GLMM; Baayen, 2008) and, depending on the nature of the response variable, with one of the following error structures and link functions: Poisson (model 1a), Zero inflated negative binomial (model 1b), Binomial (models 2, 5, and 6), Gamma (models 3), and Gaussian error structure (models 4); and log link (models 1a, 3), logit/log (model 1b), logit (models 2, 5, and 6), or identity (models 4) link function.

In the first set of analysis (a) two levels were considered for recipient age: adult and peer. For the subset of data used in the second set of analyses (b) we employed the difference between the recipient's age and the signaller's age in days as a measure, allowing us to account for both the valency and the magnitude of age difference. An exception was made when analysing the diversity of gestures (1b) where relative proportions were required. For this analysis we considered again two levels for recipient age, but this time with younger-peer and older-peer as categories.

In all models, we controlled for the interaction between signaller age and signaller gender. To control for confounding effects, we also included group as further fixed effect into the model. As random effects (intercepts) we included the identity of the signaller (Signaller's ID). We included recipient age within Signaller's ID to keep type I error rate at the nominal level of 5% (Barr et al., 2013; Schielzeth & Forstmeier, 2009). An exception was made for Models 5 and 3b as including the random slope prevented the models from converging. For the other fixed effects (gender, age, and group), we did not include random slopes as they were constant within signaller's ID. To test the overall significance of our key predictor (recipient age; Forstmeier & Schielzeth, 2011) we compared the full models with reduced models lacking the key predictor using a likelihood ratio test (Dobson & Barnett, 2018).

5.3.6. Model implementation

We fitted models in R (version 4.0.2, R Core Team, 2020) using the functions glmer and lmer of the R-package lm4 (Bates et al., 2014). The zero-inflated model (1b) was fitted using the function glmmTMB (Brooks et al., 2017). Prior to fitting the model, we z-transformed signaller age and the difference between recipient and signaller's age to a mean of zero and a standard deviation of one to provide more easily interpretable estimates (Schielzeth, 2010). We also log transformed the duration of gestures to provide an approximately symmetrical distribution and mitigate against the effects of any influential cases. To control for collinearity, we determined Variance Inflation Factors (VIF, Quinn & Keough, 2002) from the equivalent standard linear models including only the fixed main effects and lacking the interaction, using the function vif of the R-package car (Fox & Weisberg, 2011). This check showed that collinearity was not an issue in any of the models (maximum VIF 1.87).

5.3.7. Ethical note

This study was observational, and participation was voluntary. All parents gave their written informed consent for their children to take part in the study. The parents could decide at any time to pause or stop their child's participation in the study and request that their child's video data be deleted. We anonymized all data to ensure that toddlers could not be identified during data analysis and in the presentation of the results. The study was approved by the ethical committee of ISPA – Instituto Universitário.

5.4. Results

5.4.1. Adult-directed gestures vs peer-directed gestures

Of the 1595 gesture tokens produced by the signallers (n=53), 672 gesture tokens were directed toward adults and 923 towards peers. Toddlers used 65 gesture forms: 49 when communicating towards adults, and 59 when communicating towards peers. Toddlers employed 6 gesture forms towards adults that were not seen in their communication with peers, and 15 gesture forms towards peers that were not seen in their communication with adults (Table 19). Examining the cumulative frequency of gesture forms directed towards adults and peers, suggests that our sample repertoire had reached asymptote within our observed contexts (adult-directed communication: 622; peer-directed communication: 829;Appendix C 2;Appendix C 3).

The age of the recipient influenced some features of the toddlers' gesturing, in particular the complexity of their vocabulary and their temporal patterns (Appendix C 4 - Appendix C 6). Vocabulary complexity, as measured by the diversity of gesture forms used, increased in communication directed towards peers (full-null model comparison: $\chi2$ =28.064, df=31, p<0.001). Toddlers used a more diverse set of gesture forms towards peers as compared to the set of gesture forms they used towards adults (estimate= 0.634±0.117, z=5.43, p>0.001,Figure 21, Appendix C 7). The full-null model comparison revealed no significant impact of recipient age on the use of sequences (χ^2=0.473, df=1, p=0.49).

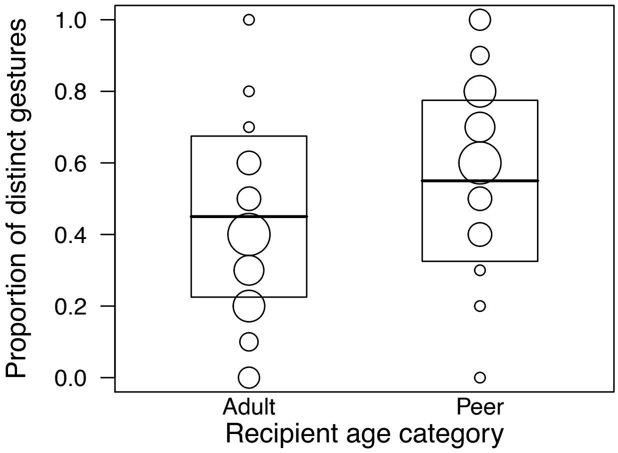


Figure 21. Proportion of different gesture forms directed towards adult and peer recipients. In total, 49 different forms of gesture actions were used towards adults and 59 towards peers. Larger bubbles represent more toddlers with a given proportion. Boxes indicate 25th, 50th, and 75th percentiles. The proportions were calculated for each toddler by dividing the number of distinct gesture forms directed towards adults or peers by the total number of the distinct gesture forms produced by each toddler.

In terms of temporal patterns, there was no clear effect of recipient age on gesture rate (full-null model comparison: χ^2=1.880, df=1, p=0.170), but recipient age did affect gesture duration (full-null model comparison: χ^2=16.709, df=1, p<0.001) with toddlers directing longer gestures towards adults (estimate= -0.118±0.043, t-value=-2.711, df=25.641, p=0.012, Figure 22).

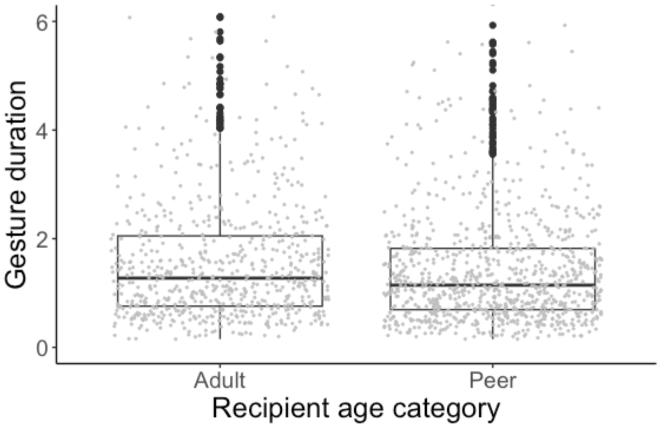


Figure 22. Difference in the gesture duration between gestures directed towards adults and peers. Boxplots show the gesture (PAU) durations of 1595 gestures: 672 directed towards adults and 923 towards peers. Raw data are represented by the grey dots.

Finally, the prominence of the toddler's gestures did not vary with the recipient's age. Toddlers were similarly likely to use repetition in their gesturing (full-null model comparison:

χ^2=0.655, df=1, p=0.418) and to use objects in their gestures (full-null model comparison: χ^2=1.349, df=1, p=0.246) when communicating towards adults and peers.

5.4.2. Peer-directed gestures: younger vs older recipients

Within the subset of communication directed towards peers, toddlers (n=52) directed 379 gesture tokens from 51 gesture forms towards younger peer partners and 499 gesture tokens from 48 gesture forms towards older peer partners.

Toddlers were able to adjust their vocabulary complexity and temporal patterns to their partner's age (Appendix C 8 - Appendix C 10). Recipient age did impact the diversity of gestures used (full-null model comparison: χ^2=6.130, df= 1, p=0.013). Across signallers a larger number of gesture forms were used to communicate to younger peers, with n=3 gesture forms used to younger peers that were not recorded used towards older peers. However, individual repertoires of gesture forms that toddlers produced towards younger peers was typically smaller than those used towards older peers (estimate= -0.378±0.146, z=-2.582, p=0.01;Figure 23, Appendix C 11). In contrast, we found no effect of recipient age on the likelihood of using gesture sequences (full-null model comparison: χ^2=0.861, df= 1, p=0.353).

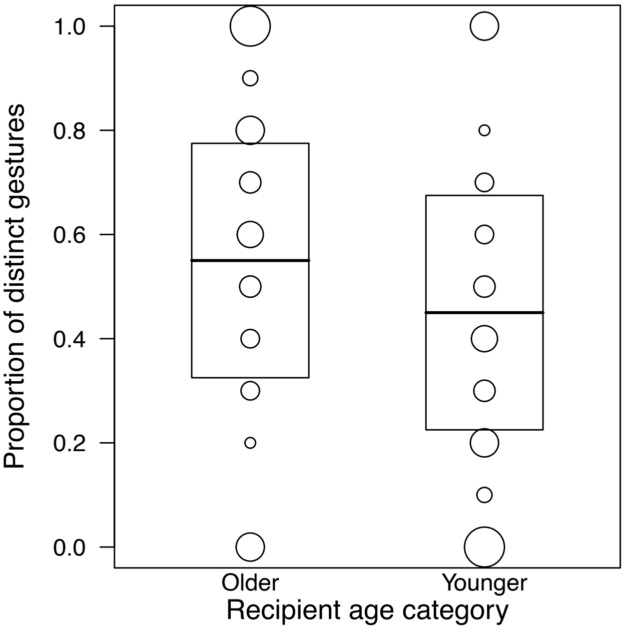


Figure 23. Proportion of different gesture forms directed towards younger and older peer recipients. Larger bubbles represent more toddlers with a given proportion. Boxes indicate 25th, 50th, and 75th percentiles. The proportions were calculated for each toddler, by dividing the number of distinct gesture forms directed towards younger or older peers by the number of the total distinct gesture forms produced by each toddler.

In terms of temporal patterns, peer recipient age did impact gesture rate (full-null model comparison: χ^2=4.876, df= 1, p=0.027): toddlers gestured more slowly towards younger peers (estimate= 0.066±0.03, z=2.217, p=0.027;Figure 24). However, partner age had no impact on the performed action unit (PAU) duration (full-null model comparison: χ^2=0.309, df= 1, p=0.578).

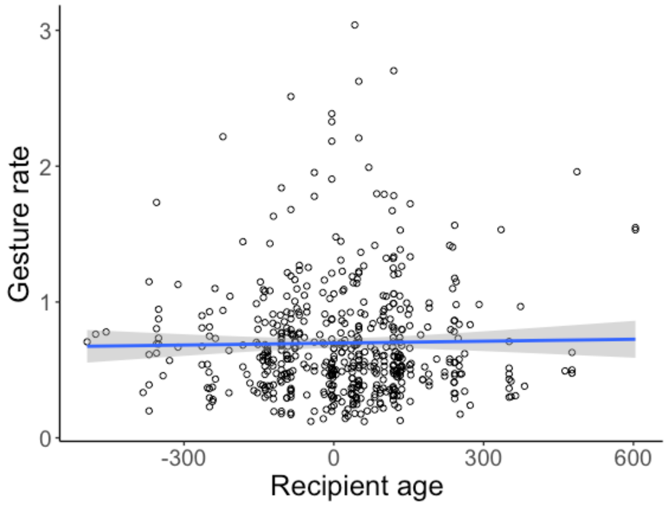


Figure 24. Effect of recipient age on the gesture rate. Gesture rate represents the number of gestures per sequence divided by the sequence duration. Each point in the plot represents a sequence.

Again, the prominence in gesturing did not vary with recipient age when comparing the communications directed towards younger and older peers. We found no variation in the use of repetition in gesturing (full-null model comparison: χ^2=0.065, df=1, p=0.799), nor in the inclusion of objects in gestural communication (full-null model comparison: χ^2=0.017, df= 1, p=0.895).

5.5. Discussion

We describe the emergence of our ability to accommodate communication to partners of different ages. We focused on the gestures produced by toddlers during free play and investigated the influence of recipient age on three dimensions usually explored in child-directed communication: vocabulary complexity, tempo, and prominence. We first compared whether toddlers address peers and adults in different ways. We then explored the same features in peer-directed communication to assess whether toddlers were sensitive to more subtle age differences, differently adjusting their communication to younger and older individuals within their peer group. Toddlers were able to adjust the vocabulary complexity and the temporal patterns of their gestures to their recipient's age but did not appear to change the prominence of their communication. When communicating with younger peers, some of the patterns of child-directed communication described in language use already appear present in toddlers' non-linguistic gestures: they communicated with younger peers at a slower pace and using a simpler vocabulary. However, when comparing adult-directed with peer-directed communication, we found an opposite pattern: toddlers used a more diverse set of gestures and shorter gestures when communicating with their peers as compared to adults.

Based on the ability of very young children to discriminate levels of social competence in their recipients, we predicted we would find patterns of accommodation towards their peers, as compared to adults, resembling those already described in child-directed communication, as they should recognise that younger partners are less proficient communicators. Interestingly, our finding of an opposite trend in the adult-peer comparison suggests that toddlers can accommodate their communication within different registers when communicating with peers and adults, but that there may be factors other than age or associated communicative competence driving this accommodation. For example, toddlers may recognise that adults, as compared to peers, have different motivations, expectations, or goals in mind (Kachel et al., 2021). The fact that the cumulative number of gesture forms directed towards adults also reached asymptote, makes it unlikely that the reduced diversity of gestures were a by-product of the fewer number of gestures produced towards adults. However, if toddlers engage with adults for different goals, or for a more restricted set of goals, they might use a specific subset of gesture actions to do so – apparently 'limiting' their vocabulary. Determining the meaning of gestures and goals is challenging in pre-linguistic children, and to investigate this further would require data across a more diverse range of contexts (Kersken et al., 2018) and substantially larger datasets than were available in this study. Moreover, at present, we are only able to determine goals for successful imperative requests in gestural communication (Bates, 1979; Cartmill & Byrne, 2010; Hobaiter & Byrne, 2017) further limiting our ability to explore across the full range of toddlers' gesturing. Similarly, we can not rule out that our unexpected pattern of longer-gestures towards adults, as compared to peers, was the result of variation in gesture forms – rather than extension of the gesture units themselves. Gesture forms are very different from each other, with some gesture forms necessarily longer than others to produce: for example, some involve the whole body as opposed to just a limb, some have an optional holding/repetition phase, some are characterized by a particular speed (e.g., a Fling cannot be slow). As our measure of gesture duration is dependent on gesture forms, we would ideally either control for gesture form, or investigate the use of specific gesture forms across recipients of different ages.

An additional factor that may have shaped our findings, in particular the ones regarding temporal patterns, is the interaction between age and social relationship. Social relationships shape the way we communicate: for example, differences in greetings based on social familiarity and hierarchy (Gallois et al., 2005; Giles et al., 1987), or our ability to communicate more efficiently with friends compared to strangers, based on shared common ground (Savitsky et al., 2011; Van Der Wege et al., 2021). The influence of common ground on some language properties is already well documented, affecting the use of syntax, vocabulary, accent, and intonation (e.g.: Clark, 1996; Hwang et al., 2015). In a nursery school context, the toddlers we observed may have shared more similar language competences and experiences with the other toddlers, interacting with them more often as compared to the adult teachers. This increased common ground may have contributed to their use of shorter gestures with peers. It would be interesting to compare toddlers' gesturing towards adult recipients of different social relationships and familiarities – for example, teachers and caretakers as compared to parents.

Another dimension of our social relationships that shapes our daily interactions is dominance and hierarchy (Gallois & Others, 1992; Giles et al., 1987). For example, in some cultures, the way we address more dominant individuals, such as the matriarch of a family, or a university professor is more formal and, as a result, more energetically 'expensive' in the sense that we choose to use more complex and longer structures. In our observations the adults were familiar with our toddlers, but also individuals in positions of social authority (teachers and classroom assistants). If similar sensitivity to social hierarchy is already present in early ontogeny, toddlers may have perceived the adults as more distant and more dominant individuals, and consequently employed longer gestures. In these types of socially stratified relationships children may also want to 'display' newly acquired communication skills to create a positive impression in someone that can acknowledge their skills (as one might put more effort into preparing a meal for a friend who is a chef).

Finally, nursery schools provide a very specific social setting in which there are diverse sources of interest, such as objects and social partners (usually a greater variety as compared to the ones that they would have at home), but also more competition for those same objects and partners. Particularly, where there is a small ratio of adults/toddlers - toddlers experience greater competition for the attention of the adults as compared to peers. In our study there was usually a maximum of 3 adults, excluding the researcher, per room (the teacher and up to 2 classroom assistants) in groups that varied from 12 to 18 toddlers. As a result, to get an adult's attention, toddlers might have to hold a gesture for longer while waiting for the adult to pay attention to them. Audience effects are well established in communication (Alibali & Don, 2001; Cartmill & Byrne, 2007; Galati & Brennan, 2010); and although we focused on dyadic interactions, the presence of other individuals in their environment – such as the large number of peers contrasting with the fewer adults who needed to divide their attention among them – could also have influenced the children to compete for adult's attention.

To better understand the influence of friendship, familiarity, dominance, and competition on toddlers' gestural accommodation, future studies could incorporate a range of different settings, cultures, and social relationships across a wider range of recipient ages. For example, further research could investigate how gestural accommodation varies between close family relationships and more formal relationships with non-family members (such as teachers). Similarly, exploring gesture between different states of attention and within different social audiences would help disentangle the diverse possible effects in this complex phenomenon.

It is somehow a little surprising that we did not find any change in the 'prominence' of the gestures used by the toddlers. One function of child-directed communication is to get the attention of the recipient, and we selected two features that we anticipated would capture some of the potential variation related to prominence: repetition and the use of objects. Repetition is one of the most well documented features of child-directed communication (Cameron-Faulkner et al., 2003; Masataka, 1992; Papoušek et al., 1987); however, there are several possible explanations for the apparent lack of an effect in this study. We may have missed describing the ways in which prominence was varied, such as with additional acoustic signals, or in other variations in the use of space, movement, and energy in gesture production. For example, more expansive gestures are usually wider and exploring more the peripheral space, which involves more energic demanding movements, but they could attract/maintain the recipient's attention more easily. Increased energic demand could also be reflected in more forcefully produced gestures that make louder or harder contact with other objects or individuals. While we did consider emphasis across gestures in our coding, we were only able to do so where two instances of the same gesture action were produced in the same communication. The signaller might use other strategies outside of the specific gesture production to capture and hold the recipient's attention, such as moving into the recipient's line of sight, or by producing attention getting signals in other modalities – such as a vocal or facial signal. Some of these possible patterns in gestural prominence of child-directed communication may only emerge if we consider the full multimodal nature of the communication.

Alternatively, accommodation through adjusted prominence might not be present at this stage of development. Repetition at this stage may only be used in persistence towards a goal that was initially declined, or to repair a miscommunication. Although younger recipients may be more likely to misunderstand or to take more time to understand the goal, any effect might remain undetected by our methods and in this specific social context. For example, play contexts in nursery schools represents a non-urgent context in which children, regardless of their age, are free to move around their environment. This freedom of movement could influence gestural production and the use of accommodation as the signaller is able to easily move to the front of the recipient to capture their attention, move to a new partner to interact with instead, or they could find something else to do and give up on the interaction entirely. Additionally, using objects in gesturing makes the gestures themselves more salient. For instance, hitting an object with another object, or extending an arm (Reach) while holding an object, are both more noticeable than their non-object counterpart actions. However, toddlers did not vary their object use based on interaction partner (adults or either type of peers, younger or older). These findings suggest that toddlers may not use objects as attention getters (i.e., to capture the attention of the recipient and subsequently communicate about other things), but instead, that the communication itself is likely to be about the objects.

A closer look at peer-directed gestural communication suggests that our ability to accommodate our communication to younger individuals is already present during toddlerhood, and that toddlers use of this register partially follows the patterns described in infant-directed speech. In this study, we found that when communicating with younger partners, toddlers opted for using simpler vocabulary (reflected on the use of a more restricted set of gesture actions) and at a slower pace (lower gesture rate). The use of fewer gesture actions may, again, be related to a more limited range of interactions and goals, which we suggest may have occurred in gestures directed to adults. However, here this bias would be in line with the predictions of the

Interactional Artifact Theory, which suggests that gesture modification may be a by-product of the semantic simplicity of interactions with infants (O'Neill et al., 2005; Pine, 1994).

Our analyses of the temporal patterns in toddlers' peer-directed gestures showed that the pace of their communication was also adjusted when communicating with younger individuals. We used the total duration of the sequence, and accounted for pauses between gestures in calculating gesturing rate. Thus, a slower rate may reflect longer gestural units or longer pauses between them or both. The fact that we did not find an effect of peer age on the duration of the gesture (Performed Action Unit), strongly supports the suggestion that it was the length of the pauses that were adjusted – aligning with the findings that longer pauses are an established feature of child-directed communication (e.g.; Fernald et al., 1989). In the future, exploring this feature by directly measuring pause lengths, and by looking more generally at the whole communication, including pauses between distinct sequences that may reflect persistence or exchanges, could provide a better understanding of how distinct structural elements are adjusted.

Some of the measures chosen for this study did not reveal any effect of the recipient's age on the gestures directed to them, suggesting that these features are not (yet) adjusted by toddlers in their gesturing. However, child-directed communication registers are not universal, and not all features are present across all cultures and contexts. Conversely, other features in child-directed communication may already be in place but were not explored in this study, such as the use of space, the number of exchanges, or the use of deictic gestures. Specificities in the Portuguese language, culture, or in the school environmental context of free play may also promote and shape the use of certain features in gestural accommodation. We chose free play due to the richness of opportunities this context provides, particularly as it is often free of more formal scaffolding and instructions. However, these freedoms also provide a challenging context for analysis, perhaps masking patterns that would be present in other communicative contexts.

Here, we provide a first case-study that showed how and where child-directed communication registers could emerge in the gesturing of toddlers in Portuguese nursery schools during free play. Further study across a more diverse set of contexts, communities, relationships, and features of interest is needed to assess how these findings might generalise more broadly. Nevertheless, we establish that toddlers can accommodate their gestural communication, and that they do so both by varying these patterns in unexpected ways when gesturing with adults, and by adopting similar patterns to adults in child-directed communication registers in their gesturing with younger peers.

CHAPTER 6: General Discussion

The aim of this doctoral thesis was to investigate how the ability to accommodate our communication emerges and evolved. We focused on gestural communication because of its relevance in language evolution and human ontogeny, and because it offers a rare opportunity to directly compare the communicative behaviour of young children and other apes. We started by conducting a systematic review to understand the current landscape of gestural research in human and nonhuman primates. We then tackled the study of communicative accommodation using observational studies of chimpanzees and children; asking questions at the ultimate level by exploring its evolutionary origins through the study of one of our closest phylogenetic relatives: chimpanzees; and at the proximate level by looking at how it emerges in human early development.

Within this evolutionary-developmental framework we explored the ability to accommodate communication from different perspectives. We looked at how chimpanzees adjusted their communication in the contexts of greeting and leave-taking, exploring the broader social context, including the effects of the recipient and the wider audience. We also took a more detailed perspective, looking at whether specific features of child-directed communication from human language use were expressed in the gestural communication of chimpanzee mothers. We found that social aspects of relationships, such as kinship and rank, influenced the likelihood of communication, and that kinship also shaped more subtle features of the gestures produced, such as prominence and temporal patterns. At the more proximate level, we applied the same detailed child-directed communication framework to explore whether toddlers adapted their pre-linguistic gestures to their social partners. A particular feature of child-directed communication is accommodation to the age of your social partner. We found that chimpanzees were able to accommodate their communication to young individuals, but in ways that applied opposite patterns to those typically described in human adults' child-directed communication. Chimpanzees used shorter gesture units towards immature individuals and used more repetition towers older offspring. In contrast, we found that human toddlers already adapted their gestures following the patterns described for human adults' child-directed communication: they used less complex gestural vocabulary and gestured at a slower tempo when communicating with younger peers.

6.1. The challenges of comparative research

A first step of this project was to understand where the similarities and discrepancies between human and nonhuman gestural research current lie. Chapter 2 highlights how methodological transparency and detail are central to robust comparative research. By conducting a systematic review, we established that very few empirical studies include both human and nonhuman primates and, as a result, the comparative patterns on which evolutionary arguments are made are usually inferred from comparison across different studies and datasets. However, human and nonhuman research used different approaches and focused on different domains: gestural research in nonhuman primates often focused on the form of gestures, often analysing communicative repertoires (e.g., De Waal, 1988; Fröhlich et al., 2021; Hobaiter & Byrne, 2011), an essential step when studying the communication of nonhuman species. Nevertheless, the absence of equivalent systematic descriptive studies of human gesture forms continues to pose challenges when it comes to comparing gesture use with nonhuman primates (c.f., Kersken et al., 2018).

Other methodological differences emerged as consistent patterns in our field: most human research is conducted in unfamiliar environments, such as research laboratories, through experimental approaches; whereas nonhuman primates were most often studied in environments that were familiar to them and through observational approaches. As a result, we need to be cautious in comparing and interpreting our findings across these areas, because, when not taken into account, species differences in testing conditions could easily be mistaken for species differences in cognition (Bard & Leavens, 2014; Leavens et al., 2019).

Human research holds a very different position than that on nonhuman primates, one in which core definitions and descriptions are taken for granted, and meanings and functions are often inferred. We know humans can point, and that their communication is intentional. Thus, we often do not include steps to establish these types of features and, at times, assume their presence in even very young humans. Doing so allows us to ask a range of other questions, and a divergence in interests and methodologies is not inherently problematic; the issue arises only when, as researchers, we make comparisons of things that are not comparable. One fundamental set of differences lie in what researchers consider a gesture. Definitions and details of the coding schemes varied substantially and were not always made available. When they were available, we showed that different studies used different definitions of which movements and body parts constitute a gesture, and different criteria to define their intentional use. A substantial portion of studies conducted in humans often lacked any clear definition of gesture or failed to determine whether the gestures are intentionally produced. Consequently, when researchers attempt to compare findings across different studies without a clear understanding of the concepts they are addressing, it can again lead to unfair comparisons.

Scholars have previously noted that human research may have underestimated the number of gestures we produce, because only considered empty-handed gestures (Petito, 1988; Pika, 2008). In many cases, actions resembling gestures but that involved objects were considered functional object usage (Goldin-Meadow et al., 2007), and thus, were regarded as meaningful actions rather than gestures. In our analysis in Chapter 2, we did not specifically examine the incorporation of objects, but we did identify a bias toward manual gestures in human research. However, it is worth noting that the concept of mechanical ineffectiveness is not commonly considered in human research. This criterion is frequently employed in nonhuman primate studies to define gestures but is rarely observed in human gestural research. For example, an effective push could qualify to be a gesture in research conducted in humans, whereas in nonhuman research, its mechanically effectiveness would exclude it from consideration. Consequently, while research on human gesturing has been very restrictive in some aspects of its definitions, research on nonhuman primate gesture has been more restrictive in others.

Another area in which nonhuman primate gesture is often more restrictive than human gesture is in only including actions that show signs of being intentionally produced. Even though the criteria of intentionality were initially derived from studies involving preverbal human children, our findings revealed that research involving humans often takes intentionality for granted. Out of 80 studies including humans, only five explicitly applied intentional criteria, whereas more than half of the 87 studies of nonhuman primates provided explicit intentionality criteria. Although humans clearly possess the capacity for intentional communication, we are also fully capable of generating involuntary signals such as a spontaneous yelp or laugh (Kawakami et al., 2007; Provine, 1992). Incorporating all human gesture-like movements, regardless of whether there is substantial evidence of their communicative and intentional nature, while restricting nonhuman primate data to only those gestures backed by clear evidence of intentional use, once again, hinders our capacity to establish meaningful comparisons between human and nonhuman gesturing.

Asking for a uniform definition of gesture with precisely the same criteria would be too restrictive, and, for example, focusing exclusively on manual gestures or intentional gestures does not pose any specific issue. Our argument is not that comparative research must stick to fixed and universal definitions and methodologies for studying different species, especially because there are often important species, population, or culturally-specific variables that need to be taken into account (Graham et al., 2022). A diversity of focus, methods, and socio-ecological contexts can help bridge significant gaps, increase our ability to generalise findings to a species-level, and offer valuable comparative insights, but only where the sources of variation are transparent. When they are transparent, these features of our datasets can be considered when attempting to fit any one puzzle piece into the larger picture.

After describing the current state of the field, and offering practical steps to address current gaps, we planned a series of studies that applied comparable methods in human toddlers and chimpanzees to explore their ability accommodate communication. We include two chimpanzee communities from two different subspecies and four groups of children, but we are cautious in drawing species-level generalisations. Our goal instead is to highlight what capacities are present in both species, and to provide a first illustration of when and how these abilities can emerge.

6.2. Did the ability to accommodate our communication emerge before language?

To answer this question, we explored the flexibility of two distinct communicative systems: the communicative system of our closest phylogenetic relatives: chimpanzees, and the communicative system of humans before language is fully developed. In this way, we can address two of Tinbergen’s four questions: when and how did the ability to accommodate our communication emerge in the evolutionary context (section 6.2.1 based on Chapters 3 and 4) and in ontogeny (section 6.2.2. based on Chapter 5).

6.2.1. Was this ability already present in our last common ancestor?

In Chapter 2, we showed that studies of nonhuman primate gestural communication are largely limited to chimpanzees and bonobos. However, this is for good reason, as our closest phylogenetic relatives they often provide a first point of comparison and our shared physiology and commonalities in our social behaviour allow for detailed and nuanced comparison. Thus, we also chose to conduct the comparative part of this thesis with chimpanzees. In Chapter 3 we explored whether greeting and leave-taking behaviour are present in chimpanzees, suggesting that they preceded the emergence of the linguistic communication that characterizes our human lineage. In humans, greetings and leave-takings show strong variation depending on our social relationships with our communicative partner, and the wider audience, and are thus ideal starting points for exploring when and how communication shows social adjustment. Recognized as important moments in every day human routines, (Giles et al., 1987), we analysed the probability that chimpanzees would greet or take-leave of their partners and, when they do, which type of signals they used. To avoid preconceived categorizations about what constitutes a greeting or leave-taking, we analysed all forms of communication that took place during social fusions (arrivals) and fissions (departures).

Our findings indicate that the occurrence and form of communication during arrivals and departures are influenced by social factors. Communication was observed in both situations, but more than twice as often during arrivals than during departures, which supports previous suggestions that leave-takings appear absent in chimpanzees and may not have been present in our last common ancestor (McGrew & Baehren, 2016). As we assessed each opportunity for an individual to engage with any member present in the party, we observed that these interactions were highly selective. Only a small portion of the available opportunities to communicate were made use of and were more likely to be directed towards specific individuals: in particular those of higher social rank and non-kin individuals. Additionally, we observed that towards higher ranking individuals, chimpanzees also adjusted the type of signals used in greetings, using fewer gestures and more vocalizations. Finally, we demonstrated that these dyadic interactions during arrivals and departures were influenced by the presence of other individuals, notably males. When there were more individuals present, especially mature males, it reduced the likelihood of greetings taking place.

In Chapter 4 we explored whether the ability to accommodate more subtle features of communication to specific aspects of your partner's identity might be present in chimpanzees. We looked specifically at how chimpanzee mothers adjusted the expression of their gestural communication to the attributes and relationship of their children and other communicative partners. Our findings revealed that mothers adjusted their gestures to the age of their partners and to their kin relationship, but not to the sex of their partners. Across the community, mothers used shorter gesture units towards immature individuals, but this trend did not hold when we analysed the subset of mother-offspring communication: mothers did not use shorter gestures towards younger offspring, suggesting that kinship may play an important mediating role. In fact, we found that kinship impacted gesturing in several ways: mothers used shorter Performed

Action Units (the key informative section of the gesture), communicated at a faster pace, with a more diverse set of gesture forms, and were less likely to use repetitions towards non-kin individuals. With their offspring, chimpanzee mothers were more likely to use repetitions towards older offspring. The slower and more repetitive nature of their gesturing with kin may be due in part to a more relaxed context of communication with close kin, but also reflect aspects of the recipient's responsiveness. Communication is a two-way street and the need to repeat gestures more often towards older offspring may be due to their lack of response (or mother's ability to simply enact their goals on younger infants without 'asking a second time').

Taken together, the findings of these two chapters show that chimpanzees are highly selective with their communicative partners, being able to accommodate the type of signal used and diverse features of their gesture production to attributes of their partners such as social rank, and age, and kinship. Our studies suggest that the ability to accommodate communication is shared with chimpanzees and was likely present in our common ancestor, extending back at least 6 to 7 million years ago (Young et al., 2015).

6.2.2. Do we accommodate our communication before acquiring language?

Chapter 5 investigated the spontaneous gestural communication of four groups of toddlers in three nursery schools to further explore whether our capacity for accommodating our communication is a by-product of language or if it is already present before language is fully developed. In this chapter, our focus was on the toddlers' ability to adjust their communication to the age of their partner. Given the existence of both linguistic and non-linguistic modifications in our communication with young children (child-directed communication), we examined whether toddlers exhibited the capacity to accommodate and whether their behaviours aligned with the established patterns described for this special register in adult child-directed communication.

Our results showed that toddlers adjusted the complexity of their vocabulary and the temporal patterns of their gestures to their recipient's age but did not adjust the prominence of their communication. Toddlers used simpler vocabulary at a slower pace when interacting with younger peers. However, when comparing communication directed towards adults with that directed towards their peers in general, we observed the opposite trend: toddlers employed a wider range of gestures and shorter gestures when communicating with their peers, as opposed to their interactions with adults. This aspect of our results highlights that communicative adjustments rely on more than just partner age, and that aspects of status and social relationship might similarly impact the expression of gesturing in humans as well. Despite not adjusting all the gestural elements we studied, our research revealed that toddlers indeed have the capacity to adapt their gestural communication. They adopt similar patterns to those used by adults in child-directed communication when communicating with their younger peers but accommodate their communication to adults in different ways.

6.3. What can the absence of communication or its accommodation tell us and why is it important?

In this thesis we repeatedly observed the absence of communication and/or its accommodation throughout the different studies. In Chapter 3 we reported the absence of communication in specific circumstances (leave-takings) as well as towards specific individuals. In Chapter 4, we saw that chimpanzee mothers did not accommodate their gestural communication towards recipient sex, or in many of the features of their gesturing with their offspring. In Chapter 5 we also saw that toddlers did not accommodate certain gestural features when communicating with individuals of different ages that are often employed by adults in child-directed communication. What does the absence of accommodation – or communication – mean in an interaction or relationship? Importantly, the absence of communication or accommodation in certain instances of use does not imply that individuals must lack the ability to communicate or adapt that specific aspect of their communication. It could be an active choice by them not to do so, or also a result of our limitations in our ability to describe gestural communication in these relatively new areas and understudied groups.

6.3.1. Absence in specific circumstances

Our findings in Chapter 3 are consistent with the observation that leave-taking behaviour appears absent among chimpanzees (McGrew & Baehren, 2016). If such behaviours do exist among them, they seem to be extremely rare, as chimpanzees engaged in communication in less than 5% of the occasions when they had the opportunity to do so before leaving. Even for the signals produced during departures we need to be cautious in assigning them as leave-takings as none of the signals displayed were exclusive to this specific context, with the most frequent signal observed, the ‘big loud scratch’ gesture, being also produced during situations where adult chimpanzees were requesting that others travel with them (Fröhlich et al., 2016; Hobaiter & Byrne, 2014). The absence of leave-taking would be in line with the claim that other great apes do not use declarative signals in their natural environments (e.g., Tomasello & Camaioni, 1997). However, the way researchers have approached describing meaning relies on observable behavioural responses, which do not allow us to discriminate a failed imperative 'Travel with me' from a declarative 'I'm leaving'.

Although an extensive questionnaire involving numerous researchers and diverse field sites suggested a widespread absence of leave-taking (McGrew & Baehren, 2016), we must also remain open to the possibility that leave-takings could be present in other communities. The Bossou community in which we explored it is particularly small and cohesive, perhaps making leave-taking less likely to occur. If leave-taking is more broadly absent in chimpanzees, it may be because there was no social pressure acting to promote their use of these signals. It could be the case that chimpanzees do not possess the imaginative capacity to project into the future, or to anticipate the length of period of separation from their social partners. Although there is evidence to the contrary from studies of their travel planning (Janmaat et al., 2014). Perhaps more importantly, for the individual leaving, the highly complex nature of their fission–fusion society makes it difficult to predict whether they will be absent for a longer period. Most critically, their use of long-distance signals that convey location, identity, and activity (Arcadi et al., 1998; Eleuteri et al., 2022), may mean that chimpanzees are rarely effectively out of contact with each other. Where they are, it may be more efficient to invest in signalling their relationship upon their return, when the circumstances requiring communication are more clearly defined.

6.3.2. Absence to specific individuals

With Chapter 3 we also showed that chimpanzees are highly selective in who—among the individuals present—they chose to communicate with during fission-fusion events. This pattern could represent a choice to communicate with targeted individuals, and/or a choice not to communicate with specific others. In other words, the decision to communicate may include both the relationship between the two individuals (who can both act as potential signaller and recipient), and their relationships with these two individuals and others who are present.

Accommodation occurs after the decision of whether to communicate with a certain individual has been made. And, as we mention above, not accommodating, especially when we are able to do so, can be very informative of the social context or relationship. As suggested in Communication Accommodation Theory (Giles et al., 1987), one of the function of accommodation is in regulating our 'social distance' with our communicative partner. This ability does not seem to be automatic, as suggested by Interactive Alignment Model (Pickering & Garrod, 2004), and being under individual control – signallers may choose to regulate social distance by either converging or diverging their communicative style from the recipient, or by not accommodating at all and maintain their communicative style regardless of their partner.

6.3.3. Absence of accommodation towards certain attributes of the recipient

In the context of each chapter, we included variables, such as recipient attributes and relationships, that we believed would have an impact on communication based on their presence in patterns of accommodation in human language. In general, we found that the variables included in our models influenced some of the features we were analysing (even if the opposite direction to our predictions). A striking exception was found in Chapter 4 regarding the effect of the recipient's sex on the chimpanzee mothers' signalling.

Accommodation towards the sex or gender of your recipient is a widespread feature of human language use (Cherry & Lewis, 1976; Kitamura et al., 2001). Some sex differences have already been reported in the gestural development of chimpanzees, with immature males employing a larger repertoire as compared to immature females (Fröhlich et al., 2017). These differences could result from distinct communicative styles directed towards male and female chimpanzees from an early age. The fact that the recipient's sex did not influence the analysed communicative features of the gestures analysed in Chapter 4 suggests that the impact of partner sex on gesturing may be more subtle in chimpanzees – requiring larger datasets to detect it in, or that other aspects of chimpanzee social behaviour likely have a more significant influence.

As observed in Chapter 3, chimpanzees appear to exhibit a high degree of selectivity in choosing their communication partners during greetings. However, within fission-fusion societies, they must make another higher-level decision regarding the individuals with whom they associate and spend time with. From a mother's perspective it could be more crucial to modify other social behaviours, such as their gregariousness (Murray et al., 2014), rather than their communication. For instance, researchers have found that mothers with male offspring socialised more, providing immature males with more opportunities to interact with a wider range of different social partners (Murray et al., 2014). Thus, while a mother may not adapt her gesturing to the sex of her offspring, she may influence her infants' gestural environment in other ways, controlling for other aspects such as the number and range of available social partners through selective subgrouping.

6.3.4. Absence of certain gestural features

In Chapters 4 and 5 we focused on variation in more subtle features of chimpanzees' and human toddlers' gestural communication relating to its complexity, tempo, and prominence. In Chapter 4, which focused on chimpanzee interactions, we showed that mothers were able to adjust all these aspects of their communication to the recipient; although these were more prominently adjusted outside of mother-offspring communication. Chapter 5 revealed that toddlers were able to adjust the complexity and tempo of their communication, but not their prominence, and that they adjusted for partner age in different ways with different groups.

Chimpanzee mothers directed shorter gestures, including shorter hold/repetition phases towards immature individuals. However, these patterns did not hold when we analysed the subset of mother-offspring data, suggesting a possible interaction between kinship and age of the recipient. It is possible that this trend may only become apparent in larger datasets or that it could be influenced by non-kin individuals with whom the mother is likely less familiar and interacts less frequently. Kinship seems to play a very important role in chimpanzee communication. While mothers create a secure and permissive environment that fosters the exploration and development of various skills in their offspring (Goodall, 1986), older individuals beyond the mother-offspring pair can represent a significant risk, and thus justifying an increased investment in communication when interacting with non-kin individuals.

When exploring the ontogeny of the human ability to accommodate communication, we showed that toddlers were able to adjust the vocabulary complexity and the temporal patterns of their gestures to their recipient's age. However, they did not modify the prominence of their communication, especially in terms of how often they used repetition or incorporated objects into their communication. While one option is that the capacity to employ prominence is not present at such an early age, it is also possible that we were not able to detect how toddlers modified the prominence in their communication. One of the reasons for making our communication more noticeable when talking with young children is to get the attention of the recipient. Toddlers may adjust different aspects of their communication, such as incorporating extra acoustic components, more exaggerated movements, or using strategies beyond the production of gestures to capture and hold their recipient's attention (for example, by positioning themselves in the recipient's line of sight).

Finally, it is important to note that child-directed communication registers are not universal, and not all features are present across cultures and contexts (Soderstrom, 2007). Therefore, we should not rule out the possibility that toddlers do not modify the prominence of their communication for various reasons, including that there may be no need for such adjustments in the gesturing.

6.4. What do different accommodation patterns suggest?

6.4.1. Importance and complexity of relationships

In Chapter 3, by exploring the specific context of fissions and fusions, we showed that the occurrence and form of communication events are mediated by social factors, specifically rank and kinship. We observed that more communication tends to occur towards higher-ranking individuals and between non-kin individuals. In fact, in these events it might be particularly important to reassert the positive and hierarchical aspects of chimpanzees' relationships. The same types of pressure seem to extend to subtler aspects of communication, indicated by a more efficient – faster, shorter – communication style when individuals interact with non-kin partners. In addition, chimpanzee mothers employed a more diverse range of gesture forms when communicating with non-kin, suggesting that chimpanzees may feel the need to invest and nurture their friendships and alliances, or that they are communicating across a more diverse range of social goals, when interacting with individuals with whom they are not closely related.

Although not as critical as in chimpanzee societies, hierarchical relationships also shape interactions in humans, influencing the way we communicate (Gallois & Others, 1992; Giles et al., 1987). For example, we may address more dominant individuals in a more formal way, elaborating our vocabulary and language structure. As suggested in Chapter 5, if our sensitivity to social hierarchy is already present in early ontogeny, this aspect of relationships may explain why toddlers unexpectedly employed longer gestures when interacting with adults, who in our study corresponded to teachers and classroom assistants that could be seen as figures of social authority.

6.4.2. Accommodating to young individuals: child-directed communication patterns

In Chapter 5 we showed that some features of child-directed communication emerge before language is fully developed. Toddlers were able to adjust both the complexity of their vocabulary and the temporal patterns of their gestures when communicating with younger peers, adopting similar patterns to those used by adults when addressing children. When interacting with younger partners, toddlers employed a more limited repertoire of gesture forms. The use of simpler vocabulary could be a result of deliberately selecting a specific subset of signals to reduce input complexity and facilitate comprehension. Alternatively, it could arise from the simple nature of interactions usually associated with very young individuals (O'Neill et al., 2005; Pine, 1994).

The pace of toddlers' communication was also adjusted following patterns used in child-directed communication, with toddlers gesturing at a slower rate. The rate was calculated by the number of gestures per sequence divided by the duration of the sequence. As we did not find evidence for the use of longer gestures (measured by the duration of the Performed Action Unit, PAU) the slower pace was likely driven by longer pauses instead. In child-directed communication, the use of longer pauses has been suggested to facilitate comprehension, discrimination, and segmentation of the communicative elements (Cooper & Aslin, 1990; Fernald et al., 1989) and, together with the complexity of the vocabulary we use, it seems that this important feature already emerges early in development in toddlers' pre-linguistic gestures.

6.4.3. Accommodating to young individuals: counter-CDC patterns

Chimpanzee mothers adjusted the tempo and prominence of their gestures, but in the opposite direction to that predicted using child-directed communication in human languages: they produced shorter gestural units (including shorter PAUs and hold/repetition phases) towards immature individuals, and more repetition towards their older offspring.

A possible explanation for these counter-child-directed communication patterns of accommodation towards younger chimpanzees, may relate to gestural complexity. If hold/repetition phases encode complexity, gestures with longer hold/ repetition phases would be more complex and could contain information in addition to the core meaning of the gesture action. Mothers could opt for these more complex variants when interacting with older individuals but prefer to use simpler structures (in the form of shorter gestures or with no or shorter optional hold/repetition phases) towards immature individuals to avoid misunderstanding. As we included all types of repetitions, where repetition of the action within a gesture encodes additional information, it may also explain the use of more repetitions towards older offspring. The repetitive patterns usually found in child-directed communication (more repetition towards younger individuals) have been described in other great apes (Luef and Liebal 2012). However, repetition is a broad term that may include repetitions within the gesture action (e.g., Hitting), or within the same sequence or after response waiting within different sequences in the same communication (e.g., Hit, Hit, response wait, Hit). Repetition in child-directed communication is often related to structural generalization of elements and vocabulary acquisition. While promoting interaction with the child by inviting their response, it also serves to disambiguate or reinforce the performance of the child (Schwab & Lew-Williams, 2016). However, this will likely correspond to repetitions that are spaced in time (more equivalent to persistence) and may serve a distinct function or convey different information to the use of rhythmic repetition included within the gesture form.

In humans, one of the main function of child-directed communication is argued to be facilitating communication learning (Schick et al., 2022). Child-directed communication is part of a more general package of child-directed behaviours that serve to pass on cultural knowledge and skills to the next generation, known as natural pedagogy and, although likely derived from capacities expressed by nonhuman primates, it is argued to be uniquely human (Schick et al., 2022). In chimpanzees, child-directed communication might have been shaped by different pressures and evolved with other functions. For example, one of the functions for accommodating our communication suggested in Communication Accommodation Theory is to signal social closeness or distance to a partner. In a highly hierarchical species such as chimpanzees, regulation of social distance in gestural signals - not necessarily by converging or diverging their communicative style, but by acknowledging the rank of the recipient adjusting the way they gesture - might be more important than fostering the communicative skills of the young individuals, which can be promoted in other ways. In fact, when compared with monkeys, the prolonged and more differentiated nature of social relationships among apes, along with their extended period of dependency and close physical proximity with their offspring, are two important aspects that might have shaped the way accommodation of communication looks in great apes. By providing their offspring with a safe and relaxed environment to learn and acquire their communicative skills, it is possible that mothers' signalling closeness or distance in our evolutionary past was the main driving force for adjusting communication. While the role of signalling social distance may have originated in earlier ancestors and been retained in humans and other modern apes, the accommodation of communication to specifically assist immature individuals in developing their communicative abilities may have emerged later in our species' lineage; perhaps with the transition from an independent breeding system to one that is more cooperative (Burkart et al., 2009).

Finally in Chapter 5, as toddlers are sensitive to different levels of competence (Chow et al., 2008; Zmyj et al., 2010), we predicted that we would find child-directed communication patterns in the communication of toddlers directed towards peers when compared to adults. Instead, we found precisely the opposite: toddlers directed fewer types of gestures and longer gestures towards adults. In addition to the dominance effect mentioned earlier (with teachers being perceived as figures of authority), there could be alternative reasons for this pattern. Toddlers might interact with adults for specific purposes that differ from, or form a subset of, their interactions with peers, and that might require a more limited range of gesture actions. Furthermore, because we could not control the duration of individual gesture actions, it is possible that toddlers used gesture types that are inherently longer to produce when targeting specific goals with adults.

6.5. Limitations and future directions

As demonstrated earlier, the study of gestures is not conducted in isolation, and our current approach relies on other behaviours as indicators to examine their intention and meaning. However, relying on briefly expressed behavioural cues does not allow us to differentiate between declarative signals and, for example, unsuccessful imperative signals. Our findings suggest that chimpanzees rarely communicate during departures, but when they do, they often use the 'big loud scratch' gesture, which is commonly used to ask someone to join them for the travel. Despite the current limitations in our methods that prevent us from distinguishing between a failed 'travel with me' request and a simple 'goodbye', it is through unbiased exploration of these contexts, without assumptions about what constitutes a greeting or a leave-taking, that we are most likely to find a way forward in our research.

As observed in our systematic review, gestural research has the potential to incorporate information from other co-occurring sources, such as vocalizations and facial expressions. Research conducted with humans is more likely to incorporate these additional sources, but it has remained challenging to do so in other primate species (Liebal et al., 2022; Slocombe et al., 2011). In our first empirical study on chimpanzee greetings and leave-taking (Chapter 3), we included vocalizations and facial expressions. Research conducted on greetings has been focused on vocal communication, but when we integrated gestures into these contexts, it became evident that they play an important role. For instance, our findings suggest that chimpanzees are more likely to use gesture-only communication with individuals of higher social status. When analysing the accommodation of more subtle gestural features to young individuals (Chapters 4 and 5) we were not able to include information of these other sources, but it is plausible – even likely – that the integration of additional sources to gesture would complement, strengthen, or even change some of the patterns we identified.

Social relationships exhibit a high degree of complexity, arising from the interplay of numerous interconnected factors. While our findings across chapters confirmed that communication is accommodated to relationships in different ways, there were certain crucial aspects that we could not include in all our analyses. For instance, we did not include dominance relationships in the studies exploring accommodation to young individuals (in Chapter 4 with chimpanzee mothers, and in Chapter 5 in toddlers). Another significant factor that was not addressed in any of our empirical studies was the influence of friendship or familiarity, and conducting further research in this area would contribute to a more nuanced understanding of the multi-layered impact of social dynamics on our capacity to accommodate our communication.

In our systematic review we encourage empirical researchers to explicitly test hypothesis in language evolution. We recognize the importance of diversity in the ways we tackle this topic, but we emphasize the importance of our research being transparent in our methodologies and definitions. In well-established fields we can take core definitions for granted, but our review revealed that – when available – these differ a lot. When not available, it is likely that the diversity we see in studies with definitions is similar or greater in those without, but we cannot access it and control for it, making essential comparisons across studies impossible. With this thesis we assemble a set of detailed studies with data and methodological details available – while these were not identical across chapters, species, and datasets, we hope that in being transparent it is clear what can (and cannot yet) be compared. In this way we hopefully contribute to the understanding of our ability of accommodate communication. Nevertheless, these represented a first step – the study of accommodation in gesturing in humans or other apes is in its infancy, and we only selected a subset of the gestural features available to explore. Within the research conducted on accommodation, and specifically in our ability to accommodate to young individuals, we know that there is substantial variation on the accommodation of communicative features in different groups and cultures. Therefore, extending these studies to other features and to other groups of chimpanzees and humans will allow us to grasp a more complete picture of the emergence of this ability as we go forward.

Finally, the evolutionary origins of communication accommodation are not yet well understood and, as we have seen, it is possible that the motivations and skills involved in this ability are not unique to humans but shared with other animals. At the beginning we outlined three possible scenarios for the emergence of the ability to accommodate our communication, including towards immature individuals: i) uniquely derived in humans; ii) shared with other great apes and thus present in our common ancestor, and iii) shared with more distant related species (evolved convergently). In this thesis we provide clear evidence supporting the suggestion that this ability is shared with chimpanzees, and as a consequence was likely present in our last common ancestor. However, the other two scenarios are not necessarily then excluded: some of the communicative features may have started to be adjusted after we diverged from other modern apes, and are only present in humans; and – until we have data on more biologically remote species with whom we share similar social cognitive capacities, such as elephants or cetaceans – it remains possible that this ability may have emerged via convergent evolution as a result of the specific communicative pressures that modern apes, including humans, might share with some other species. To distinguish between the different scenarios, further research is needed exploring accommodation in communication across other communicative features and in other model species and systems.

6.6. Final remarks

The patterns seen in adults' use of child-directed communication seems to emerge early in ontogeny, well before language, with toddlers using simpler vocabulary and gesturing at a slower pace towards younger individuals. However, even though the ability to adjust our communication is shared with chimpanzees and was likely present in our last common ancestor, the way in which it is expressed appears to differ, perhaps in response to differences in our social contexts of communication. This is evident by the counter patterns to adult human child-directed communication that we found in chimpanzees: they used shorter gestures towards immature individuals and used more repetitions towards older offspring.

The studies assembled in this thesis have shown that the ability to accommodate our communication, including to young individuals, is present in other communicative systems, namely in the gestures of our closest phylogenetic relatives (chimpanzees) and in our spontaneous use of gestures in early childhood, before language is fully developed. We propose that our ability to accommodate our language, and particularly to young individuals, is not a consequence of language itself but instead represents one of the foundational abilities upon which language was likely constructed. Moreover, there are numerous communicative features and social factors that likely play a role in the way we – and other apes – accommodate our communication to our social partners and offer exciting avenues for future research .

REFERENCES

Acquistapace, P., Aquiloni, L., Hazlett, B. A., & Gherardi, F. (2011). Multimodal communication in crayfish: Sex recognition during mate search by male Austropotamobius pallipes. *Canadian Journal of Zoology*. https://doi.org/10.1139/z02-171

Alfaro, J. L. (2008). Scream–embrace displays in wild black-horned capuchin monkeys. *American Journal of Primatology*, *70*(6), 551–559. https://doi.org/10.1002/ajp.20528

Alibali, M. W., & Don, L. S. (2001). Children's gestures are meant to be seen. *Gesture*, *1*(2), 113–127. https://doi.org/10.1075/gest.1.2.02ali

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3/4), 227–266. https://doi.org/10.1163/156853974X00534

Arcadi, A. C., Robert, D., & Boesch, C. (1998). Buttress drumming by wild chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary evidence for individual distinctiveness. *Primates*, *39*(4), 505–518.

Arensburg, B., Tillier, A. M., Vandermeersch, B., Duday, H., Schepartz, L. A., & Rak, Y. (1989). A Middle Palaeolithic human hyoid bone. *Nature*, *338*(6218), 758–760. https://doi.org/10.1038/338758a0

Armstrong, D. F., Stokoe, W. C., & Wilcox, S. E. (1994). Signs of the origin of syntax. *Current Anthropology*, *35*(4), 349–368.

Aureli, F., & Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters*, *3*(2), 147–149. https://doi.org/10.1098/rsbl.2007.0041

Baayen, R. H. (2008). *Analyzing Linguistic Data: A practical introduction to statistics using R*. Cambridge University Press.

Babiszewska, M., Schel, A. M., Wilke, C., & Slocombe, K. E. (2015). Social, contextual, and individual factors affecting the occurrence and acoustic structure of drumming bouts in wild chimpanzees (Pan troglodytes). *American Journal of Physical Anthropology*, *156*(1), 125–134. https://doi.org/10.1002/ajpa.22634

Bard, K. A. (1992). Intentional Behavior and Intentional Communication in Young Free-Ranging Orangutans. *Child Development*, *63*(5), 1186–1197. https://doi.org/10.1111/j.1467-8624.1992.tb01688.x

Bard, K. A., Dunbar, S., Maguire-Herring, V., Veira, Y., Hayes, K. G., & Mcdonald, K. (2014). Gestures and social-emotional communicative development in chimpanzee infants. *American Journal of Primatology*, *76*(1), 14–29. https://doi.org/10.1002/ajp.22189

Bard, K. A., & Hopkins, W. D. (2018). Early Socioemotional Intervention Mediates Long-Term Effects of Atypical Rearing on Structural Covariation in Gray Matter in Adult Chimpanzees. *Psychological Science*, *29*(4), 594–603. https://doi.org/10.1177/0956797617740685

Bard, K. A., & Kishimoto, T. (2023). Early communicative gestures in human and chimpanzee 1-year-olds observed across diverse socioecological settings. *Learning & Behavior*, *51*(1), 15–33. https://doi.org/10.3758/s13420-022-00553-1

Bard, K. A., & Leavens, D. A. (2014). The Importance of Development for Comparative Primatology. *Annual Review of Anthropology*, *43*(1), 183–200. https://doi.org/10.1146/annurev-anthro-102313-030223

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, M. B., & Walker, S. C. (2014). Fitting linear mixed-effects models using lme4. *arXiv:1406.5823 [Stat]*. http://arxiv.org/abs/1406.5823

Bates, E. (1979). Intentions, conventions, and symbols. *The Emergence of Symbols: Cognition and Communication in Infancy*, 33–68.

Bates, E., Camaioni, L., & Volterra, V. (1975). The acquisition of performatives prior to speech. *Merrill-Palmer Quarterly of Behavior and Development*, *21*(3), 205–226.

Bates, L. A., Poole, J. H., & Byrne, R. W. (2008). Elephant cognition. *Current Biology*, *18*(13), R544–R546.

Bekken, K. E. (1989). *Is there" motherese" in gesture?* [PhD Thesis]. The University of Chicago.

Berg, J. K. (1983). Vocalizations and Associated Behaviors of the African Elephant (Loxodonta africana) in Captivity. *Zeitschrift Für Tierpsychologie*, *63*(1), 63–79. https://doi.org/10.1111/j.1439-0310.1983.tb00741.x

Biau, E., Morís Fernández, L., Holle, H., Avila, C., & Soto-Faraco, S. (2016). Hand gestures as visual prosody: BOLD responses to audio–visual alignment are modulated by the communicative nature of the stimuli. *NeuroImage*, *132*, 129–137. https://doi.org/10.1016/j.neuroimage.2016.02.018

Biersack, S., Kempe, V., & Knapton, L. (2005). Fine-tuning speech registers: A comparison of the prosodic features of child-directed and foreigner-directed speech. *Ninth European Conference on Speech Communication and Technology*.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, *6*(4), 213–223.

Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and Cultural Propagation of Tool Use by Wild Chimpanzees at Bossou, Guinea: Case Studies in Nut Cracking and Leaf Folding. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive Development in Chimpanzees* (pp. 476–508). Springer-Verlag. https://doi.org/10.1007/4-431-30248-4_28

Blake, J., McConnell, S., Horton, G., & Benson, N. (1992). The gestural repertoire and its evolution over the second year. *Early Development and Parenting*, *1*(3), 127–136. https://doi.org/10.1002/edp.2430010302

Boesch, C. (2007). What Makes Us Human (Homo sapiens)? The Challenge of Cognitive Cross-Species Comparison. *Journal of Comparative Psychology*, *121*(3), 227–240. https://doi.org/10.1037/0735-7036.121.3.227

Boesch, C. (2020). The Human Challenge in Understanding Animal Cognition. In L. S. M. Johnson, A. Fenton, & A. Shriver (Eds.), *Neuroethics and Nonhuman Animals* (pp. 33–51). Springer International Publishing. https://doi.org/10.1007/978-3-030-31011-0_3

Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, *26*(4), 325–338. https://doi.org/10.1006/jhev.1994.1020

Bolhuis, J. J., Tattersall, I., Chomsky, N., & Berwick, R. C. (2014). How Could Language Have Evolved? *PLoS Biology*, *12*(8), e1001934. https://doi.org/10.1371/journal.pbio.1001934

Bourjade, M., Cochet, H., Molesti, S., & Guidetti, M. (2020). Is Conceptual Diversity an Advantage for Scientific Inquiry? A Case Study on the Concept of ‘Gesture’ in Comparative Psychology. *Integrative Psychological and Behavioral Science*, *54*(4), 805–832. https://doi.org/10.1007/s12124-020-09516-5

Bourjade, M., Dafreville, M., Scola, C., & Jover, M. (2023). Six-month-old infants’ communication in a comparative perspective: Do maternal attention and interaction matter? *Journal of Experimental Child Psychology*, *231*, 105651. https://doi.org/10.1016/j.jecp.2023.105651

Brand, R. J., Baldwin, D. A., & Ashburn, L. A. (2002). Evidence for ‘motionese’: Modifications in mothers’ infant-directed action. *Developmental Science*, *5*(1), 72–83. https://doi.org/10.1111/1467-7687.00211

Brentari, D., Coppola, M., Mazzoni, L., & Goldin-Meadow, S. (2012). When does a system become phonological? Handshape production in gesturers, signers, and homesigners. *Natural Language & Linguistic Theory*, *30*(1), 1–31. https://doi.org/10.1007/s11049-011-9145-1

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.3929/ethz-b-000240890

Brownell, C. A., & Carriger, M. S. (1990). Changes in Cooperation and Self-Other Differentiation during the Second Year. *Child Development*, *61*(4), 1164–1174. https://doi.org/10.1111/j.1467-8624.1990.tb02850.x

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise: Regulation of call characteristics in a New World monkey. *Journal of Experimental Biology*, *207*(3), 443–448. https://doi.org/10.1242/jeb.00768

Bruner, J. S. (1981). The social context of language acquisition. *Language & Communication*, *1*(2–3), 155–178. https://doi.org/10.1016/0271-5309(81)90010-0

Bürkner, P.-C. (2017). **brms**: An *R* Package for Bayesian Multilevel Models Using *Stan*. *Journal of Statistical Software*, *80*(1). https://doi.org/10.18637/jss.v080.i01

Butterworth, G. (2003, June 20). *Pointing Is the Royal Road to Language for Babies*. Pointing. https://doi.org/10.4324/9781410607744-6

Bygott, J. (1979). Agonistic behaviour, dominance, and social structure in wild chimpanzees of the Gombe National Park. *The Great Apes*, 405–428.

Byrne, R. W., Cartmill, E. A., Genty, E., Graham, K. E., Hobaiter, C., & Tanner, J. E. (2017). Great ape gestures: Intentional communication with a rich set of innate signals. *Animal Cognition*, *20*(4), 755–769. https://doi.org/10.1007/s10071-017-1096-4

Cairns, R. (1979). *Social development: The origins and plasticity of interchanges.*

Call, J., & Tomasello, M. (2007). *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Mahwah, New York.

Cameron-Faulkner, T., Lieven, E., & Tomasello, M. (2003). A construction based analysis of child directed speech. *Cognitive Science*, *27*(6), 843–873. https://doi.org/10.1207/s15516709cog2706_2

Cartmill, E. A. (2008). *Gestural communication in orangutans (Pongo pygmaeus and Pongo Abeli): A cognitive approach* [PhD]. University of St Andrews.

Cartmill, E. A., & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, *17*(15), 1345–1348. https://doi.org/10.1016/j.cub.2007.06.069

Cartmill, E. A., & Byrne, R. W. (2010). Semantics of primate gestures: Intentional meanings of orangutan gestures. *Animal Cognition*, *13*(6), 793–804. https://doi.org/10.1007/s10071-010-0328-7

Carvalho, S., Biro, D., McGrew, W. C., & Matsuzawa, T. (2009). Tool-composite reuse in wild chimpanzees (Pan troglodytes): Archaeologically invisible steps in the technological evolution of early hominins? *Animal Cognition*, *12*(1), 103–114. https://doi.org/10.1007/s10071-009-0271-7

Chen, Y., Matheson, L. E., & Sakata, J. T. (2016). Mechanisms underlying the social enhancement of vocal learning in songbirds. *Proceedings of the National Academy of Sciences*, *113*(24), 6641–6646. https://doi.org/10.1073/pnas.1522306113

Cheney, D. L., & Seyfarth, R. M. (2018). Flexible usage and social function in primate vocalizations. *Proceedings of the National Academy of Sciences*, 201717572. https://doi.org/10.1073/pnas.1717572115

Chow, V., Poulin-Dubois, D., & Lewis, J. (2008). To see or not to see: Infants prefer to follow the gaze of a reliable looker. *Developmental Science*, *11*(5), 761–770. https://doi.org/10.1111/j.1467-7687.2008.00726.x

Christiansen, M. H., & Chater, N. (2015). The language faculty that wasn't: A usage-based account of natural language recursion. *Frontiers in Psychology*, *6*, 1182. https://doi.org/10.3389/fpsyg.2015.01182

Clark, H. H. (1996). *Using Language*. Cambridge University Press.

Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, *20*(1), 37–46.

Conner, R. N. (1985). Vocalizations of Common Ravens in Virginia. *The Condor*, *87*(3), 379–388. https://doi.org/10.2307/1367219

Cooke, A., Smith, D., & Booth, A. (2013). Qualitative Health Research Beyond PIC : The SPIDER Tool for Qualitative Evidence Synthesis. *Qualitative Health Research*, *22*(10), 1435–1443. https://doi.org/10.1177/1049732312452938

Corballis, M. C. (2002). *From Hand to Mouth: The Origins of Language*. Princeton University Press. https://doi.org/10.1525/jlin.2006.16.1.146

Crais, E., Watson, L., & Baranek, G. (2009). Use of Gesture Development in Profiling Children's Prelinguistic Communication Skills. *American Journal of Speech-Language Pathology*, *18*(1), 95–108. https://doi.org/10.1044/1058-0360(2008/07-0041)

Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour*, *142*(4), 397–421. https://doi.org/10.1163/1568539054012047

Crockford, C., Gruber, T., & Zuberbühler, K. (2018). Chimpanzee quiet hoo variants differ according to context. *Royal Society Open Science*, *5*(5), 172066. https://doi.org/10.1098/rsos.172066

Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild Chimpanzees Produce Group-Specific Calls: A Case for Vocal Learning? *Ethology*, *110*(3), 221–243. https://doi.org/10.1111/j.1439-0310.2004.00968.x

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1755), 20122765. https://doi.org/10.1098/rspb.2012.2765

De La Torre, S., & Snowdon, C. T. (2002). Environmental correlates of vocal communication of wild pygmy marmosets, Cebuella pygmaea. *Animal Behaviour*, *63*(5), 847–856. https://doi.org/10.1006/anbe.2001.1978

De Waal, F. (2007). *Chimpanzee politics: Power and sex among apes*. JHU Press.

De Waal, F. (2016). *Are we smart enough to know how smart animals are?* WW Norton & Company.

Defolie, C., Malassis, R., Serre, M., & Meunier, H. (2015). Tufted capuchins (Cebus apella) adapt their communicative behaviour to human's attentional states. *Animal Cognition*, *18*(3), 747–755. https://doi.org/10.1007/s10071-015-0841-9

DePaulo, B. M., & Coleman, L. M. (1986). Talking to children, foreigners, and retarded adults. *Journal of Personality and Social Psychology*, *51*, 945–959. https://doi.org/10.1037/0022-3514.51.5.945

Dobson, A. J., & Barnett, A. G. (2018). *An Introduction to Generalized Linear Models*. CRC Press.

Dunn, J., & Kendrick, C. (1982). The speech of two- and three-year-olds to infant siblings: 'Baby talk' and the context of communication. *Journal of Child Language*, *9*(3), 579–595. https://doi.org/10.1017/S030500090000492X

Eckerman, C. O., Peterman, K., Bremner, G., & Fogel, A. (2001). *Blackwell handbook of infant development*.

Edds-Walton, P. L., & Edds-Walton, P. L. (1997). Acoustic communication signals of mysticete whales. *Bioacoustics*, *8*(1–2), 47–60. https://doi.org/10.1080/09524622.1997.9753353

ELAN (6.4). (2022). [Computer software]. Max Planck Institute for Psycholinguistics, The Language Archive. https://archive.mpi.nl/tla/elan

Falk, D. (2004). Prelinguistic evolution in early hominins: Whence motherese? *Behavioral and Brain Sciences*, *27*(4), 491.

Fedurek, P., Neumann, C., Bouquet, Y., Mercier, S., Magris, M., Quintero, F., & Zuberbühler, K. (2019). Behavioural patterns of vocal greeting production in four primate species. *Royal Society Open Science*, *6*(4), 182181. https://doi.org/10.1098/rsos.182181

Fedurek, P., Tkaczynski, P. J., Hobaiter, C., Zuberbühler, K., Wittig, R. M., & Crockford, C. (2021). The function of chimpanzee greeting calls is modulated by their acoustic variation. *Animal Behaviour*, *174*, 279–289. https://doi.org/10.1016/j.anbehav.2021.02.002

Fedurek, P., Zuberbühler, K., & Dahl, C. D. (2016). Sequential information in a great ape utterance. *Scientific Reports*, *6*(1), Article 1. https://doi.org/10.1038/srep38226

Ferguson, C. A. (1964). Baby Talk in Six Languages. *American Anthropologist*, *66*(6), 103–114.

Ferguson, C. A. (1976). The structure and use of politeness formulas. *Language in Society*, *5*(2), 137–151. https://doi.org/10.1017/S0047404500006989

Fernald, A., Taeschner, T., Dunn, J., Papousek, M., Boysson-Bardies, B. de, & Fukui, I. (1989). A cross-language study of prosodic modifications in mothers' and fathers' speech to preverbal infants*. *Journal of Child Language*, *16*(3), 477–501. https://doi.org/10.1017/S0305000900010679

Fernandez, A. A., & Knörnschild, M. (2020). Pup Directed Vocalizations of Adult Females and Males in a Vocal Learning Bat. *Frontiers in Ecology and Evolution*, *8*. https://www.frontiersin.org/articles/10.3389/fevo.2020.00265

Field, A., Miles, J., & Field, Z. (2012). *Discovering Statistics Using R*. Sage Publications Ltd.

Firth, R. (1972). Verbal and bodily rituals of greeting and parting. *The Interpretation of Ritual*, *1972*, 1–38.

Fletcher, A. W. (2006). Clapping in chimpanzees: Evidence of exclusive hand preference in a spontaneous, bimanual gesture. *American Journal of Primatology*, *68*(11), 1081–1088. https://doi.org/10.1002/ajp.20308

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, *65*(1), 47–55. https://doi.org/10.1007/s00265-010-1038-5

Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression*. SAGE Publications.

Fox, J., & Weisberg, S. (2019). An R companion to applied regression (Third). *Thousand Oaks CA: Sage*.

Franco, F., Perucchini, P., & March, B. (2009). Is Infant Initiation of Joint Attention by Pointing Affected by Type of Interaction? *Social Development*, *18*(1), 51–76. https://doi.org/10.1111/j.1467-9507.2008.00464.x

Fröhlich, M., & Hobaiter, C. (2018). The development of gestural communication in great apes. *Behavioral Ecology and Sociobiology*, *72*(12), 194. https://doi.org/10.1007/s00265-018-2619-y

Fröhlich, M., Kuchenbuch, P., Müller, G., Fruth, B., Furuichi, T., Wittig, R. M., & Pika, S. (2016). Unpeeling the layers of language: Bonobos and chimpanzees engage in cooperative turn-taking sequences. *Scientific Reports*, *6*(1), 1–14. https://doi.org/10.1038/srep25887

Fröhlich, M., Lee, K., Mitra Setia, T., Schuppli, C., & van Schaik, C. P. (2019). The loud scratch: A newly identified gesture of Sumatran orangutan mothers in the wild. *Biology Letters*, *15*(7), 20190209.

Fröhlich, M., Müller, G., Zeiträg, C., Wittig, R. M., & Pika, S. (2017). Gestural development of chimpanzees in the wild: The impact of interactional experience. *Animal Behaviour*, *134*, 271–282. https://doi.org/10.1016/j.anbehav.2016.12.018

Fröhlich, M., Sievers, C., Townsend, S. W., Gruber, T., & Schaik, C. P. (2019). Multimodal communication and language origins: Integrating gestures and vocalizations. *Biological Reviews*, *94*(5), 1809–1829. https://doi.org/10.1111/brv.12535

Fröhlich, M., Wittig, R. M., & Pika, S. (2016a). Play-solicitation gestures in chimpanzees in the wild: Flexible adjustment to social circumstances and individual matrices. *Royal Society Open Science*, *3*(8), 160278. https://doi.org/10.1098/rsos.160278

Fröhlich, M., Wittig, R. M., & Pika, S. (2016b). Should I stay or should I go? Initiation of joint travel in mother–infant dyads of two chimpanzee communities in the wild. *Animal Cognition*, *19*(3), 483–500. https://doi.org/10.1007/s10071-015-0948-z

Fröhlich, M., Wittig, R. M., & Pika, S. (2018). The ontogeny of intentional communication in chimpanzees in the wild. *Developmental Science*, *22*(1), e12716. https://doi.org/10.1111/desc.12716

Galati, A., & Brennan, S. E. (2010). Attenuating information in spoken communication: For the speaker, or for the addressee? *Journal of Memory and Language*, *62*(1), 35–51. https://doi.org/10.1016/j.jml.2009.09.002

Gallois, C., Ogay, T., & Giles, H. (2005). Communication accommodation theory: A look back and a look ahead. In *Theorizing about intercultural communication* (pp. 121–148). Thousand Oaks: Sage.

Gallois, C., & Others, A. (1992). *Communication Accommodation between Chinese and Australian Students and Academic Staff*. https://eric.ed.gov/?id=ED353606

Gelman, A., Jakulin, A., Pittau, M. G., & Su, Y.-S. (2008). A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics*, *2*(4), 1360–1383. https://doi.org/10.1214/08-AOAS191

Genty, E. (2019). Vocal–gestural combinations in infant bonobos: New insights into signal functional specificity. *Animal Cognition*, *22*(4), 505–518. https://doi.org/10.1007/s10071-019-01267-0

Genty, E., Breuer, T., Hobaiter, C., & Byrne, R. W. (2009). Gestural communication of the gorilla (Gorilla gorilla): Repertoire, intentionality and possible origins. *Animal Cognition*, *12*(3), 527–546.

Ghazanfar, A. A., & Rendall, D. (2008). Evolution of human vocal production. *Current Biology*, *18*(11), R457–R460. https://doi.org/10.1016/j.cub.2008.03.030

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381. https://doi.org/10.1007/s00265-012-1457-6

Gilby, I. C., & Wrangham, R. W. (2008). Association patterns among wild chimpanzees (Pan troglodytes schweinfurthii) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, *62*(11), 1831. https://doi.org/10.1007/s00265-008-0612-6

Giles, H., Mulac, A., Bradac, J. J., & Johnson, P. (1987). Speech Accommodation Theory: The First Decade and Beyond. *Annals of the International Communication Association*, *10*(1), 13–48. https://doi.org/10.1080/23808985.1987.11678638

Giles, H., & Powesland, P. F. (1975). *Speech style and social evaluation* (pp. viii, 218). Academic Press.

Gillespie-Lynch, K., Greenfield, P. M., Lyn, H., & Savage-Rumbaugh, S. (2014). Gestural and symbolic development among apes and humans: Support for a multimodal theory of language evolution. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01228

Goffman, E. (1967). *Interaction ritual: Essays on face-to-face interaction*. Aldine.

Goldin-Meadow, S. (1993). When does gesture become language? A study of gesture used as a primary communication system by deaf children of hearing parents. *Tools, Language and Cognition in Human Evolution*, 63–85.

Goldin-Meadow, S., & McNeill, D. (1999). *The role of gesture and mimetic representation in making language the province of speech*. Oxford University Press, USA.

Goldin-Meadow, S., & Yang, C. (2017). Statistical evidence that a child can create a combinatorial linguistic system without external linguistic input: Implications for language evolution. *Neuroscience & Biobehavioral Reviews*, *81*, 150–157. https://doi.org/10.1016/j.neubiorev.2016.12.016

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge University Press.

Grafe, T. U., Preininger, D., Sztatecsny, M., Kasah, R., Dehling, J. M., Proksch, S., & Hödl, W. (2012). Multimodal Communication in a Noisy Environment: A Case Study of the Bornean Rock Frog Staurois parvus. *PLOS ONE*, *7*(5), e37965. https://doi.org/10.1371/journal.pone.0037965

Graham, K. E., Badihi, G., Safryghin, A., Grund, C., & Hobaiter, C. (2022). A socio-ecological perspective on the gestural communication of great ape species, individuals, and social units. *Ethology Ecology & Evolution*, *34*(3), 235–259. https://doi.org/10.1080/03949370.2021.1988722

Graham, K. E., Furuichi, T., & Byrne, R. W. (2017). The gestural repertoire of the wild bonobo (Pan paniscus): A mutually understood communication system. *Animal Cognition*, *20*(2), 171–177. https://doi.org/10.1007/s10071-016-1035-9

Graham, K. E., & Hobaiter, C. (2023). Towards a great ape dictionary: Inexperienced humans understand common nonhuman ape gestures. *PLOS Biology*, *21*(1), e3001939. https://doi.org/10.1371/journal.pbio.3001939

Graham, K. E., Hobaiter, C., Ounsley, J., Furuichi, T., & Byrne, R. W. (2018). Bonobo and chimpanzee gestures overlap extensively in meaning. *PLOS Biology*, *16*(2), e2004825. https://doi.org/10.1371/journal.pbio.2004825

Grund, C., Badihi, G., Graham, K. E., Safryghin, A., & Hobaiter, C. (2023). GesturalOrigins: A bottom-up framework for establishing systematic gesture data across ape species. *Behavior Research Methods*. https://doi.org/10.3758/s13428-023-02082-9

Gupta, S., & Sinha, A. (2016). Not here, there! Possible referential gesturing during allogrooming by wild bonnet macaques, Macaca radiata. *Animal Cognition*, *19*(6), 1243–1248. https://doi.org/10.1007/s10071-016-1012-3

Hall, M. L., Ahn, Y. D., Mayberry, R. I., & Ferreira, V. S. (2015). Production and comprehension show divergent constituent order preferences: Evidence from elicited pantomime. *Journal of Memory and Language*, *81*, 16–33. https://doi.org/10.1016/j.jml.2014.12.003

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Hawley, P. H. (1999). The Ontogenesis of Social Dominance: A Strategy-Based Evolutionary Perspective. *Developmental Review*, *19*(1), 97–132. https://doi.org/10.1006/drev.1998.0470

Hawley, P. H., & Little, T. D. (1999). On Winning Some and Losing Some: A Social Relations Approach to Social Dominance in Toddlers. *Merrill-Palmer Quarterly*, *45*(2), 185–214.

Hayashi, M., & Inoue-Nakamura, N. (2011). From Handling Stones and Nuts to Tool-Use. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 175–182). Springer Japan. https://doi.org/10.1007/978-4-431-53921-6_19

Hayes, D. P., Ahrens, M. G., & Tsay, R. (1987). *Tight and loose coupling: Effects on accommodation in conversation*. Cornell University, Department of Sociology.

Heesen, R., Bangerter, A., Zuberbühler, K., Iglesias, K., Neumann, C., Pajot, A., Perrenoud, L., Guéry, J.-P., Rossano, F., & Genty, E. (2021). Assessing joint commitment as a process in great apes. *iScience*, 102872. https://doi.org/10.1016/j.isci.2021.102872

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). Most people are not WEIRD. *Nature*, *466*(7302), 29–29.

Hewes, G. W., Andrew, R. J., Carini, L., Choe, H., Gardner, R. A., Kortlandt, A., Krantz, G. S., McBride, G., Nottebohm, F., & Pfeiffer, J. (1973). Primate communication and the gestural origin of language [and comments and reply]. *Current Anthropology*, *14*(1/2), 5–24.

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, *11*(1), 1–17. https://doi.org/10.2307/2800384

Hobaiter, C., Badihi, G., Daly, G. B. de M., Eleuteri, V., Graham, K. E., Grund, C., Henderson, M., Rodrigues, E. D., Safryghin, A., Soldati, A., & Wiltshire, C. (2021). *The Great Ape Dictionary video database* (1.0.0) [dataset]. Zenodo. https://doi.org/10.5281/zenodo.5600472

Hobaiter, C., & Byrne, R. W. (2011a). Serial gesturing by wild chimpanzees: Its nature and function for communication. *Anim Cogn*, *14*, 827–838. https://doi.org/10.1007/s10071-011-0416-3

Hobaiter, C., & Byrne, R. W. (2011b). The gestural repertoire of the wild chimpanzee. *Animal Cognition*, *14*(5), 745–767. https://doi.org/10.1007/s10071-011-0409-2

Hobaiter, C., & Byrne, R. W. (2012). Gesture use in Consortship: Wild chimpanzees' use of gesture for an 'evolutionarily urgent' purpose. *Developments in Primate Gesture Research*, *6*, 129–146.

Hobaiter, C., & Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology*, *24*(14), 1596–1600. https://doi.org/10.1016/j.cub.2014.05.066

Hobaiter, C., & Byrne, R. W. (2017). What is a gesture? A meaning-based approach to defining gestural repertoires. *Neuroscience & Biobehavioral Reviews*, *82*, 3–12. https://doi.org/10.1016/j.neubiorev.2017.03.008

Hobaiter, C., Byrne, R. W., & Zuberbühler, K. (2017). Wild chimpanzees' use of single and combined vocal and gestural signals. *Behavioral Ecology and Sociobiology*, *71*(6), 96. https://doi.org/10.1007/s00265-017-2325-1

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2009). Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: Feeding dynamics in a human-influenced environment. *American Journal of Primatology*, *71*(8), 636–646. https://doi.org/10.1002/ajp.20698

Hockings, K. J., Humle, T., Anderson, J. R., Biro, D., Sousa, C., Ohashi, G., & Matsuzawa, T. (2007). Chimpanzees Share Forbidden Fruit. *PLOS ONE*, *2*(9), e886. https://doi.org/10.1371/journal.pone.0000886

Hoff, E. (2006). How social contexts support and shape language development. *Developmental Review*, *26*(1), 55–88. https://doi.org/10.1016/j.dr.2005.11.002

Holzrichter, A. S., & Meier, R. P. (2000). Child-directed signing in American sign language. *Language Acquisition by Eye*, 25–40.

Hopkins, W. D., Dunham, L., Cantalupo, C., & Taglialatela, J. (2007). The Association between Handedness, Brain Asymmetries, and Corpus Callosum Size in Chimpanzees (Pan troglodytes). *Cerebral Cortex*, *17*(8), 1757–1765. https://doi.org/10.1093/cercor/bhl086

Hopkins, W. D., Taglialatela, J. P., Meguerditchian, A., Nir, T., Schenker, N. M., & Sherwood, C. C. (2008). Gray matter asymmetries in chimpanzees as revealed by voxel-based morphometry. *NeuroImage*, *42*(2), 491–497. https://doi.org/10.1016/j.neuroimage.2008.05.014

Hsieh, S., & Plotnick, R. E. (2020). The representation of animal behaviour in the fossil record. *Animal Behaviour*, *169*, 65–80. https://doi.org/10.1016/j.anbehav.2020.09.010

Hwang, J., Brennan, S. E., & Huffman, M. K. (2015). Phonetic adaptation in non-native spoken dialogue: Effects of priming and audience design. *Journal of Memory and Language*, *81*, 72–90. https://doi.org/10.1016/j.jml.2015.01.001

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *111*(2), 159.

Itani, J. (1963). Vocal communication of the wild Japanese monkey. *Primates*, *4*(2), 11–66. https://doi.org/10.1007/bf01659149

Iverson, J. M., Capirci, O., & Caselli, M. C. (1994). From communication to language in two modalities. *Cognitive Development*, *9*(1), 23–43. https://doi.org/10.1016/0885-2014(94)90018-3

Iverson, J. M., Capirci, O., Longobardi, E., & Cristina Caselli, M. (1999). Gesturing in mother-child interactions. *Cognitive Development*, *14*(1), 57–75. https://doi.org/10.1016/S0885-2014(99)80018-5

Iverson, J. M., & Goldin-Meadow, S. (1998). Why people gesture when they speak. *Nature*, *396*(6708), 228–228. https://doi.org/10.1038/24300

Iverson, J. M., & Goldin-Meadow, S. (2005). Gesture Paves the Way for Language Development. *Psychological Science*, *16*(5), 367–371. https://doi.org/10.1111/j.0956-7976.2005.01542.x

Janmaat, K. R. L., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences*, *111*(46), 16343–16348.

Junqua, J.-C. (1996). The influence of acoustics on speech production: A noise-induced stress phenomenon known as the Lombard reflex. *Speech Communication*, *20*(1), 13–22. https://doi.org/10.1016/S0167-6393(96)00041-6

Kachel, G., Moore, R., Hepach, R., & Tomasello, M. (2021). Toddlers Prefer Adults as Informants: 2- and 3-Year-Olds' Use of and Attention to Pointing Gestures From Peer and Adult Partners. *Child Development*, *n/a*(n/a). https://doi.org/10.1111/cdev.13544

Kalan, A. K., Mundry, R., & Boesch, C. (2015). Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour*, *101*, 1–9. https://doi.org/10.1016/j.anbehav.2014.12.011

Kawakami, K., Takai-Kawakami, K., Tomonaga, M., Suzuki, J., Kusaka, F., & Okai, T. (2007). Spontaneous smile and spontaneous laugh: An intensive longitudinal case study. *Infant Behavior and Development*, *30*(1), 146–152. https://doi.org/10.1016/j.infbeh.2006.08.004

Kemper, S. (1994). Elderspeak: Speech accommodations to older adults. *Aging, Neuropsychology, and Cognition*, *1*(1), 17–28. https://doi.org/10.1080/09289919408251447

Kersken, V., Gómez, J.-C., Liszkowski, U., Soldati, A., & Hobaiter, C. (2018). A gestural repertoire of 1- to 2-year-old human children: In search of the ape gestures. *Animal Cognition*. https://doi.org/10.1007/s10071-018-1213-z

Kim, H. I., & Johnson, S. P. (2013). Do young infants prefer an infant-directed face or a happy face? *International Journal of Behavioral Development*, *37*(2), 125–130.

Kitamura, C., Thanavishuth, C., Burnham, D., & Luksaneeyanawin, S. (2001). Universality and specificity in infant-directed speech: Pitch modifications as a function of infant age and sex in a tonal and non-tonal language. *Infant Behavior and Development*, *24*(4), 372–392. https://doi.org/10.1016/S0163-6383(02)00086-3

Knapp, M. L., Hart, R. P., Friedrich, G. W., & Shulman, G. M. (1973). The rhetoric of goodbye: Verbal and nonverbal correlates of human leave-taking. *Speech Monographs*, *40*(3), 182–198. https://doi.org/10.1080/03637757309375796

Knox, A., Markx, J., How, E., Azis, A., Hobaiter, C., van Veen, F. J. F., & Morrogh-Bernard, H. (2019). Gesture Use in Communication between Mothers and Offspring in Wild Orang-Utans (Pongo pygmaeus wurmbii) from the Sabangau Peat-Swamp Forest, Borneo. *International Journal of Primatology*, 1–24. https://doi.org/10.1007/s10764-019-00095-w

Kudo, H. (1987). The study of vocal communication of wild mandrills in Cameroon in relation to their social structure. *Primates*, *28*(3), 289–308. https://doi.org/10.1007/BF02381013

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*(10), 840–851. https://doi.org/10.1002/ajp.20711

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour*, *80*(3), 467–473. https://doi.org/10.1016/j.anbehav.2010.06.005

Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2010). BIZARRE chimpanzees do not represent “the chimpanzee”. *Behavioral and Brain Sciences*, *33*(2–3), 100–101. https://doi.org/10.1017/S0140525X10000166

Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2019). The mismeasure of ape social cognition. *Animal Cognition*, *22*(4), 487–504. https://doi.org/10.1007/s10071-017-1119-1

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, *34*(5), 813. https://doi.org/10.1037/0012-1649.34.5.813

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science*, *14*(4), 185–189. https://doi.org/10.1111/j.0963-7214.2005.00361.x

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005a). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (Pan troglodytes). *Child Development*, *76*(1), 291–306. https://doi.org/10.1111/j.1467-8624.2005.00845.x

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2010). Multimodal communication by captive chimpanzees (Pan troglodytes). *Animal Cognition*, *13*(1), 33–40. https://doi.org/10.1007/s10071-009-0242-z

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: Effects of community size on wild chimpanzee (Pan troglodytes verus) social organisation. *Behavioral Ecology and Sociobiology*, *56*(3), 207–216. https://doi.org/10.1007/s00265-004-0781-x

Liebal, K., Call, J., & Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology*, *64*(4), 377–396. https://doi.org/10.1002/ajp.20087

Lieven, E. V. M. (1994). Crosslinguistic and crosscultural aspects of language addressed to children. In *Input and interaction in language acquisition* (pp. 56–73). Cambridge University Press. https://doi.org/10.1017/CBO9780511620690.005

Liszkowski, U. (2010). Deictic and other gestures in infancy. *Acción Psicológica*, *7*(2), 21–33.

Liszkowski, U., Carpenter, M., Henning, A., Striano, T., & Tomasello, M. (2004). Twelve-month-olds point to share attention and interest. *Developmental Science*, *7*(3), 297–307. https://doi.org/10.1111/j.1467-7687.2004.00349.x

Lock, A. (2004). Preverbal Communication. In *Blackwell Handbook of Infant Development* (pp. 379–403). John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470996348.ch14

Loukatou, G., Scaff, C., Demuth, K., Cristia, A., & Havron, N. (2022). Child-directed and overheard input from different speakers in two distinct cultures. *Journal of Child Language*, *49*(6), 1173–1192. https://doi.org/10.1017/S0305000921000623

Lowe, A. E., Hobaiter, C., Asiimwe, C., Zuberbühler, K., & Newton-Fisher, N. E. (2020). Intra-community infanticide in wild, eastern chimpanzees: A 24-year review. *Primates*, *61*(1), 69–82. https://doi.org/10.1007/s10329-019-00730-3

Luef, E. M., & Liebal, K. (2012). Infant-Directed Communication in Lowland Gorillas (Gorilla gorilla): Do Older Animals Scaffold Communicative Competence in Infants? *American Journal of Primatology*, *74*(9), 841–852. https://doi.org/10.1002/ajp.22039

Luef, E. M., & Pika, S. (2017). Reciprocal greeting in chimpanzees (Pan troglodytes) at the Ngogo community. *Journal of Neurolinguistics*, *43*, 263–273. https://doi.org/10.1016/j.jneuroling.2016.11.002

Luef, E. M., & Pika, S. (2019). Social relationships and greetings in wild chimpanzees (Pan troglodytes): Use of signal combinations. *Primates*, *60*(6), 507–515. https://doi.org/10.1007/s10329-019-00758-5

MacLarnon, A. M., & Hewitt, G. P. (1999). The evolution of human speech: The role of enhanced breathing control. *American Journal of Physical Anthropology*, *109*(3), 341–363. https://doi.org/10.1002/(SICI)1096-8644(199907)109:3<341::AID-AJPA5>3.0.CO;2-2

Masataka, N. (1992). Motherese in a signed language. *Infant Behavior and Development*, *15*(4), 453–460. https://doi.org/10.1016/0163-6383(92)80013-K

Matsuzawa, T. (1994). Field Experiments on Use of Stone. *Chimpanzee Cultures*, 350.

Matsuzawa, T., Humle, T., & Sugiyama, Y. (2011). *The chimpanzees of Bossou and Nimba*. Springer Science & Business Media.

McCarthy, M. S., Jensvold, M. L. A., & Fouts, D. H. (2013). Use of gesture sequences in captive chimpanzee (Pan troglodytes) play. *Animal Cognition*, *16*(3), 471–481. https://doi.org/10.1007/s10071-012-0587-6

McElreath, R. (2020). *Statistical Rethinking: A Bayesian Course with Examples in R and STAN*. CRC Press.

McGraw, K. O., & Wong, S. P. (1996). Forming inferences about some intraclass correlation coefficients. *Psychological Methods*, *1*(1), 30–46. https://doi.org/10.1037/1082-989X.1.1.30

McGrew, W. C., & Baehren, L. (2016). ‘Parting Is Such Sweet Sorrow’, But Only for Humans? *Human Ethology Bulletin*, *31*(4), 5–14. https://doi.org/10.22330/heb/314/005-014

McGrew, W., Ham, R., White, L., … C. T.-I. J. of, & 1997, U. (1997). Why don’t chimpanzees in Gabon crack nuts? *International Journal of Primatology*, *18*(3), 353–374. https://doi.org/10.1023/A:1026382316131

McNeill, D. (1992). *Hand and Mind: What Gestures Reveal about Thought*. University of Chicago Press.

Meguerditchian, A., Molesti, S., & Vauclair, J. (2011). Right-handedness predominance in 162 baboons (Papio anubis) for gestural communication: Consistency across time and groups. *Behavioral Neuroscience*, *125*(4), 653–660. https://doi.org/10.1037/a0023823

Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2010). Captive chimpanzees use their right hand to communicate with each other: Implications for the origin of the cerebral substrate for language. *CORTEX*, *46*(1), 40–48. https://doi.org/10.1016/j.cortex.2009.02.013

Meunier, H., Fizet, J., & Vauclair, J. (2013). Tonkean macaques communicate with their right hand. *Brain and Language*, *126*(2), 181–187. https://doi.org/10.1016/j.bandl.2013.05.004

Micheletta, J., Engelhardt, A., Matthews, L., Agil, M., & Waller, B. M. (2013). Multicomponent and multimodal lipsmacking in crested macaques (Macaca nigra). *American Journal of Primatology*, *75*(7), 763–773. https://doi.org/10.1002/ajp.22105

Mielke, A., Samuni, L., Preis, A., Gogarten, J. F., Crockford, C., & Wittig, R. M. (2017). Bystanders intervene to impede grooming in Western chimpanzees and sooty mangabeys. *Royal Society Open Science*, *4*(11), 171296. https://doi.org/10.1098/rsos.171296

Morita, M. (2011). Sex Differences in Human Greeting Behaviors in Waiting and Meeting Situations: A Field Study in Japan. *Journal of Human Ergology*, *40*(1_2), 79–83. https://doi.org/10.11183/jhe.40.79

Müller, C. (2005). Gestures in human and nonhuman primates: Why we need a comparative view. In *Gesture* (Vol. 5, Issue 1, pp. 259–283). https://doi.org/10.1075/gest.5.1.17mul

Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (Pan troglodytes schweinfurthii). *Behavioral Ecology and Sociobiology*, *55*(4), 332–340. https://doi.org/10.1007/s00265-003-0713-1

Murillo, E., Montero, I., & Casla, M. (2021). On the Multimodal Path to Language: The Relationship Between Rhythmic Movements and Deictic Gestures at the End of the First Year. *Frontiers in Psychology*, *12*. https://www.frontiersin.org/articles/10.3389/fpsyg.2021.616812

Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall, J., & Pusey, A. E. (2014). Early social exposure in wild chimpanzees: Mothers with sons are more gregarious than mothers with daughters. *Proceedings of the National Academy of Sciences*, *111*(51), 18189–18194. https://doi.org/10.1073/pnas.1409507111

Nakamura, M., McGrew, W. C., Marchant, L. F., & Nishida, T. (2000). Social scratch: Another custom in wild chimpanzees? *Primates*, *41*(3), 237–248. https://doi.org/10.1007/BF02557594

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*(4), 911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Newton-Fisher, N. E. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates*, *45*(2), 81–87. https://doi.org/10.1007/s10329-003-0064-6

Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. *Primates*, *9*(3), 167–224. https://doi.org/10.1007/BF01730971

Nishida, T. (1980). The leaf-clipping display: A newly-discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution*, *9*(2), 117–128. https://doi.org/10.1016/0047-2484(80)90068-8

Ochs, E., & Schieffelin, B. (1984). Language acquisition and socialization. *Culture Theory: Essays on Mind, Self, and Emotion*, 276–320.

O’Neill, M., Bard, K. A., Linnell, M., & Fluck, M. (2005). Maternal gestures with 20-month-old infants in two contexts. *Developmental Science*, *8*(4), 352–359. https://doi.org/10.1111/j.1467-7687.2005.00423.x

Oshima-Takane, Y., Goodz, E., & Derevensky, J. L. (1996). Birth Order Effects on Early Language Development: Do Secondborn Children Learn from Overheard Speech? *Child Development*, *67*(2), 621–634. https://doi.org/10.1111/j.1467-8624.1996.tb01755.x

Ouattara, K., Zuberbühler, K., N’goran, E. K., Gombert, J.-E., & Lemasson, A. (2009). The alarm call system of female Campbell’s monkeys. *Animal Behaviour*, *78*(1), 35–44. https://doi.org/10.1016/j.anbehav.2009.03.014

Papoušek, M., Papoušek, H., & Haekel, M. (1987). Didactic adjustments in fathers’ and mothers’ speech to their 3-month-old infants. *Journal of Psycholinguistic Research*, *16*(5), 491–516. https://doi.org/10.1007/BF01073274

Parr, L. A., Cohen, M., & Waal, F. de. (2005). Influence of Social Context on the Use of Blended and Graded Facial Displays in Chimpanzees. *International Journal of Primatology*, *26*(1), 73–103. https://doi.org/10.1007/s10764-005-0724-z

Parr, L. A., & Waller, B. M. (2006). Understanding chimpanzee facial expression: Insights into the evolution of communication. *Social Cognitive and Affective Neuroscience*, *1*(3), 221–228. https://doi.org/10.1093/scan/nsl031

Partan, S. (2002). Single and multichannel signal composition: Facial expressions and vocalizations of rhesus macaques (Macaca mulatta). *Behaviour*, *139*, 993–1028.

Partan, S., & Marler, P. (1999). Communication goes multimodal. *Science*, *83*, 1272–1273.

Petito, L. A. (1988). Language'in the prelinguistic child. *The Development of Language and Language Researchers. Hillsdale, NJ: Erlbaum*.

Pickering, M. J., & Garrod, S. (2004). The interactive-alignment model: Developments and refinements. *Behavioral and Brain Sciences*, *27*(2), 212–225. https://doi.org/10.1017/S0140525X04450055

Pika, S. (2008). Gestures of apes and pre-linguistic human children: Similar or different? *First Language*, *28*(2), 116–140. https://doi.org/10.1177/0142723707080966

Pika, S., & Liebal, K. (2012). *Developments in Primate Gesture Research*. John Benjamins Publishing.

Pika, S., & Mitani, J. (2006). Referential gestural communication in wild chimpanzees (Pan troglodytes). *Current Biology*, *16*(6), R191–R192. https://doi.org/10.1016/j.cub.2006.02.037

Pine, J. M. (1994). The language of primary caregivers. In *Input and interaction in language acquisition* (pp. 15–37). Cambridge University Press. https://doi.org/10.1017/CBO9780511620690.003

Pinker, S., & Jackendoff, R. (2005). The faculty of language: What's special about it? *Cognition*, *95*(2), 201–236. https://doi.org/10.1016/j.cognition.2004.08.004

Plooij, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gestures, and symbol: The emergence of language* (pp. 111–132).

Pollick, A. S., & de Waal, F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(19), 8184–8189.

Prieur, J., Barbu, S., Blois-Heulin, C., & Lemasson, A. (2020). The origins of gestures and language: History, current advances and proposed theories. *Biological Reviews*, *95*(3), 531–554. https://doi.org/10.1111/brv.12576

Prieur, J., Lemasson, A., Barbu, S., & Blois-Heulin, C. (2018). Challenges Facing the Study of the Evolutionary Origins of Human Right-Handedness and Language. *International Journal of Primatology*, *39*(2), 183–207. https://doi.org/10.1007/s10764-018-0038-6

Provine, R. R. (1992). Contagious laughter: Laughter is a sufficient stimulus for laughs and smiles. *Bulletin of the Psychonomic Society*, *30*(1), 1–4. https://doi.org/10.3758/BF03330380

Pruetz, J. D., & McGrew, W. C. (2001). What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. *Care and Management of Captive Chimpanzees*, 16–37.

Pusey, A., Williams, J., & Goodall, J. (1997). The Influence of Dominance Rank on the Reproductive Success of Female Chimpanzees. *Science*, *277*(5327), 828–831. https://doi.org/10.1126/science.277.5327.828

Quinn, G. P., & Keough, M. J. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge University Press.

R Core Team. (2020). *R: A language and environment for statistical computing.* (4.0.2) [Computer software]. https://www.R-project.org/

Reilly, J. S., & Bellugi, U. (1996). Competition on the face: Affect and language in ASL motherese. *Journal of Child Language*, *23*(1), 219–239. https://doi.org/10.1017/S0305000900010163

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour*, *78*(2), 233–240. https://doi.org/10.1016/j.anbehav.2009.06.007

Reynolds, V. (2005). *Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation*. Oxford University Press.

Richerson, P., Biolinguistics, R. B.-, & 2010, U. (2010). Why Possibly Language Evolved. *Biolinguistics*, *4*(2–3), 289–306.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. In *Trends in Neurosciences* (Vol. 21, Issue 5, pp. 188–194).

Roberts, A. I., Vick, S.-J., & Buchanan-Smith, H. M. (2012). Usage and comprehension of manual gestures in wild chimpanzees. *Animal Behaviour*, *84*(2), 459–470. https://doi.org/10.1016/j.anbehav.2012.05.022

Rodrigues, E. D., Marôco, J., & Frota, S. (2021). Communicative gestures in 7–12-month infants: A phylogenetic comparative approach. *Infant and Child Development*, *30*(5), e2262. https://doi.org/10.1002/icd.2262

Rodrigues, E. D., Santos, A. J., Hayashi, M., Matsuzawa, T., & Hobaiter, C. (2022). Exploring greetings and leave-takings: Communication during arrivals and departures by chimpanzees of the Bossou community, Guinea. *Primates*, *63*(5), 443–461. https://doi.org/10.1007/s10329-021-00957-z

Rodrigues, E. D., Santos, A. J., Veppo, F., Pereira, J., & Hobaiter, C. (2021). Connecting primate gesture to the evolutionary roots of language: A systematic review. *American Journal of Primatology*, *83*(9), e23313. https://doi.org/10.1002/ajp.23313

Ruch, H., Zürcher, Y., & Burkart, J. M. (2018). The function and mechanism of vocal accommodation in humans and other primates. *Biological Reviews*, *93*(2), 996–1013. https://doi.org/10.1111/brv.12382

Rutz, C., & Webster, M. M. (2021). Ethology adopts the STRANGE framework for animal behaviour research, to improve reporting standards. *Ethology*, *127*(2), 99–101. https://doi.org/10.1111/eth.13118

Sachs, J., & Devin, J. (1976). Young children's use of age-appropriate speech styles in social interaction and role-playing. *Journal of Child Language*, *3*(1), 81–98. https://doi.org/10.1017/S030500090000132X

Saito, A., Hayashi, M., Takeshita, H., & Matsuzawa, T. (2014). The Origin of Representational Drawing: A Comparison of Human Children and Chimpanzees. *Child Development*, *85*(6), 2232–2246. https://doi.org/10.1111/cdev.12319

Salo, V. C., Rowe, M. L., & Reeb-Sutherland, B. C. (2018). Exploring Infant Gesture and Joint Attention as Related Constructs and as Predictors of Later Language. *Infancy*, *23*(3), 432–452. https://doi.org/10.1111/infa.12229

Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R. M., & Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1888), 20181643. https://doi.org/10.1098/rspb.2018.1643

Savitsky, K., Keysar, B., Epley, N., Carter, T., & Swanson, A. (2011). The closeness-communication bias: Increased egocentrism among friends versus strangers. *Journal of Experimental Social Psychology*, *47*(1), 269–273. https://doi.org/10.1016/j.jesp.2010.09.005

Sayigh, L. S., El Haddad, N., Tyack, P. L., Janik, V. M., Wells, R. S., & Jensen, F. H. (2023). Bottlenose dolphin mothers modify signature whistles in the presence of their own calves. *Proceedings of the National Academy of Sciences*, *120*(27), e2300262120. https://doi.org/10.1073/pnas.2300262120

Schamberg, I., Cheney, D. L., Clay, Z., Hohmann, G., & Seyfarth, R. M. (2016). Call combinations, vocal exchanges and interparty movement in wild bonobos. *Animal Behaviour*, *122*, 109–116. https://doi.org/10.1016/j.anbehav.2016.10.003

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee Alarm Call Production Meets Key Criteria for Intentionality. *PLoS ONE*, *8*(10). https://doi.org/10.1371/journal.pone.0076674

Scheumann, M., Linn, S., & Zimmermann, E. (2017). Vocal greeting during mother-infant reunions in a nocturnal primate, the gray mouse lemur (Microcebus murinus). *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/s41598-017-10417-8

Schick, J., Fryns, C., Wegdell, F., Laporte, M., Zuberbühler, K., Schaik, C. P. van, Townsend, S. W., & Stoll, S. (2022). The function and evolution of child-directed communication. *PLOS Biology*, *20*(5), e3001630. https://doi.org/10.1371/journal.pbio.3001630

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., & Carvalho, S. (2019). Chimpanzee face recognition from videos in the wild using deep learning. *Science Advances*, *5*(9), eaaw0736. https://doi.org/10.1126/sciadv.aaw0736

Schwab, J. F., & Lew-Williams, C. (2016). Repetition across successive sentences facilitates young children's word learning. *Developmental Psychology*, *52*(6), 879–886. https://doi.org/10.1037/dev0000125

Seyfarth, R., & Cheney, D. (2003). Meaning and emotion in animal vocalizations. *Annals of the New York Academy of Sciences*, 32–55.

Seyfarth, R. M., & Cheney, D. L. (2003). Signalers and Receivers in Animal Communication. *Annual Review of Psychology*, *54*(1), 145–173. https://doi.org/10.1146/annurev.psych.54.101601.145121

Shatz, M., & Gelman, R. (1973). The Development of Communication Skills: Modifications in the Speech of Young Children as a Function of Listener. *Monographs of the Society for Research in Child Development*, *38*(5), 1–38. https://doi.org/10.2307/1165783

Slocombe, K. E., Waller, B. M., & Liebal, K. (2011). The language void: The need for multimodality in primate communication research. *Animal Behaviour*, *81*(5), 919–924. https://doi.org/10.1016/j.anbehav.2011.02.002

Slocombe, K. E., & Zuberbuhler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228–17233. https://doi.org/10.1073/pnas.0706741104

Smith, J. E., Powning, K. S., Dawes, S. E., Estrada, J. R., Hopper, A. L., Piotrowski, S. L., & Holekamp, K. E. (2011). Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour*, *81*(2), 401–415. https://doi.org/10.1016/j.anbehav.2010.11.007

Smuts, B. B., & Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (Papio cynocephalus anubis). *International Journal of Primatology*, *11*(2), 147–172.

Snow, C. E. (1977). The development of conversation between mothers and babies*. *Journal of Child Language*, *4*(1), 1–22. https://doi.org/10.1017/S0305000900000453

Soderstrom, M. (2007). Beyond babytalk: Re-evaluating the nature and content of speech input to preverbal infants. *Developmental Review*, *27*(4), 501–532. https://doi.org/10.1016/j.dr.2007.06.002

Sogabe, A., & Yanagisawa, Y. (2007). The function of daily greetings in a monogamous pipefish Corythoichthys haematopterus. *Journal of Fish Biology*, *71*(2), 585–595. https://doi.org/10.1111/j.1095-8649.2007.01523.x

Sousa, C., Biro, D., & Matsuzawa, T. (2009). Leaf-tool use for drinking water by wild chimpanzees (Pan troglodytes): Acquisition patterns and handedness. *Animal Cognition*, *12*(1), 115–125. https://doi.org/10.1007/s10071-009-0278-0

Stamp, R., Schembri, A., Evans, B. G., & Cormier, K. (2016). Regional Sign Language Varieties in Contact: Investigating Patterns of Accommodation. *The Journal of Deaf Studies and Deaf Education*, *21*(1), 70–82. https://doi.org/10.1093/deafed/env043

Stan Development Team. (2020). *RStan: The R interface to Stan*. R package version 2.21.1. http://mc-stan.org/

Stivers, T., Enfield, N. J., Brown, P., Englert, C., Hayashi, M., Heinemann, T., Hoymann, G., Rossano, F., de Ruiter, J. P., Yoon, K.-E., & Levinson, S. C. (2009). Universals and cultural variation in turn-taking in conversation. *Proceedings of the National Academy of Sciences*, *106*(26), 10587–10592. https://doi.org/10.1073/pnas.0903616106

Suddendorf, T., & Corballis, M. C. (2010). Behavioural evidence for mental time travel in nonhuman animals. *Behavioural Brain Research*, *215*(2), 292–298. https://doi.org/10.1016/j.bbr.2009.11.044

Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology*, *124*(2), 154–165. https://doi.org/10.1002/ajpa.10345

Sugiyama, Y., & Koman, J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates*, *20*(3), 323–339. https://doi.org/10.1007/BF02373387

Taglialatela, J. P., Russell, J. L., Schaeffer, J. A., & Hopkins, W. D. (2011). Chimpanzee Vocal Signaling Points to a Multimodal Origin of Human Language. *PLoS ONE*, *6*(4). https://doi.org/10.1371/journal.pone.0018852

Tempelmann, S., & Liebal, K. (2012). Spontaneous use of gesture sequences in orangutans. In *Developments in Primate Gesture Research* (pp. 73–92). https://doi.org/10.1075/gs.6.05tem

Tomasello, M., & Call, J. (1997). *Primate Cognition*. Oxford University Press.

Tomasello, M., Call, J., & Gluckman, A. (1997). Comprehension of Novel Communicative Signs by Apes and Human Children. *Child Development*, *68*(6), 1067–1080. https://doi.org/10.2307/1132292

Tomasello, M., Call, J., Nagell, K., Jaakkola, K., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, *35*, 137–154. https://doi.org/10.1007/BF02382050

Tomasello, M., George, B. L., Kruger, A. C., Jeffrey, M., Farrar, & Evans, A. (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution*, *14*(2), 175–186. https://doi.org/10.1016/S0047-2484(85)80005-1

Townsend, S. W., Deschner, T., & Zuberbühler, K. (2008). Female Chimpanzees Use Copulation Calls Flexibly to Prevent Social Competition. *PLoS ONE*, *3*(6), e2431. https://doi.org/10.1371/journal.pone.0002431

Townsend, S. W., Koski, S. E., Byrne, R. W., Slocombe, K. E., Bickel, B., Boeckle, M., Braga Goncalves, I., Burkart, J. M., Flower, T., Gaunet, F., Glock, H. J., Gruber, T., Jansen, D. A. W. A. M., Liebal, K., Linke, A., Miklósi, Á., Moore, R., van Schaik, C. P., Stoll, S., … Manser, M. B. (2017). Exorcising Grice's ghost: An empirical approach to studying intentional communication in animals: Intentional communication in animals. *Biological Reviews*, *92*(3), 1427–1433. https://doi.org/10.1111/brv.12289

Van Der Wege, M., Jacobsen, J., Magats, N., Mansour, C. B., & Park, J. H. (2021). Familiarity breeds overconfidence: Group membership and shared experience in the closeness-communication bias. *Journal of Experimental Social Psychology*, *94*, 104097. https://doi.org/10.1016/j.jesp.2020.104097

Van Lawick-Goodall, J. (1968). The Behaviour of Free-living Chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161-IN12. https://doi.org/10.1016/S0066-1856(68)80003-2

Vehtari, A., Simpson, D., Gelman, A., Yao, Y., & Gabry, J. (2019). Pareto Smoothed Importance Sampling. *arXiv:1507.02646 [Stat]*. http://arxiv.org/abs/1507.02646

Waller, B. M., Liebal, K., Burrows, A. M., & Slocombe, Katie. E. (2013). How Can a Multimodal Approach to Primate Communication Help Us Understand the Evolution of Communication? *Evolutionary Psychology*, *11*(3), 147470491301100. https://doi.org/10.1177/147470491301100305

Webster, M. M., & Rutz, C. (2020). How STRANGE are your study animals? *Nature*, *582*(7812), 337–340. https://doi.org/10.1038/d41586-020-01751-5

Wheeler, B. C. (2010). Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (Cebus apella nigritus). *Behavioral Ecology and Sociobiology*, *64*(6), 989–1000. https://doi.org/10.1007/s00265-010-0914-3

Whitehead, H., & Rendell, L. (2014). *The cultural lives of whales and dolphins*. University of Chicago Press.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685. https://doi.org/10.1038/21415

Whitham, J. C., Gerald, M. S., & Maestripieri, D. (2007). Intended Receivers and Functional Significance of Grunt and Girney Vocalizations in Free-Ranging Female Rhesus Macaques. *Ethology*, *113*(9), 862–874. https://doi.org/10.1111/j.1439-0310.2007.01381.x

Whitham, J. C., & Maestripieri, D. (2003). Primate Rituals: The Function of Greetings between Male Guinea Baboons. *Ethology*, *109*(10), 847–859. https://doi.org/10.1046/j.0179-1613.2003.00922.x

Wich, S. A., Krützen, M., Lameira, A. R., Nater, A., Arora, N., Bastian, M. L., Meulman, E., Morrogh-Bernard, H. C., Atmoko, S. S. U., Pamungkas, J., Perwitasari-Farajallah, D., Hardus, M. E., Noordwijk, M. van, & Schaik, C. P. van. (2012). Call Cultures in Orang-Utans? *PLOS ONE*, *7*(5), e36180. https://doi.org/10.1371/journal.pone.0036180

Wilke, C., Kavanagh, E., Donnellan, E., Waller, B. M., Machanda, Z. P., & Slocombe, K. E. (2017). Production of and responses to unimodal and multimodal signals in wild chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour*, *123*, 305–316. https://doi.org/10.1016/j.anbehav.2016.10.024

Wilke, C., Lahiff, N. J., Sabbi, K. H., Watts, D. P., Townsend, S. W., & Slocombe, K. E. (2022). Declarative referential gesturing in a wild chimpanzee (*Pan troglodytes*). *Proceedings* *of the National Academy of Sciences*, *119*(47), e2206486119. https://doi.org/10.1073/pnas.2206486119

Wittig, R. M., & Boesch, C. (2003). Food Competition and Linear Dominance Hierarchy Among Female Chimpanzees of the Taï National Park. *International Journal of Primatology*, *24*(4), 847–867. https://doi.org/10.1023/A:1024632923180

Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour*, *77*(4), 873–885. https://doi.org/10.1016/j.anbehav.2008.12.014

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, *106*(3), 283–295. https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O

Youssouf, I. A., Grimshaw, A. D., & Bird, C. S. (1976). Greetings in the desert1. *American Ethnologist*, *3*(4), 797–824. https://doi.org/10.1525/ae.1976.3.4.02a00140

Zhang, Y. B., & Giles, H. (2018). *Communication Accommodation Theory* (pp. 95–108). https://doi.org/10.1002/9781118783665.ieicc0156

Zmyj, N., Buttelmann, D., Carpenter, M., & Daum, M. M. (2010). The reliability of a model influences 14-month-olds' imitation. *Journal of Experimental Child Psychology*, *106*(4), 208–220. https://doi.org/10.1016/j.jecp.2010.03.002

APPENDICES

APPENDIX A: Supporting information for Chapter 3

Appendix A 1. Filemaker coding scheme with the coded variables, their descriptions, and respective values

Variable	Values	Description
Clip name	Free text	Name of the file.
Date	Free text	Date in the format year-month-day.
Clip length	Free text	Length in seconds.
Clip time	Free text	Time of the event.
Record number	Free text	Unique numeric identifier for each opportunity to communicate
Possible interaction number	Free text	Numeric identifier for each possible dyad. The same Possible Interaction Number comprises two individual opportunities to communicate (with the traveller being focal or partner for each possible interaction).
Event number	Free text	Numeric identifier for each individual event. The same event number includes all the possible interactions of one individual that joins or leaves the party.
Travel number	Free text	Numeric identifier for each fission or fusion. The same travel number includes all events (individual fissions or fusions) of individuals traveling together (same direction, separated by less than 5 min).
Type of event	Fission; Fusion	Indicates whether the individual joins (Fusion) or leaves (Fission) the party.
Possible Joint travel	Yes; No; Unknown	Indicates whether individuals travelled together (separated by less than 5 min from/into the same direction).
Focal	Tua; Kai; Nina; Na; Fana; Foaf; Fotaiu; Fanle; Fokaiye; Flanle; Fanwa; Jire; Jeje; Velu; Vui; Vuavua; Veve; Yo; Yolo; Pama; Pili; Poni; Peley	The name of the possible signaller. Table 9 contains further details on the individuals.

Focal age	2-57	Age of the focal in years (see also Table 9).
Focal rank	Alpha; Alpha-female; Beta; Gama; High-ranking female; Immature-1; Immature-2; Low-ranking female	Rank of the focal (see also Table 9).
Focal position	Traveller; Party-member	Indicates whether the focal is the individual travelling or remaining in the party.
Focal context	Affiliation; Agonism; Begging; Consortship; Displace; Feeding; Grooming; Sexual; Moving canopy; Moving up/down tree; Resting; Solitary Play; Social play; Travelling; Unknown; Other	Behavioural context of the focal prior fissions or after fusions. Categories were defined based on Hobaiter et al 2017. We divided Play into ‘Social Play’, ‘Solitary Play’, and we excluded ‘Hunting’ and ‘Intercommunity encounter’ because they were never observed.
Partner	Tua; Kai; Nina; Na; Nto; Fana; Foaf; Fotaiu; Fanle; Fokaiye; Flanle; Fanwa; Jire; Juru; Jeje; Velu; Vui; Vuavua; Veve; Yo; Yolo; Pama; Pili; Poni; Peley	The name of the possible recipient for the communicative signals emitted by the focal. Table 9 contains further details on the individuals.
Partner age	2-57	Age of the partner in years.
Partner rank	Alpha; Alpha-female; Beta; Gama; High-ranking female; Immature-1; Immature-2; Low-ranking female	Rank of the partner.
Partner context	Affiliation; Agonism; Begging; Consortship; Displace; Feeding; Grooming; Sexual; Moving canopy; Moving up/down tree; Resting; Solitary Play; Social play; Travelling; Unknown; Other	Behavioural context of the partner prior fissions or after fusions.
Kinship	Kin; Non-kin	Kin relationship between the focal and partner. Only maternal relationships were considered: mother-infant, grandmother-infant, maternal siblings.
Rank relation	Focal > Partner; Focal = Partner; Partner>Focal	The rank relation between the focal and the partner.

Group size	Free text	Number of individuals in the party (excluding the traveller).
Males	Alpha; Alpha and Other; Other; None; Unknown	Type of males present in the audience (excluding the traveller).
Communication	Yes; No; Unknown	Indicates whether the focal produces any communicative signals towards the partner.
Multi-channel	Yes; No; Unknown	Indicates whether the focal used more than one channel of communication (facial expression, gesture, or vocalization).
Gestural	Yes; No; Unknown	Indicates whether the focal used gestures.
Vocal	Yes; No; Unknown	Indicates whether the focal used vocalizations.
Facial	Yes; No; Unknown	Indicates whether the focal used facial expressions.
Type of signal	Facial expression; Gesture; Vocal	Channel of communication used. Four boxes were available and if more signals were emitted, they were mentioned in the notes section.
Signal	See Appendix A2Table 9	Type of gesture, vocalization, or facial expression emitted by the focal.
Notes	Free text	Additional comments.

Appendix A 2 - Frequency and description of the signal types observed during fusions and fissions. Gestural repertoire based on Hobaiter and Byrne (2011, 2017) Hobaiter and Byrne (2011, 2017); vocal repertoire based on Crockford and Boesch (2005); and facial repertoire based on Parr et al. (2005). Clarifications to the descriptions taken from the original sources have been marked in square brackets. Additional signals or edits to these repertoires are indicated using footnotes. [1] Graham et al. (2018); [2] Kersken et al. (2019); [3] Previously observed in Bossou (Catherine Hobaiter, personal communication); [4] Parr et al. (2005).

Type	Definition	Fusions	Fissions	Total
Gestures				
Arm over stance [3]	Signaller pauses while standing with one or both arms held over the recipient's body. In full form signaller's body forms a bridge over the recipient.	6	0	6
Arm raise	Raise arm and/or hand vertically in the air.	5	1	6
Arm shake	Small repeated back and forth motion of the arm.	0	0	0
Arm shake on	As 'Arm shake', but in contact with recipient's body.	0	0	0
Arm shake with object	As 'Arm shake', while holding object.	0	0	0
Arm out [1]	Arm is extended out from the shoulder to the side of the body, elbow and hand held in line [Previously labelled as 'Arm up'.]	6	1	7
Arm wave	Large repeated back and forth movement of the arm raised above the shoulder.	1	0	1
Arm wave with object	As 'Arm wave', while holding object.	0	1	1
Beckon	Hand is moved in an upward sweep from the elbow or wrist towards signaller.	1	0	1
Big loud scratch	Loud exaggerated scratching movement on signaller's own body. [Scratches associated with stress/ displacement activity (typically small and/or rapid in movement) or followed by self-maintenance/grooming were excluded.]	5	36	41
Bipedal rocking	Stand or walk bipedal, rock forward and back or side to side, repeated (rarely also quadrupedal).	11	0	11
Bipedal stance	Signaller stands bipedally and holds position.	15	1	16
Bite	Recipient's body is held between the teeth of the signaller. [Includes Bite:kiss (gentle contact with the mouth that doesn't hold the recipient's body in the way that a 'Bite' does. Includes the 'share air' kiss type where they breath on each other while almost touching).]	12	0	12
Bounce	Up and down movement of whole body flexing elbows or knees, typically while quadrupedal.	6	0	6
Bow	Signaller bends forward from the waist (typically while standing).	2	0	2
Clap	Both palms moved towards each other and are brought together with an audible contact.	0	0	0
Cover	Face is hidden by the hands and/or arms. [Previously labelled as 'Hide face'.]	0	0	0

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.	0	0	0
Dangle with legs shake	As ‘Dangle’ but signaller incorporates an additional shake movement of the legs.	0	0	0
Embrace	Signaller wraps [one or] both arms around the recipient and maintains physical contact.	0	0	0
Feet shake	Repeated back and forth movement of feet from the ankles.	0	0	0
Fling	Rapid movement of the hand or arm in the direction of the recipient.	1	1	2
Grab	The hand is firmly closed over part of the recipient's body.	1	1	2
Grab hold	Same as ‘Grab’ but hand/foot of signaller stays closed around recipient's body for more than 2 seconds.	0	1	1
Grab-pull	Same as ‘Grab’ but closed hand/foot contact is maintained, and a force exerted to move the recipient from their current position.	1	1	2
Grab-pull 2-handed	As ‘Grab pull’ but with both hands.	1	1	2
Hand shake	Repeated back and forth movement of hand from the wrist.	0	1	1
Head butt	Head is briefly and firmly pushed into the body of the recipient.	0	0	0
Head shake	Repeated back and forth [or up and down] movement of the head. [Includes gestures previously labelled as ‘Head nod’.]	13	3	16
Head stand	Signaller bends forward and places head on the ground.	0	0	0
Hit object/ground	Movement of the arm from the shoulder with hard short contact of the open palm or closed fist to an object or the ground.	0	1	1
Hit object/ground 2-handed	As ‘Hit object/ground’ but with both hands.	0	0	0
Hit other	As ‘Hit object/ground’ but the hand is brought into contact with the recipient’s body.	0	2	2
Hit other 2-handed	As ‘Hit other’ but with both hands.	0	0	0
Hit with object: object/ground	As ‘Hit object/ground’ but the hand holds an object which is brought into contact with another object or the ground.	0	0	0
Hit with object: other	Signaller brings object into short hard contact with recipient’s body.	0	0	0
Hitting object/ground	As ‘Hit object/ground’ but there is regular rhythmic repetition of the action	0	0	0
Hitting object/ground 2-handed	As ‘Hit object/ground 2-handed’ but there is regular rhythmic repetition of the action.	0	0	0

Hitting other	As ‘Hit other’ but there is regular rhythmic repetition of the action.	0	0	0
Hitting other 2-handed	As ‘Hit other 2-handed’ but there is regular rhythmic repetition of the action.	0	0	0
Hitting with object: other	As ‘Hit with object: other’ but there is regular rhythmic repetition of the action.	0	0	0
Jump	While bipedal both feet leave the ground simultaneously, accompanied by horizontal displacement through the air.	1	1	2
Knock object	Back of the hand or knuckles are brought into short hard audible contact with an object.	0	0	0
Knocking object	As ‘Knock object’ but there is regular rhythmic repetition of the action.	0	0	0
Leaf clipping	Strips are torn from leaf (or leaves) held in the hand using the teeth; produces conspicuous sound.	0	0	0
Locomote: Gallop	An exaggerated running movement where the contact of signaller’s hands and feet is deliberately audible.	15	10	25
Locomote: Stiff walk	Walk quadrupedally with a slow, exaggerated movement.	7	2	9
Locomote: Tandem walk	Subject positions arm over the body of the recipient and both walk forward while maintaining position.	0	1	1
Look	Signaller stops the current activity and holds an eye-contact position with the recipient— minimum duration 2 s [accompanied by response waiting and in the absence of other signals].	1	9	10
Object in mouth	Signaller approaches recipient while carrying an object in the mouth.	0	0	0
Object move	Object is displaced in one direction, contact is maintained through movement.	1	0	1
Object on head	Signaller faces or approaches recipient while balancing an object on the head.	0	0	0
Object shake	Repeated back and forth movement of an object.	6	0	6
Poke	Firm, brief push of one or more fingers into the recipient's body.	0	0	0
Poking	Same as ‘Poke’ but there is regular rhythmic repetition of the action.	0	0	0
Pounce	Signaller displaces through the air to land quadrupedally on the body of the recipient.	0	0	0
Present	Body or body part moved to deliberately expose an area to the recipient's attention.	1	3	4
Present genitals backwards	Signaller approaches recipient backward and deliberately exposes swelling or groin area to the recipient's attention.	25	1	26
Present genitals forwards	Signaller approaches recipient and exposes swelling or groin area while facing the recipient.	1	0	1
Push	Palm in contact with recipient's body and force is exerted in attempt to displace recipient.	0	0	0

Push (directed)	A light short non-effective push that indicates a direction of desired movement, immediately followed by the recipient moving as indicated. [Previously labelled as ‘Directed push’.]	2	1	3
Rake self[3]	Signaller holds hands in distinctive position with fingers stiff and spread and pulls them over their body (typically head).	0	0	0
Rake ground[3]	As ‘Rake self’, but in the ground.	0	0	0
Reach – palm	Arm extended to the recipient with the palm held vertically or upwards and the fingers in an open position.	0	0	0
Reach – wrist	Arm extended to the recipient with the wrist bent and the palm shielded.	5	0	5
Reach directed[2]	As ‘Reach palm’ but arm is extended towards a third party or object, while audience checking, response waiting, and/or other signals are directed to recipient.	0	0	0
Rocking	Sitting, rock forward and back or side to side, repeated.	2	0	2
Roll over	Signaller rolls onto their back exposing their stomach normally accompanied by repeated movements of the arms and/or leg.	0	0	0
Rump rub	Push/rub rump against the body/ swelling of recipient.	1	0	1
Shake hands	Signaller grasps recipient’s hand in their own hand and then makes small repeated back and forth movements from the wrist.	0	0	0
Spin	Signaller rotates around their body’s axis while also displacing along the ground. Includes pirouette, somersault, and side roulade.	0	0	0
Stomp	Sole of the foot is lifted vertically and brought into short hard audible contact with ground of object, usually this is the surface the signaller is standing upon.	0	0	0
Stomp other	As ‘Stomp’ but contact is made with recipient.	0	0	0
Stomp 2-feet	As ‘Stomp object/ground’ but both feet used, normally alternately.	1	0	1
Stomp 2-feet other	As ‘Stomp other’ but both feet used, normally alternately.	0	0	0
Stomping 2-feet object/ground	As ‘Stomp 2-feet object/ground’ but there is regular rhythmic repetition of the action.	1	0	1
Stomping 2-feet other	As ‘Stomp 2-feet other’ but there is regular rhythmic repetition of the action.	0	0	0
Stomping object/ground	As ‘Stomp object/ground’ but there is regular rhythmic repetition of the action.	0	0	0
Stomping other	As ‘Stomp other’ but there is regular rhythmic repetition of the action.	0	0	0
Stroke	Signaller’s palm and fingers are repeatedly run over the mouth area of the recipient.	0	0	0

Swing	Large back and forth movement of arm(s) or leg(s) from shoulder or hip.	4	0	4
Swing (with object)	As ‘Swing’ but hand or foot holds an object.	2	0	2
Tap object	Movement of the arm from the wrist or elbow, with firm short contact of the fingers to the object.	0	0	0
Tap other	As ‘Tap object’ but contact is with recipient's body.	0	0	0
Tapping object	As ‘Tap object’ but there is regular rhythmic repetition of the action.	0	0	0
Tapping other	As ‘Tap other’ but there is regular rhythmic repetition of the action.	0	0	0
Throw object	Object is moved and released so that there is displacement through the air after moment of release.	1	1	2
Throw threat [3]	Object is lifted into position to throw it but is held in that position (typically above the shoulder) without release.	0	0	0
Thrust	Hips are brought into repeated contact with the recipient’s body.	0	0	0
Touch	Light contact of the palm and/or fingers on the body of the recipient or object, contact under 2 seconds.	6	2	8
Touch: long other	Light contact of the palm and/or fingers on the body of the recipient, contact longer than 2 seconds. [Previously labelled as ‘Hand on’.]	2	1	3
Water splash	Hand is moved vigorously through the water so that there is audible displacement of the water.	0	0	0
Other gesture	Gestures that do not fit into the categories mentioned above.	6	2	8

Bark	Loud and sharp but varies in pitch. The main energy of the call is at the onset. [4]	2	0	2
Grunt	Low-pitched tonal call. May be an intermediate stage between barking, pant-grunting and other similar calls. Cough is similar but the vocal comes from a rush of exhaled air during mild threats. [4]	10	2	12
Hoo	Short, hooting vocalizations ‘oo .. oo’. Highly tonal with clear harmonic structure.	1	3	4
Hoo grunt	Series of ‘Hoos’, ‘Grunts’ or intermediate forms joined with voiced inhaled elements; ‘Hoo’/ ‘Grunt’ elements are generally more tonal than the ‘Grunt’ elements of the ‘Pant grunt’.	1	0	1
Laughter	Rapid inhaled and exhaled elements, generally quiet and voiced, grading to unvoiced.	0	0	0
Pant	Unvoiced, rapid inhaled and exhaled elements.	8	2	10
Pant-grunt	Series of ‘Grunts’ joined together by voiced inhaled elements. [Includes distinct acoustic variants - could be noisy ‘Pants’ in which we hear both inhale and exhale elements, grading to ‘Pant-	51	4	55

	barks’ where ‘Pants’ are combined with higher-fundamental frequency calls.]			
Pant-hoot	Comprised of up to four phases: introduction: ‘Hoos’; build-up: series of ‘Hoos’ interspersed with voiced inhaled elements; climax: ‘Screams’ and sometimes ‘Barks’; let down: similar to build-up but ‘Hoos’ having decreasing pitch.	4	1	5
Scream	Loud harsh screaming like ‘aach – aach’.[4]	5	1	6
Squeak	Shorter and more tonal than “Screams” [often accompanied by bared-teeth expression].	0	0	0
Whimper	Highly tonal series of “Hoo-like” calls.	0	0	0
Other vocalization	Vocalizations that are difficult to isolate into any one discrete category as they are too graded in intensity.	2	0	2

Alert face	This is described as lower-lip depressed and lips parted, lips parted with mouth open, or lips parted with lower lip relaxed.	0	1	1
Bared-teeth	The mouth may be slightly open or closed, lips withdrawn, and mouth corners retracted laterally, and the teeth fully exposed. Eyes may be open or squinted.	9	1	10
Pant-hoot Face	Lips are pursed with rounded mouth and forward pursed lips. Mouth can be slightly open as louder, rhythmic breathing hoot vocalizations ‘hoo-hoo’ occur.	0	0	0
Play face	The mouth corners are in their usual position, or slightly withdrawn, but the lower lip hangs open to expose the bottom teeth. The top teeth can be slightly visible, otherwise the top lip folds over them.	3	1	4
Pout	Eyes are open and mouth is rounded with corners pursed forward. Lips are pursed into a round shape. No teeth are visible. No vocalizations are present.	0	0	0
Scream	The eyes are squinted or closed, ears flat, eyebrows lowered, body posture is typically crouched. Mouth is partially open, lips withdrawn as in screaming or staring bared-teeth face, but teeth are fully exposed.	1	0	1
Tight lips	Individual stares ahead, eyes open, mouth closed with the lips bulging out as though individual is blowing air. Ears should be flat against scalp. Lips are together and mouth corners neutral. [Previously labelled as ‘Bulging-lips face’.]	5	0	5
Whimper	The lips are slightly puckered/pursed while being slightly withdrawn to expose the teeth, and mouth corners are pushed forward. Eyes are partially closed, and mouth is partially open.	0	0	0
Other facial expression	Faces that are difficult to isolate into any one discrete category as they are too graded in intensity, are produced during feeding, or are other non-expressive movements, such as yawns.	1	0	1

APPENDIX B: Supporting information for Chapter 4

Appendix B 1. Gesture form definitions and the frequency with which they were directed towards any individual in each community: Bossou and Sonso. Gestures directed towards their offspring are presented in brackets.

Gesture forms	Definitions	Bossou	Sonso
Beckon	A scooping movement from one or more of the joints (e.g. fingers, wrist, elbow), movement extends towards recipient and then back to the signaller in one active motion	7(2)	6(5)
Big loud scratch	Loud exaggerated scratching movement on signaller's own body (must not be followed by self-grooming)	15(7)	174 (114)
Bite	Signaller's mouth/teeth close on the recipient's body - this may be very brief, or could be held in place	0	7(4)
Bite: kiss	Gentle contact with the mouth that doesn't hold the recipient's body (see "Bite"). Includes the 'share air' kiss type where they breath on each other while almost touching	28(0)	2(1)
Bite: object	Signaller's mouth/teeth close on an object - this may be very brief, or could be held in place	0	0
Bite: self	Signaller's body is held between the teeth/in the mouth of the signaller	0	0
Bite: threat	Signaller opens mouth rapidly as if preparing for a bite (often with a movement towards recipient) but moves past or away quickly before making contact	0	0
Bounce	Rhythmic vertical up-down movement (or 'bobbing') of the body - typically with all four feet remain on the ground (rarely hands may be free of ground)	7(0)	0
Bow	Signaller bends forward from the waist while standing bipedally	0	0
Butt	Signaller's head is briefly and firmly pushed into the body of the recipient	0	0
Clap	Both palms moved towards each other and brought together with audible contact (may be repeated)	0	0
Crouch	Signaller lowers body by bending knees and/or elbows, while maintaining at least three points of contact with ground	2(0)	1(0)
Dangle	To hang from one or both hands (or feet) from a branch with at least one limb not in contact with branch, some movement of body as a result of hanging	2(0)	4(0)
Dangle: with shake	Same as "Dangle" but signaller produces an additional shake of arm(s) or leg(s)	0	0
Drum	Signaller's hand or foot makes short hard (long-distance) audible contact with an object (single or repeated). Specifically for long-distance communication, even if a single beat	0	3(0)
Embrace	Signaller wraps one or both arms/legs around recipient	5(0)	11(4)
Finger(s) in mouth	Signaller insert finger(s) - usually palm down - in the mouth of recipient with contact	3(2)	0
Fling	Rapid movement of hand (from wrist) or arm (from elbow or shoulder; rarely with foot or head) away from the signaller's body, typically towards recipient. Energy of stroke is focused on way out away from signaller, more relaxed on way back	68(9)	16(0)
Grab	The hand or foot is firmly closed over part of the recipient's body or a handful of hair	8(2)	17(7)

Grab hold	Same as "Grab" but hand/foot of signaller stays closed around recipient's body for >2 seconds	4(1)	11(10)
Head stand	Signaller bends forward and places head on or very near to ground and pauses, at least briefly, in this position. Contact may be made with recipient's body	0	1(1)
Hit object/ground	Signaller makes a short hard contact with the ground/object; energy in movement is focused on the way out, contact can be brief or remain in place for longer. Typically occurs in front of or to the side of the signaller's body (rather than straight up and down as in Stomp). Produced with a variety of body parts - typically hand, fingers, kuckles, fist, foot	8(1)	9(1)
Hitting object/ground	See Hit object/ground but repeated at least once	2(2)	2(0)
Hit recipient	See Hit object/ground, but signaller makes deliberate contact with recipient as part of action	13(5)	16(3)
Hitting recipient	See Hit recipient but repeated at least once	0	3(0)
Hit recipient: clap on	See Hit recipient but always with two of hands/feet who make contact with recipient's body while facing each other (as for "Clap" but with recipient's body between the signaller's hands/feet)		
Hitting recipient: clap on	See Hitting recipient but always with two of hands/feet who make contact with recipient's body while facing each other (as for "Clap" but with recipient's body between the signaller's hands/feet)	0	0
Hit self	See Hit object/ground, but signaller makes deliberate contact with own body as part of action	0	0
Hitting self	See "Hit self" but repeated more than once	0	0
Hit non recipient	See Hit object/ground, but contact is made with third party (not the recipient) while the communication is clearly only directed to the recipient and not as part of a triadic communication	0	0
Hitting non recipient	See Hitting recipient but contact is made with third party (not the recipient) while the communication is clearly only directed to the recipient and not as part of a triadic communication	0	0
Hit with object: object/ground	An object is brought into short hard contact with another object or ground	0	0
Hitting with object: object/ground	Same as "Hit with object: object/ground" but repeated at least once	0	0
Hit with object: recipient	An object is brought into short hard contact with the body of the recipient	0	0
Hitting with object: recipient	Same as "Hit with object: recipient" but repeated at least once	0	0
Hit soft object/ground	See Hit object/ground but contact is gentle (as in tap, pat etc.)	1(0)	0
Hitting soft object/ground	See Hit soft object/ground but repeated at least once	0	0
Hit soft recipient	See Hit soft object/ground but contact is deliberatly made with recipient's body	3(1)	7(1)
Hitting soft recipient	See Hit soft recipient but repeated at least once	0	1(1)
Hit soft self	See Hit soft object/ground but contact is deliberatly made with signaller's body	0	0
Hitting soft self	See Hit soft self but repeated at least once	0	0
Hit soft non recipient	See Hit soft object/ground but contact is made with third party (not the recipient) while the communication is clearly only directed to the recipient and not as part of a triadic communication	0	0

Hitting soft non recipient	See Hitting soft recipient but contact is made with third party (not the recipient) while the communication is clearly only directed to the recipient and not as part of a triadic communication	0	0
Jump	While bipedal both feet leave the ground simultaneously, while qudrapedal all four limbs free of ground simultaneously; accompanied by horizontal displacement.	1(1)	1(0)
Leaf clipping	Strips are torn from leaf (or leaves) held in the hand using the teeth; produces conspicuous sound	0	1(0)
Leaf clipping: leaf drop	Leaf or leaves are plucked off with fingers or mouth and silently dropped. Note that there is no tearing action on the leaves as seen in "Leaf Clipping"	0	0
Locomote: bipedal	Signaller stands bipedally and takes at least one step with each foot	2(0)	0
Locomote: gallop	An exaggerated running movement where the limbs movements are typically stiff (straightened)	0	0
Locomote: over	Signaller finishes a locomote gesture (bipedal, gallop, stiff walk) by moving over the body of the recipient; includes some contact	0	0
Locomote: stiff walk	An exaggerated walking movement with stiff limbs and fore-limbs held in a straightened position. (potentially rename to strut walk)	0	0
Lunge	Signaller's body is rapidly thrust towards recipient. No contact is made	0	1(0)
Object in mouth: attached	See "Object in mouth: detached" but the object being held in the mouth remains attached to the environment, e.g. a sapling	0	0
Object in mouth: detached	Signaller holds an object (e.g. small branch) in mouth. Hands should not normally be involved	0	0
Object move: attached	See "Object move: detached" but object remains attached to the environment (e.g. sapling)	0	7(0)
Object move: detached	Object is displaced, contact is maintained through movement. While movement may not be in a single direction it does not include the rapid back and forth of "Object shake". Object is free to move and not attached to environment (e.g. fallen branch)	0	0
Object on head	Signaller places detached object on their head and leaves it in place. Hand may remain in contact with object for balance	0	0
Object shake	Repeated back and forth movement of an object (typically one still attached in the environment, e.g. sapling). Object movement must be controlled by the signallers hand/foot actively shaking the object and not a biproduct of the flexibility of the object	1(0)	8(0)
Out	Typical form is "arm out". Arm is extended out from the shoulder to the side of the body, elbow and hand held in line	2(1)	0
Over stance	Signaller pauses while standing with at least one limb that has been moved into position and held over the recipient's body. In full form signaller's body forms a bridge over the recipient	6(1)	0
Poke	Short firm contact made with the signaller's fingers held straight and 'pushed' briefly into the recipient's body	2(0)	1(1)
Poking	See "Poke" but repeated at least once	0	0
Present	Body or body part moved to deliberately expose an area to the recipient's attention	2(2)	14(11)
Present (directed)	Same as "Present", but recipient's behaviour must be directed to the body part presented afterwards	68(28)	69(45)

Present: genitals backwards	Same as "Present", but signaller exposes swelling or groin area while facing away from the recipient	36(4)	57(0)
Present: genitals forwards	Same as "Present", but signaller exposes swelling or groin area while facing the recipient	0	0
Pull	Same as "Push" but hand/foot (typically) contact - usually in a grab position - is maintained and a force exerted away from the recipient's body, to move the recipient from their current position	5(0)	4(4)
Pull (directed)	Same as "Pull" but signaller displaces recipient toward a specific target location	10(10)	21(18)
Push	Contact with recipient's body (typically hand or foot) and force is exerted into the recipient's body as if to displace recipient	13(8)	24(18)
Push (directed)	Same as "Push" but signaller displaces recipient toward a specific target location	37(29)	109(102)
Raise	Raise body part (typically hand or arm) in a generally vertical movement, often with a brief near the top of the movement	2(0)	0
Rake ground/object	Signaller holds hands with fingers stiff and spread in order to displace objects towards their body, e.g. dry leaves	0	0
Rake self	Signaller holds hands in distinctive position with fingers stiff and spread and pulls them over their body (e.g. over head, may be repeated code as a single gesture unless a clear break/change in movement)	3	0
Reach	Body part (typically arm) extended towards the recipient (or in their direction) with no contact	43(16)	53(20)
Rocking: bipedal	Signaller moves body back and forth while standing bipedally	2(0)	0
Rocking: sitting	Signaller moves body back and forth while sitting (includes single/half 'Rock' movement where the signaller moves back and holds)	0	3(2)
Roll over	Signaller rolls or rocks so that their back is on the object/ground exposing their stomach and holds position	0	1(1)
Rub	Signaller push/rubs body part up and down against body of recipient (typically with hands or genitals)	1(0)	1(0)
Rub self	Signaller push/rubs body part against part of their own body (typically with hands)	0	0
Shake	Signaller moves part of their body quickly and repeatedly back and forth (typically hand/arm or head). Movement is loose	10(1)	5(1)
Shake recipient	Signaller holds body part of other individual or object and moves it quickly and repeatedly back and forth	0	0
Spin	All spin gesture actions need to include a full 360 degrees of turn, as this indicates that the movement is more than would be required for locomotion	0	0
Spin: pirouette	Signaller stands and turns around their bodies vertical axis while also displacing along the ground	0	0
Spin: side roulade	Signaller is lying down and turns around their bodies vertical axis while also displacing along the ground	0	0
Spin: somersault	Signaller's body is curled into a compact position on the ground and rolled forward or backward so the feet are brought over the head and returned to sitting position	0	0

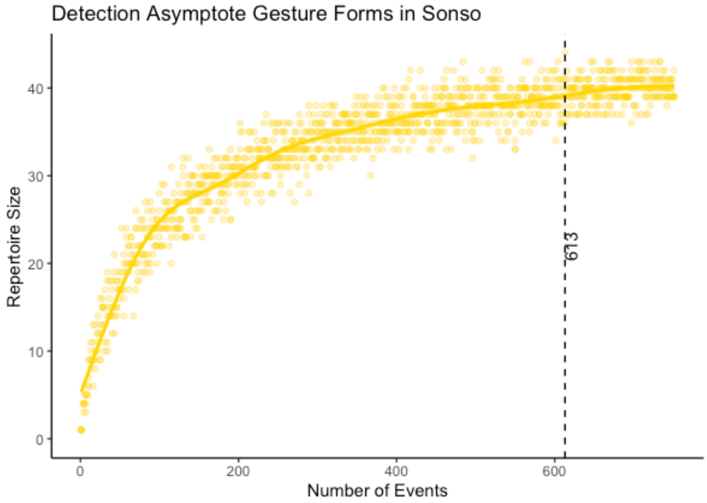
Stance: bipedal	Signaller moves into bipedal stance and holds position (must not be in order to achieve other action e.g. standing to see something arriving)	5(2)	0
Stiff stance	Signaller holds stiff quadrupedal body position with straight limbs forelimbs (often accompanied by 'tight lips' facial expression in gorillas)	0	0
Stomp object/ground	The foot (or sometimes hand) is lifted vertically and brought into short hard contact with the ground (or object). Usually this is the surface that the signaller is standing/sitting on	3(1)	5(0)
Stomping object/ground	See Stomp object/ground but repeated at least once	1(0)	3(1)
Stomp recipient	See Stomp object/ground but contact is deliberatly made on recipient's body	0	0
Stomping recipient	See Stomp recipient but repeated at least once	0	0
Stroke	Active gentle movements of the signaller's palm and/or fingers (rarely other) on the recipient's body. May include movements in more than one direction	0	4(2)
Swing	Smooth continuous motion of body part (normally arm of leg) back and forth	4(1)	4(0)
Swing (directed)	As "Swing" but direction of motion used to draw attention to specific target (e.g. travel direction, object, other individual)	0	2(1)
Throw object	Object is moved and released so that there is displacement of the object through the air after moment of release	0	0
Throw threat	Object is lifted into position to throw it but is held in that position (typically raised above shoulder) without release	1(0)	0
Thrust	Groin is pushed forward towards recipient (may be repeated)	0	0
Touch	Light contact (typically of the fingers, knuckles, hand, or foot, rarely other) on the body of the recipient, contact <2 seconds	30(5)	30(17)
Touch: long recipient	Same as "Touch" but contact is held for 2 seconds or longer	5(1)	16(11)
Touch: object/ground	Same as "Touch" but contact is made with a specific object/ground in a location between the signaller and recipient, and this location is typically involved in the subsequent behaviour	0	0
Water splash	Hand is moved vigorously through the water so that there is audible displacement of the water	0	0
Wave	Large loose back and forth movements of the arms while raised above the shoulder. Similar to Raise but with additional movements	0	0

Appendix B 2. Definition of the goals used in this study. Goals have been firstly coded with more subcategories but were lumped afterwards in these categories for further analyses.

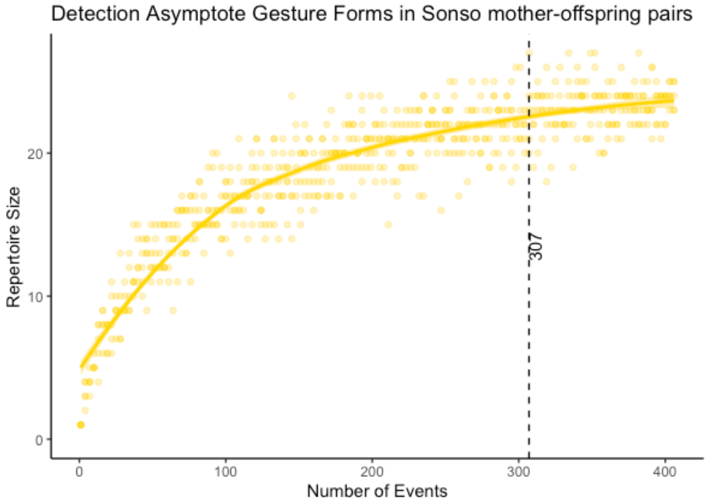
Goal	Definition
Affiliation	Body contact may occur. Initiation of affiliation behaviour can be by signaller or recipient.
Attend	Includes "attend to me" and "direct your attention". Signaller requests that the recipient change their behaviour in order to visually monitor the behaviour of the signaller; or that the recipient changes the location of this behaviour by focusing their attention on a different body part.
Climb	Recipient moves (climbs) onto the signaller, usually infant climbs onto mother or another individual
Travel	Includes "follow me" and "travel". Signaller requests that the recipient follow them in order to perform another activity in another location; or signaller gestures to another individual in the party, and response waits or checks back to recipient, ending with both travel in the same direction and within sight.
Give	Object/food is exchanged from the recipient to the signaller. Includes when recipient allows signaller to nurse.
Groom	Recipient and signaller start grooming together.
Move Away	Recipient typically stops current behaviour and increases physical distance between themselves and signalller (more than 2-steps back).
Move Close	Physical distance between signaller and recipient decreases, normally because recipient moves closer.
Play	Includes "play start", "play continue", and "play change". Signaller gestures to recipient to initiate, resume or change type of play (contact to non-contact and vice-versa).
Position	Signaller gestures for the recipient to change their position so that the signaller can continue their behaviour in a different location (i.e. groom the recipient at a different spot, nurse from the other nipple).
Sexual Attention	Behaviour linked to reproductive sexual activities (copulation, inspection, etc.). Includes penetration when female is in swelling, inspection (sniffing, tasting, poking) of female genitals at any stage by a male individual who is older than an infant.
Socio Sexual Attention	Behaviour that involves gential contact that is not linked to reproductive activities. Include all same sex interactions, and opposite sex interactions where there are none of the sexual behaviours described above.
Stay Same	Essentially there is no change in the recipient's behaviour but the signaller behaves as if they are satisfied with this outcome.
Stop Behaviour	The recipient stops the behaviour they were in before the gesture and pause or rest for a (brief) time. Includes "stop behaviour at this place" when the recipient's behaviour does not completely stop but is continued at a different place; and "stop behaviour: don't leave" when the signaller gestures and the recipient, that is standing up about to leave, does not leave but stays close
Support	After the gestural interaction signaller and recipient direct behaviour - typically aggressive/agonistic - toward another individual. Aggression is one possible outcome, but other outcomes would be vocal support (bark), and the support should include behaviour that is directed to a third party.

Take	Object/food is exchanged from the signaller to the recipient. Includes when recipient nurses from signaller, after the signaller gestures toward recipient.

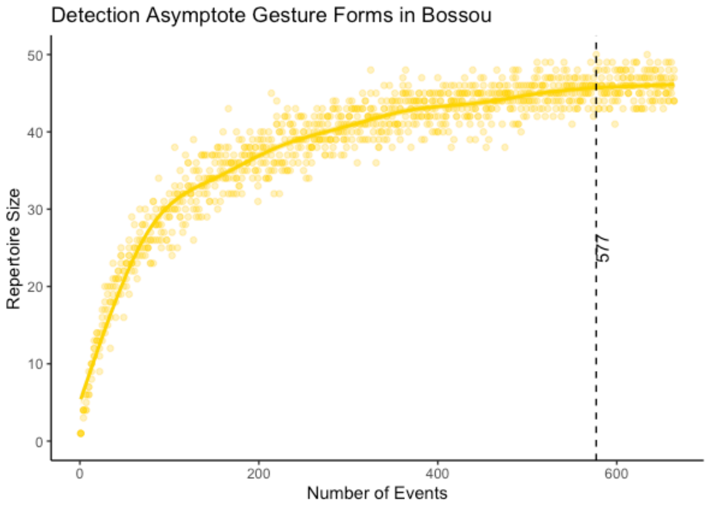
Appendix B 3. Cumulative record of gesture forms in the communication of Sonso mothers directed to any individual of the community, obtained through a function that takes random subsamples of the data and check how many of the gesture forms are identified in each subsample.



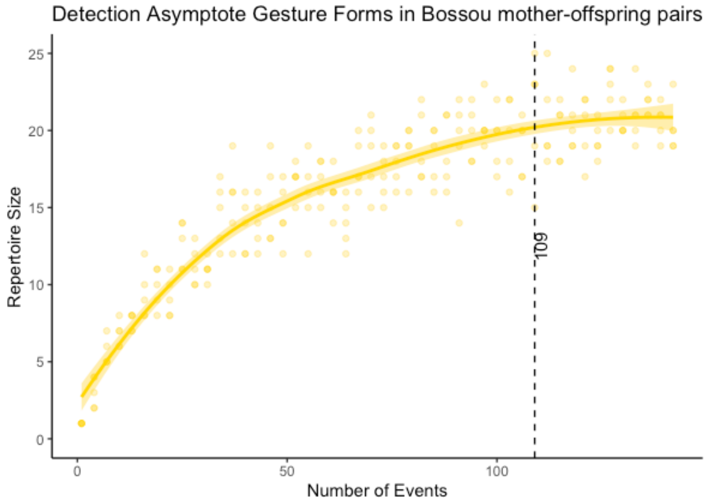
Appendix B 4. Cumulative record of gesture forms in the communication of Sonso mothers directed to their offspring, obtained through a function that takes random subsamples of the data and check how many of the gesture forms are identified in each subsample.



Appendix B 5. Cumulative record of gesture forms in the communication of Bossou mothers directed to any individual of the community, obtained through a function that takes random subsamples of the data and check how many of the gesture forms are identified in each subsample.



Appendix B 6. Cumulative record of gesture forms in the communication of Bossou mothers directed to their offspring, obtained through a function that takes random subsamples of the data and check how many of the gesture forms are identified in each subsample.



Appendix B 7. Factors influencing (1a) the Performed Action Unit duration, (2a) the Hold/repetition phase duration of mothers' mothers' gestural communication towards any individual of the community. Significant factors are highlighted in bold, and control factors in italic.

Term	Estimate	Std. Error	lower CI	upper CI	df	t	P-value
(1a) Performed Action Unit duration							
Intercept	0.856	0.133	0.597	1.108			(1)
Signaller age	*0*	*0.035*	*-0.069*	*0.07*	*42.535*	*0.009*	*0.993*
Recipient age (infant)	**-0.199**	**0.096**	**-0.382**	**-0.012**	**248.59**	**-2.078**	**0.039**
Recipient age (juvenile)	**-0.335**	**0.089**	**-0.516**	**-0.163**	**191.87**	**-3.761**	**<0.001**
Recipient age (subadult)	-0.132	0.108	-0.344	0.065	264.21	-1.217	0.225
Kinship (non-kin)	**-0.257**	**0.067**	**-0.392**	**-0.128**	**665**	**-3.832**	**<0.001**
Recipient sex (male)	-0.088	0.071	-0.225	0.049	69.76	-1.242	0.218
Social unit (Sonso)	*0.106*	*0.091*	*-0.063*	*0.284*	*36.588*	*1.162*	*0.253*
(1b) Hold/repetition phase duration							
Intercept	0.361	0.149	0.059	0.633			(1)
Signaller age	*-0.071*	*0.039*	*-0.148*	*0.002*	*33.204*	*-1.816*	*0.078*
Recipient age (infant)	**-0.393**	**0.123**	**-0.629**	**-0.151**	**222.51**	**-3.195**	**0.002**
Recipient age (juvenile)	**-0.374**	**0.117**	**-0.595**	**-0.144**	**195.57**	**-3.204**	**0.002**
Recipient age (subadult)	0.055	0.15	-0.261	0.35	255.15	0.366	0.715
Kinship (non-kin)	**-0.204**	**0.102**	**-0.405**	**0.018**	**479.46**	**-1.999**	**0.046**
Recipient sex (male)	-0.07	0.077	-0.213	0.082	57.312	-0.912	0.366
Social unit (Sonso)	*0.068*	*0.088*	*-0.117*	*0.237*	*22.223*	*0.767*	*0.451*

(1) Significance test not indicated because it has no meaningful interpretation

Appendix B 8. Factors influencing (4a) the Gesture rate of mothers' gestural communication towards any individual of the community. Significant factors are highlighted in bold, and control factors in italic.

Term	Estimate	Std. Error	lower CI	upper CI	t	P-value
Intercept	-0.752	0.125	-1.118	-0.406		(1)
Signaller age	*-0.086*	*0.034*	*-0.198*	*0.031*	*-2.514*	*0.012*
Recipient age (infant)	0.098	0.099	-0.247	0.421	0.992	0.321
Recipient age (juvenile)	0.158	0.094	-0.171	0.457	1.689	0.091
Recipient age (subadult)	0.104	0.102	-0.268	0.476	1.018	0.308
Recipient sex (male)	0.064	0.082	-0.191	0.301	0.778	0.436
Kinship (non-kin)	**0.194**	**0.058**	**-0.022**	**0.413**	**3.335**	**0.001**
Social unit (Sonso)	*-0.16*	*0.09*	*-0.438*	*0.109*	*-1.783*	*0.075*

(1) Significance test not indicated because it has no meaningful interpretation

Appendix B 9. Factors influencing (3a) the probability of repetition, and (5a) the type/token ratio of mothers' gestural communication towards any individual of the community. Significant factors are highlighted in bold, and control factors in italic.

Term	Estimate	Std. Error	lower CI	upper CI	z	P-value
(3a) Probability of repetition						
Intercept	-1.299	0.466	-2.246	-0.31		(1)
Signaller age	*0.05*	*0.173*	*-0.234*	*0.356*	*0.287*	*0.774*
Recipient age (infant)	**-0.788**	**0.337**	**-1.48**	**-0.072**	**-2.338**	**0.019**
Recipient age (juvenile)	-0.416	0.3	-0.998	0.184	-1.385	0.166
Recipient age (subadult)	-0.043	0.362	-0.775	0.673	-0.12	0.905
Kinship (non-kin)	**-0.59**	**0.244**	**-1.086**	**-0.11**	**-2.414**	**0.016**
Recipient sex (male)	-0.038	0.225	-0.471	0.408	-0.17	0.865
Social unit (Sonso)	*1.28*	*0.387*	*0.554*	*2.076*	*3.305*	*0.001*
(5a) Type/token ratio						
Intercept	0.028	0.232	-0.405	0.528		(1)
Recipient sex (male)	-0.242	0.131	-0.497	0.015	-1.839	0.066
Kinship (non-kin)	**0.626**	**0.154**	**0.34**	**0.927**	**4.077**	**<0.001**
Recipient age (infant)	0.371	0.186	-0.036	0.735	1.993	0.046
Recipient age (juvenile)	0.047	0.168	-0.294	0.364	0.277	0.781
Recipient age (subadult)	**0.67**	**0.252**	**0.177**	**1.164**	**2.655**	**0.008**
Social unit (Sonso)	*-0.522*	*0.191*	*-0.908*	*-0.151*	*-2.73*	*0.006*

(1) Significance test not indicated because it has no meaningful interpretation

Appendix B 10. Factors influencing (1b) the Performed Action Unit duration, (2b) the Hold/repetition phase duration of mothers' gestural communication towards their offspring. Significant factors are highlighted in bold, and control factors in italic.

Term	Estimate	Std. Error	Lower CI	Higher CI	df	t	P-value
(1b) Performed Action Unit duration							
Intercept	0.539	0.127	0.286	0.778			(1)
Signaller age	*0.014*	*0.057*	*-0.106*	*0.122*	*27.314*	*0.254*	*0.801*
Recipient age	-0.015	0.046	-0.107	0.076	109.7	-0.327	0.744
Recipient sex (male)	-0.086	0.101	-0.304	0.12	35.56	-0.851	0.401
Social unit (Sonso)	0.192	0.116	-0.024	0.422	12.592	1.656	0.122
(2b) Hold/repetition phase duration							
Intercept	0.023	0.128	-0.223	0.299			(1)
Signaller age	*-0.09*	*0.053*	*-0.191*	*0.012*	*25.483*	*-1.69*	*0.103*
Recipient age	0.081	0.055	-0.032	0.186	274.98	1.463	0.145
Recipient sex (male)	-0.03	0.101	-0.232	0.175	37.365	-0.294	0.771
Social unit (Sonso)	*0.042*	*0.117*	*-0.195*	*0.281*	*22.96*	*0.355*	*0.726*

(1) Significance test not indicated because it has no meaningful interpretation

Appendix B 11. Factors influencing (4b) the Gesture duration of mothers' gestural communication towards their offspring. Significant factors are highlighted in bold, and control factors in italic.

Term	**Estimate**	**Std. Error**	**Lower CI**	**Higher CI**	**t**	**P-value**
Intercept	-0.624	0.138	-1.054	-0.218		[1]
Signaller age	*-0.031*	*0.071*	*-0.266*	*0.182*	*-0.439*	*0.661*
Recipient age	-0.023	0.047	-0.211	0.167	-0.476	0.634
Recipient sex (male)	0	0.1	-0.31	0.301	0.002	0.998
Social unit (Sonso)	*-0.108*	*0.145*	*-0.547*	*0.329*	*-0.745*	*0.456*

(1) Significance test not indicated because it has no meaningful interpretation

Appendix B 12. Factors influencing (3b) the probability of repetition, and (5b) the type/token ratio of mothers' gestural communication towards their offspring. Significant factors are highlighted in bold, and control factors in italic.

Term	**Estimate**	**Std. Error**	**Lower CI**	**Higher CI**	**z**	**P-value**
(3b) Probability of repetition						
Intercept	-2.725	0.538	-3.955	-1.732		[1]
Signaller age	*-0.444*	*0.21*	*-0.873*	*-0.05*	*-2.112*	*0.035*
Recipient age	**0.387**	**0.159**	**0.104**	**0.725**	**2.436**	**0.015**
Recipient sex (male)	0.525	0.347	-0.179	1.218	1.513	0.13
Social unit (Sonso)	*1.709*	*0.492*	*0.795*	*2.814*	*3.476*	*0.001*
(5b) Type/Token ratio						
Intercept	0.528	0.192	0.151	0.911		[1]
Recipient sex (male)	-0.149	0.127	-0.392	0.105	-1.17	0.242
Recipient age (infant)	0.02	0.164	-0.304	0.328	0.123	0.902
Recipient age (juvenile)	-0.21	0.155	-0.522	0.087	-1.356	0.175
Recipient age (subadult)	**0.613**	**0.249**	**0.152**	**1.113**	**2.466**	**0.014**
Social unit (Sonso)	*-0.641*	*0.179*	*-0.998*	*-0.28*	*-3.581*	*<0.001*

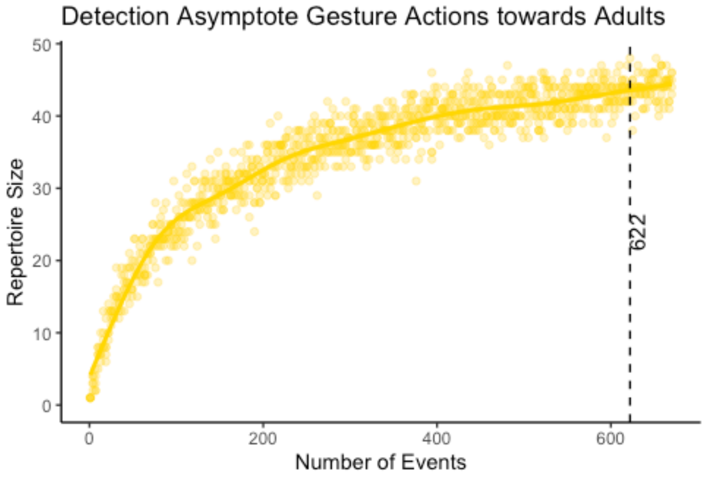
(1) Significance test not indicated because it has no meaningful interpretation

APPENDIX C: Supporting information for Chapter 5

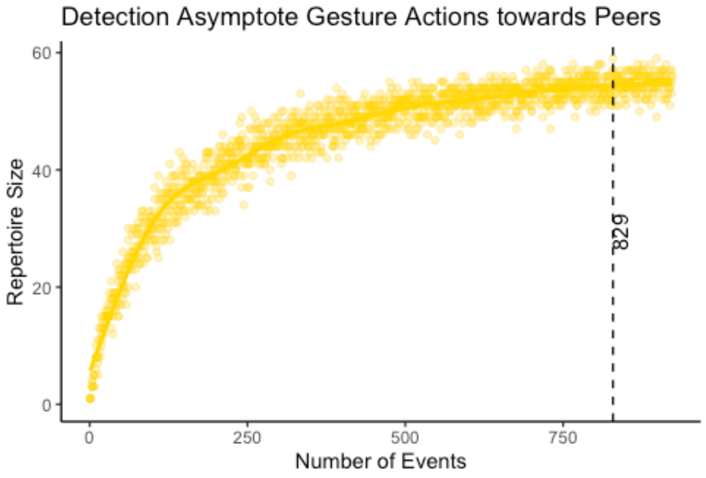
Appendix C 1. Characteristics of the focal toddlers namely their ID (code name), gender, age at the start of data collection, and the group to which they belonged.

ID	Gender	Age (days)	School
Columba	F	928	VO Laranjeiro
Cepheus	F	947	VO Laranjeiro
Antlia	M	593	VO Laranjeiro
Chamaeleon	F	725	VO Laranjeiro
Circinus	M	842	VO Laranjeiro
Dorado	F	599	VO Laranjeiro
Auriga	F	1080	VO Laranjeiro
Capricornus	M	953	VO Laranjeiro
Eridanus	M	599	VO Laranjeiro
Cygnus	M	975	VO Laranjeiro
Ophiuchus	M	472	VO Laranjeiro
Lepus	F	842	VO Laranjeiro
Coma Berenices	M	554	VO Laranjeiro
Fornax	M	716	VO Laranjeiro
Hercules	F	1076	VO Laranjeiro
Lupus	M	481	VO Laranjeiro
Octans	M	440	VO Ajuda
Apus	M	774	VO Ajuda
Corona Borealis	F	600	VO Ajuda
Delphinus	F	663	VO Ajuda
Centaurus	F	628	VO Ajuda
Mensa	F	410	VO Ajuda
Gemini	F	827	VO Ajuda
Leo	M	912	VO Ajuda
Camelopardalis	M	873	VO Ajuda
Musca	M	566	VO Ajuda
Grus	M	720	VO Ajuda
Lyra	F	692	VO Graça S3
Aquila	F	577	VO Graça S3
Microscopium	F	599	VO Graça S3
Corvus	M	659	VO Graça S3
Leo Minor	F	841	VO Graça S3
Equuleus	F	540	VO Graça S3
Libra	M	532	VO Graça S3
Carina	F	577	VO Graça S3
Canis Minor	F	571	VO Graça S3
Aries	M	600	VO Graça S3
Monocerus	F	673	VO Graça S3
Lacerta	M	499	VO Graça S3
Horologium	M	699	VO Graça S3
Corona Australis	M	579	VO Graça S3
Aquarius	F	982	VO Graça S4
Crater	M	861	VO Graça S4
Cetus	F	846	VO Graça S4
Draco	F	983	VO Graça S4
Canis Major	M	947	VO Graça S4
Crux	F	1052	VO Graça S4
Norma	F	905	VO Graça S4
Lynx	F	966	VO Graça S4
Hydrus	M	959	VO Graça S4
Bootes	M	1052	VO Graça S4
Cassiopeia	M	1001	VO Graça S4
Canes Venatici	M	1019	VO Graça S4

Appendix C 2. Cumulative record of gesture actions in toddler’s adult-directed communication obtained through a function that takes random subsamples of the data and check how many of the gesture actions are identified in each subsample.



Appendix C 3. Cumulative record of gesture actions in toddler’s peer-directed communication obtained through a function that takes random subsamples of the data and check how many of the gesture actions are identified in each subsample.



Appendix C 4. Factors influencing the following toddlers' gestural communication features: : (1a) Diversity of gestures, (2a) Use of sequences, (5a) Repetitions and (6a) Use of objects.

Term	Estimate	Std. Error	lower CI*	upper CI*	z	P-value
(1a) Diversity of gestures						
Intercept	1.24	0.221	0.82	1.633		[1]
Signaller gender (male)	-0.092	0.137	-0.355	0.183		[1]
Signaller age	0.504	0.12	0.291	0.745		[1]
Recipient age (peer)	**0.634**	**0.117**	**0.419**	**0.877**	**5.43**	**<0.001**
School (VO Graça S3)	0.326	0.235	-0.07	0.767	1.388	0.165
School (VO Graça S4)	0.077	0.251	-0.403	0.546	0.306	0.76
School (VO Laranjeiro)	0.115	0.211	-0.266	0.516	0.544	0.587
Signaller gender (male) x Signaller age	-0.154	0.144	-0.423	0.103	-1.071	0.284
(2a) Use of sequences						
Intercept	-0.372	0.232	-0.855	0.086		[1]
Signaller gender (male)	0.075	0.181	-0.262	0.427		[1]
Signaller age	0.261	0.14	-0.007	0.533		[1]
Recipient age (peer)	0.106	0.154	-0.218	0.4	0.686	0.493
School (VO Graça S3)	0.005	0.282	-0.564	0.578	0.017	0.986
School (VO Graça S4)	-0.135	0.278	-0.676	0.395	-0.487	0.626
School (VO Laranjeiro)	-0.39	0.271	-0.915	0.099	-1.438	0.151
Signaller gender (male) x Signaller age	-0.062	0.183	-0.436	0.301	-0.336	0.737
(5a) Repetitions						
Intercept	-0.584	0.189	-0.949	-0.219		[1]
Signaller gender (male)	-0.123	0.145	-0.405	0.168		[1]
Signaller age	0.276	0.112	0.061	0.495		[1]
Recipient age (peer)	-0.095	0.117	-0.32	0.142	-0.811	0.417
School (VO Graça S3)	0.158	0.229	-0.273	0.6	0.69	0.49
School (VO Graça S4)	-0.02	0.223	-0.449	0.413	-0.09	0.928
School (VO Laranjeiro)	-0.344	0.222	-0.747	0.08	-1.553	0.12
Signaller gender (male) x Signaller age	-0.38	0.144	-0.666	-0.101	-2.635	0.008
(6a) Use of objets						
Intercept	-0.533	0.317	-1.176	0.095		[1]
Signaller gender (male)	-0.005	0.264	-0.57	0.495		[1]
Signaller age	-0.18	0.195	-0.551	0.21		[1]
Recipient age (peer)	-0.309	0.256	-0.781	0.157	-1.206	0.228
School (VO Graça S3)	-1.138	0.398	-1.956	-0.402	-2.859	0.004
School (VO Graça S4)	-0.597	0.415	-1.4	0.191	-1.439	0.15
School (VO Laranjeiro)	0.045	0.392	-0.67	0.745	0.115	0.908
Signaller gender (male) x Signaller age	0.218	0.278	-0.292	0.68	0.785	0.433

[1] Not shown as lacking a meaningful interpretation

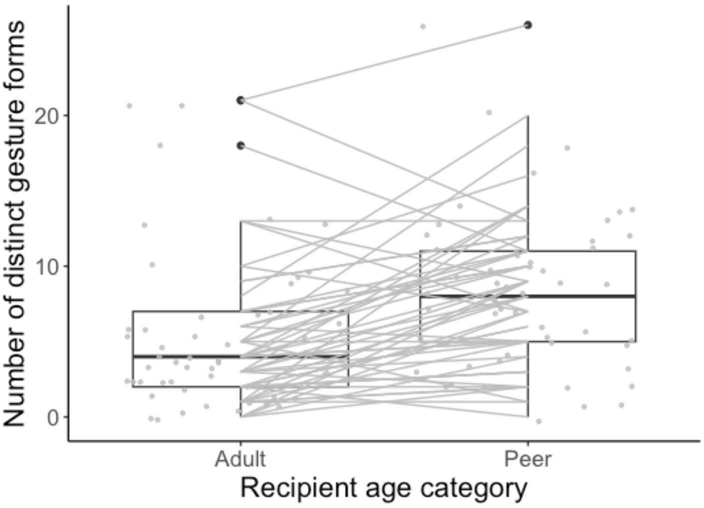
Appendix C 5. Factors influencing (3a) the gesture rate of toddlers' gestural communication.

Term	Estimate	Std. Error	lower CI	upper CI	t	P-value
Intercept	-0.353	0.1	-0.684	0.002		[1]
Signaller gender (male)	-0.097	0.077	-0.349	0.156		[1]
Signaller age	0.119	0.064	-0.081	0.33		[1]
Recipient age (peer)	0.078	0.059	-0.142	0.309	1.324	0.185
School (VO Graça S3)	-0.087	0.113	-0.496	0.296	-0.769	0.442
School (VO Graça S4)	-0.04	0.131	-0.43	0.367	-0.303	0.762
School (VO Laranjeiro)	-0.134	0.11	-0.532	0.262	-1.212	0.226
Signaller gender (male) x Signaller age	-0.091	0.078	-0.361	0.167	-1.164	0.244

Appendix C 6. Factors influencing (4a) the gesture duration of toddlers' gestural communication.

Term	Estimate	Std. Error	lower CI	upper CI	df	t value	P-value
Intercept	0.194	0.083	0.024	0.361			[1]
Signaller gender(male)	0.074	0.065	-0.056	0.204			[1]
Signaller age	-0.149	0.049	-0.248	-0.05			[1]
Recipient age (peer)	**-0.118**	**0.043**	**-0.202**	**-0.034**	**25.641**	**-2.711**	**0.012**
School (VO Graça S3)	-0.053	0.097	-0.261	0.158	46.533	-0.544	0.589
School (VO Graça S4)	-0.012	0.103	-0.221	0.205	28.244	-0.115	0.909
School (VO Laranjeiro)	0.11	0.095	-0.081	0.31	38.41	1.161	0.253
Signaller gender (male) x Signaller age	0.098	0.062	-0.023	0.231	42.126	1.585	0.121

Appendix C 7. Boxplots show the number of distinct gesture forms produced by the 53 toddlers. Each toddler is represented by a grey dot next to each box and the lines connect the number of distinct gesture forms produced by the same toddler towards adults and peers.



Appendix C 8. Factors influencing the following features of toddlers' gestural peer-directed communication: (1b) Diversity of gestures, (2b) Use of sequences, (5b) Repetitions and (6b) Use of objects.

Term	**Estimate**	**Std. Error**	**lower CI***	**upper CI***	**z**	**P-value**
(1b) Diversity of gestures						
count part - Intercept	1.650	0.233	1.193	2.108		[1]
count part - Signaller gender (male)	-0.168	0.172	-0.506	0.17		[1]
count part - Signaller age	0.661	0.161	0.345	0.976		[1]
count part - Peer recipient age category	-0.378	0.146	-0.665	-0.091	-2.582	0.010
count part - School (VO Graça S3)	0.571	0.269	0.043	1.098	2.12	0.034
count part - School (VO Graça S4)	-0.198	0.303	-0.793	0.396	-0.654	0.513
count part - School (VO Laranjeiro)	-0.047	0.276	-0.588	0.495	-0.169	0.866
count part - Signaller gender (male) x Signaller age	-0.097	0.172	-0.435	0.24	-0.564	0.572
zero part - Intercept	-1.825	0.367	-2.543	-1.106	-4.975	0.000
(2b) Use of sequences						
Intercept	-0.114	0.341	-0.814	0.521		[1]
Signaller gender (male)	-0.067	0.232	-0.497	0.389		[1]
Signaller age	0.164	0.225	-0.303	0.628		[1]
Age difference recipient-signaller	-0.117	0.125	-0.379	0.137	-0.938	0.348
School (VO Graça S3)	-0.115	0.415	-0.954	0.756	-0.277	0.782
School (VO Graça S4)	-0.085	0.415	-0.923	0.75	-0.204	0.839
School (VO Laranjeiro)	-0.68	0.388	-1.462	0.089	-1.752	0.08
Signaller gender (male)x Signaller age	-0.149	0.237	-0.61	0.288	-0.629	0.529
(5b) Use of repetitions						
Intercept	-0.635	0.105	-0.831	-0.423		[1]
Signaller gender (male)	-0.265	0.165	-0.591	0.053		[1]
Signaller age	0.115	0.109	-0.083	0.34		[1]
Age difference recipient-signaller	-0.02	0.078	-0.183	0.12	-0.254	0.8
Signaller gender (male)x Signaller age	-0.345	0.161	-0.66	-0.033	-2.138	0.033
(6b) Use of objects						
Intercept	-0.772	0.521	-1.732	0.223		[1]
Signaller gender (male)	-0.097	0.375	-0.833	0.672		[1]
Signaller age	0.114	0.338	-0.542	0.731		[1]
Age difference recipient-signaller	0.024	0.179	-0.36	0.393	0.135	0.893
School (VO Graça S3)	-1.029	0.62	-2.123	0.142	-1.661	0.097
School (VO Graça S4)	-0.218	0.671	-1.395	1.024	-0.325	0.745
School (VO Laranjeiro)	-0.56	0.597	-1.677	0.573	-0.937	0.349
Signaller gender (male)x Signaller age	-0.455	0.36	-1.216	0.27	-1.265	0.206

Appendix C 9. Factors influencing (3b) the gesture rate of toddlers' peer-directed gestural communication.

Term	Estimate	Std. Error	lower CI*	upper CI*	t value	Pr(>|z|)
Intercept	-0.261	0.117	-0.728	0.252		[1]
Signaller gender (male)	-0.069	0.085	-0.375	0.248		[1]
Signaller age	0.137	0.078	-0.17	0.43		[1]
Age difference recipient-signaller	0.066	0.03	-0.085	0.21	2.217	0.027
School (VO Graça S3)	-0.023	0.137	-0.568	0.519	-0.17	0.865
School (VO Graça S4)	-0.175	0.149	-0.754	0.413	-1.174	0.24
School (VO Laranjeiro)	-0.102	0.131	-0.647	0.412	-0.783	0.433
Signaller gender (male)x Signaller age	-0.02	0.085	-0.334	0.281	-0.231	0.818

Appendix C 10. Factors influencing (4b) the gesture duration of toddlers' gestural communication.

Term	Estimate	Std. Error	lower CI*	upper CI*	df	t value	Pr(>|z|)
Intercept	0.038	0.106	-0.178	0.255			[1]
Signaller gender (male)	0.062	0.073	-0.084	0.222			[1]
Signaller age	-0.095	0.068	-0.23	0.039			[1]
Age difference recipient-signaller	-0.02	0.035	-0.09	0.045	66.821	-0.573	0.569
School (VO Graça S3)	-0.05	0.126	-0.3	0.193	39.902	-0.393	0.697
School (VO Graça S4)	0.084	0.129	-0.152	0.336	28.851	0.651	0.52
School (VO Laranjeiro)	0.107	0.119	-0.125	0.35	34.962	0.893	0.378
Signaller gender (male)x Signaller age	0.026	0.072	-0.119	0.168	29.349	0.364	0.718

Appendix C 11. Boxplots show the number of distinct gesture forms produced by the 52 toddlers in peer-directed communication. Each toddler is represented by the grey dots and the lines connect the number of distinct gesture forms produced by the same toddler towards younger and older peers.