

**Joint Attention in Wild Chimpanzees
and Human Infants:
A Comparative Study**

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Abstract

The ability to engage in joint attention is a pivotal milestone during human development. Whether this ability is uniquely human or shared with chimpanzees is hotly debated. Progress has been hampered by testing chimpanzees and humans with different methods, which has prevented meaningful species comparisons. In addition, little is known about cultural variation of joint attention in human infants and the socio-environmental factors linked to its development.

In order to address these issues, I applied a standard set of experiments to chimpanzee, Ugandan and British mother-offspring dyads in their natural environments. I presented a novel laser stimulus into the visual field of the offspring or an offspring-mother dyad and analysed the resulting behaviour and interactions.

In all three groups, offspring showed similarly low rates of laser-related communicative behaviours, when their mothers were inattentive and instead engaged with the laser individually. When the laser was visible to both the mother and offspring, however, humans engaged significantly more in joint attention than chimpanzees who only engaged in two instances of joint attention. Furthermore, human mothers of both cultures observed their infant's interaction with the laser more and communicated more during mutual gaze than chimpanzee mothers, suggesting that mothers play an important role in scaffolding early joint attention interactions.

Socio-environmental factors that might explain this species difference were identified by collecting observational data on the participants' everyday activities. Chimpanzee offspring vocalised less and spent less time engaged in activities that may promote joint attention (social activities, dyadic play, play with objects) than human infants. The offspring's main social partner during everyday life activities did not, however, predict group-level joint attention performance. To conclude, the overall patterns of results of this thesis suggest joint attention skills are present in chimpanzees, but the motivation to engage in joint attention may be uniquely human.

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Author's declaration

I declare that this thesis represents my own work, except where due acknowledgement is made, and that it has not been previously submitted to this university or any other institution for a degree or other awards.

(Tanja Kaller)

Chapter 1 : Introduction to Joint Attention

Summary

Joint attention is a pivotal milestone for the development of spoken language. Although our closest living relatives, the chimpanzees, engage in some complex forms of communication, it is still unclear whether they engage in joint attention or whether joint attention is uniquely human.

Progress on comparative joint attention research has been hampered by a lack of agreement on a single definition of joint attention across species. In this chapter, different definitions of joint attention are discussed which results in the following definition of joint attention for this thesis: *Joint attention is the mutual awareness of having attended to the same entity between two (or more) individuals. Mutual awareness is established through communication by at least one individual during mutual gaze.* The event of joint attention which requires the coordination of attention from two social partners is distinguished from joint attention skills, such as gaze alternation, social referencing, pointing or gaze following which can be done individually and which do not necessarily result in “mutual awareness”.

Different operationalisations of joint attention are discussed which result in the following operationalisation of joint attention for this thesis: *Individual A and individual B look at the same stimulus before engaging in face to face contact. During face to face contact, individual A and/or B engage in communication. Communication consists of either vocalisations or salient facial movements.*

Introduction

Countless times during the day, humans engage in joint attention with each other in many different ways. When we are at work, we exchange ideas and concepts with others and when we enjoy our leisure time we meet up for a match of our favourite sport or play cards with our friends. All of these activities have one aspect in common: they are examples of our ability to engage with others in joint attention. This ability to coordinate attention with others enables us to share experiences, ideas and achieve common goals in collaborative activities (Tomasello, 2008; Pinker, 2010; Whiten and Erdal, 2012).

Joint Attention started to become a topic of systematic research during the 1970s (e.g. Bruner, 1974; Scaife & Bruner, 1975; Collis & Schaffer, 1975) and since then received considerable attention from developmental and comparative psychology and psychopathology (see Tomasello, 1988 and Moore & Dunham, 1995 for a review). In the last 15 years, joint attention research has further expanded into a vibrant, multidisciplinary field with inputs from philosophy, neuroscience and even robotics (see Eilan, Hoerl, McCormack & Roessler, 2005; Seemann, 2012 for a review). This high level of interest from several fields indicates that joint attention is regarded as an important skill relevant to a variety of complex behaviours (e.g. language and higher order cooperation). As a consequence, joint attention is examined on a multitude of different levels and from various different perspectives.

This variety and complexity of investigation is reflected in the fact that, until now, there is no unanimous consensus on the definition of joint attention itself, which considerably complicates comparisons between the different fields (Seemann, 2012). Some of the different definitions that have been developed over the past 40 years will be discussed in more detail later in this chapter. Since a comprehensive discussion of all aspects of joint attention is beyond the scope of this PhD, the main focus of this thesis will be on the developmental and comparative perspectives.

In this chapter, I will first highlight the importance of joint attention from an ontogenetic and phylogenetic perspective and then introduce some definitions of

joint attention. I will then outline behaviours that are similar to joint attention and evaluate them in light of the presented definitions. Finally, I will critically evaluate the different definitions of joint attention and review different strategies to operationalise joint attention for empirical investigations. This will then lead me to a conclusion of how I will try and address the operationalisation of joint attention in this thesis.

Joint Attention and the Comparative Approach

The Importance of Joint Attention from an Ontogenetic Perspective

During the ontogeny of human infants, joint attention constitutes an important building block for language acquisition and a “rich soil” for the cultivation of other socio-cognitive abilities (e.g. Adamson & McArthur, 1995; Mundy & Newell, 2007; Seemann, 2012). Tomasello and Farrar (1986) discovered that there was a link between the frequency of joint attentional episodes and early language competency in human infants. They proposed that joint attentional episodes scaffolded early mother-infant linguistic interactions which facilitated the preverbal infants’ language acquisition. This shows that joint attention provides pre-linguistic infants with a contextual framework or joint attentional frame in which they can more easily identify intended referents during linguistic interactions (Bruner, 1974; Tomasello, 1988).

Joint attention not only enables infants to learn new words or concepts, it also gives them the opportunity to exchange emotions with others about external objects or events in a coordinated way (Carpenter, Nagell & Tomasello, 1998). Therefore, joint attention “may be seen as the crossroads where human infants meet the world of collective cognition in which they will reside for the rest of their lives” (Carpenter et al., 1998, p.2).

The Importance of Joint Attention from a Phylogenetic Perspective

Since joint attention is a pivotal developmental milestone in human ontogeny, tracing its phylogenetic origins is vital to understand our cognitive evolution. The central questions are: When did joint attention emerge in the course of evolution and is it a uniquely human skill? One promising way to tackle these important

questions is to apply a comparative approach: although we cannot directly examine the abilities of the ancestors of extant species and cognitive capacities are not preserved in the fossil record, it is possible to investigate similarities and differences in living species that are closely related to each other. This approach enables us to make inferences about the abilities of the common ancestor of these two closely related species. Thus in order to trace the evolutionary roots of joint attention, it is important to know whether our closest living relatives, the chimpanzees, engage in joint attention and joint attention related behaviours. Chimpanzees and humans shared a common ancestor approximately 5-7 million years ago (Enard & Pääbo, 2004) and their genome is 98.7% identical to ours (Enard, Khaitovich et al., 2002). This genetic similarity and, in evolutionary terms, recent divergence is mirrored by resemblances in physical appearance, behaviour and comparatively sophisticated cognitive skills. Therefore, studying the behaviours of chimpanzees enables us to estimate which abilities the last common ancestor of chimpanzees and humans possessed.

Despite the genetic similarity to chimpanzees, humans display some remarkable social abilities that may be uniquely human. Some of these abilities include, firstly, and most distinctively, spoken language. Characterised by a high degree of complexity and generativity, recursiveness and grammar, it is unparalleled throughout the whole animal kingdom (Hauser, Chomsky & Fitch, 2002; Pinker, 2010). Secondly, humans are highly cooperative and are able to coordinate large groups to achieve common goals (Tomasello, Carpenter, Call, Behne & Moll, 2005; Tomasello, 2008, Whiten & Erdal, 2012). Thirdly, humans transmit their knowledge from generation to generation through intentional and active teaching (Thornton & Raihani, 2008). This transfer of knowledge results in a “rich trans-generational knowledge database”, or cumulative culture, and far exceeds the skill set that individuals of one generation alone could invent (Whiten, 2000; Whiten & Erdal, 2012).

Joint attention forms the basis of all these potentially uniquely human characteristics. Without jointly attending to the same entity, a linguistic exchange about that entity would be impossible. Human cooperation, teaching and

cumulative cultural build on joint attention and language: in order to coordinate larger scale operations, the participants need to commit to a shared goal to which every member of the group jointly attends (Tomasello et. al, 2005; Tomasello, 2008). Effective and active teaching can only be achieved if the learner jointly attends to the same entity as the teacher.

Although these joint attention based social abilities are widely regarded as uniquely human, there is some evidence indicating that precursors for these abilities may have been present in our last common ancestor and therefore can be observed in chimpanzees. Despite chimpanzees not possessing the genetic or anatomical preconditions for speech (Enard, Przeworski, et al., 2002), there is a growing body of evidence that our closest living relatives possess a relatively complex communication system using gestures, vocalisations and facial expressions (Goodall, 1986). Although chimpanzee communication exhibits some of the characteristic of human language such as intentionality (Leavens & Hopkins, 1998; Hobaiter & Byrne, 2011), flexibility (Slocombe & Zuberbühler, 2007; Slocombe et al., 2010), some degree of reference (Slocombe & Zuberbühler, 2005) and generativity (Arnold & Zuberbühler, 2006) in their natural communication, it seems to lack recursion and hierarchical syntax (Hauser et al., 2002; Pinker, 2010).

Chimpanzees engage in mutualistic cooperation to solve tasks when they face an immediate pay-off (Melis, Hare & Tomasello, 2006). Compared to humans, however, chimpanzees show a much lower motivation to cooperate with unrelated individuals (Melis & Semmann, 2010). In addition, there is no evidence that chimpanzees commit to common goals and collaborate based on an action plan (Tomasello et al., 2005).

Knowledge is transmitted in chimpanzee communities from older individuals to offspring through social learning processes which results in the existence of different cultures across different wild populations (Whiten, Goodall et al., 1999; Whiten, 2000; Whiten, 2005). Although there are two reported instances of potentially active teaching in wild chimpanzees (Boesch, 1991), the majority of the data indicates that wild chimpanzees do not actively and intentionally teach their offspring (Matsuzawa, 2007). Therefore, the underlying cognitive mechanisms for

social learning in chimpanzees may be quite different to human cultural transmission (Whiten, 2000; Tomasello, 2008).

Summary

To summarise, although chimpanzees possess some social skills that are similar to those of humans, they seem not to be as sophisticated as in humans and the motivations behind the behaviours may be different (Tomasello, 2008). As previously shown from a developmental perspective, joint attention is a pivotal developmental milestone for human language, cooperation and teaching. It seems possible that phylogenetically, joint attention may be the missing link between the social skills of our closest living relatives and humans.

After having established the importance of research into joint attention and before I review the empirical work that has been done on joint attention in humans and in chimpanzees (Chapter 2), it is important to first discuss how joint attention has been defined and operationalised in the literature. At the end of this chapter, I will then present the definition and operationalisation of joint attention that I have adopted throughout this thesis.

Joint Attention – Definitions and Similar Phenomena

Definitions of Joint Attention

As outlined above, joint attention has been investigated from several different perspectives over the past 40 years. Based on the multidisciplinary nature of the approaches to joint attention, there are many competing definitions of joint attention that emphasize slightly different aspects of the component behaviours of joint attention. Disagreements within and between different fields of investigation are often rooted in the use of different definitions for joint attention (Carpenter & Liebal, 2012).

To add more confusion to the definitional debate of joint attention, there is some variation with respect to the terms used to refer to “joint attention”. The terms “joint attention” and “shared attention” are most commonly used in the literature

(Seemann, 2012) and are in most cases interchangeable. The term “joint engagement” mostly refers to more extended periods of joint attention (i.e. that last at least a few seconds) (Carpenter et al., 1998), but for some authors, “joint engagement” also includes shorter joint attention interactions (e.g. Bakeman & Adamson, 1984; Hobson & Hobson, 2012). In this thesis, I will use the term “joint attention” which will be defined at the end of this chapter. It is also important to note that joint attention can occur in different sensory domains such as visual, tactile or auditory domains. In this thesis, I will focus only on joint visual attention. From now on, the term “joint attention” refers to “joint visual attention”.

An exhaustive theoretical analysis of joint attention across all disciplines is beyond the scope of this PhD, thus, I will focus on definitions of joint attention relevant to developmental and comparative psychology.

Early definition of joint attention

Bakeman and Adamson (1984) originally defined joint engagement as two individuals coordinating their attention with each other about an object or event of mutual interest. They further distinguished “passive joint engagement” in which mothers and their infants were attending to the same toys, but the infants were relatively unaware of the mother’s involvement or even presence, and “active joint engagement” in which the “infant is actively involved with and coordinates his or her attention to both another person and the object that person is involved with” (Bakeman and Adamson, 1984, p.1281).

Since then, different researchers have modified this definition and emphasized different aspects of this early concept of joint attention. The aspect of coordination of attention, however, remained central to most researchers (e.g. Tomasello, 1995; Carpenter et al., 1998; Mundy, Delgado, Block, Venezia, Hogan & Seibert, 2003; Leavens & Bard, 2011; Carpenter & Liebal, 2012).

Joint attention as intentional co-orientation to a common locus

The main proponents of a more behaviour-based definition of joint attention are Leavens, Bard, Hopkins, Racine and others whom I will subsequently refer to as “Leavens and co-workers”. They based their definition of joint attention on the

original concept of Bakeman and Adamson (1984) with the emphasis on coordinated joint engagement (Leavens, 2012, personal communication). Leavens and co-workers defined joint attention as “the ability of social partners to intentionally co-orient to a common focus of attention” (Leavens and Bard, 2011, p.11). The term “intentional” refers to the presence of intentional communication from at least one of the interactants (e.g. overt looking, pointing, verbal or non-verbal deixis) about a third entity. The ability to engage in joint attention becomes manifest in the interaction between two (or more) organisms. For example, individual A points to an object and subsequently, individual B follows A’s point and looks at the object. In this case, the behaviour of individual B is contingent on the behaviour of individual A and therefore, joint attention is established. Consequently, instances of passive joint engagement in which one of the partners is oblivious to the actions of the other, are excluded from this definition. In addition, since Leavens and Bard’s (2011) definition of joint attention requires at least one individual to display goal-directed behaviour, it also excludes instances of parallel attention in which two (or more) organisms shift their attention simultaneously and independently of each other to an external event (e.g. a sudden blast) with no one initiating it.

Leavens and co-workers distinguish between the event of joint attention as defined above and joint attention skills. The latter can be displayed irrespective of the social responsiveness of the partner. For example, I can point to food for my rabbit, but he fails to understand my pointing. In this case, no joint attention would have occurred between me and the rabbit, but I could be credited with joint attention skills.

Joint Attention through “knowing together”

Definition based on knowing together

The main proponents of a stricter and more cognitive definition of joint attention are Tomasello and his colleagues (Carpenter, Liszkowski, Liebal and others) who are subsequently referred to as “Tomasello and colleagues”. Like Leavens and co-workers, Tomasello and colleagues also base their definition of joint attention on Bakeman and Adamson’s (1984), but they have developed a more cognitive

approach (Tomasello 1995; Tomasello 2008, Carpenter & Liebal, 2012) in which joint attention is defined as the active sharing of attention about an object, event or an idea. More specifically, “sharing” means that both individuals are not just attending to the same entity, but they “know together” that they are attending to the same entity (Tomasello, 1995; Carpenter & Liebal, 2012; Carpenter & Call, in press). According to Tomasello (1995, 2008), sharing attention is a mental event and each social partner requires the ability to understand herself and the other as intentional agents in the sense that they know that others can intentionally direct their attention to a specific focus. Based on this ability, the social partners can actively and intentionally direct, follow or share attention.

What is similar between Tomasello and colleagues’ and Leavens and co-worker’s definition is that joint attention is regarded as a social interaction between two individuals which requires the active participation of both parties to occur. In Tomasello and colleagues’ view, however, there is no joint attention without both parties “knowing together” that they are attending to the same entity (Tomasello, 1995). It is not enough if only one individual is trying to share attention with the other and the recipient of a communicative act subsequently co-orient to a common locus, but in addition the social partners need to be mutually aware that they are focussing on the same thing and make that awareness mutually manifest (Carpenter & Liebal, 2012). In this sense, Leavens and co-workers’ definition of joint attention is over-inclusive. Since the sharing aspect of joint attention is central to the personal experience we have when we engage in joint attention ourselves, it is vital to include it into the definition of joint attention.

If Leavens and co-workers’ definition of joint attention serves as the basis for empirical comparative research, it may result in too many false positives, i.e. counting instances in which there is no sharing as joint attention such as A points to x, B follows the point and sees x, picks x up and walks away (Carpenter, 2012, personal communication).

“Knowing together” through communication

The interesting question now is: how can “knowing together” be achieved? The original proposition was that “knowing together” essentially requires recursive

mindreading of “I know that you know that I know ... we are attending to the same thing” (e.g. Schiffer, 1972; Tomasello, 1995). Recursive mindreading is a complex mental activity that requires a third-person representation (Gómez, 1995).

Alternatively, Gómez (1995) suggested his concept of “attention contact” in which two individuals attend to each other’s attention. Carpenter and Liebal (2012) illustrated attention contact by comparing it to two mirrors infinitely reflecting each other. Although attention contact is simpler and more direct, it still contains an infinite loop of recursion. Therefore, it does not fulfil the criterion of “sharing” or “togetherness” that is required for true joint attention, because the experiences of both interactants would still be separate whilst each partner individually assesses the knowledge state of the other (Carpenter & Liebal, 2012).

To resolve this issue, Carpenter and Liebal (2012) proposed that to establish knowing something *together* with someone requires *both partners* openly and actively making it mutually manifest to each other *through communication* that they share attention about a specific referent. Consequently, the key element that makes joint attention truly joint is communication, because it “turns a mutually experienced event into an interaction, into something joint” (Carpenter & Liebal, 2012, p.168). Figure 1.1 illustrates the resulting joint attention triangle.

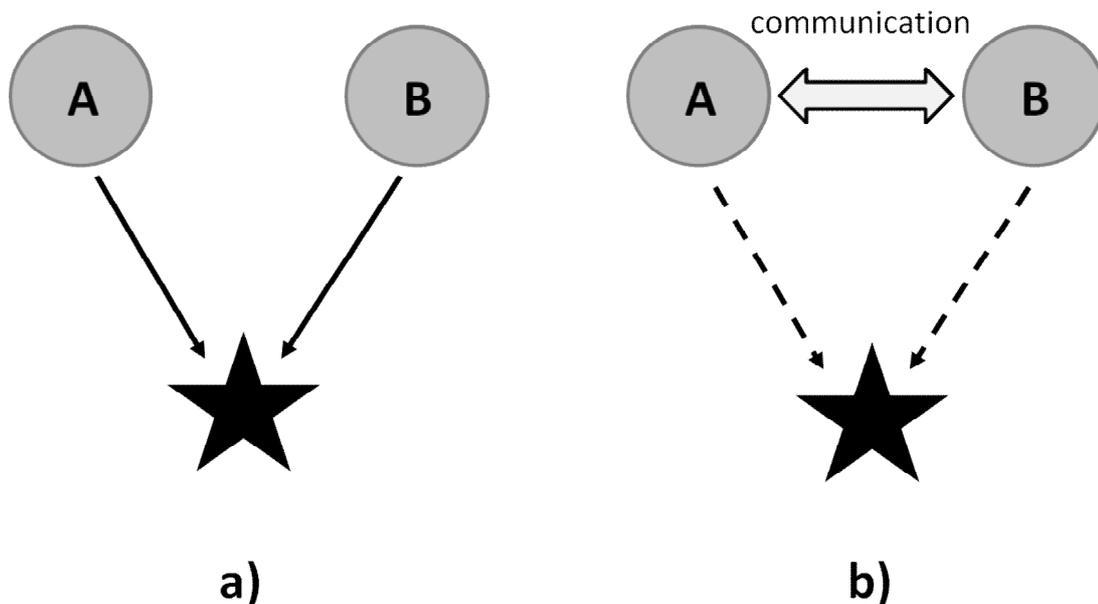


Figure 1.1: Joint attention triangle as illustrated by one possible example on how joint attention can be established. a) Individual A and B are both looking at the star (object of mutual interest). After that, in b) A and B are connected through “knowing together” of having attended to the star (the dashed lines indicates that A and B are no longer looking at the star). Knowing together through communication closes the triangle between A, B and the star.

It is important to note that whilst both Leavens and co-workers and Tomasello and colleagues stress the importance of communication during joint attention interactions, they do so for different stages within the interaction. Communication in Leavens and Bard (2011) refers to communication for establishing the co-orientation (e.g. pointing and point following) whilst Tomasello and colleagues refer to communication during or *after* the social partners have attended to the same entity (i.e. the sharing aspect). Pointing, gaze following and gaze alternation are joint attention behaviours or skills, but according to Carpenter and Liebal (2012) not enough by themselves to constitute a full-fledged instance of joint attention (see discussion below).

The simplest form of communication to share attention could be a mutual look. According to Carpenter & Liebal (2012), however, this alone does not necessarily constitute an act of joint attention either, because the involved parties may only check each others' focus of attention and accidentally make eye contact. Instead, the look must at least be a “sharing look” (Carpenter & Liebal, 2012, p.161ff) which

carries some degree of expressive communication. According to Carpenter and Liebal (2012), sharing looks “are intentional, they are referential, and they have content – they convey a message about the object or event” (e.g. Isn’t that great?) (p.170). Sharing looks can be accompanied by emotional cues, such as smiling. Based on Hobson and Hobson’s criteria (2007), sharing looks can be distinguished from checking looks. In contrast to sharing looks, checking looks only function to gather information unilaterally without the motivation to share mental states. In addition to sharing looks, the social partners may also show more obvious forms of communication such as vocalisations or facial expressions such as a smile, a wink or, in response to a negative stimulus, frowning.

One difficulty with Tomasello and colleagues’ adoption of sharing looks from Hobson and Hobson (2007) into the definition of joint attention is that the concept of sharing looks in the absence of any additional communicative behaviours cannot be meaningfully applied to other species. This will become more apparent below, when I present the operationalisation of a sharing looks.

It is important to note that this emphasis on the importance of communication within the interaction is quite recent and, in earlier studies, Carpenter and colleagues regarded gaze alternation as a sufficient indicator for joint attention in human infants and non-human primates (Carpenter et al., 1995, Tomasello & Carpenter, 2005). This shows how active the joint attention field is and that the definition of joint attention changes dynamically even within research groups. Consequently, we need to be careful when comparing the results from older studies with more recent ones and, because they may be based on different definitions of joint attention.

The motivation to share attention

In addition to the coordination of attention between social partners, Tomasello and colleagues also emphasize that the motivation to share attention with others should be a sharing one (Carpenter & Liebal, 2009; Carpenter & Liebal, 2012). With the motivation to share attention, knowledge or emotion, joint attention is not just a means to an end (i.e. instrumental action), but an end in itself (Carpenter & Liebal, 2012). This includes some gestures, such as pointing to an object with the

motivation to share attention and interest about this object (declarative pointing, see below) and holding up objects towards a social partner with the motivation to show it to her, because they are communicative acts that reflect the actor's motivation to engage in joint attention about an object with a social partner (Carpenter & Liebal, 2012). In contrast, since Leavens and co-workers' do not make inferences about the motivations behind the actor's actions, they include instrumental actions such as a chimpanzee's pointing for a human to see a banana that he should bring for him (imperative pointing) into the definition of joint attention.

How is joint attention established?

According to the Carpenter and Liebal (2012) definition, joint attention can be established in two different ways. In "person-driven" joint attention, the signaller actively initiates joint attention by redirecting the recipient's focus of attention. For example, whilst you are reading, I see a beautiful bird flying by and point at it which then actively draws your attention to it. When you have seen the bird, you then turn towards me and say: "Wow, I haven't seen that one for a while!". The complete joint attention interaction here involves first directing, then following and finally sharing attention. The directing and following of attention is mirrored in Leavens and Bard's (2011) definition, but the sharing aspect is unique to Carpenter and Liebal's (2012) concept of joint attention (and other proponents of a richer view, e.g. Hobson & Hobson, 2007).

The second way of establishing joint attention is "stimulus-driven" joint attention. Imagine you are walking down the street in the city centre with your friend and suddenly you both see an elephant coming around the corner. In this scenario, you would probably both orient towards the elephant without anyone initiating it, because the stimulus (elephant) draws attention to itself. The triangle is then closed through communication and the expression of surprise like "Wow, did you see that?" (Carpenter & Liebal, 2012).

Critical evaluation of the definitions of joint attention

Since in stimulus-driven joint attention, only sharing attention takes place, no intentional co-orientation sensu Leavens and Bard (2011), instances of stimulus-driven joint attention would not be captured by Leavens and Bard's (2011) definition. This shows one important weakness of their definition and highlights an important point about the underlying concept of Leavens and co-workers' definition of joint attention: the main focus lies on communicative behaviours that cause the coordination of attention, whilst little emphasis is given to the sharing aspect of joint attention after the social partners have oriented towards a third entity. Joint attention is more than just an intentional co-orientation to a stimulus. Instead, it is a "meeting of minds" in which both partners also share the awareness that they are attending to the same object or event (Tomasello, 1995; Carpenter et al, 1998; Hobson, 2005; Carpenter & Liebal, 2012).

The big advantage of Tomasello and colleagues' definition of joint attention is that it tries to catch the very essence of joint attention, the "jointness" itself and the richness of a joint attention interaction (Carpenter & Liebal, 2012). This definition manages to theoretically disentangle joint attention from similar phenomena in which attention may not be shared in the stricter Tomasello sense, but which are included in Leavens and co-workers' definition. Therefore, Tomasello and colleagues' definition, if operationalised well, could be very useful in reducing false positives (e.g. social referencing, gaze following, imperative pointing).

With the Tomasello and colleagues strict definition, it may be argued, however, that it potentially leads to several false negatives as sometimes we may not pick up on subtle behavioural cues (e.g. sharing looks). Nevertheless, I think it is preferable to be strict whilst adjusting and developing the method rather than being over-inclusive which may lead to a lack of precision and hence cause confusion.

Similar Phenomena

In the following section, I will present some joint attention behaviours/skills and relate them to the previously outlined definitions of joint attention. These include gaze following, pointing and social referencing.

Gaze following

Gaze following is defined as the ability to recognize that another's gaze is not directed towards oneself and then to follow the line of sight of the other individual to find out his focus of attention (Emery, Lorincz, Perrett, Oram & Baker, 1997; Emery, 2000). Gaze following (including point following) may occur, but not necessarily, in the beginning of a joint attention interaction (see person-driven joint attention above). Gaze following without communication between the individuals, however, is unidirectional and is better described as the individualistic exploitation of a cue by another individual (Tomasello, 2008). In this case, the looker may not even be aware that his gaze is being followed. For Leavens and co-workers, gaze following if accompanied by any intentional communication is regarded as an instance of joint attention, (Leavens & Bard, 2011). In Tomasello and colleagues' view, gaze following only results in joint attention if the attention is shared at the end of the interaction, regardless of whether the looking of the social partners was initiated by one of them.

Pointing

Pointing is a communicative body movement that projects a vector from a body part with the function to direct another individual's attention to an external object or event (Kita, 2003). Pointing can be executed with different motivations such as imperative or requestive "Give me the chocolate" or declarative "Look at the beautiful butterfly" (Tomasello, 2008). Tomasello, Carpenter and Liszkowski (2007) distinguished a third type of pointing, i.e. informative pointing, which is a sharing of knowledge, but may not, like declarative pointing, be an end in itself. For Tomasello and colleagues, only declarative pointing is communication to establish joint attention (Carpenter & Liebal, 2012). In contrast, Leavens and co-workers *do not support this distinction, because they reject the attribution of motivations to individuals in order to define joint attention (Leavens & Bard, 2011).*

Pointing and the subsequent co-orientation of the recipient to a common locus is one of the most important indicators for joint attention in Leavens and co-workers' studies. According to Tomasello and co-workers, however, pointing constitutes a joint attention skill, but is not joint attention in itself, until both partners have shared

attention and “know together” that they are attending to the same entity (Carpenter, 2012, personal communication).

Social referencing

Social referencing is defined as the seeking of information from another individual's reaction to a particular object or event in the environment by monitoring his reaction in relation to this object (Russell, Bard & Adamson, 1997). Social referencing does not constitute true joint attention *sensu* Tomasello and co-workers, because it can be done individualistically without the sharing aspect of joint attention (Carpenter et al., 1998).

Social referencing is much harder to distinguish from true joint attention, because it involves gaze alternation of one individual between another and an object in the environment. Social referencing is similar to joint attention, because, in contrast to parallel attention, one individual takes into account the reaction of the other *in relation* to an external object or event. Therefore, the information seeker needs to have some ability to coordinate his attention between two external entities (Russell et al., 1997; Carpenter et al., 1998).

There is, however, one main difference between joint attention and social referencing: social referencing is unidirectional. Like in gaze following, the individual who is already focused on the object does not need to be aware of the other individual's behaviour. One animal can simply observe the other's behaviour without engaging with him/her about it. When the information-seeker looks back at the social partner, he could just be checking his reaction to the object. In this case, there is no intentional communication displayed by either of the social partners (Leavens & Bard, 2011) and there is no “knowing together” (Tomasello, 1995) and thus, joint attention is not established.

Like pointing and gaze following, social referencing could transform into joint attention. Imagine the individual who focused on the object first, then looks at the information seeker and both then show some overt signs of sharing attention, this would qualify as joint attention in the Tomasello sense. It is not clear, however, whether this scenario would qualify as joint attention according to Leavens and

Bard's (2011) definition, because there was no goal-directed behaviour involved in order to establish the co-orientation of both individuals. Social referencing without subsequent sharing of attention was accepted as being an instance of joint attention, however, in a more inclusive definition of Leavens and Racine (2009).

Summary

To summarise, according to Leavens and Bard's (2011) definition of joint attention, one individual's orientation to the common locus has to be contingent on the other's intentional communicative behaviour. This, however, does not yet constitute real joint attention for Tomasello and colleagues, because they stress the importance of "knowing together" and the jointness of the interaction regardless of whether the co-orientation was caused by the (intentional) behaviour of one of the individuals or whether the stimulus drew attention to itself. In addition, Tomasello and colleagues take the motivation of the actor into account of definition whether joint attention has occurred or not. Leavens and co-workers reject this, because according to them, motivations are mental states that cannot be directly observed.

Joint attention can involve several different joint attention skills, such as gaze following, pointing, gaze alternation and social referencing that do not necessarily constitute a joint attention event by themselves. It becomes evident that there is no unanimous agreement on a single definition for joint attention. Therefore, it is a tremendous challenge but at the same time essential to bridge the gap between the different approaches and find an agreement on a single definition for joint attention. So far, this has not been achieved which poses a serious challenge for operationalising joint attention for empirical research.

Operationalisation of Joint Attention

It is important to note that most of the operationalisations for joint attention are developed based on studies with human participants and are therefore anthropocentric. This might cause difficulties in trying to operationalise and investigate joint attention across species.

Assessing the infant's joint attention skills

Seibert, Hogan and Mundy (1982) developed a test battery to assess early social-communication skills of infants including joint attention skills. Their nomenclature was later adopted by Mundy et al. (2003) to assess joint attention skills in human infants as an early indicator for autism. Mundy et al.'s (2003) test battery has not only been applied in developmental psychopathology; Leavens and colleagues have also adopted it to examine joint attention skills in non-human primates (Leavens & Racine, 2009).

Mundy et al. (2003) generally operationalised joint attention behaviours as “the child's skill in using non-verbal behaviours to share the experience of objects or events with others” (p.1). According to different underlying motivations and roles of the infant, he further divided joint attention behaviours into four sub-categories: “initiating joint attention” which includes behaviours such as eye contact, pointing and showing objects to a social partner in order to share attention, “responding to joint attention” which includes gaze and point following, “initiating behavioural requests” such as eye contact, reaching and pointing to elicit help in getting an object and “responding to behavioural requests” which includes behaviours like giving a requested object to the tester (Mundy et al., 2003, pp.1-2). Mundy (2003) solely focused on the infant's behaviour and thus can only establish joint attention skills in the infant, but not whether a joint attention event has occurred. In order to establish whether joint attention as an event has occurred, both, the mothers' and the infants' reactions need to be taken into account.

Intentional communication and joint attention

Leavens and colleagues stressed intentional communication to be vital for joint attention to occur. Behavioural indicators for intentional communication in the signaller include (1) “gaze alternation, visual checking, response waiting, etc”, (2) displaying “sensitivity to the attentional state of the social partner” and (3) “persistence or elaboration of signalling when initial attempts to communicate fail” (Leavens & Bard, 2011, p.11). These criteria were also used in several other studies on intentional communication of humans and non-human primates (Cartmill & Byrne, 2007; Leavens, Russell & Hopkins, 2005; Pika, Liebal, Call & Tomasello, 2005).

The advantage of the behavioural indicators for intentional communication mentioned above is that they focus on non-verbal behaviours and are therefore well suited for the assessment of joint attention skills in pre-verbal infants and potentially non-human primates. Leavens and Bard’s (2011) claim that chimpanzees do engage in joint attention mainly rests on their ability to learn pointing gestures in captivity. When these chimpanzees pointed, and either a human experimenter or in rare cases another language trained chimpanzee responded to the point, they credited chimpanzees with joint attention and not just joint attention skills. In Tomasello and colleagues’ view, however, this is not joint attention, because no sharing has taken place (yet). Since Leavens and colleagues did not define and operationalise this aspect of joint attention, I will now present the Tomasello lab’s operationalisation as they stressed the importance of the presence of “sharing” and “knowing together”.

Operationalising “knowing together”

According to Carpenter and Liebal (2012), there are two things to look for when investigating joint attention: (1) the motivation to engage in joint attention and (2) knowing together. The motivation to engage in joint attention can be operationalised by examining behaviours whose sole purpose is to share attention, such as showing and declarative pointing. A study by Liszkowski, Carpenter, Henning, Striano and Tomasello (2004) revealed that 12 months old infants pointed declaratively by manipulating the reactions of an experimenter to the

infants' pointing gesture. The infants were only satisfied with the reaction of the experimenter, if she engaged in joint attention with the infant *about* the object the infant pointed to.

To identify "knowing together", Tomasello and colleagues, in earlier studies, also focused on the subjects' joint attention skills. Gaze alternation of the infant between the social partner and a third entity was the main criterion determining the presence or absence of joint attention (Tomasello, Savage-Rumbaugh & Kruger, 1993; Carpenter, Tomasello & Savage-Rumbaugh, 1995; Tomasello & Carpenter, 2005). Recently, however, Carpenter and Liebal (2012) proposed a stricter way of operationalising joint attention and included the social partners' active participation, because gaze alternation is not a sufficient indicator for joint attention. In order to score joint attention, some form of overt and active sharing must be observable from *both* social partners, because only the presence of communicative signs and expressions between the social partners after they have both seen the stimulus is a clear and reliable indicator of joint attention (Carpenter & Liebal, 2012). Sharing can be expressed either through verbal communication (e.g. "Wow, how cool is that?"), or "just a meaningful, expressive look" (Carpenter and Liebal, 2011, p.167).

How can we measure a meaningful or expressive look? Hobson and Hobson (2007) have proposed an operationalisation to distinguish "sharing looks" that indicate true joint attention through interpersonal experience, from "checking looks" which are unilaterally glances from the subject and "orientation looks" that happen in direct response to the social partner's behaviour such as moving or making noises. Sharing and checking looks are distinguished on three dimensions: (1) reciprocity, (2) depth and (3) contact (Hobson & Hobson, 2007). Whilst sharing looks are characterised by the subject's awareness that the social partner is looking at them, the look itself being deep *into* their partner's eyes and manifesting affective *contact* with the social partner, checking looks are unilateral, superficial, i.e. a glance *at* the eyes of the social partner, and impersonal in the sense that the subject may only be monitoring the social partners actions (Hobson & Hobson, 2007). Despite the highly subjective and subtle nature of the criteria used to distinguish sharing from

checking looks, they achieved good to excellent inter-observer reliability in making this distinction, because “it was straightforward to ‘feel’ (and judge) whether the looks seen on the videotape were sharing (...) or checking” (Hobson & Hobson, 2007, p.419).

Whereas this highly subjective, yet admittedly very reliable, operationalisation of sharing looks may be very successful in diagnosing autism in human infants, it appears to be unsuitable to investigate whether joint attention is uniquely human. We have to admit that as humans we cannot have the same degree of intuitive understanding of non-human animals’ interactions. How do we know whether a look from a chimpanzee is deep or superficial or whether they have registered that the social partner is looking at them? The answer is clear: we lack objective criteria that allow us to operationalise sharing looks across species. For that reason, subjective measures like those of Hobson and Hobson (2007) cannot be meaningfully used in comparative psychology.

The importance of natural communication

What is important to take into account when operationalising a concept across species is each species’ natural way of communicating. For instance, although we know that chimpanzees have several anatomically homologous expressions to humans, they can differ in function (e.g. smiling and bared teeth expression) (Parr, Waller & Vick, 2007). In addition some human expressions are not seen in our closest living relatives (e.g. disgust expression). Furthermore, eye contact serves a different function in chimpanzees. In contrast to human interactions, adult chimpanzees avoid direct gaze, because it can constitute a signal for aggression (Goodall, 1986). Mutual gaze between mothers and their infants, however, has been observed in two captive chimpanzee populations (Bard, Myowa-Yamakoshi, Tomonaga & Tanaka, 2005). Nevertheless, it is thinkable that eye contact between chimpanzees as a way to share attention may be shorter than in humans. As a consequence, if we applied Hobson and Hobson’s (2007) coding scheme, we may code sharing looks of chimpanzees as checking looks because they appeared to be superficial glances at the eyes to a human observer. In addition, based on the finding of Kawai and Matsuzawa (2000) which shows the impressive speed with

which chimpanzees processed visual stimuli, expressive eye-contact between chimpanzees could happen in a split second. Furthermore, chimpanzees may exchange affect very quickly and very subtly which may easily be missed the human observer's eye. As a consequence, I think that before we have understood the intricacies of chimpanzee communication, we are not in a good position to assess joint attention across species on this subtle level.

Summary

While Mundy's operationalisation of joint attention is focused on joint attention skills in infants, Leavens and co-workers definition mainly focus on measuring intentional behaviour that serves to establish the co-orientation of the two individuals to a common focus. Although the operationalisations from Mundy and Leavens are helpful to identify joint attention skills in pre-verbal infants and non-human primates, they did not operationalise the joint attention event itself. The motivation to share attention was operationalised by Tomasello and colleagues as showing objects or pointing declaratively. Joint attention which is characterised by "knowing together", was operationalised as communication between the social partners, identified as "sharing looks", emotional exchange or vocal communication.

Conclusions

Based on the definitions discussed in this Chapter, joint attention was defined in this thesis as follows:

Joint attention is the mutual awareness of having attended to the same entity between two (or more) individuals. Mutual awareness is established through communication by at least one individual during mutual gaze.

It is possible to establish mutual awareness without mutual gaze, but this usually entails either referential language or tactile communication. Since this thesis focussed on non-verbal individuals and joint visual attention, the above-mentioned definition was sufficient. The term "mutual awareness" carries an almost identical meaning to "knowing together". The reason for using the term "mutual awareness" instead of "knowing together" was, that "mutual" has a stronger connotation of

reciprocity and it emphasizes each participants' role in the joint attention event. "Awareness" was used over "knowing", because it has a stronger connotation of attention. As for Tomasello and colleagues, communication as a way of making the mutual awareness of having attended to a common object of interest mutually manifest, was central to my definition of joint attention. "Having attended to the same entity" emphasizes that two individuals can only be mutually aware of something, if both had perceived the same entity before communicating about it. My definition of joint attention, however, does not address how "having attended to the same entity" has come about. This is addressed by Leavens' and co-workers' definition. Therefore, my definition only focuses on joint attention as an event. Joint attention skills were defined as the ability (i.e. gaze alternation, pointing, point/gaze following) or the motivation to share attention which did not necessarily result in a joint attention event.

In the above mentioned definition of joint attention, it was essential that, in addition to mutual gaze, at least one individual had to overtly communicate. In contrast to Carpenter and Liebal's (2012) concept, communication through "sharing looks" in the absence of other communicative signs was not sufficient for my definition of joint attention. Although it is possible that a "sharing look" can be sufficient for mutual awareness to be established, we lack the objective criteria to operationalise "sharing looks" across species. In contrast, my definition requires the use of vocalisations or salient facial movements as 'communication', because these signals can be objectively and fairly identified across species.

It could be argued that in pre-linguistic infants or non-linguistic primates it can never unequivocally be known whether mutual awareness was established, even in the presence of overt communication from both sides. For example, after attending to an object with her mother, the infant could switch her attention from the object to her mother, the mother then smiles to share attention about the object, and the infant responds to the mother's smile by smiling back. The infant's smile, despite being contingent on "having attended to the same entity", could be a dyadic reaction to the mothers smile and not a sharing smile *about* the object. This unavoidable uncertainty occurs whenever researchers try to make inferences

about the mental states of non linguistic beings, however I do not believe that this should prevent us from trying to investigate these issues. I hope therefore, that the definition of joint attention used in this thesis is a very close approximation to capturing true joint attention, because, in addition to gaze alternation, it includes mutual gaze AND communication.

Joint attention was operationalised for this thesis in the following way:

Individual A and individual B looked at the same stimulus before engaging in face to face contact. During face to face contact, individual A and/or B engaged in communication. Communication consisted of either vocalisations or salient facial movements.

It is important to note that communication had to be present in addition to face to face contact for joint attention to be scored.

Joint attention skills examined in this thesis were attention directing, attention following, gaze alternation and observing the social partner's engagement with an object. Behaviours that indicate the motivation to share attention that were examined in this thesis were anticipatory facial movements and triadic attention getters.

Chapter 2 : Joint attention in Human Infants and Chimpanzees

Summary

The development of joint attention skills and the age of emergence for joint attention are reviewed for chimpanzee and human infants. Human and chimpanzee socio-cognitive development is similar in many ways until approximately 9 months of age. They engage in dyadic interactions and mutual gaze with their mothers and start to manipulate objects. At 9 months, human infants start to engage in first instances of joint attention and display a strong motivation to share attention and interest through the emergence of anticipatory smiling and the 'showing' gesture. Regardless of age, there is currently no evidence that chimpanzees engage in joint attention.

Differences in joint attention skills of chimpanzees are discussed with a special focus on whether the chimpanzee subjects interacted with humans or conspecifics. The importance of the rearing history in chimpanzees for the development of joint attention skills is revealed. I conclude that only studies on intra-species communication in wild chimpanzees can reveal whether chimpanzees naturally engage in joint attention in an environment they are adapted to. In addition, due to cultural variation of socio-environmental factors, the need of cross-cultural studies in joint attention research is highlighted.

Finally, methodological issues of previous research into joint attention are discussed which motivated an original cross-species and cross-cultural approach that included chimpanzees, Ugandan and British mother – offspring dyads. The age of the human infants is chosen to be 11 months and all dependent offspring of chimpanzee mothers (0-12 years) are included in this study. Two experiments using a novel stimulus that aimed at triggering triadic interaction in the dyads are combined with an observational study in which joint attention related factors of the social environment of all three study groups are examined.

Joint Attention in Human infants

Development of communication and joint attention in human infants

Joint attention requires the infant's coordination of attention between an object and a social partner. In the following section, I will outline the emergence of socio-cognitive and motivational behaviours that are relevant for understanding the emergence of joint attention skills and sharing attention.

0-9 months

From birth human infants are very social. Neonates are sensitive to social stimuli (Striano & Reid, 2005) and they prefer to look into a face whose eyes directly gaze at them compared to a face with averted gaze (Farroni, Csibra, Simion & Johnson, 2002). In addition, soon after birth, infants engage in neonatal imitation, e.g. they imitate tongue protrusion (Meltzoff & Moore, 1977, Anisfeld, 1991).

Figure 2.1 shows that, at 2 months of age, young infants start to engage in dyadic interactions with their caregivers (Trevarthen & Hubley, 1978; Adamson & McArthur, 1995). The term *dyadic interaction* describes episodes of engagement between the infant and a social partner which are often characterised by emotional exchange such as smiling and sharing affect between mothers and their infants (Striano & Reid 2006). Dyadic social interactions can be mediated through tactile modalities, such as body contact or through the visual modality, such as mutual gaze. The preference of either the visual or tactile modality in dyadic interactions varies in dependence of the cultural background of the mother (Keller, Lohaus et al. 2004).

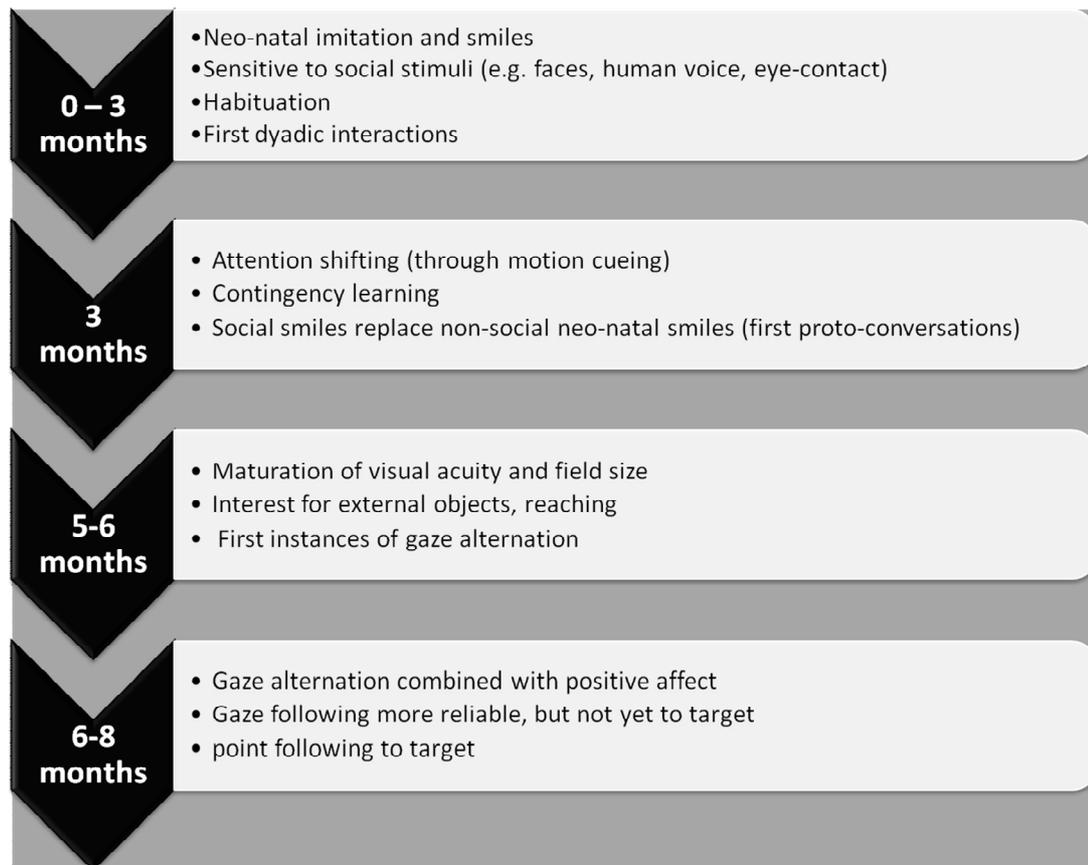


Figure 2.1: Flow chart for most important aspects of the development of Western human infants from birth to 8 months of age

In the first two months of life, infants have very limited control over their social attention which means that the infants' gaze mainly orients to faces and does not easily disengage from them. Figure 2.1 shows that at approximately 3 months, however, infants are able to briefly disengage from the experimenter's face in response to her gaze shift. As a consequence, the infants showed a first tendency to follow the adult's gaze (D'Entremont, Hains & Muir, 1997; Gredebäck, Fikke, Melinder, 2010; Perra & Gattis, 2010), but at this age, these brief "gaze following motions" were mainly due to motion cueing and the infants were unlikely to be able to establish the focus of the adults' attention (Deák & Triesch, 2006). The ability to briefly disengage from a stimulus (e.g. the mother's face) may be mediated by habituation. Habituation is characterised by the infant's decreasing interest in the mother's face over time which then facilitates the gaze shift (Deák & Triesch, 2006). In addition, after following the motion of the adult's gaze shift, some infants looked back at the adult (Perra & Gattis, 2010). This shows that some

infants as young as 3 months showed a very basic form of gaze alternation which is a pivotal element of joint attention. The infants' tendency to look back at the adult's face may be mediated by the infants' preference for looking at faces which exists from birth (see Figure 2.1).

At approximately 3 months (Figure 2.1), infants begin to detect contingencies in their social and non-social environment (Striano & Rochat, 1999). Contingency learning is a process in which the infant uses their experiences about previous sequences of events to generate predictions about ongoing or future sequences of events. For example, when exposing infants to a patterned sequence of alternating lights, infants learned to anticipate the location of the next light by shifting their head before the next light was visible (Deák & Triesch, 2006). Deák and Triesch (2006) suggested that contingency learning is vital for the subsequent acquisition of joint attention skills such as gaze following. With infants now starting to be sensitive to contingencies and engaging in dyadic interactions, they have started the process of becoming shaped by their respective cultural and social environment (Keller, 2007).

At 3 months of age, infants have also become more responsive to their parents and display first social smiles (Tomasello & Carpenter, 2005; Deák & Triesch, 2006). Interactions that involve mutual gaze, touch, smile and vocalisations become more and more frequent (Figure 2.1). These dyadic interactions have also been referred to as *proto-conversations* and they are characterised by an exchange of emotions and affect (Trevarthen, 1979; Carpenter et al., 1998). At 3 months, infants begin to initiate dyadic interactions, for example through smiling (Striano & Reid, 2006) and they are sensitive to a delay as short as 1 second during the flow of dyadic interactions (Striano, Henning & Stahl, 2006). Striano and Stahl (2005) showed that 3 month old infants discriminated between dyadic and triadic interactions by measuring variations in gazing and smiling.

Triadic interactions not only involve the infant and a social partner, but in addition, an external object or event that becomes the topic of the interaction (Carpenter et al., 1998). The visual field size and acuity of young infants starts to mature between 3-6 months of age (Atkinson, 2000). Reid and Striano (2005) showed,

using a habituation paradigm, that 4 month old infants not only followed an adult's gaze, but also processed some information concerning the target object by reacting stronger to a novel object than the object the adult was gazing at. Infants were also sensitive to social cues (e.g. eye contact, tone of voice) that indicate whether information was intended for them (Farroni, Johnson & Csibra, 2004).

At 5 months, enabled by improved vision, infants start to become more interested in the external world and to manipulate objects. Infants now have developed some basic abilities to engage in the two elementary components of joint attention: dyadic interaction and object manipulation. In addition, between 5 and 6 months of age, infants begin to reach for objects (Deák & Triesch, 2006) which may be a precursor to pointing (Figure 2.1).

Legerstee, Markova and Fisher (2007) showed that at 5 months, infants showed their first signs of coordinating attention, measured by gaze alternation. Whilst infants were playing with their mothers and an object, some infants (60%) alternated their gaze between the object and their mothers face. The number of infants who engaged in gaze alternation did not increase significantly in 7 (77%) and 10 months old infants (66%). A similar result was obtained by Bakeman and Adamson (1984) who did not find a significant difference in the average amount of time spent in joint engagement (defined by gaze alternation) between 6 and 9 months old infants. Furthermore, Legerstee et al. (2007) found that the infants' gaze monitoring during dyadic interactions at 3 months was related to coordinating attention at 10 month. They suggested that an increased rate of maternal attunement (i.e. maintaining attention and warm sensitivity) from 3-10 months to be an important factor to foster the link between infant gaze monitoring and gaze alternation during triadic interactions.

Do these early instances of gaze alternation mean that infants between 5-10 months already engage in joint attention, being "mutually aware" that they have attended to the same object? Legerstee et al. (2007) did not code whether face to face contacts occurred and whether there were any communicative behaviours of the infants present during gaze alternation. Therefore, although the infants were able to engage in gaze alternation, it is not possible to conclude whether infants

looked to the social partner in order to communicate or only to check whether she was still there. To my knowledge, there has been no evidence that infants younger than 9 months share attention through communication with their social partner by engaging in showing, giving or declaratively pointing to an object. Therefore, it is likely that the gaze alternation behaviour of 5 month old babies may have a different underlying cognitive structure than later joint attention.

In the second half of the first year of life, gaze following and gaze alternation become more sophisticated. Figure 2.1 shows that between 6 and 8 months, human infants were more likely to combine their gaze alternation between an object and their mother with positive affect (Striano & Bertin, 2005a). Infants alternated their gaze not only with their mothers, but also with adult strangers. In addition, infants follow an experimenter's gaze more reliably (Gredebäck et al, 2010), but it is not until 9 month of age that infants follow gaze to a specific target in their frontal visual field (Deák & Triesch, 2006, Figure 2.2). In another study by Striano and Bertin (2005b), almost $\frac{3}{4}$ of the tested 7 months old infants succeeded in localizing an object on the wall that the experimenter pointed to, but only one third followed the experimenter's gaze (Figure 2.1).

A study by Cleveland, Schug and Striano (2007) suggests that joint attention interactions contributed to infant learning before they showed signs of engaging in joint attention themselves. They revealed that, at 7 months, the social context in which an object was experienced impacted the infants' object processing outcomes. Having experienced a target object in joint attention with someone lead to habituation to that object in contrast to having observed the experimenter inspecting the object on her own.

To sum up, during the first 9 months of life, infants have frequently engaged with others in dyadic interactions, they have developed visual acuity, the basic cognitive skills of social attention control and an increasing interest for objects. In addition, they have been shaped by their social environment through contingency learning and interaction routines. The early and stepwise emergence of joint attention related skills reviewed above suggests a gradual development from dyadic to triadic interactions (Cleveland, Schug & Striano, 2007). Infants younger than 9

months show some joint attention skills by alternating their gaze between objects and social partner and some ability to follow gaze and pointing, but they have not yet displayed any overt communication to convey that they are “mutually aware” that they share attention with their social partner (Chapter 1, p.22). It has been suggested that infants undergo several fundamental changes starting from 9 months of age and therefore this time period is called the “9-month revolution” (Carpenter et al., 1998; Tomasello, 2008). In the following section, I will review the developmental changes that infants undergo from 9 months until they reach 2 years.

Nine - 24 months

For Tomasello (1995, 2008) understanding others as intentional agents that act towards a goal, is an important precondition for joint attention. There is some evidence that 9 months old infants begin to understand goals of others. In a study by Behne, Carpenter, Call and Tomasello (2005), 9 months old infants (but not 6 months olds) distinguished between identical actions that had been motivated by different goals. The authors concluded that infants at this age recognized the goal-directed nature of the experimenters’ actions and therefore understood others as intentional agents (Tomasello, 1999, 2008) (Figure 2.2). Corkum and Moore (1995) opposed Tomasello’s (1995) rich interpretation of 9 month old infants’ behaviour and pointed out that conditioning and contingency learning may as well account for the infants’ abilities at this age. There is a wider consensus, however, that infants from 15 months understand other’s underlying intentional states (Baldwin & Moses, 2001; Deák, Walden, Kaiser & Lewis, 2008).

By the age of 9-10 months, infants have started to engage in social referencing (Campos & Sternberg, 1981; Deák & Triesch, 2006) and most typically developing infants use gaze alternation during playing episodes with adults (Carpenter et al., 1998; Adamson & Bakeman, 1991; Bard & Leavens, 2009). Whilst dyadic interactions are frequently accompanied by mutual gaze and affective displays at a younger age, between 9-12 months, infants start to engage in mutual gaze with adults *about* an object (Carpenter & Call, in press) (Figure 2.2). Whilst mutual gaze and affective displays used to be the central topic of dyadic interactions, they

become now a means to share attention in triadic interactions about the external topic of interest (Adamson & Bakeman, 1984).

At 10 months, infants increased their use of anticipatory smiling during joint attention interactions (Venezia, Messinger, Thorp & Mundy, 2004; Parlade, Messinger, Delgado, Kaiser, van Hecke & Mundy, 2009). Anticipatory smiling is different to reactive smiling in that it is already present before the infant looks into the adult's face. Anticipatory smiles are therefore not contingent on the smile of a social partner. They may be an indicator for the motivation to share positive affect during joint attention episodes (Figure 2.2). Therefore, it is at 9-12 months when the first instances of joint attention as defined in this thesis (p.22) occur. For the first time, the infants' gaze alternation between an object and a social partner is combined with face to face contacts that are characterised by communication and affective displays, such as smiles and vocalisations (Figure 2.2).

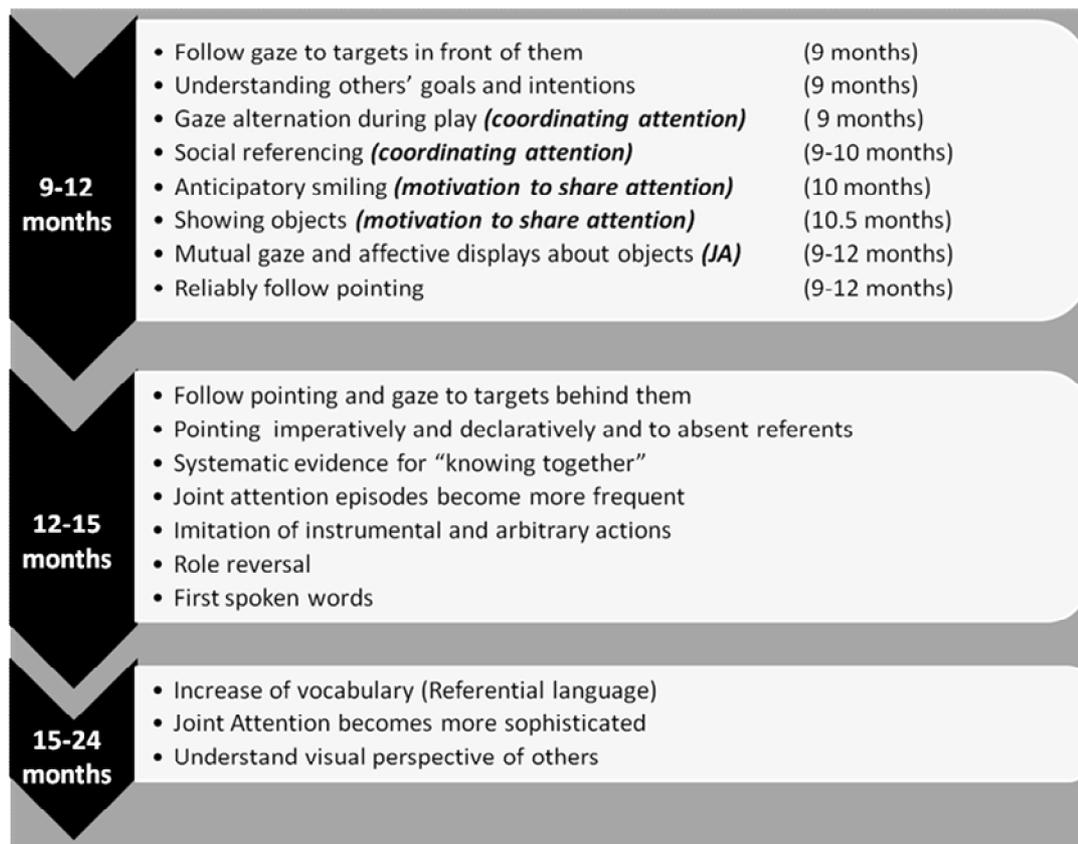


Figure 2.2: Flow chart for most important aspects of the development of Western human infants from 9 - 24 months of age. JA = joint attention

The emergence of joint attention is soon followed by the appearance of communicative gestures. 'Showing' emerged at 10.5 months and declarative pointing at approximately 12 months (Figure 2.2). Furthermore, infants were able to follow the adult's pointing reliably and successfully at an average of 11.5 months of age and the adult's gaze at an average of 13 months of age (Carpenter et al., 1998).

Figure 2.2 shows that 12 months old infants also followed an adult's gaze or point to targets behind them even when there were distracters present (Deák, Flom & Pick, 2000) or when the target was behind opaque barriers (Moll & Tomasello, 2004). This shows that the infants understood something about the line of sight of the adult. In addition 12 months old infants followed an adult's head turn significantly more often when he had his eyes open than when he either had them closed (Brooks & Meltzoff, 2005), but when he was blindfolded, only 14 months olds could distinguish that from someone wearing a head band (Brooks & Meltzoff, 2002).

A study by Liszkowski, Carpenter and Tomasello (2007) showed that 12 months old infants point with the aim to share attention about something specific. They showed persistence if they did not reach their communicative aims. For example, when the experimenter misunderstood the referent of the infant's declarative point, they continued pointing and thereby repaired the misunderstanding about the exact referent of their point. In addition, infants were not satisfied if the experimenter reacted to the infants' pointing gesture to an interesting sight merely with attention to the infant and ignoring the object the infant was pointing to (Liszkowski et al., 2004). These two studies showed that 12 month old infants pointed about something specific and did not just want to prolong the rewarding social interaction as previously suggested by D'Entremont & Seamans (2007). Sharing attention can also take place on an abstract level. Liszkowski et al. (2007) showed that 12 month old infants would also point to an absent referent in reference to the object that had just disappeared (Figure 2.2).

At 14 months there is more evidence for infants' "knowing together" (see p.22, Chapter 1) during triadic interactions with a social partner (Figure 2.2). In a study by Moll, Richer, Carpenter & Tomasello (2008), infants responded to the experimenter's request based on what they knew together with the experimenter. The authors ruled out the possibility that the infant responded based on what either they knew individually or what the experimenter knew individually. The infants reliably chose the object that both knew together (Moll et al., 2008). A similar study was conducted by Liebal, Behne, Carpenter & Tomasello (2009). Fourteen months old infants were able to interpret an experimenter's ambiguous point based on their shared experience with that experimenter. This also shows the 14 months olds remarkable ability to keep track of what they have shared with whom. These two studies show that infants know when they have shared something with someone and that they used this experience to figure out what an adult wanted from them. In contrast, 14 months old infants were not able to point selectively to an object that was relevant to previously shared experience with a particular person they are pointing for (Liebal, Carpenter & Tomasello, 2010). This means that 14 month old infants comprehended communication about a referent that they shared experience about with someone else, before they could produce requests based on shared experience until 18 months of age.

Since the emergence of the first joint attention episodes at 9-12 months, joint attention episodes become more frequent in the infants' second year of life (Figure 2.2). In addition, the infants' joint attention skills become more sophisticated (Carpenter et al., 1998) and the production of pointing with gaze alternation and sharing of attention has become robust (Figure 2.2). It seems that the ability to engage in Joint Attention then paves the way for the development of a whole array of communicative skills. Infants also begin to imitate instrumental and arbitrary actions (Carpenter et al., 1998) and they start to engage in games that include role reversal (Tomasello & Carpenter, 2005). In addition, first spoken words are learnt (Figure 2.2) and Tomasello (1988) and Carpenter et al. (1998) stressed the importance for joint attention skills in early language acquisition. For example, infants' gaze following ability at 10 months was linked to their language capacity at 18 months (Baldwin & Moses, 2001). After 15 months, the infants' vocabularies

increase explosively from a median of 40 words at 16 months to a median of 280 words at 21 months (Fenson, Dale et al, 1994; Figure 2.2).

To sum up, at 9 months of age, infants undergo some fundamental developmental changes. They understand something about other's goals and they are able to follow gaze to targets in front of them. Gaze alternation during play and social referencing are first signs of the infants' increasing ability to coordinate their attention between objects and a social partner. With the emergence of showing and anticipatory smiling, they have now acquired all necessary preconditions to engage in true joint attention. Sometime between 9 and 12 months of age, the coordination of attention is finally combined with mutual gaze and affective display. Hence, first instances of joint attention have occurred. At 12 months, infants point declaratively to share their experience about something specific. Shortly after, they begin to imitate and reverse roles. At 14 months, there is clear evidence for human infants' "knowing together" with a social partner. They understand what they have shared with whom and can use this knowledge to interpret an adult's request. At 18 months, they are then able to produce request based on shared knowledge themselves. During the second year of life, the infants' vocabularies explode and they start to use referential language. At the end of the second year of life, human infants' joint attention becomes more sophisticated and they start to understand the visual perspectives of others may be different from their own.

The Role of Human Mothers

Mothers play a central role in the development of joint attention (Kennedy & Bakeman, 1984; Bakeman & Adamson, 1984, Tomasello & Farrar, 1986). Infants from 9-15 months coordinated their attention more with their mothers than with same aged peers. This may be due to the mothers' ability to tailor their actions to suit the current attention state of the infant (Adamson & Bakeman, 1985).

In addition, human infants spend a considerable amount of time with their mothers. Therefore, mothers are key players in shaping the social environment of the infants. Infants whose mothers tuned more into their current focus of attention rather than re-directing the infant's attention to other objects, showed a bigger

vocabulary at 21 months of age (Tomasello & Farrar, 1986; Carpenter et al., 1998). In addition, the amount of time that infants engaged with their mothers in joint episodes also correlated with their linguistic communication skills (Carpenter et al., 1998). The mothers' interactive style also correlated with the infants' joint attention abilities. Infants of non-depressive mothers who were highly sensitive to the signals of the infants and who supported their infants verbally during problem solving showed better joint attention skills than infants of mothers with a poorer interactive style (Legerstee et al, 2007). Maternal responsiveness to the infants during the first 6 months of life also predicted spoken vocabulary size (Ruddy & Bornstein, 1982) and language comprehension (Tamis-LeMonda & Bornstein, 1989) at 12 months. In addition, the mothers' sensitivity and teaching skills at 6 months were predictive for joint attention (gaze alternation) at 9 months (Gaffan, Martins, Healy & Murray, 2010). Therefore, early mother-infant interactions are critical for an infant's social, emotional and cognitive development (Markova & Legerstee, 2006).

In the course of the first year of life, infants and their caregivers have established several routines (Deák & Triesch, 2006). During these routines, mothers provide infants with a supportive structure in shared activities such as picture book reading or mutual object play (Bakeman & Adamson, 1984). Therefore, mothers appear to play a key role in supporting infants' joint attention development.

Summary

To sum up, joint attention is a complex social skill that emerges based on a multitude of other skills during the first year of life and further develops during the 2nd year of life. First instances of true joint attention occur between 9-12 months which may be characterised by anticipatory smiling, and 'showing'. Joint attention develops from basic perceptual, cognitive and affective processes and is shaped by reinforcement learning and habituation. In addition to that, the social environment feeds the developing infant with experiences and the mothers play a key role in the development of joint attention (Deák & Triesch, 2006).

Finally, it is important to highlight the fact that the developmental timeline as outlined above is solely based on research with Western infants. Since the social

environment is very important for infant development and infants are shaped by different cultures from as early as 3 months of age (Keller, 2007), it is possible that joint attention follows a different developmental trajectory in other human cultures. The importance and the nature of the influence of the social environment on joint attention and related skills will be discussed later in this chapter.

Joint attention in Chimpanzees

Are the ability and the motivation to engage in joint attention a uniquely human trait in the primate lineage? As mentioned in Chapter 1, the human genome is 98.7 % identical to that of chimpanzees (Enard, Khaitovich et al., 2002), our closest living relative, and this is reflected in many physical and behavioural similarities. Despite having a complex social network and a variety of communicative signals, chimpanzees do not use human-like language. Since joint attention skills are strongly linked to language acquisition in human ontogeny (Tomasello & Farrar, 1986), an absence of joint attention in chimpanzees may indicate that joint attention is the missing link that makes human communication unique. On the other hand, the existence of joint attention in chimpanzees would indicate that this important foundation that language builds upon was present in the chimpanzee-human common ancestor.

Since the first half of the 20th century, chimpanzees have been systematically studied from a psychological perspective (Köhler, 1925; Goodall, 1986) and countless studies have been conducted on chimpanzees' social cognition (e.g. Tomasello and Povinelli). When reviewing evidence for joint attention in chimpanzees, it is important to take into account the different rearing histories of the subjects, because it has been repeatedly shown how important early life experiences are for the development of particular behaviours (Keller 2007; Bard & Leavens 2009). According to Leavens and Bard (2011), chimpanzees can be classified into three different categories with regard to their different socialisation histories: (1) home-raised or language-trained chimpanzees who were either cross-fostered by human caregivers and treated like human children (e.g. Gardner & Gardner 1969; Savage-Rumbaugh, 1994) or had extensive contact with a human caregiver from early on, (2) institutionalised captive chimpanzees who live in

biomedical research centres or zoos and who are exposed to humans during their everyday lives, but contact with humans is limited and (3) wild chimpanzees who have been raised by their biological mothers and have very limited exposure to humans. The great majority of joint attention studies have been conducted with either language-trained, home-raised or institutionalised captive chimpanzees and most of them are based on communication between chimpanzee subjects and human experimenters (e.g. Tomasello & Carpenter, 2005), whereas few have investigated joint attention skills amongst chimpanzees (e.g. Madsen, 2010; Tomonaga, Tanaka et al., 2004).

I will first outline the developmental timeline of joint attention related skills in chimpanzees and highlight the rearing background of the respective study subjects. After that, I will take a closer look at which joint attention capacities in chimpanzees vary as a function of who they interact with (humans or conspecifics).

Development of communication and joint attention skills in chimpanzees

Available Data

Chimpanzee development has not been studied extensively and therefore, it is difficult to accurately portray the development of chimpanzee infants. The following section on chimpanzee ontogeny is based on the few available studies and it is sometimes based on just a single chimpanzee individual. In addition the data used to estimate chimpanzee developmental patterns are derived from studies using different methodologies. In some studies, human experimenters were used and in others, intra-species behaviour was observed.

The main sources for this review on chimpanzee ontogeny derive from the Primate Research Institute at Kyoto where 1-3 mother-reared chimpanzee infants were studied in interaction with their mothers and/or human experimenters (e.g. Matsuzawa, 2006) and the Yerkes National Primate Research Centre (e.g. Bard, 1996; Bard & Gardener, 1996) where the influence of different rearing histories on the development of nursery-raised chimpanzees was investigated. To this end, Bard and Gardener (1996) divided orphaned chimpanzee infants into two nursery

groups that received a differential amount of one-to-one interaction time with their human caregivers. Chimpanzees exposed to standard care spent most of their time in peer groups with only a small amount of interactions with humans, whereas the chimpanzee infants of the responsive care group received 20 hours of human-chimpanzee interactions per week in addition to that experienced by standard care individuals (Bard, 1996).

The results of the two laboratories are complemented with some data from wild chimpanzees and other laboratories. The paucity of developmental data from the wild calls for more research with wild populations to create a clearer and more complete picture of chimpanzee ontogeny in an ecologically valid setting. This will enable us to better compare chimpanzee development with human development and identify the ontogenetic similarities and differences in the two species.

Birth-3 months

Postnatal brain growth of chimpanzees and humans is almost the same. From birth until reaching adulthood, the chimpanzee brain triples in size (3.20 times). This is very similar to humans whose brain grows to 3.26 times the size of a new born (Matsuzawa, 2007). If we combine this with the duration of dependency from the mother which lasts up to 12 years in the wild (Goodall, 1986), chimpanzees, like humans, have a long period in which they can learn flexibly and be shaped by their cultural environment.

Just like humans, chimpanzee neonates are responsive to human faces and engage in neonatal imitation with a human experimenter (Figure 2.3) (Bard, Platzman, Lester & Suomi, 1992; Myowa-Yamakoshi, Tomonaga, Tanaka & Matsuzawa, 2004). Bard et al. (1992) used the Brazelton Neonatal Assessment Inventory (BNAI) which assesses the neuro-behavioural skills such as the capacity to habituate to stimuli and self-regulation, response to stress and social-interactive capacities of newborns (0-2 months), to compare chimpanzee and human neonates (Figure 2.3). They found that chimpanzee neonates generally showed similar results to human babies (Bard et al, 1992). According to Bard (1999), orphaned chimpanzees express positive emotions through facial expressions and vocal greetings, and negative emotions through pouts, fussiness and whimpering. These

expressions also exist in mother-raised chimpanzee infants, but they are much harder to detect (Bard, 1999).

In general, the development of chimpanzee and human infants in the first three months of life is similar in many respects (Matsuzawa, 2007; Tomonaga et al., 2004). Chimpanzee neonates attend to social stimuli and enjoy social interaction. Chimpanzee babies recognize their mother's face at 1 month of age (Figure 2.3) and started to engage in social facial movements at approximately 2 months of age (Tomonaga et al. 2004). Like human infants, 2 months old chimpanzee infants preferred to look at faces that directly look at them as opposed to an averted gaze (Myowa-Yamakoshi, Tomonaga, Tanaka & Matsuzawa, 2003). In addition, the occurrence of mutual gaze (Figure 2.3) increased over the first 2 months of life and resulted in an average of 28 face to face contacts with their mothers per hour (Tomonaga et al. 2004), but Bard et al. (2005) reported only 8-10 instances of mutual gaze per hour in the chimpanzees housed at Yerkes National Primate Research Center. This shows that the frequency of mutual gaze varies between different chimpanzee groups. Mutual gaze has also been observed in the wild by van Lawick-Goodall (1968). Like in humans, the frequency of mutual gaze between chimpanzee infant and mother was negatively correlated to the frequency of physical contact with her (Tomonaga, et al, 2004). Little is known, however, as to whether chimpanzees also exchange emotions during these dyadic face to face interactions.



Figure 2.3: Flow chart for the most important aspects of the development of chimpanzee infants from birth to 24 months of age. The data derives from captive as well as wild chimpanzees. This flow chart is only a tentative portrait of the development of chimpanzees. More research is needed to establish the exact dates of emergence for the chimpanzees' abilities. BNAI: Brazelton Neonate Assessment Inventory. MDI = Mental Development Index of the Bayley Scale for Infant Development.

Three months – 24 months

Chimpanzee infants are more mobile than human babies and begin to move away from their mothers and explore their immediate surroundings for brief periods at 4 months of age (Tomonaga et al. 2004). At 5-7 months, they start to locomote on their hands and feet which is earlier than humans start crawling or walking (Figure 2.3) (Bard, 2012). At this point chimpanzee infants also begin to interact with conspecifics (Matsuzawa, 2007) and begin to manipulate objects (Tomonaga et al. 2004; Figure 2.3). At 6-8 months, chimpanzee infants interact with conspecifics more regularly and at 8-9 months of age, the chimpanzees' object manipulations become more complex (Hayashi & Matsuzawa, 2003).

In order to compare chimpanzees' cognitive development to humans, Bard and Gardner (1996) applied the Bayley Scales of Infant Development (which was originally designed for human infants) to 29 orphaned chimpanzee infants. They found that chimpanzee infants scored significantly higher on the mental development index than the human norm at 4-7 months. At 8-9 months, there was no difference between the chimpanzees and the human norm in general, but the chimpanzees who received responsive care performed better than the human norm and standard care chimpanzees below the human norm (Bard, 2012). Finally at 10-12 month, all chimpanzees performed significantly below the human norm. This may be due to the use of items that included human artefacts, such as specific toys (see Appendix).

One chimpanzee infant has been shown to follow human pointing at 9 months, the human head turn at 10 months and an eye-gaze cue at 13 months (Tomonaga et al. 2004). In addition, at 21 months of age, a chimpanzee infant reliably followed the human experimenter's cues to a target behind him, thereby displaying advanced gaze following abilities similar to those found in human infants (Okamoto, Tanaka & Tomonaga, 2004). According to Bard and Leavens (2009), joint attention emerges in chimpanzees at the same age as in humans: at 9 months of age. This age of emergence, however, was solely based on the chimpanzees' begging gesture. The chimpanzee begging gesture is characterised by the infant holding her hand palm up at the mouth of the mother while she is eating in the expectation of obtaining some food. Although there is an external object (food) and communication (begging gesture) involved, it is unclear whether the infant engaged in mutual gaze with the mother which is an important component of true joint attention (see Chapter 1, p. 22).

At 12 months of age, wild chimpanzees started to use communicative gestures (Figure 2.3). They began to initiate interactions with their mothers using gestures to initiate grooming or begging for food (Plooij, 1979; Goodall, 1986; Pika, 2008). There is no evidence, however, that chimpanzees use declarative gestures such as showing or giving objects to human experimenters without being prompted (Tomonaga et al, 2004; Carpenter & Call, in press). In addition, in response to a

novel object (i.e. a remote controlled car) the 1 and 2 year old chimpanzees did not alternate their gaze between the toy and their mothers whilst simultaneously engaging with the toy (Kosugi, Murai, Tomonaga, Tanaka, Ishida & Itakura, 2003; Tomonaga et al. 2004). The infants engaged with the object simultaneously with their mother, but neither of them exchanged looks with each other (Tomonaga et al. 2004). One infant chimpanzee, however, showed some form of social referencing (Figure 2.3), because after observing his mother engaging with the object, he overcame his initial fear and started manipulating the object himself (Tomonaga et al. 2004). This shows that the chimpanzee was able to coordinate his attention between the object and the mother, but he did not share his attention with his mother. At 14 months, chimpanzees engaged in social referencing with a human caregiver, alternating their gaze between a novel object and the caregiver and reacted based on the emotional value of the caregiver's facial expressions to the object (Russell, Bard et al. 1997).

Tomasello and Carpenter (2005) conducted a comprehensive study with three nursery-reared chimpanzees on joint attention and joint attention related skills similar to Carpenter et al's (1998) study with human infants. It is important to note that the chimpanzees were tested with their human caregivers and one of the chimpanzees was exposed to considerably more human contact than the other two. They established the following order of emergence for joint attention related abilities in the three chimpanzees: attention following (at 17, 36, 36 months), communicative gestures (at 21, 40, 40 months), but gaze alternation during social play and joint attention never occurred. The chimpanzee with the lowest ages of emergence was the one who had most human exposure.

Over 24 months

5 year old chimpanzees have been shown to point to out-of-reach food, thereby directing the experimenter's attention to an external entity (Leavens & Hopkins, 1998). When pointing, however, chimpanzees did not understand the roles of the experimenter's eyes for seeing (Povinelli & Eddy, 1994; 1996). They pointed equally often for an experimenter who was blindfolded, looking upwards or having a bucket on their head as for an experimenter who was wearing a head band,

directly gazed at them or held the bucket next to his head (Povinelli & Eddy, 1996). All they distinguished is whether the experimenter's body faced them or not, regardless of what the eyes were doing.

To sum up, whilst chimpanzees and humans become interested in objects at around the same age, chimpanzee infants are mobile considerably earlier than human infants. Chimpanzees engage in gaze following and social referencing and juvenile chimpanzees pointed to humans in captivity to obtain food. There is no evidence, however, that chimpanzee infants engage in joint attention with conspecifics or humans that involve the communicative display of "mutual awareness" and the sharing of attention.

The role of chimpanzee mothers

Chimpanzee mother-infant dyads have a very close social bond (Goodall, 1986) and chimpanzee infants spend the first 3 months of their lives in constant body contact with their mothers (Matsuzawa, 2007). Even after that, the majority of the care giving activities such as protecting the infant and grooming are done by the mothers (Goodall, 1986). In addition, chimpanzee mothers support the development of their infants mainly through the tactile rather than the visual modality which is similar to a non-Western parenting style (Bard, 1994; 2002). Chimpanzee mothers habitually play with their infants, but there was no mutual gaze during a tickle game (Bard, 2008). In addition, chimpanzee mothers rarely manipulated objects with the function to engage the attention of their infants. In addition, chimpanzee mothers do not overtly teach their infants or provide positive/ negative feedback on their offspring's actions (Matsuzawa, 2007). This is in stark contrast to human mothers (at least in the Western culture) who frequently and habitually manipulate objects to stimulate their infants or to teach them something about them (Bard & Vauclair, 1984).

Joint Attention in Adult Chimpanzees

By only considering data from chimpanzee infants and juveniles, it is not possible to get a complete picture about the chimpanzees' joint attention skills and whether or not they engage in joint attention. In fact, the majority of the studies on social

cognition and communication have been conducted with sub-adult and adult chimpanzees. Since it is undebated that human adults of all cultural backgrounds engage in joint attention in a variety of ways, most studies focus on infants in order to understand the development of this universal human skill. For chimpanzees, however, there is still a great debate on whether they engage in joint attention at all, regardless of their age. Therefore, it is important to consider evidence from all studies that have been conducted with chimpanzees on joint attention and related skills. In the following section, I will present evidence for joint attention (skills) from human-chimpanzee interactions and chimpanzee-chimpanzee interactions separately, because the chimpanzee behaviour varies as a function of whom they interacted with (Bard & Vauclair, 1984). In addition, disentangling inter-species from intra-species communication enables me to draw a more valid conclusion when comparing evidence for joint attention in chimpanzees with evidence from human infants which originated exclusively from intra-species communication.

Evidence from human – chimpanzee interactions

As mentioned above, Tomasello (1995, 2008) highlighted the importance of understanding the goal-directed nature of others' behaviour. There is some evidence that institutionalised chimpanzees understood something about a human experimenter's intentions. Just like the 9 months old infants in Behne et al.'s (2005) study, chimpanzees reacted differently to an experimenter who was either unwilling or unable to give them food. In addition, Call and Tomasello (1998) showed that chimpanzees distinguished between the intentional and accidental actions of a human experimenter. These results show that chimpanzees perceived the human experimenter's actions as intentional and goal-directed.

Following attention

Chimpanzees were able to follow the gaze of a human experimenter to external objects (Povinelli & Eddy 1996; Itakura & Tanaka 1998) even when the target objects were located outside of their visual field or behind barriers (Povinelli & Eddy, 1996; Tomasello, Hare & Agnetta, 1999). In addition, chimpanzees even looked back at the experimenter when they did not find anything interesting

(Bräuer, Call & Tomasello, 2005). These studies show that chimpanzees possess some advanced skills for following the gaze of a human experimenter.

Some institutionalised chimpanzees were also capable of following pointing to locate an object, but it was not spontaneous and took them some time and repeated experience to learn (Povinelli, Reaux, Bierschwale, Allain & Simon, 1997). Other institutionalised chimpanzees were unable to understand the meaning of human pointing gestures in a cooperative context altogether (Hare & Tomasello 2004). Several studies in which adult chimpanzees had to not only follow the communicative cues of the human experimenter, but also had to identify the target of this gesture, revealed that chimpanzees were unable to use human cues to find hidden food in object choice tasks (Call, 2004).

Chimpanzees performed much better, however, when a signal was embedded in a competitive rather than a cooperative context. Hare and Tomasello (2004) showed that chimpanzees found the food significantly more when the experimenter was reaching at the food rather than pointing at it. Language trained and home-raised chimpanzees displayed far better skills in understanding human pointing (performing above chance) even in cooperative contexts compared to institutionalised chimpanzees (Leavens & Racine, 2009; Lyn, Russell & Hopkins, 2010; Leavens & Bard, 2011).

Directing Attention

Leavens, Bard and Hopkins (2010) reported that approximately 50% of all tested institutionalised chimpanzees point and 100% of language-trained or home-raised chimpanzees. The majority of chimpanzee pointing is done for a human experimenter to request an out of reach food (e.g. Leavens, Hopkins & Bard, 1996; Leavens, 2004; Leavens, 2012). Chimpanzees not only point to food, but also to other objects such as tools that were required to open containers with food (e.g. Bullinger, Zimmermann, Kaminski & Tomasello, 2011). This is also called informative pointing (Tomasello et al., 2007), but it can occur without “mutual awareness” (see Chapter 1, p.22). Whilst pointing, chimpanzees displayed sensitivity to the attentional state of a communicative partner (Leavens & Hopkins 1998). In addition, more than 80% of the sub-adult chimpanzee subjects showed

gaze alternation between the experimenter and the food (Leavens, Russell & Hopkins, 2005). Chimpanzees also persisted in their communicative attempts if the experimenter did not deliver the full reward or elaborated their signals if the experimenter did not deliver the specific item they wanted. Both persistence and elaboration are important indicators for intentional communication (Leavens et al., 2005).

Declarative pointing which is characterised by a sharing motive and does not serve as a means to an end (e.g. getting food), does not occur in institutionalised chimpanzees (Tomasello, 2006) and there is very little convincing evidence that home-raised or language trained chimpanzees do (Carpenter & Liebal, 2012). Even Leavens who is one of the main proponents of the view that chimpanzees point declaratively (Leavens, 2012) admits that declarative pointing in chimpanzees is “not nearly as frequent as in typical Western human infants” (Leavens & Racine, 2009, p.256).

Joint Attention

Mutual gaze is an important component of joint attention (see Chapter 1, p.22). Carpenter et al. (1995) found that looks to the experimenter’s face during an imitation study of language-trained and institutionalised chimpanzees were significantly shorter than those of human infants (~1.1s vs. 2.1s). This shows that chimpanzees may not engage in prolonged mutual gaze, but it does not necessarily mean that they cannot share attention during the brief face to face contacts they had. In addition, language-trained chimpanzees showed more joint attentional engagement with the experimenter than institutionalised chimpanzees, but this is only based on gaze alternation and not on the occurrence of communication during face to face contact (Carpenter & Liebal, 2012). In Tomasello and Carpenter’s (2005) study, the three nursery-reared chimpanzees did not spontaneously show or give objects to humans and there was no evidence for gaze alternation or joint attention with humans (Tomasello & Carpenter, 2005).

Summary

To sum up, adult chimpanzees follow a human's gaze in quite sophisticated ways. They also point frequently for humans in order to obtain an object or food. Chimpanzee pointing is intentional (Leavens et al., 2005), and referential (Leavens et al., 1998), but there is currently no evidence that chimpanzees point to share attention (Tomasello et al., 2007). In addition, there is currently no evidence that chimpanzees engage in joint attention as defined in Chapter 1 (p.22) with human experimenters.

It is important to note that with the exception of home-raised chimpanzees, captive chimpanzees do not have as much exposure to human interaction as human infants do. As a consequence, when chimpanzees are tested with a human experimenter, they are automatically put at a disadvantage compared to human infants. Humans interact with a member of their own species for the majority of their time and they are tested by another human, whilst chimpanzees are often put into a situation in which they have to understand the signals of a different species (a human experimenter) to successfully complete a task (e.g. Povinelli et al., 1997; Tomasello & Carpenter, 2005; Herrmann, Call, Hernandez-Lloreda, Hare & Tomasello, 2007). In addition, the apparatuses and objects used in many experimental studies had been designed for its use with infants and have later been adopted and modified for being used with chimpanzees (Tomasello & Carpenter, 2005; Liszkowski et al., 2007). Finally, several of the chimpanzees who have participated in human-chimpanzee interaction studies are orphaned or removed from their mothers at an early age and thus have had a disrupted and possibly traumatic early life history, which again puts them at a disadvantage compared to the majority of human infants that they are compared to who have been raised by their mothers and had the opportunity to show normal socio-emotional development. As a consequence, these factors may have prevented chimpanzees from showing their real abilities. In order to overcome these issues and to understand how chimpanzees interact with each other, it is vital to consider evidence for joint attention skills and events from chimpanzee-chimpanzee interactions.

Evidence from chimpanzee – chimpanzee interactions

Following Attention

In addition to following the gaze of humans (see above), institutionalised chimpanzees also followed the gaze of conspecifics (Tomasello, Call & Hare, 1998).

Directing Attention

It has been observed in wild chimpanzees that if they scratch a particular body part during grooming, it is more likely that the groomer subsequently shifts his efforts to the scratched body part (Pika & Mitani, 2006). Is this evidence for a referential gesture in wild chimpanzees? Although referential gestures such as pointing for humans in captivity are accompanied by gaze alternation and attention monitoring of the pointer (Leavens & Hopkins, 1999; Leavens et al., 2005), this was not observed during directed scratching. In addition, the scratching chimpanzees might just have been itchy at that particular body part which functionally drew the attention of the groomer to this body part (local enhancement). Since there were no markers of intentional signalling reported, it cannot be concluded that directed scratching is a real self-referential gesture.

There is one example of two language trained apes pointing for each other as they were engaging in a food sharing task (Savage-Rumbaugh, 1986). It is unclear, however, whether the chimpanzees were spontaneously communicating with each other and monitoring each others' attention or whether they just followed a well-conditioned behavioural routine (Leavens & Racine, 2009). With the exception of one reported instance in bonobos (Véa & Sabater-Pi, 1998), there is no evidence for wild chimpanzees to direct others' attention by pointing; at least not with their arms (Leavens & Racine, 2009; Tomasello, 2008).

During play, wild chimpanzees draw the attention of potential playmates to themselves using objects (Hobaiter & Byrne, 2011), but there were no signs of the objects serving any other purpose than helping to initiate dyadic play. The interaction was not *about* the object unlike in human infants (Liszkowski et al., 2004).

Joint Attention

There is currently no evidence for joint attention as defined in Chapter 1 (p.22) during chimpanzee-chimpanzee interactions (Tomonaga et al, 2004; Madsen, 2010). More studies are needed to systematically investigate joint attention amongst chimpanzees.

Summary

This review highlights that there have not been enough studies conducted on chimpanzee- chimpanzee interactions to draw a meaningful conclusion about joint attention (skills) during intra-specific communication. This is especially true for wild chimpanzees.

Do chimpanzees engage in Joint Attention?

Taking all the evidence across chimp-human and chimp-chimp interactions is it possible to conclude whether chimpanzees engage in joint attention? Bard, Leavens and colleagues suggest that captive chimpanzees do engage in joint attention by following other's gaze, pointing and social referencing (e.g. Bard & Leavens 2009, Leavens & Racine, 2009; Leavens & Bard, 2011). As discussed in Chapter 1, several researchers (including ourselves) do not include these joint attention skills by themselves into their definition of true joint attention (Carpenter & Liebal, 2012). This is based on the argument that attention following and attention directing behaviours do not necessarily have to be joint (Carpenter & Liebal, 2012). Gaze following can be done unilaterally and attention directing without closing the referential triangle through "mutual awareness" (see Chapter 1, p.22). Although it is evident from the previous sections that some captive chimpanzees display some joint attention skills (e.g. Lyn et al., 2010), there is currently no evidence for actual joint attention events in chimpanzees, especially when they had little exposure to human-typical interactions. It is important to note, however, that there have been no studies to date that directly address the "knowing together" or "mutual awareness through communication" aspect of joint attention in chimpanzees and particularly during chimpanzee-chimpanzee interactions (Carpenter & Liebal, 2012).

Summary

Whilst human infants start to engage in their first instances of joint attention between 9-12 months, there is still a large controversy about whether chimpanzees engage in joint attention or not. Scientists who suggest that joint attention is uniquely human, state that the “9-month revolution” of humans and the subsequent emergence of joint attention does not occur in chimpanzee (Tomasello & Carpenter, 2005). Proponents of the existence of joint attention in chimpanzees use a more inclusive definition of joint attention, but they also point out that the presence or absence of joint attention in chimpanzees is highly dependent on the different life histories and socialisation experiences of the subjects (Bard & Leavens 2009).

I conclude that whilst some joint attention skills such as gaze alternation and pointing (Leavens et al., 2005) have been shown in human-chimpanzee interactions, there is currently no evidence for “mutual awareness that was established through communication” (p. 22) in any chimpanzees regardless of whether the social partner was a human or another chimpanzee. Since human-chimpanzee interactions put chimpanzees at a disadvantage when behaviour is compared to human-human interactions, it is important to focus on chimpanzee-chimpanzee interactions. The paucity of data on chimpanzee-chimpanzee interactions addressing this aspect of joint attention, however, makes a final conclusion about the existence of joint attention in chimpanzees impossible. Therefore research on intra-specific joint attention studies especially in an ecologically more valid setting are necessary to answer the question of whether or not chimpanzees engage in joint attention.

Joint Attention and the Social Environment

Since the joint attention skills displayed by captive chimpanzees vary considerably as a function of their rearing and socialisation histories, it is very important to take the social environment of the study groups into account when studying joint attention. In the following sections, I will review different socio-environmental contexts of humans and chimpanzees and conclude that it is important to study joint attention in wild chimpanzees and across different human cultures.

What can Evidence from Captive Chimpanzees tell us?

So far, the vast majority of joint attention studies on chimpanzees have been conducted in captivity which implies that all subjects had human contact to some extent. Although there is currently no evidence for joint attention in chimpanzees (Carpenter & Call, in press), captive chimpanzees who have been raised by humans or who had extensive human contact displayed more joint attention skills than captive chimpanzees with limited human contact (Bard & Gardner, 1996; Lyn et al., 2010; Leavens & Bard, 2011). Whilst studying captive chimpanzees gives us an idea about what this species is capable to do under certain conditions, it does not tell us how wild chimpanzees naturally behave in the environment they are best adapted to. The existence of some joint attention skills in home-raised and language trained chimpanzees only reveals their cognitive flexibility to adapt to new environmental challenges.

One such challenge is the “Referential Problem Space” (Leavens et al., 2005). Physical restraint is a characteristic of captivity that wild chimpanzees do not usually face. Leavens et al. (2005) argue that chimpanzees in the wild do not point, because they can go and get everything they want themselves. In captivity, however, chimpanzees are restrained by cages and learn to use cooperative humans as tools to obtain items out of their reach. This situation is very similar to that of human infants who face the same referential problem space until they can crawl or walk. Therefore, being exposed to the same problem, both human infants and chimpanzees come up with a similar solution: a referential gesture (i.e. pointing). This example shows the great flexibility of the chimpanzee mind, but it does not show whether pointing is an adaptive functional behaviour in the environment the chimpanzees evolved in. The absence of pointing in wild chimpanzees indicates that it is not in the natural behavioural repertoire of wild chimpanzees and therefore is not an adaptive behaviour in their socio-ecological environment. Therefore, when investigating the evolutionary pathway of a specific behaviour (e.g. joint attention), it is vital not only to consider the cognitive capacity of an animal to engage in a behaviour, but also, critically, to consider why the behaviour evolved and therefore the selective pressures that may have made the behaviour adaptive. This can only be done by investigating the behaviour of

interest in an environmental context that constitutes the best estimate of the environment the last common ancestor of chimpanzees and humans lived in. As a consequence, focussing exclusively on captive chimpanzees is not sufficient. Therefore, investigating the chimpanzees' joint attention skills and whether they engage in joint attention in their natural environment is vital to shed light on the evolution of joint attention. So far, this area of research has been neglected.

Differences between the Wild and the Captive Environment

What characterises and distinguishes the wild chimpanzees' environment from the captive chimpanzees' environment? Firstly, in the wild, chimpanzees do not interact with humans and infants grow up with their biological mothers. Orphaned captive chimpanzees may have had some traumatic experiences in their early infancy that may affect socio-emotional development (Bard & Gardner, 1996; Bard & Leavens, 2009). When orphaned chimpanzees are adopted by humans or receive extensive human care, they are exposed to human emotions and contingencies and therefore their socialisation is very different to that of mother-raised chimpanzee infants (Bard & Leavens, 2009). These chimpanzees show better skills of understanding human communication and are more motivated to tune into human-like interactions than captive chimpanzees who have been raised by their biological mothers (Gardner & Gardner, 1969; Bard & Leavens, 2009; Lyn et al., 2010).

Second, wild chimpanzees can move freely and they are not constrained by enclosure walls. This has two important consequences: (1) chimpanzees do not face the referential problem space faced by human infants and captive chimpanzees and (2) they can adopt their natural fission-fusion social system that cannot be supported by most captive enclosures. Fission-fusion behaviour relates to chimpanzees having a very fluid social organisation within a community. Chimpanzees form small groups which are called parties (Goodall, 1986), whose composition changes regularly as groups fuse and divide. This allows them to choose whom to associate with and whom to avoid. In zoos, chimpanzees are usually forced to stay as one coherent group, generally always within sight of each other and thus unable to exhibit fission-fusion behaviour. In addition, some

chimpanzees in biomedical research centres are deprived of social contact or have highly impoverished physical and/or social conditions (e.g. single / pair housed).

Other important differences between wild and captive groups include (1) in captivity the composition of the social group is often unnatural, with contraceptive implants preventing births and adult males sometimes being removed to reduce aggression. (2) Institutionalised chimpanzees do not have to forage for their food. Therefore, in captivity, chimpanzees have very different activity time-budgets to their wild counterparts. Consequently, they are able to dedicate more time to social interactions including grooming of their infants and infants may have more contact with other chimpanzees and their offspring (Kanngießler, Sueur, Riedl, Grossmann & Call, 2011) which may foster social interaction competence. These environmental differences undoubtedly lead to different early life experiences in chimpanzees which in turn may influence joint attention behaviours (Bard & Leavens 2008).

To conclude, in order to understand the evolutionary pathway of joint attention, we need to study wild chimpanzees, to reveal whether joint attention is an adaptive behaviour for chimpanzees in their natural socio-ecological environment. If we then aim to compare the natural joint attention abilities of chimpanzees to those of humans, one big question arises: which cultural group in humans should we choose? Given the impact of the social environment on developing chimpanzees, it is likely that different parenting strategies and socio-environmental factors may lead to different developmental pathways for joint attention in humans. In the next section, I will discuss the impact of the different cultural environments of humans on the development of joint attention behaviours.

Joint Attention and Human Culture

Despite few explicit cross-cultural studies examining joint attention, the ability for adults to share attention with others seems to be a very robust, universal human ability, similar to pointing. Pointing exists in all human cultures, but there is some cultural variation on how humans point. Whilst Europeans prefer to point with their index finger, other societies use whole hand pointing or prefer using their lips

to direct others' attention to an object in the environment (Kita, 2003). With regard to joint attention, the main question therefore is not so much whether joint attention exists in other cultures, but rather whether joint attention follows the same developmental patterns across cultures and whether infants of different cultures share attention in the same way.

Most studies on infant social cognition and also joint attention have been conducted in highly educated, urban, middle-class Western societies (Henrich, et al., 2010). Therefore, the ontogenetic pathway of joint attention described above refers to this "Western" context. Although many researchers generalise their findings from "Western" societies to all humans, Henrich et al. (2010) have shown that the "Western" context is rarely representative for all humans. In fact, Western societies are frequent outliers when compared with non-Western and small-scale societies. In addition to that, there is a growing body of evidence that early life experiences have a significant influence on development and our subsequent behaviour (Markus & Kitayama, 1991; Bard et al., 2005; Keller, 2007). Keller and colleagues, for example, found that cultural differences in parenting at 3 months become manifest in the children's behaviour later on (Keller, 2007). Therefore, it is absolutely essential to refrain from generalising results from Western participants to all humans.

There are several ways in which cultural differences in the social environment might be expected to influence the development of joint attention. Deák and Triesch (2006) proposed that one important factor for the development of joint attention in human infants is a structured social environment, i.e. every day interaction routines with the caregivers, such as face to face play and general care giving activities (e.g. nappy changing, feeding, bathing). These activities create a predictable context in which infants can learn contingencies that they can later generalize to other contexts. The nature of this structured social environment is highly dependent on the cultural values and parenting practises in a given society.

Different cultural parenting practices may have important consequences for the development of joint attention. First, although mutual gaze is considered to be a universal human activity, the amount of mutual gaze, varies a lot as a function of

parenting practices and cultural beliefs. For example, mother-infant dyads from Western cultures engage more in mutual gaze than African dyads (Keller, Lohaus, Kuensenmueller et al, 2004).

Second, Western mothers devote much time exclusively to their infants and frequently engage in proto-conversational face to face interactions with them (Keller, 2000). In contrast, African mothers do not dedicate as much time to exclusive play with their babies (Keller, 2007).

Third, Keller (2007) reported that US mothers already engaged with their infants in proto-joint attention interactions using objects at 3 months of age, long before the infants were able to coordinate their attention between their mother and the objects. This type of maternal object stimulation might have an accelerating effect on the development of joint attention by providing the baby with a joint attention scaffold that becomes embedded into playing routines and may later facilitate the emergence of joint attention (Bruner, 1999; Deák & Triesch, 2008). African mothers, however, engage more in body stimulation rather than in object stimulation (Keller, 2000). Therefore, joint attention skills might emerge later in relation to other abilities such as motor abilities whose development is more promoted and adaptive in the mostly rural environment of African villages (Keller, 2007).

Summary

Both chimpanzee and human infants are shaped by their social environment and consequently develop different skill sets. Investigating joint attention in wild chimpanzees enables us to reveal whether engaging in joint attention is part of the chimpanzees' natural behavioural repertoire: a vital step for understanding the evolutionary pathway for human joint attention. The considerable cultural variation of parenting practices and socio-cultural environments in humans may have important influences on the ontogenetic pathway and nature of joint attention in humans, yet this has not been systematically investigated to date. Studying joint attention in different cultures addresses this need and it may also help us understand the factors that are vital for the emergence of joint attention. If joint attention follows a similar developmental trajectory across cultures, despite

differing social environments, we can start to identify the factors that play a pivotal role in joint attention and are thus present across cultures and factors that are not necessary for the development of joint attention due to their absence in some cultures.

Concept and Approach

General Concept

In addition to the lack of consensus on a single definition for joint attention which was addressed in Chapter 1, comparative research into joint attention has been hampered by three main problems:

(1) Whilst research with captive chimpanzees can only show us their capacity to flexibly adapt to a novel social and physical environment and deal with the cognitive demands of joint attention behaviours, it cannot tell us what chimpanzees naturally do in the environment they are best adapted to. Therefore, in order to make inferences about the evolutionary pathway of joint attention, our closest living relative's natural behaviour in their species typical environment needs to be examined.

(2) Chimpanzees and human infants have been tested with different methods (i.e. inter-species vs. intra-species designs). For example, human infants were not separated by cage mesh from the experimenter and interacted with a member of their own species using human toys and human games (Carpenter et al., 1998). Chimpanzees, however, were separated from the experimenter through mesh or plexiglas, interacted with a human who was using human artefacts and tried to engage them in human games (Tomasello & Carpenter, 2005; Herrmann et al., 2007). In addition, it is important to note that many human studies were conducted in laboratories which constitutes an unusual environment with much less distraction than encountered in everyday life (Deák & Triesch, 2006). Based on all these differences, it can be argued that chimpanzees were put at a considerable disadvantage. Therefore, it is vital to compare human-human

interactions with chimpanzee-chimpanzee interactions in their everyday life environment and to use experimental stimuli that have a similar impact on humans and chimpanzees.

(3) Conclusions on species differences have been drawn without taking different socialisation histories of the chimpanzee and human participants into account. Since human and chimpanzee infants are shaped by their social environment, joint attention itself is a product of a multidimensional genetic and developmental network. Therefore, it cannot be investigated as an isolated entity. Since parenting and the social environment that may shape the development of joint attention vary across cultures, only studying Western infants may not be representative for humans as a species and may therefore make species comparisons less valid (Henrich et al., 2010). Therefore, it is vital to expand joint attention research to other cultures in order to gain a more representative view of human joint attention and critically to identify specific socio-environmental factors that do and do not influence the emergence of joint attention.

All of these three issues were addressed in the research of this PhD by adopting an original cross – species and cross – cultural approach:

(1) For the first time, joint attention was experimentally investigated in wild chimpanzees in order to find out whether chimpanzees naturally engage in joint attention in their species typical environment.

(2) The design included a species comparison in which both chimpanzees and humans interacted with familiar conspecifics in their everyday environment. That means I followed chimpanzees wherever they decided to go and visited human children at their homes. I used an experimental paradigm that could be applied with only minor modifications to both humans and chimpanzees. The experimental stimulus used was identical across all three groups: the moving red dot of a laser pointer which was salient and novel to the participants in each group. The use of the laser pointer was motivated by its successful use in previous studies investigating communication in adult captive chimpanzees (Madsen, 2010). In

addition, the experimenter who presented the laser stimulus was identical across all three groups.

(3) The design included a cross-cultural approach to examine variation in joint attention (skills) across two different cultures. In addition to the experimental investigation of joint attention, observational data on joint attention related factors in the social environment of the three study groups was collected. These data, in conjunction with the joint attention behaviours shown in the experiments, enabled us to identify factors that were and were not likely necessary for the emergence of joint attention.

Choice of study groups and participants

As mentioned above the first study group in this PhD were chimpanzees (*Pan troglodytes*). The two human study groups originated from the UK and Uganda. The British study group represents the “Western” context and the Ugandans the “non-Western” context (Henrich et al., 2010). The Western context is characterised by a modern, urban lifestyle with generally high levels of education and the non-Western context as represented by Ugandans is characterised by a rural, modest lifestyle with generally low levels of formal education. As reviewed above and described in more detail in Chapter 3, these two human cultures differ on several important dimensions.

Within the study groups, I chose to examine the behaviour of mother –offspring dyads. There are two reasons why I did this: first, previous research has shown that human mothers are very important for the development of joint attention and language (Tomasello & Farrar, 1986; Carpenter et al., 1998; Bruner, 1999). Second, in chimpanzees and humans, the emotional bond between mother-offspring dyads is very strong (Bard, 1994). Since joint attention requires a cooperative communication and chimpanzees generally have a very competitive nature (Hare & Tomasello, 2004), chimpanzee mother-offspring pairs may be more cooperative and less competitive than adults (Bard et al., 2005).

Age of offspring

The age of the human infants to be studied was carefully chosen. Since wild chimpanzees have never been observed to engage in joint attention or pointing (Tomasello, 2008; Carpenter & Call, 2011) and do not have a spoken language, we know that once human infants are pointing and speaking there is a clear species difference in behaviour. I was therefore interested in examining the fundamental basis upon which pointing and linguistic behaviours build: early joint attention. I therefore chose to focus on human infants who do not yet point or speak. Consequently, they had to be below the age of 12 months (Carpenter et al., 1998, Liszkowski et al., 2007). At the same time, I required their early joint attention skills to be as well developed as possible. First instances of joint attention including gaze alternation and communication emerge in human infants at 9 months of age and become more stable in the following months (Carpenter et al., 1998; Carpenter & Call, in press.). Therefore, the best compromise between the presence of joint attention and the infants not yet engaging in uniquely human behaviour was the age of 11 months. 11 months old infants in the Western context are able to engage in joint attention, but pointing and spoken language are still infrequent.

Since there is currently no evidence that chimpanzees engage in joint attention (as defined in this thesis), an age of emergence cannot be stated. There was therefore no theoretical rationale for choosing a specific age group in chimpanzees. In practical terms, in order to maximise the number of subjects, I decided to include all chimpanzee offspring into the study who were still dependent on the mother. This state of dependence lasts from age 0 to 12 years (Reynolds, 2005).

Additional Methodological Improvements

The big strength of this study was that it was designed to suit three different groups from the outset and it was improved through pilot studies before the final procedure was applied. Some previous research was completed with one species first and the method later adapted to another species (e.g. Tomasello & Carpenter, 2005; Liszkowski et al., 2007). In addition, two different species and two different

cultures are compared in one single study. Two of these groups have never been tested in a joint attention paradigm (Ugandans and wild chimpanzees).

Summary

To sum up, the studies conducted during this PhD focused on two human cultural groups (Ugandans and British) and wild chimpanzees. Mother-offspring dyads were chosen as the participants. The human infants were 11 months old during the study, because at this age, most typically developing Western human infants are able to engage in joint attention with others, but they are not regularly displaying behaviours (i.e. pointing and speaking) that are naturally unique to humans. Since a potential age of emergence is unknown for joint attention in chimpanzees, all dependent chimpanzee offspring were included in this study to maximise the sample size.

The research of this PhD included some significant methodological improvements over previous research in this area: all offspring grew up with their biological mothers and all mother-offspring dyads were tested in their habitual environment. Chimpanzees interacted with chimpanzees, humans interacted with humans. The overall design of this research was to attempt to trigger joint attention behaviours in all three groups in two different laser experiments and correlate the findings of the laser experiments with parameters in the social environment of the participants.

Thesis Outline

In Chapter 3, I will present the three study groups together with the socio-demographic data I collected for the Ugandan and the British study groups. In addition, I will establish that the infants of the two human groups had reached the same stage of cognitive development when they engaged in the laser experiments.

The first laser experiment, the 'Infant Only' laser experiment, will be presented in Chapter 4. In the 'Infant Only' laser experiment, a novel laser stimulus was presented to the chimpanzee, Ugandan and British offspring when the mother was nearby, but not attending to the offspring or laser stimulus. The aim of this study was to investigate whether the offspring would (1) engage in social referencing

before engaging with the novel stimulus and (2) monitor the attention of others whilst engaging with the laser. Furthermore, I investigated whether (3) the offspring attempted to communicate with conspecifics *about* the laser and whether (4) the communicative behaviours used were dyadic or triadic.

In Chapter 5, the Social laser experiment will be reported. In the Social laser experiment, the novel laser stimulus was presented to both the offspring and a social partner. In addition to investigating whether joint attention occurred between offspring and a social partner in the chimpanzee, Ugandan and British dyads, several different joint attention skills, such as gaze alternation, attention directing and attention following were examined.

In order to identify parameters of the social environment of the study participants that may explain the differences found between the three groups in the Infant Only and Social laser experiments, an observational study was conducted and is presented in Chapter 6. I established the general time budget of the offspring and the mothers of the three study groups and analysed some specific behaviours that are relevant for the development of joint attention (e.g. social activities, object play and vocalisations).

Finally, in Chapter 7, the results of the laser experiments and the observational data will be drawn together to identify factors that were and were not likely to be important in the emergence of joint attention behaviours. I will end this thesis by indicating future directions for research into joint attention.

Chapter 3 : The Study Groups

Summary

This chapter summarises the key characteristics of the three study groups: habituated wild chimpanzees, Ugandan humans and British humans. The wild chimpanzee study group is characterised by a male-dominated fission-fusion society in which offspring are dependent on their mothers until 12 years of age. Wild chimpanzees spend the majority of their time foraging and the most important social activity is grooming.

The Ugandan sample represents a rural subsistence farmer's lifestyle in which people widely lack formal education and comprehensive health care and which is characterised by a strong focus on the infants' developing into perceiving themselves as part of the community (Keller, 2002). Household sizes are big and parental investment is comparatively low (Keller, 2000).

The British sample represents Western culture that is generally characterised by a highly developed urban lifestyle with small and highly educated nuclear families who engage frequently in exclusive dyadic interaction involving regular face to face contact (Lohaus, Keller et al., 2011). Parental investment is high and the number of children born is low (Keller, 2000).

In order to control for potential differences in general development in the 11 months old Ugandan and British infants, I tested their cognitive, language and motor skills using the Bayley Scale of Infant Development III (Bayley, 2006), in addition to measuring their height, weight and head circumferences. Although Ugandan infants were shorter and lighter than British infants, the human infants did not differ in their head circumference and in their cognitive, receptive and expressive language abilities. There was a trend for the Ugandan infants' gross motor skills to be more developed than in British infants. It can be concluded that Ugandan and British infants were at a comparable developmental stage when they participated in my studies.

The Chimpanzee Study Group

General Information

Ecology

Wild chimpanzees are distributed across Equatorial Africa and their current population in the wild is estimated to be approximately 150 000 – 250 000 individuals (WWF, 2012). Chimpanzees face serious predation threat from lions (Tsukahara, 1993; Nishida et al., 2003), leopards (Boesch, 1991a) and most significantly humans. The prevalence of the predators is highly variable depending on the habitat and location of each chimpanzee population.

Chimpanzee diet mainly consists of fruits including several types of figs (McGrew, Baldwin & Tutin, 1988; Newton-Fisher, 1999; Tweheyo, Lye & Weladji, 2004). In addition, chimpanzees feed on young leaves, seeds and some terrestrial herbs (Wrangham, Conklin-Brittain & Hunt, 1998). Hunting for meat is also observed at highly variable rates across Africa with chimpanzees' main prey being arboreal monkeys and occasionally antelopes and birds (Goodall, 1986). To obtain highly nutritious foods such as ants (Goodall, 1964; Nishida, 1973; McGrew 1974), termites (McGrew et al., 1979; McGrew & Collins, 1985), honey (Gruber, Muller, Strimling, Wrangham & Zuberbühler, 2009) and nuts (Sugiyama & Koman, 1979; Boesch & Boesch, 1984; Hannah & McGrew, 1987), wild chimpanzees have frequently been observed to use tools. The presence and type of the different tool using techniques vary highly across several study sites in Africa (Whiten et al, 1999; Whiten et al, 2001) and several studies have revealed that in addition to environmental factors, cultural factors determine which tool-use technique is used to obtain food (McGrew et al., 1997; Whiten, Horner & de Waal, 2005).

Social Structure and female life history

Chimpanzees form communities that usually contain between 20 to over 100 members (Nishida & Hiraiwa-Hasegawa, 1987). Within a community, chimpanzees are relatively tolerant with each other, share the same territory and engage in social and affiliative behaviours such as grooming (Goodall, 1986). Chimpanzees are territorial and the males (and sometimes also females) patrol the community

borders on a regular basis. Upon close encounters with other chimpanzee communities, the territory is fiercely defended and chimpanzees react with fear and hostility towards outsiders. These inter-group encounters occasionally lead to lethal aggression (Goodall, 1986).

Within a community, chimpanzees live in a fission-fusion society, i.e. they usually split up into smaller travelling and foraging units and may re-unite later on. These smaller units are referred to as parties (Goodall, 1986) and this fluid organisation is characterised by constantly changing party composition (Lehmann & Boesch, 2004; Reynolds, 2005).

When females reach sexual maturity at an age of 10-11 years (Nishida, Corp et al, 2003), they usually leave their community, potentially to avoid inbreeding. The percentage of emigrating females, however, is highly variable across field sites (varying between 90% and 50%) and it was proposed that it is dependent on the number and size of the adjacent territories and communities. At Mahale, the median age for female emigration was 11 years (Nishida et al, 2003).

Chimpanzee males are philopatric and therefore do not leave their native territory (Nishida et al., 2003). Males are very gregarious and have a clear dominance hierarchy. They spend a considerable amount of time on maintaining or improving their social status within the community through dominance displays and alliance formations (Goodall, 1986). In contrast, non-oestrus females are less gregarious than males and spend most of their time either alone with their offspring or in small nursery parties with other females (Goodall, 1986). Therefore, it is much harder to decode the dominance structure of females. When females meet, however, it becomes evident that they also have a hierarchical organisation amongst themselves (Goodall, 1986). Adult males are usually dominant to all females within the community (Goodall, 1986).

The median age of chimpanzee females at their first birth was 13-15 years (Tutin, 1979) and their inter-birth intervals varied from 4.4 to 7.6 years and was therefore considerably longer than in both human groups (see below) (Goodall, 1983; Sugiyama, 1984). The mean age at weaning was 64.6 months for males and 62.3

month for female offspring (Pusey, 1983). After weaning, chimpanzee offspring still associated with their mothers and most of the time stayed within 15m of her for another 5-7 years (Pusey, 1983). Since non-human primates (and humans) in general, especially chimpanzees, have a prolonged infant and juvenile phase, chimpanzee offspring have the opportunity to acquire advanced social skills and other cultural behaviours such as food processing techniques through social learning processes (Joffe, 1997; Kaplan et al, 2000; Whiten & Erdal, 2012). Tutin (1994) also calculated how many babies a chimpanzee female can produce during an estimated lifespan of 55 years. Tutin's estimation of 7 offspring per female was higher than the observed mean number of offspring which was 3.85 (N = 26) (Nishida et al, 2003). Infant mortality in chimpanzees is high. Nishida et al. (2003) observed that 50% of infants died before weaning and only 20% reached maturity. In Bossou-Guinea, infant mortality was 18% within the first three years (Sugiyama, 1984). That corresponds to an average of 180 deaths out of 1000 births. This infant mortality rate is considerably higher than in both human groups (note, however, that infant mortality in humans is defined as deaths from birth to the first birthday).

Although chimpanzees are relatively tolerant within their community and mostly gentle with offspring (Goodall, 1986), they occasionally display fatal aggressive behaviours towards other community members (Fawcett & Muhumuza, 2000). In addition, female-led infanticide has also been observed (Townsend, Slocombe, Emery-Thompson & Zuberbühler, 2007) which may have occurred due to an increasing competition for resources amongst females. In contrast, there were several cases of orphaned infants that had been adopted by another community member (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987).

Social Behaviour and Communication

Chimpanzees engage in a variety of social behaviours with other community members. Adult males spent a considerable amount of time grooming each other. In addition to having a hygienic function, grooming also has an important social function (Dunbar, 1991). It serves to reduce tension (Terry, 1970) and strengthens social bonds with potential allies and females. Several studies show that there is a

correlation between grooming and a subsequent support in agonistic interactions (Schino, 2007) and a females' preference for copulating with long term grooming partners (Tutin, 1979).

Females have also been observed to groom each other, but at much lower frequencies and the interaction tends to be much shorter than male-male or male-female grooming. Amongst kin, grooming is very common (personal observation). Female chimpanzees spend a considerable amount of time grooming their offspring, especially the youngest. This may serve to enhance the mother-infant bond (Nishida, 1988). Grooming techniques vary across different wild chimpanzee populations resulting in different grooming "cultures" across the African continent (McGrew, Marchant, Scott & Tutin, 2001; Nishida, Mitani & Watts, 2004; Whiten et al., 1999; Whiten, 2001).

Another important social behaviour is play. During the dry season, when parties include several females with offspring, especially infants and juveniles play at high frequencies. Playing supports the offspring's motor development and agility. In addition, playing also has an important social function: it helps offspring to assess their strengths (Palagi, Cordoni & Borgognini-Tarli, 2004) and to form bonds to other kin and non-kin playmates.

Chimpanzees also share food (Goodall, 1986; de Waal, 1989, Mitani & Watts, 2001; Jaeggi & van Schaik, 2011). Active sharing, in which an individual actively offers food to another is very rare, and most instances of food sharing are, in fact, tolerated scrounging (Blurton & Jones, 1984). Adult males mainly share meat with other males or females after a successful hunt, but chimpanzee mothers also share other food items such as fruits and other plant parts with their offspring (Silk, 1978). The likelihood for a mother to share with her offspring correlated with the relative processing difficulty of the respective food item (Jaeggi & van Schaik, 2011).

Chimpanzees communicate with each other using different modalities, i.e. vocalisations, gestures and facial expressions (Goodall, 1986; Slocombe, Waller & Liebal, 2011). The chimpanzee vocal system is graded, but there are approximately

13 distinct calls (Marler & Tenaza, 1977) and chimpanzees also use call combinations (Crockford & Boesch, 2005). There is a growing body of evidence that chimpanzee vocalisations are functionally referential (Slocombe & Zuberbühler, 2005a) and they are used flexibly in different contexts (Slocombe & Zuberbühler, 2005b; Slocombe, Kaller et al., 2010). Gestural communication has been described as intentional, elaborate and flexible and more than 60 distinct gesture types have been identified in wild chimpanzees (Hobaiter & Byrne, 2011a). Gestures can be acquired during individual development and therefore, cultural variations of gestures exist between different chimpanzee communities (Whiten et al., 1999; Whiten, 2005). Chimpanzees also display facial expressions in a variety of contexts, including during affiliative (e.g. play face) and agonistic interactions (e.g. silent-bared teeth) (Goodall, 1986).

The Study Site

The data were collected on the Sonso group of wild chimpanzees inhabiting the Budongo Forest Reserve in the Masindi District of Uganda. The forest is located between 31°8 and 31°42 East and 1°35 and 1°55 North and is classified as moist, semi-deciduous tropical forest. It covers an area of 435km² which makes it the largest area of forest in Uganda (Reynolds, 2005). The study site is located at an altitude of 1100 metres and has an annual rainfall of approximately 1600mm. There are two rainy seasons from mid-March to May and from October to November and a dry season from December to February (Newton-Fisher, 1999). Having been subjected to selective logging in the past, Budongo Forest mainly consists of secondary forest (Schaab, Khayota, Eilu, & Wägele, 2010).

The Sonso study site was established in 1991 and has since been run by the Budongo Forest Project (BFP), later renamed as Budongo Conservation Field Station. BFP established a trail system of parallel north-south and east-west bisections running through the central part of the Sonso chimpanzees' home range and thereby allowing researchers to follow the chimpanzees more efficiently in the forest.

The Participants

Approximately 650 chimpanzees live in Budongo forest and they belong to the Eastern subspecies of chimpanzees (*Pan troglodytes schweinfurthii*). At the beginning of the study the Sonso community included 74 chimpanzees, 20 of which were males (10 adult males) and 54 females (24 adult females). The group was first sighted by Prof. Vernon Reynolds in 1962 and systematic habituation without provisioning started in 1990. All known members of the Sonso community have been named and given two-letter codes usually according to their maternal relations.

The adult males of the Sonso community were usually better habituated as they spent more time in the central area of their territory and were therefore easier to locate and to follow. There were some females who were very gregarious and spent much time with the males in the central part of their territory, but other females sometimes spent days or weeks on their own, only followed by their dependent offspring, and stayed in the periphery of the community home range. Therefore, the habituation level of central females were almost as high as of their male counterparts, but the habituation level of the peripheral females was considerably lower and it was much harder to follow them, especially when they were travelling on the ground. Table 3.1 shows all participants of my study.

Table 3.1: Study subjects and their birthdates (* indicated individuals who changed their age group during the study period. The chimpanzee was assigned to the age class we had more data from and subsequently only the data from the indicated age class was used). The age classes are based on Reynolds (2005).

Name of offspring	Code	Mother	Sex	Birthdates	Uncertainty	Age class
Heri	HR	Harriet	female	01/11/2009	5 days	Infant
Mbotella	MB	Melissa	male	30/12/2008	1 week	Infant
Kaspa	KP	Kigere	female	28/10/2008	exact	Infant
Kathy	KH	Kutu	female	26/07/2008	1 day	Infant

Name of offspring	Code	Mother	Sex	Birthdates	Uncertainty	Age class
Marion	MI	Mukwano	female	15/10/2007	2 weeks	Infant
Rafia	RF	Ruhara	female	29/06/2007	5 days	Infant
Kox	KX	Kewaya	female	07/02/2007	1 month	Infant
Karibu	KB	Kwera	female	09/01/2007	1 day	Infant
Sokomoko	SK	Sarine	male	01/10/2006	2 weeks	Infant
Klauce	KC	Kalemma	male	03/09/2006	2 days	Infant
James	JS	Janie	male	04/04/2006	1 month	Infant
Gorea	GR	Gladys	female	01/03/2006	4 months	Infant
Honey	HY	Harriet	female	02/10/2005	1 day	Infant*
Kasigwa	KS	Kutu	male	15/08/2003	2 weeks	Juvenile
Monika	MN	Melissa	female	22/06/2003	2 weeks	Juvenile
Night	NT	Nambi	female	06/02/2003	exact	Juvenile
Zak	ZK	Zimba	male	21/11/2002	1 day	Juvenile
Ramula	RM	Ruhara	female	06/09/2002	1 week	Juvenile
Karo	KR	Kwera	female	01/11/2001	1 day	Juvenile
Helen	HL	Harriet	female	15/02/2001	3 weeks	Juvenile
Kumi	KM	Kalema	female	17/09/2000	2 days	Subadult*
Janet	JT	Janie	female	01/10/1999	3 days	Subadult
Katia	KA	Kewaya	female	30/12/1998	exact	Subadult
Kana	KN	Kutu	female	29/10/1998	1 day	Subadult
Zig	ZG	Zimba	male	24/06/1997	2 weeks	Subadult

The final participants

Data were collected on 16/18 available mothers and 28/34 available offspring but not all individuals contributed data to each study (see Chapters 4, 5 and 6). The offspring consisted of 13 infants (9 females and 4 males), 7 juveniles (5 females and 2 males) and 5 sub adults (4 females and 1 male). Table 3.2 shows the definitions for the age classes.

Table 3.2: Chimpanzee offspring age classes as defined by Reynolds (2005) and as defined for this thesis.

Age Class	Age Range	Age class in this thesis	Sample size
Infant	0-4 years	Infant	13
Juvenile	5-9 years	Non-Infant	7
Sub adult	10-14 years (females)	Non-Infant	5
	10-15 years (males)		

Chimpanzee offspring ranged from 5 months (HR) to 163 months (ZG) of age. The chimpanzee offspring's mean age was 74.8 months (SD= 43.2 months) for the main study period in 2010/11. The participating chimpanzee offspring had an average number siblings who were still dependent on the mother of 1.2 (SD = 0.62) and three of the 25 (12%) chimpanzee offspring that were included into the final sample had no living older siblings.

The Study Period

The data for the chimpanzee study group were collected between February and May 2009 and between March 2010 and January 2011.

The Ugandan Study Group

The majority of the statistics presented for the Ugandan population originated from a census conducted in 2002. The results of this census were published by the Ugandan Bureau of Statistics (UBOS) in 2007 under the name “The 2006 Uganda Demographic and Health Survey” and were based on a sample of 8531 women aged 15-49 and 2503 men aged 15-54. There is currently a new census under way, but the results were not available before the submission of this thesis.

General Information

Uganda is a landlocked East African country with a total area of 241 038 km² (Figure 3.1). It lies on the Equator between 1° 29' South and 4° 12' North latitude and 29° 34' East and 35° 0' East longitude (UBOS, 2007).



Figure 3.1: Map of Uganda. The black arrow indicates the study area.

The climate of the country is equatorial, but moderated through its altitude. Uganda received an annual rainfall between 750mm and 2100mm that mainly occurred in two rainy seasons from March to May and from September to November (UBOS, 2007). The country's vegetation ranges from tropical rainforest (study area) to semi arid vegetation in the North.

Uganda had a population of 33.8 million in 2010 (United Nations, 2010) and is currently divided into 4 regions and 112 districts. The study population of this thesis was located in the Western region, Masindi District, Bujenje County, Budongo and Kabango Sub-counties and Nyabyeya and Kabango Parishes. The villages of the Ugandan study group were located at an altitude of approximately 1100 metres, had an average annual rainfall of 1600 mm and an average temperature of 27^o Celsius during the day (Newton-Fisher, 1999). According to the sub-national projections of the Uganda Bureau of Statistics (2006), the total population of Masindi district in 2010 was 602100, in Kabango parish 16700 and in Nyabyeya parish 8700. The majority of the Ugandan population were farmers, especially in rural areas (UBOS, 2007). The Ugandan population is composed of a highly diverse ethnic population originating from 56 different tribes (UBOS, 2007).

Ugandan households were composed of an average of 5.1 persons in rural areas. Ugandans live in a male dominated society with the husband usually being the head of the family and in control of most of the decisions in the household (UBOS, 2007). For 68.9% of the rural population the drinking water source was more than 30min (roundtrip) away from the home and only 62.7% of all rural households had access to an improved water source (e.g. borehole). The main people to collect water were females above 15 years (72.3%). 91.3% of rural households did not have an improved latrine (e.g. pit latrine with slab) and only 3% of the rural population had access to electricity. 84.8% of rural households had floors made of earth, sand or cow dung and 44.3% only had one room for all household members to sleep in (UBOS, 2007).

Uganda had a very high fertility rate with an average of 7.3 births per woman in the Western region (UBOS, 2007). Child bearing started very early in Ugandan women, especially in those from rural areas with a median age of 18.5 years at

their first birth. Child bearing is almost universal in Uganda. Only 2 in 10 women in the age group of 20-24 had never given birth. In rural areas 62.2% of the births were carried out at home. The median inter-birth-interval in rural areas was 29.6 months (UBOS, 2007). Uganda had a high infant mortality rate of 88 in 1000 births for rural areas and 76 in 1000 births for the Western region. Infant mortality was strongly associated with their mother's education. Infants of mothers with secondary education were less likely to die within the first year than infants of mothers with no education (UBOS, 2007). Breastfeeding was nearly universal in Uganda with 98% of all babies having been breastfed at some point. Weaning took place after a median of 20.6 months in rural areas (UBOS, 2007). Looking at the median for inter-birth intervals it becomes apparent that in most cases the reason for weaning was pregnancy with the next child. Bottle feeding is not common in Uganda (UBOS, 2007) and I only observed it in one family.

Although Uganda had introduced universal primary education in 1999 and universal secondary education in 2007, some children in rural areas did not complete the seven years of primary school (UBOS, 2007). In addition, under- and malnutrition still remains a serious problem in Uganda. 40% of rural children under the age of 5 are stunted (more than 2 standard deviations below the mean height-for-age ratio), 17% underweight and 74% suffer from anaemia (UBOS, 2007).

The Study Site

The majority of the Ugandan mother-infants pairs lived in two villages bordering the Budongo Forest: Nyakafunjo and Nyabyeya. One participant lived in Kabango and another in Nyabyegoma. Nyakafunjo, Nyabyeya and Nyabyegoma are part of the Nyabyeya parish and the sub-county Budongo and all villages were located in Masindi District. Nyabyeya parish consisted of little villages and the local population were mainly subsistence farmers.

The Participants

Recruitment

The participants were recruited through a local field assistant, Ms. Helen Biroch (HB), who registered willing participants as closely as possible to their babies' birthdates. This was done to increase the accuracy of their ages at the time of observation, because most mothers who participated in the pilot study did not know the exact birthdates of their babies. In total, Helen registered more than 150 mother-infant dyads. The final participants were selected according to their ages, sex and the location of their compounds. Busy areas with many people passing through the compound were avoided to minimise disturbances during the experiments.

Health monitoring visits

In order to monitor the infants' health before the data collection, Helen conducted one-monthly health monitoring visits for at least 3 months prior to the data collection period at 11 months. Since the chimpanzee data collection was also conducted during the same period as for the Ugandan infants, only two to three infants could be visited by the author each month for the main experimental sessions. For each month, the infants with the least health difficulties were chosen to participate in the study to reduce the potential confound that Ugandan infants were less healthy than British infants. Common reasons for exclusion were repeated illness such as fever or diarrhoea and a general lack of alertness in combination with external signs of illnesses.

Exclusions and the final participants

The babies were 11 months old (defined as between 315 and 355 days) at the time of the study. During the whole study period, a total of 24 Ugandan infants and their mothers participated in at least some part of the study. One baby had to be excluded completely, because her mother moved away during the study period. From 23 Ugandan families, I obtained demographic, socio-economic and socio-cultural data using questionnaires. The same 23 mother-infant dyads also participated in the time budget study (see Chapter 6). Two dyads, however, had to

be excluded later, because after applying a stricter age criterion, one baby was too young (313 days) and another one too old (379 days). A third dyad had to be excluded, because of a lack of data (see Chapter 6, p.218). The final sample for the time budget study (Chapter 6), therefore, consisted of 8 girls and 12 boys and their mothers.

Since the data collection for the experimental parts (i.e. Laser Experiments and Bayley's Scale for Infant Development, Weighing and Measuring) were very time consuming, only 12 Ugandan infants participated in the experimental part of the study (Bayley's Scale for Infant Development below in Chapter 3, Infant Only Laser Experiment, Chapter 4; Social Laser Experiment, Chapter 5). The sample for the experimental parts of the study consisted of 7 boys and 5 girls. The Ugandan infants had an average of 2.2 (SD = 2.2) siblings. The average age of all participating mothers was 26.64 years (SD=6.69, N= 16, 4 mothers did not know their ages) at the time of data collection.

All participants grew up at least bilingually (see comparison between the Ugandan and British study group below). Ugandan infants in the study area usually learnt their mothers' language first (e.g. Alur, Lunyoro, Lugbara), followed by local Swahili (a simplified version of the modern Swahili spoken in Kenya and Tanzania) and possibly the language of their fathers should it differ from their mother's language. In general, when Ugandan children in the study area entered school, they were conversational in at least two languages (Kaller, personal observation). Fluent English was usually only spoken by individuals who finished primary education (7 years).

The Study Period

The data for the Ugandan study group were collected between April 2010 and January 2011.

The British Study Group

The majority of the data for the British study group originated from a Census conducted in 2001 by the UK Office of National Statistics (ONS) and its subsequent analyses. The Census 2001 was conducted with the entire population in the UK which was 58.8 million in 2001 (ONS, 2001). There was a new census conducted in 2011, but the results were not yet available before the submission of this thesis.

General Information

The United Kingdom is a Western European country and is composed of four different nations: England, Scotland, Wales, and Northern Ireland (Figure 3.2). England together with Wales and Scotland form an island in the North Sea. The total area of the UK is 243000 km² and it lies 54°00' North and 2°00' West.



Figure 3.2: Map of the United Kingdom.

Being located in the temperate zone, the UK has four seasons: spring, summer, autumn and winter. Due to its maritime climate and the North Atlantic Current, winters and summers are characterised by mild temperatures and high humidity with a mean annual temperature of 9.6^o Celsius in 2011. The UK received an average annual rainfall of 1166mm which was almost evenly distributed over the year (Metoffice UK, 2011). The majority of the countries' surface is used for meadows and pastures (46%), 30% are arable and 10% are forests and woodlands.

English was the main spoken language in the UK and the average household size in England and Wales was 2.4 persons (ONS, 2001). Compared to Uganda, England is ethnically much more homogenous with the following distribution among ethnic groups: 94.9% White British, 2.4% Other White and 2.7% were from a different origin (ONS, 2001). The UK can be described as a gender equal society and household decisions are mainly shared between men and women.

The total fertility rate for England was 1.96 children per women (ONS, 2009) and the average age of the mothers at childbirth was 29.4 years and 30.4 years at first birth (ONS, 2009). The majority of women in England and Wales gave birth in a hospital (ONS, 2009). The infant mortality for the UK was 4.3 per 1000 live births in 2010 and was therefore considerably lower than in Uganda (ONS, 2010).

The Study Site

The study population for this research was recruited from different parts of England. Seventeen participants lived in York, three lived in Leeds, two in London and one in Durham. All participants lived in urban or sub-urban areas.

The Participants

Recruitment

The twelve participants for the experiments were recruited through an existing participant pool of the Department of Linguistics at York University. Mothers whose infants participated in a linguistic study at their lab were asked, if they were interested in participating in another study. If they agreed, I obtained their phone

number and contacted them. The response rate was very good and the families very cooperative. On the phone, I explained the study to the mother and arranged two visits to her home that were scheduled for 2 hours each. The visit was confirmed the day before to make sure the infant was healthy at the day of the visit.

The eleven participants of the time budget study were recruited through friends and colleagues of the Psychology Department at the University of York. The visits were arranged and the data were collected by two research assistants (Kate Brook and Stephanie Burchill) who were trained in the same method that my Ugandan research assistant HB applied.

Exclusions and the final participants

A total number of 23 families participated in some part of the research for this thesis. Twelve mother infant dyads participated in the experimental part of the study (Laser experiments and Bayley's Scale, Weighing and Measuring, this Chapter) and eleven dyads participated in the time budget study (Chapter 6). This means that in contrast to the Ugandan study group, the families who participated in the laser experiments were different from those who participated in the time budget study. All 23 mothers completed the questionnaires. All twelve participants of the experimental part of the study lived in or near York, 7 were male and 5 were female (exactly as in the Ugandan study group). The participants for the time budget study lived in different parts of England, 6 were males and 5 were females. None of the participants had to be excluded from the study.

Study Period

The data collection for the experimental part started in December 2009 and was completed in March 2010. For the time budget study (Chapter 6), the data collection period started in April 2011 and ended in January 2012.

Comparison of the British and Ugandan study groups

Comparison of socio-economic, health, educational and cultural parameters between the two study groups

Introduction

In order to systematically investigate the differences and similarities between the Ugandan and British study group, I designed a questionnaire about the participants' living arrangements, the infants' habits, the mothers' and fathers' education and socio-economic background. Since Ugandan infants were exposed to a large variety of health hazards, additional regular health monitoring visits were conducted once a month for at least three months prior to the study at 11 months as mentioned above. It was not possible to visit the British participants in the months before the study, but the mother was asked whether a serious illness or injury occurred before the beginning of the data collection. No serious illness was reported for any of the British participants.

Methods

The questionnaire covered different aspects of the family background: (a) living and sleeping arrangements, (b) demographic data (e.g. number of siblings, age of mother, education of parents, ethnic background etc.), (c) feeding habits, (d) habits of baby (e.g. what did he play with yesterday), (e) languages spoken with the baby. The health monitoring questionnaire included questions about illnesses (e.g. fever, vomiting, diarrhoea, rashes, etc.) and injuries (e.g. falls from height, animal bites, cuts and scratches). The selection of items and the composition of both questionnaires were based on a comprehensive study of infancy in Uganda conducted by Ainsworth (1967).

The questionnaire was originally composed in English and tested on 16 mothers during the pilot phase in Uganda 2009. During this phase, Helen translated the questions live into either Swahili or Alur depending on the preference of the mothers. After the pilot study, the questionnaire was refined and finally applied to the British mothers. The questionnaire was sent to the mothers prior to the study and the mothers answered the questions whenever they were free to do so. I asked

them to fill in the questionnaire as closely as possible to their infant's 11 month anniversary.

For the Ugandan participants, I, together with a local field assistant, Monday Gideon Mbotella, who was fluent in English and grew up in the study area, translated the English version of the questionnaire into the local Swahili spoken by most people in the study area. Rather than adhering to correct grammar, we made sure that we used the expressions that the majority of the mothers would understand. After translating, I asked my field assistant Helen to back-translate the questionnaire into English and together with a local veterinarian (Dr. Tonny Kidega) who possessed an excellent understanding of English and Alur (the mother tongue of Helen) and a local lady who was a mother to four children (Mrs. Sarah Friday), we discussed the exact intended meaning of each question.

Before the questionnaire was administered, we explained to the mothers that she would not be judged on her answers. If the mothers did not understand the question as it was written on the sheet, Helen explained the meaning of the question in her own words. As explained above, the study area is highly heterogeneous in terms of tribes and languages and different families may use different expressions for the same concept.

For the families who also participated in the empirical part of the study, the questionnaire was completed during one of the two visits by reading out each question to the mother. For families who participated only in the time budget study (Chapter 6), the questionnaires were administered on a visit after the data collection during which I distributed the presents and thanked the mothers for their participation. Since I was unable to visit all families in person, Helen conducted 4 questionnaire-interviews on her own. After the data collection, the answers were entered into an excel file and means/medians for quantitative data were calculated.

The health monitoring visits started as soon as possible after registration, but at the latest they commenced three months before the 11th anniversary of the infant. After obtaining consent from the mothers, Helen visited the infants' families

spontaneously, without appointment, once a month. Any illness or injury that the mothers could recall since the last visit or since birth during the first visit were recorded on a data sheet.

Results

Family Background

The most important comparative findings are summarised in Table 3.3.

Table 3.3: Background information for the participating British and Ugandan infants and their families.

	Ugandans (N = 23)	British (N = 23)
Area inhabited	Rural	Sub-urban or urban
Employment of parents	Mainly rural subsistence farmers	Mainly employed or self-employed
Housing conditions	Mainly mud houses with grass thatched roofs (4 families lived in a brick house with iron sheets), latrines and water source outside the house	Permanent structures with electricity, heating, flush toilet and running water inside the house
Household size (excluding infant)	4.7 (SD = 2.6)	2.7 (SD = 1.0)
Most prevalent ethnic group	Alur	White British
Percentage of infants raised multilingually	100	8.7
Mean number of years of schooling for mothers	4.4 (SD = 3.6)	11.91 (SD = 0.29)

	Ugandans (N = 23)	British (N = 23)
Mean number of years of schooling for fathers	6.9 (SD = 3.7), N = 20	11.78 (SD = 0.52)
Mean interval after birth of infant before resuming work (months) for mothers	1.8 (SD = 1.1)	8.3 (SD = 1.28)
Percentage of mothers who were married	91.3	91.3
Percentage of mothers who cohabited with the father of the infant	91.3	95.7
Percentage of participants being the first born	30	60
Mean number of siblings	2.2 (SD = 2.2)	0.56 (SD = 0.95)
Median age of mothers at first birth (years)	18 (N = 17)	31
Percentage of mothers who had given birth before the age of 25	100	13
Percentage of infants sleeping in the same bed as mother	100	0

	Ugandans (N = 23)	British (N = 23)
Percentage of infants still breastfed at the time of the study	100	47.9
Main type of object infants played with	Any object found in the compound, e.g. sticks, bottle tops, stones, self-made banana fibre balls	Bright and colourful manufactured toys, designed for infant use

The Ugandan study group originated from a remote, rural area bordering Budongo forest. Housing conditions were simple and food was mainly obtained from people's own fields. Mothers resumed their household duties (e.g. fetching water, cleaning, collecting firewood and digging) after birth much earlier than British mothers returned to their workplace (see Table 3.3). The education of the participants' parents rarely exceeded primary education. Six Ugandan mothers never visited school and only four mothers attended secondary school. The education of Ugandan men was higher than that of women, but only 7 out of 23 fathers attended secondary school.

The British study group was comparatively wealthy and all participating mothers were either employed, self-employed or on maternity leave at the time of the study. Their housing conditions were more comfortable with adequate sanitation and water supply inside the house. There was little difference between the educational level of mothers and fathers, but both of them attended school considerably longer than their Ugandan counterparts (see Table 3.3).

The Ugandan study area was characterised by a high diversity of ethnic groups. The mothers of the participants originated from 7 different tribes and their fathers from 8 different tribes. In mothers as well as fathers, the Alur who originated from West Nile were the most strongly represented ethnic group (mothers = 57% and fathers 39%) in my study group. Intermarriage between tribes was common

(47.8%). The Ugandan infants were exposed to an average of 2.30 (SD = 0.47) languages. As already indicated above, babies were born into a multilingual environment and speak at least two languages fluently when they enter school (personal observation).

The British study group was relatively homogenous in terms of their ethnic composition. The majority of mothers and fathers were White British (74% and 83% respectively). 17% of the infants' mothers and 17% of the fathers were from a different White origin. Only 9% of the mothers and none of the fathers were of a mixed origin. All of the participating mothers, however, grew up in either the UK or another developed country. The main language spoken with the infants was English and only two infants were exposed to another language (Table 3.3).

The size of the Ugandan households was considerably bigger than the British households. This difference is mirrored by the Ugandan participants having more siblings than British infants. The percentage of Ugandan first borns in this study was much higher (30%) than in the Ugandan population, but it was still impossible to match it to the high percentage of first borns in the British sample (60%). All Ugandan mothers who cohabited with the father of the participant were also married with him, because in Ugandan culture, living together as an unmarried couple is not permitted. It was common, however, for Ugandan men to marry more than one wife. In the British, a small percentage of parents cohabited, but were not yet married (see Table 3.3). At the age of 25, all Ugandan mothers had already given birth at least once, whereas British mothers had their first birth at a much higher age (see Table 3.3).

All 23 Ugandan infants slept in one bed with their mothers (Table 3.3). In order to find out whether this sleeping arrangement was necessitated by the lack of space in Ugandan houses or whether it reflects a real cultural conviction, I asked the mothers if they would still sleep in the bed with their babies even if they had a big house with many rooms. 82.6% of the mothers answered that they would always want to sleep together with their babies. When I asked them for the reason most of them replied that it is safer, because otherwise a "wizard" might catch them at night and kill them. This is only one example of the very predominant superstitious

beliefs in the study area. In British families it was very uncommon for an 11 month old baby to sleep together with their mother in one bed (see Table 3.3). All of the 23 Ugandan participating infants were still breastfed at the time of the data collection whereas half of the British mothers had already stopped breastfeeding their babies.

Ugandan infants mainly played with simple objects found in the compound. Only one participant had a high variety of manufactured toys. Ugandan infants were observed to play with sticks, stones, sand, leaves, bottles and bottle tops, self-made balls from banana fibre and even knives and bush knives (pangas). Squeak toys were found in the villages, but they were rare. Toddlers and older children showed much imagination whilst playing with these simple self-made toys (personal observation). In contrast, British infants had a variety of brightly coloured toys that were specifically designed to stimulate the infants' motor and cognitive development.

Health monitoring visits

According to the results of the health monitoring visits, all 23 Ugandan infants with the exception of one were reported to have had Malaria at some point before their 11 months anniversary. In addition, due to the poor nutritional state Ugandan children in general (UBOS, 2007) and the exposure to diseases such as Malaria that are very weakening, it was possible that 11 month old Ugandan infants may have differed in their overall developmental from generally well-nourished and healthy 11 month old British infants. Therefore, it could be argued that potential cross cultural differences found in this thesis may be attributed to the differential cognitive development between Ugandan and British infants at 11 months old. In order to control for this potential confound, I conducted the Bayley Scale for Infant Development III (Bayley, 2006) in addition to weighing infants and measuring the height and head circumference of the infants in both cultural groups.

Comparison of development – Weighing, Measuring and the Bayley Scale for Infant Development III

Introduction

As mentioned above, national statistics indicate that Ugandan infants have a higher mortality rate than British infants and there tended to be a high percentage of Ugandan children who were stunted, underweight and anaemic (UBOS, 2007). Therefore, it was an essential part of this research to investigate a priori whether 11 month old infants of both groups had developed to the same level. In order to test that, I weighed and measured the height and head circumference of 12 participants of each human group and completed four of the five scales of the Bayley Scale for Infant and Toddler Development (Bayley, 2006): (1) Cognitive, (2) Receptive Communication, (3) Expressive Communication, and (4) Gross Motor Skills. All items that were administered to the infants are listed in the Appendix.

Methods

The participants for the developmental comparison were 12 Ugandan infants and 12 British infants who participated in the two experimental visits and in all parts of my PhD data collection.

Weighing and Measuring

During one of the two experimental visits to the participating infant, the infant's weight, height and head circumference was measured. For measuring the weight in Ugandans, the infant was put in a bag-like cloth that had two holes at the bottom for the infants' legs. The handles of the bag were attached to a hook at the end of a portable suspension scale. The scale was securely tied with a rope to one of the branches of a tree in the family compound or a stable beam of their house. In the British, if the infant was weighed between the experimental visits or not more than one week before, the data of the health centre were used. Otherwise, an ordinary weighing scale that I carried to the families' homes was used.

The heights of the infants were obtained by either measuring their height if they were able to stand or their body length, if they were unable to. The measurement

was repeated once, if the infants cooperated. If the British mothers had a recent measurement for their infant's height available, this measurement was used.

The head circumference was measured by using a flexible tape measure. Whilst the infant was keeping still, the tape measure was placed around the widest point of the infant's head. The measuring was repeated twice and the largest number was later used for analysis. The order in which the three measurements were taking varied in dependence on the infants' cooperation.

The Bayley Scale for Infant Development

The Bayley's Scale for Infant Development was split over the two visits to the infant's home and lasted between 20 min to 75 min (including breaks) during each visit. In British infants, the testing took a shorter period of time, because of less distraction in the environment. In both groups, however, items were only administered when the infant was attentive to the experimenter. In all cases, the experimental parts of the Bayley Scale were applied after the laser experiment of each visit and both, the infant and the mother, were given as many breaks as they desired. In the British infants, I performed the role as the experimenter whilst the research assistant (Vicki West or Shane Ford) distracted and played with siblings (if any) in another room.

Before I set out to test infants, I familiarised myself with the Bayley's manual and the test items that are listed in detail in the Appendix, conducted several training sessions with my research assistants and three pilot trials with infants of different ages were conducted (6 months, 18 months and 22 months). Although it is always preferable to keep the experimenter consistent across study groups, I decided to train my Ugandan field assistant in the role of the experimenter for those items that required the experimenter's interaction with the infant (mainly Cognitive sub-scale, see Appendix), because Ugandan infants were used to interact with other Ugandans and I was not sufficiently familiar with the Ugandan interaction style with infants. In addition, I did not speak the local languages as fluently as required for testing 11 month old infants. Being multilingual, my field assistant Helen was able to talk to the infants in the same languages as their mothers. Since it was the

main aim of the study to have infants behave and react in a natural way, this was best achieved with Helen as the experimenter for the Ugandan infants.

Since the Ugandan part of this study was conducted after finishing the British part, I had already gained experience in the different ways the infants may react or potential difficulties that may arise whilst applying the tests. Therefore, I trained Helen to conduct the tests in as a similar way to mine as possible. In addition, I showed Helen the administration of the items from several British children and she completed two full-day training sessions in which all items' administration were practised until I was happy with her execution. During the actual visit, I was seated behind Helen and gave further instructions whenever necessary.

Some items of the Bayley Scale needed to be administered on a table. In the British infants we used whatever table the families had available (e.g. kitchen table, high chair table). Ugandans families, however, did not all possess a table in their homes, so we carried a portable table with us that could easily be installed and uninstalled at any location in the family compound.

The Bayley Scale for Infant Development provided toys to administer the items (see 'object used' –column in the Appendix). Since the test battery was designed for infants from Western backgrounds, some items would not have been known by Ugandan infants and therefore had to be replaced. If the toys that were used for Ugandan infants differed from toys that were used for British infants, I listed them separately in the 'object used'- column of the Appendix.

In both groups, I scored the reaction of the infants live, but in order to be able to double-check ambiguous situations, the cognitive part of the Bayley's sessions were consistently recorded on video. The video camera was positioned on a tripod to capture the infants' behaviours during interactions on the table. Items that were administered in other places of the house/compound were filmed by the author whenever possible. When the infant spontaneously displayed a behaviour to be scored in the Bayley Scale (e.g. gross motor skills or expressive communication during a testing break), however, these behaviours could not be filmed, but were scored live.

In order to allow flexibility depending on the infant's concentration and interest, the items were not necessarily administered in the order they appear in the manual. Since there were several parts of my study to be conducted during any one visit, the administration of the Bayley scale was distributed over two visits. The average number of days between the two visits were 9 days (SD = 3.0) in the British infants and 10 days (SD = 2.2) in the Ugandan infants. The mean age during the first visit was 333.3 days (SD = 6.8) in British and 332.4 days (SD = 4.5) in Ugandan infants. During the second visit, British infants had an average age of 342.1 days (SD = 6.8) and Ugandan infants were an average of 342.0 days (SD = 5.0) old.

Results

Weighing and Measuring

The physical development of Ugandan and British infants was examined by measuring the weight, height and head circumference of the participating infants. Table 3.4 shows the results for these measures and establishes that the Ugandan and British infants did not differ with regard to their age on the day of weighing and measuring.

Table 3.4: Results for weighing and measuring of the Ugandan and British infants at 11 months of age. The right column shows the statistical comparison of Ugandan and British infants.

	Ugandans (N =12)	British (N = 12)	Independent sample t-tests
Mean age at weighing and measuring (days)	337.9 SD = 6.3	342.3 SD = 6.8	t (22) = 1.62, p = .120
Mean weight (kg)	7.99 SD = 0.76	10.46 SD = 1.27	t (22) = 5.77, p < .001
Mean height (cm)	67.44 SD = 3.08	72.42 SD = 2.41	t (22) = 4.14, p < .001
Mean head circumference (cm)	46.46 SD = 1.57	47.52 SD = 0.92	t (22) = 1.51, p = .146

On average, British infants were more than 2 kg heavier than Ugandans. An independent samples t-test confirmed that British infants weighed significantly more than Ugandan infants. In addition, British infants were also significantly taller than Ugandan infants. Interestingly, the head circumferences of the two human groups, however, did not statistically differ. Although Ugandan infants were lighter and shorter than British infants, their head circumference was similar to the British. This may indicate that Ugandan infants invested the little nutritional energy they had available primarily into their brain growth. Therefore, it may be possible that the slower physical development of Ugandan infants did not affect their cognitive development.

The Bayley Scale for Infant Development

Based on the variable cooperativeness and the limited attention span of the infants, not all items could be completed in some infants (0-3 items per infant). There was, however, no particular bias in the items that were missed out across participants and the scales are relatively resilient to a few component items not

being completed. The results of the Bayley Scale for Infant Development show that, the two cultures were comparable in terms of their cognitive development, despite the physical differences in growth patterns (Figure 3.3).

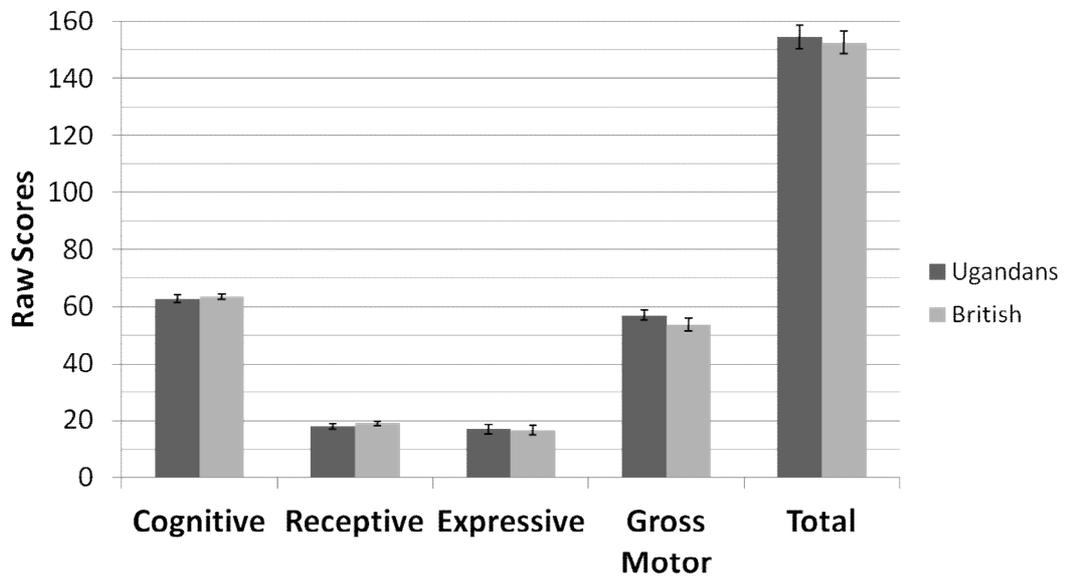


Figure 3.3: Mean raw scores for the four measured scales of the Bayley Scale for Infant Development and the total raw score for all four scales for Ugandan and British infants. The error bars represent 1 standard deviation from the mean raw score.

Independent t-tests revealed that there was no significant difference between Ugandan and British infants with respect to their raw scores on the cognitive ($t(22) = .931, p = .362$), receptive communication ($t(22) = 1.44, p = .164$) and expressive communication ($t(22) = -.329, p = .745$) scales. On the gross motor scale, however, there was a trend for Ugandan infants to score higher than British infants ($t(22) = -2.07, p = .051$).

Discussion

In contrast to the assumption that Ugandan infants may have some degree of developmental delay associated with high exposure to disease, basic sanitary conditions and nutritional state, they scored equally high compared to the British infants on three of the four examined scales and even show a slightly more advanced gross motor development than the British infants. Therefore, it will be assumed for the remainder of this thesis that Ugandan and British infants were at the same developmental level and any potential differences in the joint attention

laser experiments cannot be attributed to developmental delay in the Ugandan children due to malnutrition or serious illness (e.g. malaria).

General discussion

In some respects the environment of the chimpanzees and Ugandans was more similar than between the two human groups. Since joint attention includes an external object, it is important to highlight the big difference between Ugandan and British infants in terms of the objects they played with. Interestingly, the objects Ugandans used for play were similar to some of the objects that chimpanzee offspring played with, e.g. sticks and leaves (personal observation). As mentioned above, British infants had very salient toys available that were designed to stimulate them (e.g. toys that make sounds) and support their cognitive (e.g. puzzles) and motor development (e.g. walker). These striking cultural differences with regard to the object type infants played with were not reflected in the scores of the Bayley Scale for Infant Development. It is still possible, however, that the differential toys use has an influence on the development of joint attention. Alternatively, it may be argued that it is the quality and quantity of object stimulation by the mother that supports the development of joint attention and not the quality of the toy itself.

In Chapter 6, it was examined how much the infants engaged with objects during play and who their main playing partner was. In addition, the family size of the chimpanzees and the Ugandans was larger than the British and they had more siblings than the British infants. This could result in different amounts of contact with other children and opportunities for play which may then influence the development of joint attention. The infants' tendency to try and engage others in their play with an external stimulus and their interaction with a social partner during triadic play was examined in Chapters 4 and 5.

Conclusion

This chapter revealed that although Ugandans and the British were members of the same species, they had highly variable environmental, socio-economic and cultural backgrounds. Some parameters of the Ugandan's environment (e.g. family size, number of siblings, toys available) were arguably more similar to those of the chimpanzees, rather than the British. The following empirical chapters will reveal whether these intra-species variations and inter-species similarities correlated with the performance in the joint attention laser experiments and whether they were reflected in the time budgets of the three study groups.

Chapter 4 : The Infant Only Laser Experiment

Summary

The Infant Only experiment was designed to investigate the chimpanzee, Ugandan and British offspring's ability and motivation to coordinate their attention between a novel stimulus and their mothers in their natural environment without giving the mothers the opportunity to scaffold the behaviour of the offspring. To this end, whilst the mothers were inattentive to the offspring, the moving dot of a laser pointer was projected into the visual field of the offspring only and their joint attention skills (i.e. social referencing and triadic attention getters) analysed.

The results of the Infant Only laser experiment indicate that there was little evidence for social referencing in the offspring of the three study groups upon encounter with the novel laser stimulus. The offspring of all three groups looked to their partners at equally low rates during their engagement with the laser stimulus. Although British and Ugandan infants may have attempted to communicate with others by approaching them and, in the British, by vocalising during laser engagement, these communicative behaviours were not conditional on the presence of the laser and may therefore not have been *about* the laser.

It can be concluded that the offspring of the three groups mainly engaged with the laser individualistically and showed little evidence for coordinating their attention between the laser and their mothers which may indicate that the mothers' scaffolding may be an essential component of early joint attention interactions.

Introduction

Joint attention, the mutual awareness of having attended to an external object or event, is established through communication (Chapter 1, p.22). Although a joint attention event is, per definition, an interaction, the participants of such a joint attention interaction require some basic individual skills to engage in joint attention. First, they require the ability to coordinate their attention between an object and a social partner and, in addition, the motivation to share attention with each other (Carpenter & Liebal, 2012).

From nine months old, human infants begin to coordinate their attention between objects of interest and a social partner during play (Carpenter et al., 1998) and to engage in social referencing which is defined as the seeking of information from another individual's reaction to a particular object or event in the environment by monitoring his reaction in relation to this object (Campos & Sternberg, 1981, Russell et al., 1997). In addition, 10-11 months old infants show objects to others (Carpenter et al., 1998) and begin to engage in mutual gaze with a social partner *about* an object of interest (Carpenter & Call, in press). The pointing gesture emerges in human infants from 12 months (Carpenter et al., 1998).

Nursery reared chimpanzee infants also engaged in social referencing with a human caregiver from 14 months, but younger individuals have not been tested (Russell et al., 1997). Several captive chimpanzees point (Leavens et al., 2010) and most of them alternated their gaze between object and a human experimenter whilst pointing (Leavens et al., 2005). These studies show that captive chimpanzees are able to coordinate their attention between objects and humans. There is currently no evidence, however, that chimpanzees have the motivation to share attention with humans (Carpenter & Call, in press.). Most instances of captive chimpanzees' pointing are done with the motive of obtaining food. In addition, there is no evidence that captive chimpanzees show objects or point declaratively to share attention or interest with humans (Carpenter & Call, in press.).

As reviewed in Chapter 2, most studies on chimpanzee joint attention skills have been conducted with human experimenters in a species-untypical environment (e.g. Bard & Gardner, 1996; Tomasello & Carpenter, 2005). Such studies that require inter-species communication put chimpanzees at a disadvantage compared to the human infants that they are contrasted with. Unfortunately, there are few studies that have addressed joint attention skills in chimpanzee-chimpanzee interactions. Tomonaga et al. (2004) reported two chimpanzee infants engaging in social referencing with their mothers, but the infants did not show any motivation to share attention with their mothers. In addition, with only one exception from one bonobo (Véa & Sabater-Pi, 1998), pointing has never been observed in wild chimpanzees (Tomasello, 2008). In order to provide ecologically valid and directly comparable results across species, this chapter focused on intra-species communication with familiar conspecifics in the species' typical environment.

Since it has been suggested that Western human mothers scaffold their infants' early joint attention interactions (Deák & Triesch, 2006), the infants' individual joint attention skills can be better investigated in the absence of the mothers' (or other social partners') scaffolding. This chapter aimed at revealing the individual joint attention skills of the offspring only. In order to trigger potentially triadic behaviours of the offspring, a novel laser stimulus was projected into the visual field of the offspring only, whilst their mothers were inattentive, and the offspring's resulting behaviours analysed. Specifically, the offspring's social referencing and attention getters about the laser stimulus were compared between wild chimpanzee offspring and 11 months old Ugandan and British infants to reveal potential species differences and cultural variations in these joint attention skills.

In the following sections, I will introduce the main questions of this chapter and state what my hypotheses for each question were:

Social Referencing

Based on the studies reviewed above, 11 months old human infants and chimpanzee offspring were predicted to be able to engage in social referencing. In this experiment, the mothers were not given the opportunity to interact with the

laser. Therefore, the offspring were unable to learn from their mothers' reaction to the laser. As a consequence, I could only measure the offspring's tendency to seek information from the mother by analysing their looking behaviour to the mothers before physically engaging with the laser.

In Western humans, social referencing is often examined with stimuli that provoke uncertainty and are therefore suitable to trigger social referencing (e.g. Zaratany & Lamb, 1985). It was difficult to predict, however, whether the laser stimulus would fulfil the function of provoking uncertainty in the offspring of three groups. Since chimpanzees and Ugandan infants were less exposed and less habituated to flashing lights in their environment compared to British infants, I therefore predicted that British infants would engage less in social referencing than chimpanzee and Ugandan infants.

Monitoring the Attention of Others

The second focus of the Infant Only laser experiment was to establish whether the offspring monitored the attention of their mothers or siblings whilst they were engaging with the laser stimulus. In other words, was the offspring motivated to establish a triadic relationship with others or were they solely focused on the laser stimulus individualistically? Using a stimulus that could neither be picked up nor transferred, we could comparably measure the looking behaviours of the offspring towards conspecifics in all three groups. At this stage it did not matter why they looked to conspecifics, but whether offspring were motivated at all to look at others during laser engagement. In addition, the frequency of the offspring's looks to the mother/siblings was compared to a baseline rate of looks to mothers/siblings in which the laser stimulus was absent.

The emergence of "showing" in Western human infants at 10.5 months and its absence in chimpanzees (Carpenter et al., 1998; Tomasello & Carpenter, 2005) indicates that humans may be more motivated to share attention with others. To my knowledge, there is no study that indicates that the motivation to share attention is lower in African/Ugandan infants. Therefore, it was predicted that humans of both groups would show more looks to conspecifics than chimpanzees when the laser stimulus was present.

Directed Communication during Laser Engagement?

Although there is currently no evidence that 11 months old infants or chimpanzees in general point declaratively (Carpenter et al., 1998; Tomasello & Carpenter, 2005), it is possible that they produce other behaviours to attract the attention of their inattentive mother and siblings to the laser stimulus. One such behaviour is the human infants' "showing" of objects to social partners from 10.5 months of age, but "showing" has never been observed in chimpanzees (Tomasello & Carpenter, 2005; Carpenter & Call, in press). Since the laser stimulus could not be picked up and "shown" to others, the offspring of all three groups were placed into a novel triadic situation. This allowed me to focus on more basic behaviours that may attract the attention of others, such as approaching others, vocalisations and audible behaviours (e.g. hitting the laser, stamping on the laser or jumping against the surface it is projected onto).

In order to distinguish between the offspring of the three groups showing these basic behaviours to communicate with their mothers/siblings or whether they were simply a by-product of individualistic laser engagement, gaze alternation was used as an indicator that the behaviour was directed at the mother or sibling and thus likely communicative (Leavens et al., 2005). To this end, I analysed whether these potentially communicative behaviours occurred more before or after a look to the mothers/sibling than during laser engagement without such looks.

The central question therefore was whether the offspring of the three groups produced communicative behaviours that seemed to be directed at the mother/siblings whilst interacting with the laser stimulus and whether the three groups differed in the frequency of these behaviours. Since human infants at 11 months engage in "showing" which indicates the motivation to share attention with others (Carpenter et al., 1998), but chimpanzees did not (Tomonaga, et al., 2004; Tomasello & Carpenter, 2005), it was predicted that human infants showed more communicative behaviours directed at their conspecifics during laser engagement than chimpanzees. Again, no directional cultural hypothesis was made.

Dyadic vs. Triadic Communication

The previous section only aimed at establishing whether the offspring's behaviours that occurred during laser engagement were directed at the mother/siblings.

Therefore, it is important to examine whether the directed communicative behaviours identified above were attempts to communicate *about* the laser (triadic) or whether the offspring aimed at gaining the attention of the mother for a dyadic interaction. In order to distinguish between communicative behaviours given to initiate dyadic rather than triadic interactions, behaviours accompanying looks to the mother/sibling were compared when the laser was present and absent.

It was predicted that if the infants were motivated to initiate a triadic interaction about the laser, the offspring would display an increased rate of communicative behaviours when the laser was present compared to when it was absent. Eleven months old human infants and chimpanzees are able to coordinate their attention between an external entity and a social partner (Carpenter et al., 1998; Leavens et al., 2005), but based on the human infants' higher motivation to share attention (Carpenter & Call, in press), it was predicted that humans would show more communicative behaviours about the laser than chimpanzees. There was no reason to assume a difference between the two human cultures in this respect.

Methods

Laser stimulus

The stimulus of this study, the moving dot of a laser pointer, had been used before in experiments with captive apes (Madsen, 2010). The advantages of using a laser stimulus were that (1) it allowed the experimenter to project a stimulus close to the study subjects and control it without approaching and thereby disturbing them. This made it particularly suitable for use with wild chimpanzees, where maintaining an appropriate distance from participants is vital. (2) It was not tangible and could be removed from the situation at any time by the experimenter. This made it safe for all three groups to interact with freely and gave the experimenter considerable control over who was exposed to the stimulus (e.g. the

laser could be turned off immediately if another individual approached who I did not wish to expose), and (3) the laser stimulus was novel and unusual for all three groups, and none of the offspring could immediately associate it with its origin.

Pilot Studies

The laser paradigm used by Madsen (2010) was elaborated on and extended to humans and wild chimpanzees in this thesis. Before the final experiments, I conducted pilot trials with human and chimpanzees in order to examine their general reaction to the laser. The human pilot study was conducted at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, between October and November 2008. The participants were 8 German infants ranging from 22-24 months of age who participated in a false belief experiment in the child lab of the institute prior to the laser pilot study. The data of the pilot study were not systematically analysed as the purpose of the exposure was only to investigate whether or not the infants were scared of or interested in the laser dot. All infants looked at the laser and physically interacted with it without being fearful.

In order to check whether chimpanzees were also interested in the laser stimulus, two orphaned sub-adult chimpanzees and one orphaned sibling-sibling dyad of the Sonso group who could not be included in the experiments because of having no mother, were exposed to the laser stimulus. Three of the four individuals saw the laser. None of them were scared of the laser and all of them explored it.

After testing the general reaction of human and chimpanzee offspring to the laser, I conducted a pilot study with 16 Ugandan infants ranging from 7 month to 22 months in order to develop the final procedure. The main aim of this part of the pilot was to find the most suitable age group in human infants.

Participants

Chimpanzees

The participating chimpanzees originated from the Sonso study group described in chapter 3. Twelve different chimpanzee offspring participated in the Infant Only laser experiment. Six of the twelve chimpanzee participants were infants (5

females, 1 male), 5 were juveniles (3 females, 2 males) and 1 was a female sub-adult. The mean age of the chimpanzees during the Infant Only laser experiment was 63.0 months (SD = 30.4). Therefore, it is important to note that the term “Infant” in the Infant Only laser experiment also refers to older dependent chimpanzee offspring.

Ugandans and British

In humans, twelve Ugandan and twelve British mother-infant dyads from the communities described in chapter 3 participated in this study. Five of the 12 infants in each group were female and 7 infants were male. The mean age on the day of the Infant Only experiment was 337.17 days (SD = 7.40) for Ugandan infants and 338.08 days (SD = 7.75) for British infants.

For all three study groups, the offspring was defined as the focal during the Infant Only laser experiment. The focals’ mothers and siblings (if present) were considered to be potential interaction partners.

Design of Laser Experiments

Counterbalancing Infant Only and Social Laser Experiments

Since I aimed at investigating individual joint attention skills in the offspring as well as the occurrence of joint attention as an event and the nature of the interaction between mothers and their offspring, two types of laser experiments were conducted: the Infant Only laser experiment (this chapter) to investigate the individual joint attention skills of the offspring and the Social laser experiment (Chapter 5) to examine the joint attention interaction of mothers and their offspring. Since I planned to expose all participants to both types of laser experiments and I wanted to avoid a systematic bias for previous laser exposure, the Infant Only and the Social laser experiments were counterbalanced within the groups. Six Ugandan and British infants completed the Infant Only Experiment first and the other six infants completed the Social Laser Experiment first. Seven chimpanzees participated in both, the Infant Only and the Social laser experiment (4/7 completed the infant only first), and six chimpanzees only participated in either one of the two experiments (five in Infant Only and one in Social).

Laser Exposure

In order not to over-stimulate the participants with the laser, the required minimum time lapse between the two experiments was set to 7 days. One week seemed sufficient for the subjects to display a similar amount of interest towards the laser as during their first exposure. The average gap between experiments was 10 days (SD = 2.2) in Ugandan infants (varying from 7 to 13 days) and 9 days (SD = 3) in British infants (varying from 7 to 18 days). One British infant who participated in the Social experiment first, was exposed to the laser a second time before the Infant Only experiment due to an experimenter error. I ensured, however that there was still a gap of 7 days between the last laser exposure and the Infant Only experiment.

For the seven chimpanzees who participated in both experiments, the average time lapse between the first and the second experiment was 253 days (SD = 281) (varying from 8 to 575 days). In chimpanzees, the gap between two experiments was very variable, because some experiments were conducted in the first field period in 2009 and others in the second field period of 2010 and 2011. In chimpanzees it was impossible to influence the movement of the partner and prevent the approach of other individuals, both of which could lead to the early abortion of a trial. Therefore several chimpanzee infants had exposure to the laser for short periods before their Infant Only experiment. Table 4.1 shows the individuals who participated in the Infant Only experiment and their history of previous laser exposures.

The mean number of laser exposures for the five chimpanzees who had experience with the laser prior to the Infant Only experiment was 1.1 times and the mean number of days that had elapsed between the last previous laser exposure and Infant Only Laser Experimental was 54.6 days (SD =51.9).

Table 4.1: Overview for chimpanzees of exposures to the laser prior to the Infant Only laser experiment, completed Social experiments before the Infant Only and the minimum time that had elapsed since the last laser exposure regardless of whether it was an unsuccessful attempt or a Social laser experiment.

ID	Number of laser exposures before Infant Only Laser Experiment	Completed Social laser experiment before Infant Only?	Minimum time elapsed since the last laser exposure before the Infant Only Laser Experiment
KC	0	No	-
KS	0	No	-
NT	0	No	-
ZK	1	No	87 days
MN	0	No	-
KX	4	Yes	39 days
KM	0	No	-
KR	0	No	-
KH	1	No	5 days
MI	2	Yes	14 days
KB	5	Yes	128 days
RF	0	No	-

Procedure

Chimpanzees

The chimpanzee laser experiments were conducted between March and May 2009 and between May and December 2010.

Preconditions

Since chimpanzee mothers cannot be instructed, the laser experiments had to be conducted opportunistically whenever the following preconditions were met:

(1) The mothers were resting, feeding or grooming an individual other than the focal offspring at the beginning of the laser experiment

(2) The mother was less than 2m away from the offspring at the moment the experiment started

(3) It was possible to present the laser to the offspring without the mother seeing the laser

(4) No conspecific other than the mother was present within 5m of the focal offspring or they were unable to see the laser.

Not being in body contact with their mothers initially was a precondition during the beginning of the laser exposure to avoid tactile communication between offspring and mother during the first encounter with the laser stimulus. Given the high mobility of the chimpanzee offspring, however, the distance to the mother changed dynamically during the experiments. Therefore, brief periods with body contact could not be avoided.

Control and Experimental Periods

When the above mentioned preconditions were met, the focal mother-offspring dyad was filmed for at least 1 min, if possible, before the laser was presented. This short observation video before the experiment served as a *control period* for the laser experiment (see analysis below). If the offspring interacted with her mother for periods of more than 5s during the 1 min period before the laser was

presented, I extended the period by the duration the mother and infant's interaction.

After recording the mother-offspring dyad for approximately 1 min, the laser was switched on and presented within the visual field of the offspring. This constituted the *experimental period*. Each laser experiment was recorded by the experimenter (TK) using a Canon Digital Camera with 50x (2009 - March 2010) and later 70x optical zoom (March 2010 – Jan 2011). This allowed me to conduct experiments with chimpanzee mother –offspring dyads who were as far as 20m away from the observer.

Laser presentation pattern

Since the aim was to maximize the offspring's interest in the laser, there was no fixed pattern for the laser presentation. The experimenter alternated the movement between keeping the dot still and moving it erratically. The laser was mainly presented within reach of the offspring, but also further away if the position of the focal or the environmental situation required it. On some occasions, the laser was also projected on the body of the offspring, mainly because there was no other surface to visibly project it onto. The laser was switched off for short periods (up to 10s) to prolong the offspring's interest. The laser was also switched off when the mother or any other individual within 5m turned towards the laser presentation area and could potentially see the laser dot. In these cases, the laser remained off until the conditions allowed the experimenter to carry on with the experiment.

In addition to controlling the laser movement and filming, the experimenter operated a stop watch to keep track of the presentation time. According to the experimental protocol, it was the aim to expose the offspring to the laser stimulus for a maximum amount of 180s to give the offspring enough opportunity to show the behaviours of interest. The experiment was terminated when the maximum laser presentation time had elapsed, the offspring lost interest in the laser or any of the above mentioned preconditions were no longer met (e.g. the focal/mother moved away or another individual entered the laser presentation area).

I worked with Mr. Geresomu Muhumuza (GM), an experienced field assistant, who

noted the party composition and alerted me of any individuals entering the presentation area.

Ugandans and British

The data collection for Ugandan infants took place between April 2010 and January 2011 and for the British infants between December 2009 and March 2010. The human Infant Only laser experiment was conducted during either of the two visits to the participants' homes (Chapter 3).

Preconditions

Whenever the infant cooperated and was alert in the beginning of a visit, the laser experiments were completed before the other study parts. Since it became apparent during the pilot phase that an opportunistic execution of the laser experiment was infeasible, given the constraints of time participants were willing to volunteer for, the mother had to be given some minimal instructions to create the same experimental set up as for the chimpanzees. As part of obtaining informed consent from the mother to participate in the experiment, the mother had to be shown the laser prior to the first experiment. After both the mother and the infant had become relaxed and comfortable with the experimenters' presence, the mother was asked:

- (1) To sit in a comfortable position within 2m of her infant with no body contact. Since some of the infants were able to crawl, short periods of body contact during the experiment could not be avoided
- (2) To face away from her infant
- (3) To give the infant a familiar toy to play with and remove all other toys from within reach of the infant
- (4) To complete a visual puzzle ("Find the difference" between two pictures for Ugandan mothers and a word search for British mothers) with the instruction to find as many words/differences as possible. It was important to engage the human mothers in a visual activity, because in contrast to the chimpanzees, they knew that an experiment was going on and therefore had a higher tendency to look to

the infants. The quiz therefore helped to create a situation that was most comparable to a chimpanzee mother whose activity structure was not interrupted by an experimental visit and who was engaging in a specific activity (e.g. resting, grooming or feeding). I explained to the mothers that she would not be judged on this quiz and its purpose was only to keep her visually occupied.

(5) To interact with the infant for a short period “as she would normally do if was busily engaged with another task”, if she was under the impression that the infant was directly addressing her or wanted her attention. After a brief interaction, she was then to return her attention to the quiz.

(6) To not behave as if she had already seen the laser.

To reduce distractions during the experiment, the research assistant for the British study group invited siblings of the infant to play with her/him in a different room, before I started filming. Since in Uganda one field assistant was not enough to distract all children present in the compound, she instructed everyone present to stay beyond 5m of the presentation area and not to interfere with the experiment. In addition, she prevented arriving individuals from entering the experimental area.

Control and Experimental Periods and Laser Presentation Patterns

The mother-infant dyad was filmed for one minute (*control period*) before the laser was presented (*experimental period*) as it was also done in the chimpanzee study group. The laser presentation time and patterns were identical to those for chimpanzees (see above).

Ethics

Approval for this study was obtained from the Departmental Ethics Committee from the University of York, from the Ugandan National Council for Science and Technology (UNCST) and the Ugandan Wildlife Authority (UWA).

The laser pointer used was under 1mW in power and therefore whilst every effort was made to avoid presenting the laser near the eyes of the participants, if this happened, there was no risk of damage to the eyes of the participants.

In humans, in order to obtain informed consent from the mothers, it was necessary to show the laser to the mothers prior to the experiment. In this respect, the procedure with humans necessarily differed from the procedure of the chimpanzee study to ensure the research was conducted in an ethical manner. The only chimpanzee offspring (KS) to show signs of fear towards the laser did so when the laser was projected onto his body. Projecting the laser on to the body in subsequent trials was avoided after his reaction was observed.

Data analysis

Laser exposure and periods for analysis

As mentioned in the procedure, the aim was to present the laser for a total of 180s. In chimpanzees, this could not always be achieved, because several chimpanzee trials were prematurely aborted when the preconditions were no longer met. This happened more in chimpanzees because of the opportunistic character of the experiments. Some experiments exceeded the desired maximum exposure of 180s, because my live measurements with the stopwatch were later corrected during the exact video analysis. If the laser exposure was longer than 180s the video coding was cut off at 180s. In order to explain the *control and experimental periods* that were used for the analysis, it is important to show what the achieved laser exposure in the experiments was (see Table 4.2).

Table 4.2: The laser exposure in the Infant Only experiment for the three study groups.

N = 12	Target duration of laser exposure in seconds	Minimum duration of laser exposure in seconds	Mean duration of laser exposure in seconds (SD)
Chimpanzees	180	52.04	120.48 (44.8)
Ugandans	180	120.88	168.66 (21.44)
British	180	141.12	168.47 (13.95)

Since the analysis for “monitoring the attention of others” (see introduction, this chapter) was based on frequencies of the offspring’s looks to the mother/siblings, I required an experimental period with equal laser exposures for all participants. To this end, I standardised the experimental period for this analysis to the duration of the shortest laser exposure amongst all participants (see 52.04s in chimpanzees). As a consequence, to calculate the frequencies of monitoring the attention of others, only the first 52.04s of the experimental period (*‘52 sec experimental period’*) were analysed across the three groups.

Since all other analyses were focussed on the quality of the offspring’s behaviour, rather than the frequencies of behaviour, relevant behaviours were extracted from the entire experimental period that varied in duration between 52.04s and 180s (*‘entire experimental period’*). In addition, two types of control periods (before laser presented) were used that mirrored the two experimental periods in order to make comparisons between control and experimental periods. The first had a standardised duration of 52.04s, exactly matching the *‘52 sec experimental period’*. For the remaining analyses, the matched control periods for the *‘entire experimental period’* (52.04-180s), also consisted of the entire available control period. *‘Entire control periods’* did, however, tend to be shorter than the corresponding *‘entire experimental periods’*, because the dyads were only filmed for approximately 60s before the laser was presented.

Video Coding

All videos were coded using the Observer XT 10.5, a video coding software from Noldus. The main behaviours coded were:

- (1) Laser visible or invisible for offspring
- (2) Head direction of offspring and mothers. The precise gaze direction of the participants was not always visible, because the participants’ position relative to the experimenter was not always conducive for seeing the eye-gaze direction. In addition, the gaze direction was not equally visible across the three groups, because, in contrast to humans, chimpanzees possess a

dark sclera which makes it much harder to detect their exact gaze direction (Kobayashi & Kohshima, 1997). Therefore, the head direction of the participants was taken as an indicator for the gaze direction (Emery, 2000). “Looking at x” was therefore defined as “Head direction to x” throughout this thesis. Coded targets of the participants’ looking behaviours were: (a) laser, (b) mother/offspring (depending on who was coded), (c) sibling, (d) other conspecific (excluding experimenter) or (e) elsewhere (including experimenter)

(3) Approach of offspring to the mother or sibling

(4) Vocalisations and Sounds of offspring. Sounds had to be produced by the mouth or lips (e.g. clicking with the tongue, lip smacking)

(5) Laser engagement of offspring. The coded types of laser engagement were: (a) Eye tracking only (i.e. no physical engagement), (b) (Potentially) audible laser engagement. This was defined as any postural or limb movement in relation to the laser that potentially or definitely produced a sound

(6) Distance between offspring and mother ranging from body contact, within reach to beyond reach

Inter-observer reliability

I coded all videos of the ‘*entire*’ control and experimental periods and 25% of all videos were coded for inter observer reliability by a second independent coder who was blind to the hypotheses. For the control period ($\kappa = 0.80$) and the experimental period ($\kappa = 0.80$) kappa was excellent indicating a very good inter observer reliability between the first and the second coder (Altman, 1991).

Intentional Communication during Laser Engagement

To recap, it was the aim of this analysis to investigate whether the offspring of the three groups tried to communicate with their mothers or siblings, as opposed to being engaged with the laser individualistically. Specifically, I was interested whether some basic behaviours (see below) were used to communicate with others. Since all of these behaviours can be used individualistically as well as in

order to communicate, it was important to use a gaze alternation as a marker of intentional behaviour (Leavens et al., 2005). I will first present the behaviours of interest and then explain how communicative behaviours were distinguished operationally from behaviours that were by-products of the offspring's individualistic laser engagement.

Behaviours of interest

The following behaviours were examined as all could potentially act as communicative behaviours to attract the attention of the partner to the laser, because they all have an auditory or tactile component.

- (1) The offspring's approach to another conspecific,
- (2) Vocalisations,
- (3) Potentially audible laser engagement, behaviours (e.g. hitting the laser, stamping on the laser or jumping against the surface it is projected onto)

Approaching and possibly touching another individual may direct her attention to oneself. This can happen accidentally whilst the approacher is seeking reassurance, but it could also be done intentionally in order to get the other's attention.

Defining intervals

To distinguish whether a given behaviour was a directed communicative act or not, two types of intervals were extracted and compared in this analysis: one interval in which the offspring looked to the mother/sibling during laser engagement (hereafter: "***experimental gaze alternation intervals***") and another interval in which the offspring only looked at the laser (hereafter: "***laser engagement only intervals***"). The presence or absence of potentially communicative behaviours (approach, vocalisation and audible laser engagement) was compared between these two types of interval. If a behaviour occurred more during 'experimental gaze alternation intervals' than during 'laser engagement only' intervals, this behaviour was likely to be directed at the mother/sibling.

How were intervals extracted?

Both types of intervals were sampled from the 'entire experimental period' (min 52.04s - max 180s). It was relatively complicated to extract the two intervals of interest from the experimental trials. This section gives details on all the stages and criteria applied in order to ensure interval extraction was conducted objectively and equally across trials.

To extract and analyse an 'experimental gaze alternation interval', I (1) identified gaze alternation between laser and mother/sibling (defined as look to the laser occurring within the 3s before the look to mother/sibling) and (2) examined the communicative behaviours (see below) that occurred during the look to a conspecific and in the 5s either side of the look (see Figure 4.1).

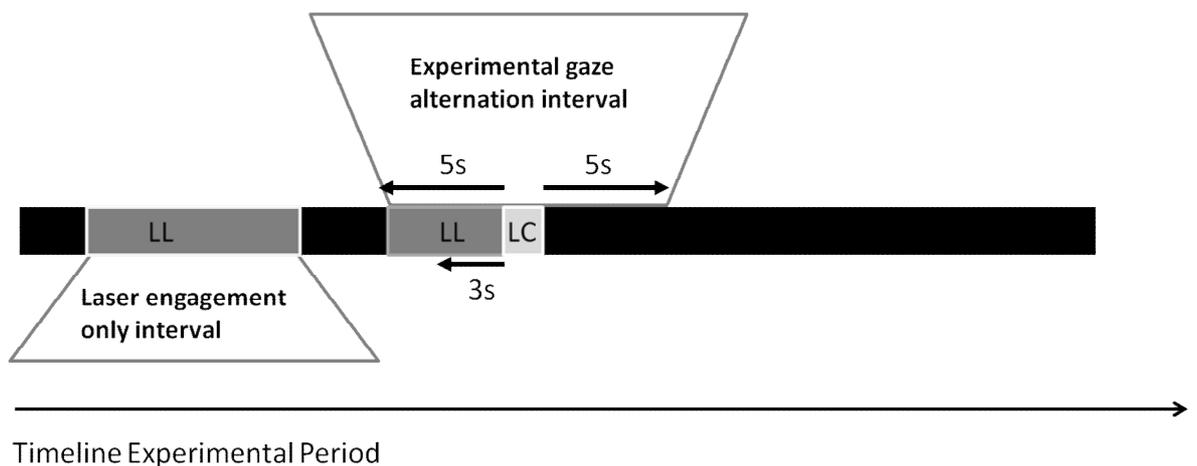


Figure 4.1: Illustration of the 'experimental gaze alternation intervals' and the 'laser engagement only intervals'. The black bar shows the focal's looking elsewhere. Dark grey areas indicate the focal's look to the laser (LL) and the light grey area shows the focal's look to a conspecific (LC). The beginning and the end of the focal's look to a conspecific determined the analysed 5s intervals.

The following rules were applied for exceptional 'experimental gaze alternation intervals':

(1) If the offspring looked to the same conspecific again within 5s after the first look ended, the gaze alternation interval was extended to include the second look as long as the offspring looked back at the laser within 3s after the last look ended.

(2) If two gaze alternation intervals of the same focal overlapped (the 5s following the look and the 5s preceding the next look partially overlapped), the overlapping period was cut into two halves and both intervals analysed separately.

(3) If a look to a conspecific lasted longer than 10s, the gaze alternation interval was ended after the offspring looked to the conspecific for 10s which resulted in a 15s interval (5s preceding the look and the look itself).

(4) If the laser was switched off or the offspring engaged with an object other than the laser during the 5s preceding or following the look to a conspecific, the duration of the absence of the laser or the engagement with another object were removed from the interval, because in both cases it could not be concluded that possible communicative behaviours were associated with the laser. As a result, some intervals were shorter than others.

How were intervals paired?

Whenever possible, 'experimental gaze alternation intervals' were paired with 'laser engagement only intervals'. These 'laser engagement only intervals' had to be at least 5s away from a look to a conspecific. The 'laser engagement only intervals' were matched with the 'experimental gaze alternation intervals' using the following criteria:

(a) The interval needed to be of similar duration (less than 1s difference) to the 'experimental gaze alternation interval'

(b) if there was no interval of equal duration, shorter 'laser engagement only intervals' were added up to match the duration of the 'experimental gaze alternation interval'

(c) The temporal distance of the 'laser engagement only interval(s)' should be as short as possible to the 'experimental gaze alternation interval' that it was matched with (see Figure 4.2)

(d) if there were not enough 'laser engagement only intervals' to match all 'experimental gaze alternation intervals' during an experiment, the 'gaze

alternation intervals' that occurred earlier in an experiment were matched first (in order to increase the similarity with the often shorter chimpanzee experiments).

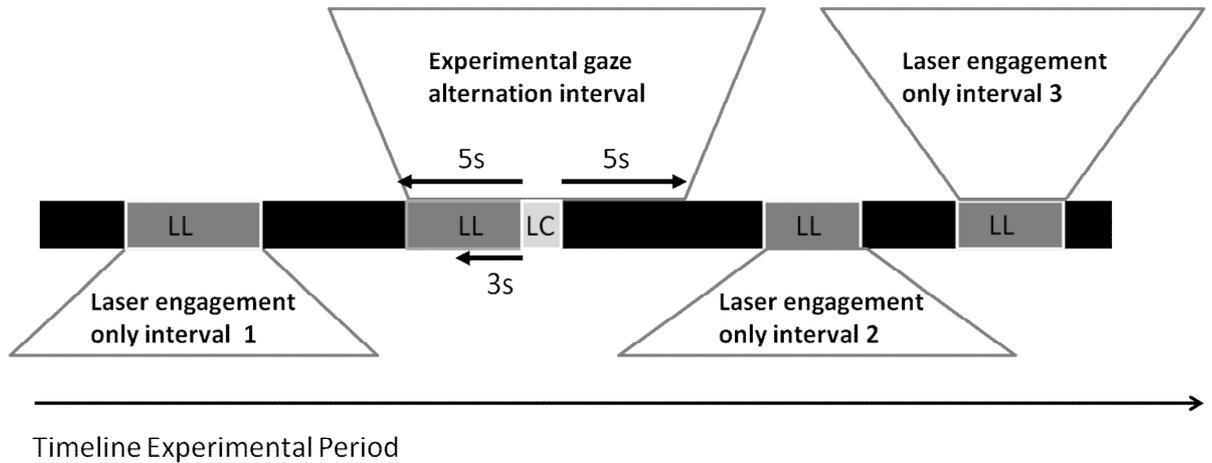
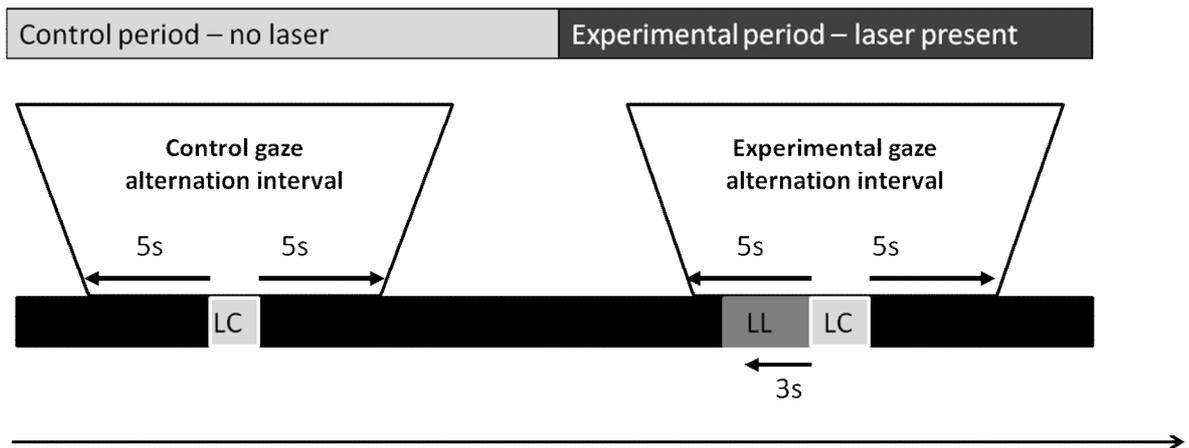


Figure 4.2: An 'experimental gaze alternation interval' was matched with two shorter 'laser engagement only intervals' (1+2) to match the total duration of the 'experimental gaze alternation interval' according to criterion (a) and (b) in the text. The 'laser engagement only intervals' were chosen to be as close as possible to the matched 'experimental gaze alternation interval' according to criterion (c). Therefore, only 'laser engagement only intervals' 1 and 2 were used, as they were closer to the 'experimental gaze alternation interval' than 'laser engagement only interval' 3. LL = look laser, LC = look conspecific.

Dyadic vs. Triadic Communication

To investigate whether communicative behaviours found in the previous analysis were *about* the laser stimulus (i.e. triadic), I compared the potentially communicative behaviours of the 'experimental gaze alternation intervals' to "**control gaze alternation intervals**" in which the laser was absent. The control intervals required a look to a conspecific in the absence of the laser stimulus during the '*entire control period*' that was recorded before the laser was presented. Therefore, the 'control gaze alternation intervals' necessarily occurred before the 'experimental gaze alternation intervals'. As in the previous analysis, the 5s of either side of the look to the mother/sibling were analysed (see Figure 4.3).



Timeline Infant Only Experiment

Figure 4.3: Example of a 'control gaze alternation interval' that originated from the '*entire control period*'. In the '*entire control period*' the laser was absent. The 'control gaze alternation interval' was identical to the 'experimental gaze alternation interval' with the exception that the focal did not look to the laser (LL) within 3s before the look to the conspecific (LC). The black bar indicates the offspring's look to "elsewhere". The 5s before and after a look to a conspecific (LC) were analysed in both the 'control gaze alternation interval' and the 'experimental gaze alternation interval'.

In addition, the control and experimental gaze alternation intervals were matched in total interval duration and extended if the focal looked to the same conspecific again within 5s after the first look ended. Periods in which the offspring engaged with an object other than the laser were excluded from the analysis. All control gaze alternation intervals were coherent intervals meaning they were not composed of some shorter intervals as in the previous analysis.

Statistical analysis

The statistical methods introduced in this section were applied throughout this thesis. When conducting a between groups analysis and comparing means of the three study groups, the data were examined prior to analyses. I investigated whether the data were normally distributed by visually inspecting the histograms and conducting a Shapiro-Wilk test of normality. If the data were normally distributed, I conducted a Levene's test to examine whether the data from all tested groups had equal variances. Based on the initial exploration of the data, the most appropriate tests for a given data set were used: If data were normally distributed either a one-Way ANOVA with Sidak post-hoc tests for data with equal

variances was used or the Welch statistics with Games-Howell post-hoc tests for data with unequal variances.

If the data were not normally distributed, the non-parametric Kruskal-Wallis test with Mann-Whitney U post-hoc pair wise comparisons were conducted and the α -level for significance was Sidak- corrected for multiple testing (see Table 4.3).

Table 4.3: Sidak-corrected α -levels to correct for a family-wise error in post-hoc tests.

Number of post-hoc tests	Sidak corrected α level for significance	Sidak corrected α level for a trend
2	.025	.051
3	.017	.035
4	.013	.026
5	.010	.020
6	.009	.017

For within-group comparisons of averages a parametric paired sample t-test was used for normally distributed data and a Wilcoxon test was used for data that was not normally distributed. For comparisons between averages in just two groups, an independent samples t-test was used for normally distributed data and a Mann-Whitney U test for other distributions.

For small sample sizes ($N < 8$), exact p-values, as opposed to asymptotic ones, were calculated, as recommended by Mundry and Fischer (1998). If asymptotic values had to be reported (in some cases the computer was unable to calculate exact statistics), this was highlighted throughout this thesis. All tests throughout this thesis were two-tailed in line recommendations given by Mundry and Fisher (1998). All above-mentioned tests were conducted with PASW 18.

In addition to interval or ratio data that were analysed using the tests specified above, I also extracted nominal (binary) data. If each individual only contributed

one data point to the data set, then binary data indicating the presence or absence of behaviours in certain intervals were analysed using General Linear Models (GLMs) with a binomial error structure. When individuals contributed more than one data point to the data set (repeated sampling) Generalized Linear Mixed effects Models (GLMMs) with a binomial error structure for data were used. The pseudo replication caused by repeated sampling of some individuals was controlled for statistically through fitting “individual” as a random factor into the GLMM (Crawley 2002) by conducting random intercepts models using the package “Lme4” (Bates & Maechler 2009). Post-hoc GLMMs were used to investigate pairwise differences between the groups and a Sidak correction was applied to the alpha level to correct for multiple comparisons (see Table 4.3).

In order to be able to conduct GLMMs it was necessary that all groups that were entered into the analysis had some variation in their data sets. This means that if behaviour X was absent (or present) in all observations for group A, behaviour X could not be entered into the analysis for group A (Zuur, 2012). This was highlighted in the results section as (0 variation) and instead, descriptive statistics were reported for this group and the GLMM was conducted for the remaining groups. In addition, there were limitations with regard to sample sizes; all GLMs and GLMMs were conducted using the software package R (i386 2.15.0).

For comparisons of just two groups with binary data, without repeated sampling, a Fisher’s exact test was used and an exact sign-rank test for within group comparisons. The Fisher’s exact test was calculated online (http://insilico.net/tools/statistics/fisher_exact_test/2x2) and the sign-rank tests were calculated in PASW 18.

Inferential statistical tests were only conducted if there were a minimum of 6 individuals per group.

Results

Excluded Experiments

In total, 26 Infant Only experiments were attempted with 15 different chimpanzee offspring, but 14 experiments had to be discarded. Thirteen out of the 14 discarded experiments were prematurely aborted, because circumstances changed, meaning the preconditions for the laser presentation were no longer met (see procedure). Therefore, the laser exposure of the offspring was too short (1s - 50s) in order to meaningfully extract data. For one individual (KC) I had two valid experiments available, one was conducted in 2009 and another one in 2010. I analysed the first valid trial available, because the lower previous laser exposure at this point made this trial more comparable to those of other participants.

For both human groups, all Infant Only laser experiments could be included into the analysis.

Activities of Mothers

Since it was the aim of the Infant Only experiment to show the laser only to the offspring, I aimed to conduct experiments when the offspring was not continuously interacting with their mothers. In humans, this was achieved by giving a visual puzzle to the mothers and asking them to sit up to 2m away from the infant. Since chimpanzee experiments were carried out opportunistically, the mothers were engaging in the following activities: Four chimpanzee mothers were feeding for the majority of the '*entire control period*' and '*entire experimental period*', two mothers were grooming an individual other than the offspring and six mothers were resting. None of the offspring of all three groups was interacting with their mothers for the majority of the '*entire control period*', except one chimpanzee sub-adult (KM) who was grooming her mother who had turned her back to KM. The constellation of individuals was not ideal in this case, but the laser was presented to the offspring during a grooming break.

Interest in laser stimulus

It is first important to establish whether chimpanzees, Ugandans and British offspring were interested in engaging with the laser dot (novel stimulus) and

whether they did so at similar rates. Table 4.4 shows the proportions of the offspring's (focal) visual or physical laser engagement during the '*entire experimental period*' and the standardised '*52 sec experimental period*'.

Table 4.4: Mean proportion and standard deviations of the focals' laser engagement (visual and physical) in the '*entire experimental period*' (52.04-180s) and the standardised '*52 sec experimental period*' (52.04s)

	Mean response to laser stimulus in '<i>entire experimental periods</i>'	Mean response to laser stimulus in '<i>52 sec experimental periods</i>'
Chimpanzees	0.73 (0.23)	0.78 (0.21)
Ugandans	0.49 (0.12)	0.69 (0.17)
British	0.44 (0.16)	0.69 (0.16)

During the '*entire experimental period*', the proportion of laser engagement in the two human groups was significantly lower than in chimpanzees (*Welch's F* (2) = 20.64, $p = .007$). With regard to the proportions of laser engagement in the standardised '*52 sec experimental period*', the interest in the laser in Ugandan and British was higher than in the '*entire experimental period*'. A one-Way ANOVA confirmed that there was no significant difference between the three groups in the shorter '*52 sec experimental period*' with respect to the focals' engagement with the laser dot (F (2, 33) = 1.12, $p = .340$).

All focals of the three groups engaged with the laser physically at some point during the '*entire experimental period*'. There was one chimpanzee (MN) and one Ugandan infant who did not engage with the laser physically during the '*52 sec experimental period*'. Both of them, however, engaged with the laser visually.

Social Referencing

It was the aim of this analysis to find out whether the offspring of all three groups showed a basic form of social referencing, i.e. whether they looked to their mothers before physically engaging with the novel laser stimulus for the first time.

It is important to note, that none of the human participants showed any obvious fear (e.g. screaming, crying) upon their first encounter with the laser stimulus. Only one chimpanzee offspring (KS), who did not avoid the laser when it was projected within his reach, subsequently showed some fear of the laser when it was projected onto his body by trying to shake it off and displaying a silent-bared teeth face.

In order to analyse whether the offspring looked to the mothers before they physically engaged with the laser, the focal's first exposure to the laser in which he physically interacted with it was examined. For chimpanzees, the first exposure to the laser could either have occurred during the Infant Only or the Social laser experiments or during an aborted trial. For the two human groups, the first exposure to the laser always was either during the Infant Only or the Social laser experiment. I then scored whether the offspring looked to the mother before physically engaging with the laser whilst the laser was visible.

The sample size for chimpanzees increased for this analysis from 12 to 15, because I could use the beginnings of laser experiments that had a shorter laser exposure than the required 52.04s for the other analyses. Two of the three additional chimpanzee focals were infants (one male, one female) and the other one was a juvenile male.

In humans, 2 Ugandan and 4 British infants had to be excluded from this analysis resulting in sample sizes of 10 for Ugandans and 8 for the British. Reasons for exclusion were (1) mothers encouraged their infants to play with the laser, before the infants had started physically engaging with it. These instances had to be excluded from this analysis, because social referencing had become unnecessary in the presence of the mothers' encouragement to engage with the laser. (2) If the infant visually engaged with the laser, the laser was then turned off for a short period and they looked to the mother whilst the laser was off. In these cases it was difficult to know why they looked at the mother when the laser was switched off. Their look to the mother could have been social referencing or it could just have reflected a wish to engage with the mother once the novel item was no longer available.

Very few offspring across all three groups looked at their mothers before physically engaging with the laser. Only 2 out of 15 chimpanzee offspring looked to the mother before physically engaging with the laser, while 1 out of 10 Ugandan infants and 0 out of 8 British infants did the same. A binomial GLM was conducted with looking to the mother before physical engagement as the dependent variable (yes/no) and group (chimpanzees, Ugandans, British) as the explanatory variable. The GLM confirmed that there was no statistical difference between the offspring of the three groups in terms of how many individuals looked at their mothers first before they physically engaged with the laser ($z = -.959, p = .337$).

Monitoring the Attention of Others

It was the aim of this analysis to reveal whether offspring monitored the attention of others whilst they were engaged with the laser. To do this, all looks of the offspring to either their mother or siblings were counted in the standardised '*52 sec experimental period*'. In order for a look to a conspecific to be regarded as being associated with laser engagement, the focal had to look at the laser within 3s of the start or end of the look to the conspecific.

Figure 4.4 shows the offspring's median number of looks to conspecifics in all three groups which indicated that they looked to conspecifics at similarly low rates.

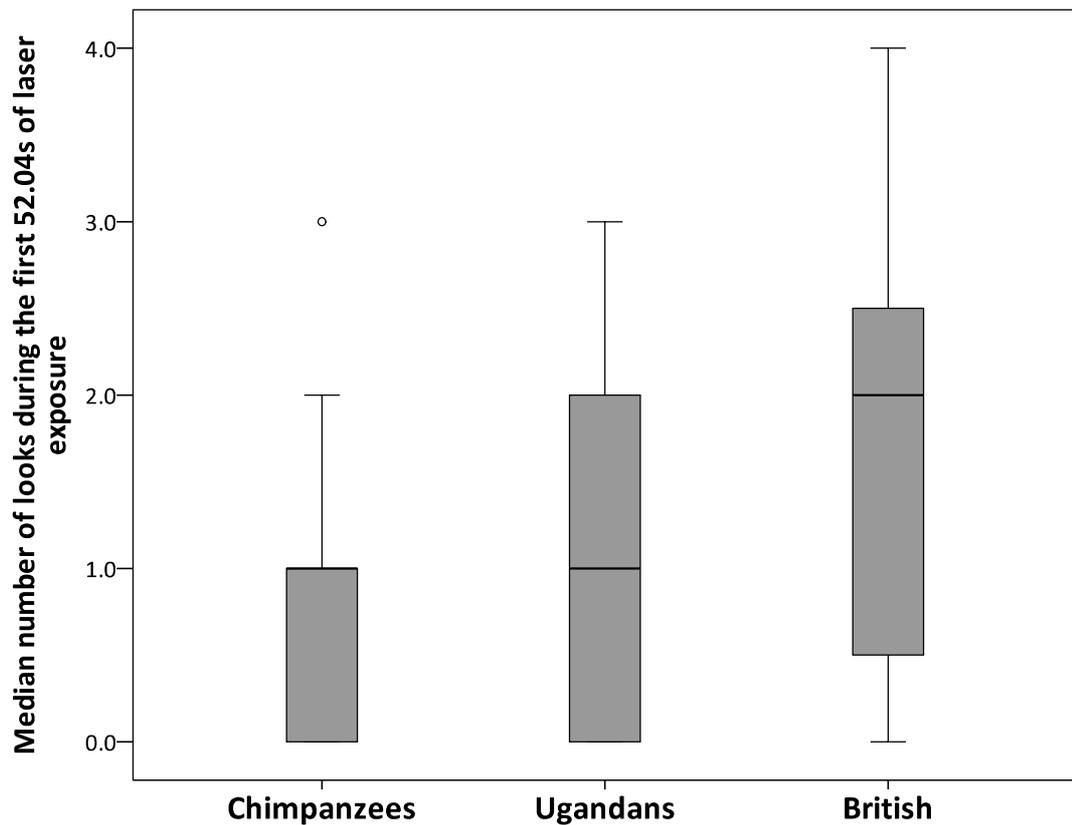


Figure 4.4: Boxplot illustrating the offspring's median number of looks to any conspecific during the standardised '52 sec experimental period'.

A Kruskal-Wallis test showed that the three groups did not differ with regard to the number of looks to their conspecifics ($\chi^2 (2) = 2.52, p = .289$).

Based on the low number of looks to a conspecific in all three groups in the '52 sec experimental period', I examined whether the offspring looked more to conspecifics in the '52 sec experimental period' compared to '52 sec control period'. Wilcoxon tests showed that regardless of group, the offspring did not look more to conspecifics in the '52 sec experimental period' than in the '52 sec control period': chimpanzees ($Z = -.41, p = .813$), Ugandans ($Z = -1.47, p = .199$) and British ($Z = -.71, p = .492$).

To sum up, the offspring of all three groups looked at conspecifics at low rates and the presence of the laser did not increase the offspring's tendency to look to conspecifics.

Directed Communication during Laser Engagement?

The aim of this analysis was to investigate whether potentially communicative behaviours of the offspring were present more in ‘experimental gaze alternation intervals’ as opposed to ‘laser engagement only intervals’ and whether chimpanzees, Ugandans and the British differed in this respect.

In the British sample, there were five ‘experimental gaze alternation intervals’ that could not be matched with an appropriate ‘laser engagement only interval’ and three in Ugandans. These periods were thus excluded from analysis. For chimpanzees, all available ‘experimental gaze alternation intervals’ could be matched with ‘laser engagement only intervals’. Table 4.5 gives an overview for the resulting dataset that was entered in to the binomial GLMM.

Table 4.5: Overview of dataset for the matched pairs of ‘experimental gaze alternation intervals’ and ‘laser engagement only intervals’ and number of individuals who contributed data to the analysis.

	Chimps	Ugandans	British
Total number of matched intervals	13	20	20
Number of individuals	9	12	11

Table 4.5 also shows that single individuals often contributed more than one data point to the analysis. This repeated sampling was controlled for by entering “individual” as a random factor into the GLMM.

Descriptives for the matched intervals

Table 4.6 shows that the ‘experimental gaze alternation intervals’ and the ‘laser engagement only intervals’ were of similar duration across the three groups. The number of looks to conspecifics in the ‘experimental gaze alternation intervals’ was comparable between the three groups, but the duration of the looks were slightly longer in the two human groups. Across groups approximately two intervals were needed to match the durations of the ‘experimental gaze alternation intervals’. It was possible to find ‘laser engagement only intervals’ closer to the

matched 'experimental gaze alternation interval' in chimpanzees whilst for humans the temporal distance between 'laser engagement only intervals' and 'experimental gaze alternation intervals' was longer.

Table 4.6: This table shows the main characteristics of analysed intervals including standard deviations for the three study groups.

	Chimps	Ugandans	British
Mean duration of 'experimental gaze alternation intervals' (SD)	10.05s (3.69)	11.32s (3.63)	10.34s (2.47)
Mean duration of 'laser engagement only intervals' (SD)	9.99s (3.72)	10.91s (4.01)	9.87s (2.49)
Mean duration of look to conspecific in 'experimental gaze alternation intervals' (SD)	1.56s (0.96)	2.94s (2.37)	2.98s (3.58)
Mean number of looks to conspecific in 'experimental gaze alternation intervals' (SD)	1.45 (0.51)	1.20 (0.52)	1.08 (0.29)
Mean number of 'laser engagement only intervals' used to match duration of 'experimental gaze alternation intervals' (SD)	2.00 (1.08)	1.90 (1.02)	2.10 (1.48)
Mean duration between 'laser engagement only intervals' and 'experimental gaze alternation intervals'	16.52s (17.88)	39.06s (83.99)	36.03s (72.43)

Between group comparisons

In order to examine group and species differences of the communicative behaviours mentioned above, I scored for each individual of the three groups whether each of the behaviours was present in the 'experimental gaze alternation interval', but absent in the 'laser engagement only interval'. If a behaviour was present only in the 'experimental gaze alternation interval', this may indicate that the behaviour was not just an individualistic interaction with the laser, but may have been communicative and possibly directed at the conspecific the focal was looking at.

To test for statistical differences between the groups, GLMMs with binomial error structure were used with Group (chimpanzee, Ugandan, British) as the explanatory variable. In addition, "individual" was entered as a random variable to control for pseudo replication. The dependent variable in each model was the presence of one of the potentially communicative behaviours in only the 'experimental gaze alternation intervals' (absent in matched 'laser engagement only interval').

There was one interval for chimpanzees and one for the British in which 'approach' could not be scored, because the offspring was already in body contact with the mother. These two intervals together with their matched interval were excluded from the 'approach' analysis.

The GLMM showed that there were no significant differences between the three groups with regard to whether the behaviours of interest were present only in the 'experimental gaze alternation intervals' (Table 4.7). There was no statistical difference between the chimpanzee, Ugandans and the British offspring with regard to potentially communicative behaviours being present only in laser engagement intervals with gaze alternation as opposed to laser engagement intervals without gaze alternation (Table 4.7).

Table 4.7: Proportion of matched intervals in each group in which the behaviour of interest was present only in the ‘experimental gaze alternation interval’ and absent in the ‘laser engagement only interval’.

	Chimpanzees	Ugandans	British	GLMM
Approach	2/12	9/20	8/19	$z = 1.24,$ $p = .215$
Vocalisations	0/13 (0 variation)	7/20	6/20	UG vs. BR $z = -.575,$ $p = .565$
Potentially audible laser engagement	1/13	4/20	2/20	$z = 0.04$ $p = .969$

Unfortunately, no inferential statistics could be conducted on chimpanzee vocalisations, because they never vocalised during any of the two types of intervals (zero variation). Descriptively, however, this absence of vocal behaviour constitutes a considerable difference from the offspring of the two human groups.

To exclude the possibility that the non-significant results could be attributed merely to the limited sample sizes, a power analysis was conducted for each behavioural variable. The effect sizes of the relationship between the dependent and explanatory variables were taken from the GLMMs of each behavioural variable. The data were subsequently simulated 100x using a custom-written power analysis script in R (Manser & Townsend, personal communication), to generate a probability of obtaining a significant p-value respective to an increase in explanatory variable sample size (N), with a given effect size (E). The upper threshold of the sample was set to $N = 200$. Figure 4.5 shows the result of the power analysis for approach between the three groups.

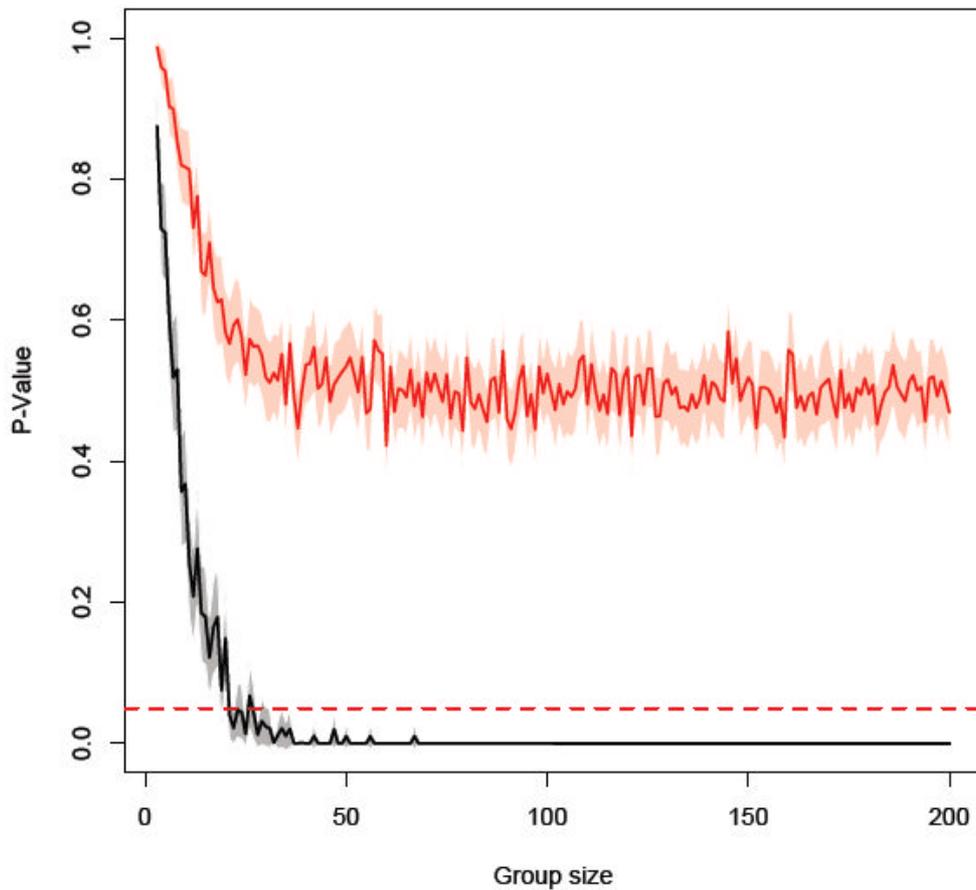


Figure 4.5: Power analysis for (potentially) audible laser engagement. The dashed line indicates the significance level of $\alpha = .05$. The red line (on top) shows the simulated p-value as a function of the increase of the sample size. The black line (below) shows the intercept of the model. The shaded areas around the two lines show the 95% confidence interval around the plotted values.

The power analysis for audible laser engagement in Figure 4.5 shows that even if we had had a sample size of 200 matched intervals, there would not have been a significant difference between the three groups. The other power analyses for approach and vocalisations also confirmed that the differences between the three groups would not have been significant with a sample size of 200 matched intervals. This showed that for each variable analysed, the limited sample size was not responsible for the non-significant differences found in the GLMMs.

Within group comparisons

Although the three groups showed similar levels of increases in potentially communicative behaviours in the 'experimental gaze alternation intervals', it is important to establish in each group whether any of the behaviours were significantly more likely to occur in the 'experimental gaze alternation interval' than the matched 'laser engagement only interval'. This would indicate that the behaviours analysed might have had some kind of communicative role, rather than just being individualistic responses to the laser. In addition, since only an increase of the potentially communicative behaviours in the 'experimental gaze alternation intervals' was analysed above, it was also important to establish whether the opposite occurred and the potentially communicative behaviours decreased in the 'experimental gaze alternation intervals' compared to the 'laser engagement only intervals'. In order to test both possibilities, three GLMMs were conducted for each group. In each model the dependent variable was the presence or absence of the potentially communicative behaviour in each interval. The explanatory variable was the type of interval ('experimental gaze alternation interval' / 'laser engagement only interval'). Individual was entered as random variable into the GLMM.

In general, chimpanzees showed very low rates of the potentially communicative behaviours. Table 4.8 shows that chimpanzee offspring never vocalised during any of the two types of intervals. None of the behaviours differed statistically between the 'laser engagement only' and 'experimental gaze alternation intervals'.

Table 4.8: The table shows the proportion of intervals in which the chimpanzee offspring engaged in the behaviour of interest for the two types of intervals. The statistical results for the comparison of intervals are shown on the right.

CHIMPANZEES	Laser engagement only interval	Experimental gaze alternation interval	GLMM
Approach	1/12	3/12	z = 0.65 p = .518
Vocalisations	0/13 0 variation	0/13 0 variation	n.a.
Potentially audible laser engagement	2/13	2/13	z = 0.98 p = .935

On a descriptive level, Ugandans showed an increase in approaches and vocalisations in the ‘experimental gaze alternation intervals’. They engaged less, however, in potentially audible behaviours towards the lasers in the ‘experimental gaze alternation interval’. However, like chimpanzees, the behaviours of the Ugandan infants did not statistically differ between the two types of intervals (See Table 4.9).

Table 4.9: The table shows the proportion of intervals in which the Ugandan infants engaged in the behaviour of interest for the two types of intervals. The statistical results for the comparison of intervals are shown on the right.

UGANDANS	Laser engagement only interval	Experimental gaze alternation interval	GLMM
Approach	0/20 0 variation	10/20	n.a.
Vocalisations	9/20	11/20	z = 0.63 p = .528
Potentially audible laser engagement	10/20	6/20	z = -1.28 p = .201

On a descriptive level, like Ugandans, British infants showed an increase in approaches in the ‘experimental gaze alternation intervals’, but no inferential statistics could be performed because they never approached others during ‘laser engagement only intervals’ (see Table 4.10). British infants did not statistically differ in their potentially audible laser engagement, but there was a trend for British infants to vocalise more in the ‘experimental gaze alternation intervals’ compared to the ‘laser engagement only intervals’.

Table 4.10: The table shows the proportion of intervals in which the British infants engaged in the behaviour of interest for the two types of intervals. The statistical results for the comparison of intervals are shown on the right.

BRITISH	Laser engagement only interval	Experimental gaze alternation interval	GLMM
Approach	0/19	8/19	n.a.
0 variation			
Vocalisations	8/20	14/20	z = 1.91 p = .056
Potentially audible laser engagement	7/20	4/20	z = -1.33 p = .184

Dyadic vs. Triadic Communication

The previous analysis indicated that British and Ugandan infants may have approached their mothers to communicate with them about the laser and the British infants’ use of vocalisations may have been a communicative signal directed at their mothers. I cannot, however, determine yet whether the Ugandan and British infants’ approach and the British infants’ vocalisations had anything to do with the presence of the laser, because the laser was present in both examined intervals. Therefore, the ‘experimental gaze alternation interval’ in which the offspring looked to their mother/sibling during laser engagement was contrasted

with a 'control gaze alternation interval' in which the offspring looked to the mother/sibling, but the laser was absent.

Since only 4 Ugandan infants looked to their mothers in the control period, they had to be excluded from the analysis. For 9 British infants I was able to match one experimental gaze alternation interval with a control gaze alternation interval and therefore, their approaches and vocalisations could be statistically investigated.

Table 4.11 summarises the characteristics of the control and experimental gaze alternation intervals for the British infants.

Table 4.11: This table shows the main characteristics of the analysed intervals including standard deviations for the British infants.

	British
Mean duration of 'experimental gaze alternation intervals' (SD)	10.58s (1.90)
Mean duration of 'control gaze alternation intervals' (SD)	10.43s (3.23)
Mean duration of look to conspecific in 'experimental gaze alternation intervals' (SD)	2.14 (1.45)
Mean duration of look to conspecific in 'control gaze alternation intervals' (SD)	2.28s (1.68)
Mean number of looks to conspecific in 'experimental gaze alternation intervals' (SD)	1.33 (0.5)
Mean number of looks to conspecific in 'control gaze alternation intervals' (SD)	1.22 (0.44)

The presence or absence of approaches and vocalisations were scored for the 'experimental gaze alternation interval' and the 'control gaze alternation interval' respectively. A Sign-ranked test showed that there was no difference between the

'control' and the 'experimental gaze alternation interval' with regard to the presence of approaches ($p = 1.00$) or vocalisations ($p = .625$) in the British infants.

Discussion

It was the aim of the Infant Only experiment to investigate some joint attention skills in chimpanzee, Ugandan and British offspring without giving their mothers the opportunity to scaffold their behaviour. To this end, a laser stimulus was projected into the visual field of the offspring only whilst the mother was inattentive. In contrast to most previous research, all offspring were tested with conspecifics in their everyday life environment to increase ecological validity and to create equal conditions for all participants. In the following sections, I will summarise and discuss the results of the Infant Only laser experiment.

Interest in laser stimulus

The offspring of all three study groups were generally interested in the laser dot as evidenced by visual or physical engagement with the laser stimulus. In the '*entire experimental period*', the chimpanzee offspring engaged with the laser more than the infants of the two human groups. Since there were more human experiments that lasted the full 180s than chimpanzee experiments, human infants were exposed to the laser for longer than chimpanzees. Therefore, the lower proportions of laser engagement in the two human groups may have been due to an increasing loss of interest in the laser dot as the experiment progressed. In the standardised '*52 sec experimental period*', however, there was no difference between the three groups and it can therefore be concluded that initially, all three groups showed equal interest in the laser dot.

Social Referencing

Although the chimpanzee, Ugandan and British offspring were interested in the laser stimulus, only a few individuals in all three groups looked to their mothers before physically engaging with the laser. Thus there was little evidence for the offspring of any group to engage in social referencing. This may not demonstrate a lack of ability, however, as they may not have regarded the laser as something

threatening and therefore the stimulus may not have 'provoked uncertainty' and was therefore unsuitable to elicit this behaviour. This was equally true for offspring of all three groups and social referencing was not observed less in the British infants as predicted. Although it may have prevented us from observing much social referencing, this did have considerable advantages, as the subjects' ease with the laser meant they interacted with it in a range of ways that we could then analyse.

Monitoring the Attention of Others

The offspring of the three groups looked at their mothers/siblings at comparably low rates during the standardised '*52 sec experimental period*'. Therefore, contrary to the prediction that the infants of the two human groups may look more to a social partner than chimpanzees, there was no difference between the three groups in the frequencies of looking at a conspecific. It may be argued that during the first minute of laser exposure, instead of monitoring the attention of conspecifics in the presence of an interesting stimulus, the offspring's attention was completely absorbed by looking at the laser. This, however, was not the case, as the offspring of all three groups did not look less to a conspecific in the '*52 sec experimental phase*' than in the '*52 sec control phase*'. What this result means is that the offspring of all three groups looked to conspecifics at generally low rates and this did not change when the laser stimulus was present.

Directed Communication during Laser Engagement?

Although the offspring of all three groups did not increase their rates of looking to their mothers/siblings when the laser was present compared to when it was absent, it was still possible that the offspring may still have had the motivation to share attention about the laser stimulus, but this was not expressed by the frequencies of looks to conspecifics but rather by potentially communicative behaviour that accompanied such looks. Therefore, I sought to identify the use of potentially communicative behaviours that were likely directed at the mothers/siblings. Operationally this meant investigating whether there was something about the offspring's behaviours that was temporally associated with a

look to a conspecific that was not present when they were solely focusing on the laser.

Overall, the offspring of the three groups were equally likely to direct potentially communicative behaviours (e.g. approaches, vocalisations, audible laser engagement) to their mothers/siblings. This indicates that there was no species or cultural difference with regard to their potentially communicative behaviours that were directed at their mothers/siblings.

As a second step, I investigated for each group separately whether the offspring of the three groups used approaches, vocalisations or audible engagement with the laser to communicate with their mothers/siblings. Interestingly, chimpanzee offspring did not vocalise during any of the analysed intervals which indicates that vocalisations may not be used by chimpanzees in this context.

Ugandans and British infants never approached their mothers during laser engagement without gaze alternation, but they did so in half of their laser engagement intervals with gaze alternation. This pattern was not found in chimpanzees. In addition, British infants showed a trend for more vocalisations that were associated with a look to their mother/sibling than during laser engagement without a look to another individual. It is possible that the trend for the increase of vocalisations during experimental gaze alternation intervals reflected the infants' motivation to attract the attention of a social partner. The lower rates of vocalisations during the 'laser engagement only intervals' exclude the alternative explanation that the infants were excited about playing with the laser and therefore vocalised more. Therefore, the finding that Ugandan and British infants, but not chimpanzees, seemed to approach their mothers/siblings and British infants also seemed to use vocalisations to communicate with them is consistent with the hypothesis that human infants would show more directed communication to their mothers than chimpanzees.

Dyadic vs. Triadic Communication

Although British offspring seemed to produce vocalisations as directed communicative signals, they were just as likely to do this when the laser was

absent as when it was present. Thus British offspring seemed to be producing vocalisations to engage in dyadic interactions with their mothers, rather than a triadic interaction about the laser. Therefore, contrary to the prediction that human infants would be more motivated to engage in triadic interactions with their mothers than chimpanzees, there was no difference between the offspring of the three groups with regard to triadic attention getters.

General Discussion and Future Directions

The Infant Only laser experiment revealed that there was no evidence for chimpanzee offspring to approach others, use vocalisation or to audibly engage with the laser to communicate with others during laser engagement. This is consistent with the prediction that chimpanzees may not be motivated to share attention with others (Carpenter & Call, in press.) and may therefore have preferred to engage individualistically with the laser stimulus. It is important to note, however, that chimpanzee offspring did not differ from the two human groups in this respect. In addition, the British infants' communication that was directed at their mothers was not *about* the laser. Therefore, human infants did not show a higher rate of triadic communication than chimpanzees.

It is unlikely, however, that the absence of joint attention skills in humans in the Infant Only experiment could merely be attributed to the laser not being an appropriate stimulus to trigger joint attention skills. The pilot study with older (12-22 months) Ugandan infants showed that they engaged in gaze alternation, vocalisations and pointing in response to the laser stimulus. In addition, the same 11 months old human infants who did not communicate about the laser stimulus with their mothers during the Infant Only experiment (this Chapter) displayed joint attention skills as a response to the laser stimulus in the Social experiment (see results, Chapter 5).

Although there was some evidence for human infants to communicate with their mothers/siblings during laser engagement, it is surprising, given the evidence of infants younger than 11 months to engage in 'showing' (Carpenter et al., 1998), that the human infants did not display any signs of trying to engage with their mothers/siblings *about* the laser. One possible explanation for the lack of

communicative attempts in the offspring is that the laser stimulus was so eye-catching and so fun to engage with that the offspring may have found individualistic engagement with it more rewarding than showing it to others. In addition, Deák and Triesch (2006) emphasized the importance of structured input from the social environment for the development of joint attention in human infants. This includes scaffolding from the mothers, but also habitual interactions that involve familiar objects. Both of these typical characteristics of the structured social environment were absent in the Infant Only experiment: the mothers could not scaffold the behaviours of the offspring, because they did not see the laser stimulus and the laser stimulus was novel and unusual in their environment. Therefore, when human infants (and possibly chimpanzees) encounter a novel and exciting object that they are not afraid of for the first time, their curiosity may override their motivation to show it to others and share attention about it. If the mothers could have also seen the laser stimulus, they could have scaffolded the infants' curiosity about it into a joint attention interaction.

In order to test the hypothesis that the infants' curiosity in the laser stimulus overrode their motivation to share attention about it, I would suggest conducting the Infant Only experiment repeatedly with chimpanzee and human infants. With repeated exposure to the laser, the infants would become familiar with the laser stimulus. The advantage of the laser stimulus is that its presentation can be varied so that the infants would not become bored by it whilst they familiarise themselves with it. It could be examined whether the infants show an increase in their communicative behaviours towards conspecifics as a function of increasing exposure with the laser stimulus.

If the infants communicate more about the laser with their mothers after repeated exposures compared to their first exposure, it could be concluded that the infants' initial excitement and curiosity first had to be exhausted before they can expand their focus and include others into their engagement. If chimpanzee offspring did not show such an increase in communicative behaviours after repeated laser exposure, it could be concluded that they either take much longer to habituate to

the stimulus or they do not have the same motivation to include other individuals into their laser engagement as human infants do.

If the 11 month old human infants do not show an increase in triadic communicative behaviours after repeated exposure to the laser, it is possible that the early joint attention interactions at 11 month require the assistance and scaffolding from the mother and that 11 month old infants may not have been able yet to purposefully attract the attention of others to show them the laser. The possibility that the mothers' scaffolding is very important for early joint attention to occur, was addressed in the Social laser experiment (Chapter 5) in which both, the offspring and a social partner, were exposed to the laser stimulus.

In order to examine whether the offspring succeeded in attracting the attention of their mothers, regardless of the intention of the offspring, and in order to identify which behaviours function to attract the attention of their mothers, it would have been necessary to code the looking behaviour of the mothers. Since human mothers knew that they were involved in an experiment and they received instructions to concentrate on the visual puzzle and chimpanzee mother did not, it was impossible to compare the behaviours of the mothers in this experiment as the instructions may have influenced the mothers' tendency to engage with the offspring. In this non- opportunistic experimental set-up for humans, that was necessary due to time constraints, it was not possible to expose only the infant to the laser without the mothers interfering and joining the infants' engagement. Therefore, they had to be distracted which enabled me to investigate the behaviour of the infant upon encounter with a novel stimulus, but I was unable to analyse the behaviour of the mothers and their reactions to the infant. Although it is not ethically possible to expose the human offspring to the laser stimulus without their mothers' informed consent, it would be possible in a future study with less time constraints to conduct the Infant Only laser experiment opportunistically with human mother-infant dyads by waiting until the mothers are occupied with their daily activities and the preconditions for the experiment are fulfilled. This study could reveal which of the offspring's behaviours attract the attention of human and chimpanzee mothers.

Since contingency learning is an important factor for the development of joint attention in human infants (Deák & Triesch, 2006), they may have to first learn the contingency between behaviours they naturally use to interact with objects and the reaction (a look) of their mothers to be able to intentionally and purposefully apply those behaviours in order to attract the attention of their mothers. It could further be revealed whether the functional attention getting behaviours of the offspring differ between chimpanzees and humans of different cultural background and whether these differences relate to whether or not and how chimpanzee and human infants engage in joint attention with their mothers.

Conclusion

The offspring of the three groups regarded the laser dot as an interesting stimulus, but they did not engage much in social referencing with their mothers and displayed equally few looks to conspecifics when engaging with the laser. There was no difference between the offspring of the three groups with regard to their communicative attempts towards others when the laser was present. When analysing the three groups separately, Ugandan and British infants showed a tendency for communicating with their mothers, but a further analysis revealed that these communicative attempts were likely used to initiate dyadic not triadic interactions. In short, when examining the behaviours of the “Infants Only” there was very little difference between wild chimpanzees, Ugandans and the British with regard to their joint attention skills. Further studies are required to reveal whether the offspring’s curiosity about the laser stimulus may have overridden their motivation to share attention and which behaviours of the offspring functioned to successfully attract the attention of their mothers. The importance of the mothers’ role in early joint attention behaviours was addressed in Chapter 5.

Chapter 5 : The Social Laser Experiment

Summary

The Social laser experiment aimed at investigating the presence and frequency of joint attention events in chimpanzee, Ugandan and British mother – offspring pairs as well as examining both the offspring's joint attention skills and the mothers' scaffolding behaviours in relation to a novel stimulus. To this end, the moving dot of a laser pointer was projected into the visual field of the mother -offspring dyad and their resulting interaction analysed.

The results of the Social laser experiment revealed that one chimpanzee mother-infant dyad engaged in two instances of joint attention. Nevertheless, the human dyads of both cultural groups showed significantly higher rates of joint attention than chimpanzees. No cultural differences were found with regard to the frequency of joint attention events.

When only considering the behaviour of the offspring, there were very few differences between the three groups. At a group level, chimpanzee offspring displayed gaze alternation at similar rates and engaged in anticipatory smiles at equally low rates as the two human groups. Human infants as a species, however, showed more gaze alternation than chimpanzee offspring.

Although Ugandan mothers had a tendency to display more intentional attention directing behaviours than British mothers, the mothers of both cultural backgrounds actively communicated with their infants during face to face contacts, whereas chimpanzee partners were never observed to do so. In addition, human mothers showed higher rates of observing their offspring's interaction with the laser than chimpanzee partners. This indicates that the human mothers may have played an important role in scaffolding the joint attention interactions and that the very low rates of joint attention in chimpanzees may be explained by a lack of the partners' motivation to scaffold the offspring into joint attention.

Introduction

As defined in Chapter 1 (p.22), joint attention is the mutual awareness of having attended to an external object or event between two or more individuals, whereby mutual awareness is established through communication of at least one individual during mutual gaze. Mutual gaze (face to face contact) is an important component of non-verbal joint attention, because it enables both individuals to exchange communication and share attention without using referential language.

At 11 months of age (the age of the human infants in this Chapter), Western human infants are able to coordinate their attention between objects of interest and an adult and they have the motivation to share attention and interest with others (Tomasello, 1995; Carpenter et al., 1998). They have started combining gaze alternation with positive affect (Striano & Bertin, 2005) and show objects to a social partner whilst alternating their gaze between object and partner (Carpenter et al., 1998). In addition, there is some evidence that 10 months old Western infants smile in anticipation of face to face contact during joint attention interactions which indicates their motivation to share attention and interest (Parlade et al., 2009). Although only the behaviour of the infant was examined in all studies mentioned above, it is likely that the infants' behaviour resulted in joint attention events (as defined above), because it is undebated that human adults are able to engage in true joint attention and were therefore able to adequately respond to the infants' behaviours. In addition, 11 months old Western human infants are able to respond to an adult's attempt to direct their attention: they are able to follow an adult's gaze to a target in front of them and to follow pointing gestures to targets in their visual periphery (Deák & Triesch, 2006).

Since the majority of joint attention studies have been conducted with Western human infants, little is known about the potential variation of joint attention skills across cultures. Since human infants are shaped by their cultures from very early on (Keller, 2007) and the social and non-social environments of the Ugandan and British infants are very different (see Chapter 3), including both cultures may enable me to establish whether joint attention emerges at the same age across

cultures. In addition, identifying cultural variants of joint attention skills can help us understand more about the cognitive infrastructure of joint attention.

The question of whether true joint attention is uniquely human is still unanswered. Chimpanzees follow the gaze of conspecifics (Tomasello et al., 1998) and some alternated their gaze between food and a human experimenter whilst pointing (Leavens et al., 2005), but chimpanzees have never been shown to actively and intentionally direct the attention of others to share interest with them (Carpenter & Call, in press). Most importantly, regardless of the social rearing history of the chimpanzees or whether they interacted with humans or conspecifics, they have never been shown to engage in joint attention as defined above (Tomonaga et al., 2004; Tomasello & Carpenter, 2005; Leavens & Bard, 2011). There has been no study to date that investigated whether wild chimpanzees engage in joint attention with each other. Since chimpanzees seem to possess some joint attention skills (e.g. gaze alternation, following gaze), it is important to investigate whether engaging in joint attention is an adaptive behaviour in their natural environment and therefore part of their natural behavioural repertoire.

Since joint attention requires the interaction of at least two individuals to occur and previous studies have mainly focussed on the behaviour of the infant, it is important to investigate the role of the mothers during joint attention interactions. Human mothers frequently scaffold early joint attention interactions with their infants which enables infants to learn the contingencies of joint attention interactions (Deák & Triesch, 2006). Although chimpanzee mothers engaged in mutual gaze with their infants (Bard et al., 2005), they did not actively stimulate their offspring with objects (Bard & Vauclair, 1984). Therefore, it is still unclear whether chimpanzee mothers have the motivation and the skills to scaffold triadic interactions with their offspring.

In this chapter, joint attention skills and joint attention itself were tackled from a multitude of different angles including behaviours before, during and after mutual gaze (face to face contact) in order to present a broad and detailed perspective on joint attention and its component behaviours in wild chimpanzees, Ugandans and the British. In the following sections, I will introduce the behaviours and

interactions that were investigated in this chapter and present my hypotheses with regard to potential species and cultural differences.

Simultaneous laser engagement

At first, it was important to establish how much the offspring and partner simultaneously engaged with the laser stimulus and whether there was a difference between the three groups. This was an important question, because the amount of the dyads' simultaneous laser engagement may reflect the dyads' inclination to engage with each other about something together and reveal how much opportunities they created for themselves to engage with each other in joint attention. This was an exploratory preliminary analysis, and therefore, no directional hypotheses were made.

Onlooking

When offspring and partner are not interacting with the laser stimulus at the same time, they could still be interested in the other's laser engagement. In other words, did one individual observe the laser related actions of the other even when not taking part in the activity? This behaviour was also coded by Bakeman and Adamson (1984, p.1281) as 'onlooking'. Although onlooking itself is not joint attention, because there is no mutual awareness in the two partners about the common focus of attention (see definition above), it is nevertheless very interesting to examine, because it could result in joint attention, if the observer and the actor establish mutual awareness (Carpenter & Liebal, 2012). In addition, human mothers often scaffold triadic interactions with their infants by either following into or redirecting the infants' focus of attention (Tomasello & Farrar, 1986; Carpenter et al., 1998). Observing the offspring's interactions with the laser may be important for mothers or older siblings to adjust their scaffolding behaviour to the offspring (Legerstee et al., 2007).

In Western humans, infants engaged in onlooking at similar rates with both mothers and peers from 6 – 15 months (Bakeman & Adamson, 1984). To my knowledge, onlooking has not yet been systematically investigated in other cultures or wild chimpanzees. Therefore, there was no directional hypothesis for

onlooking in the two cultures or the offspring's onlooking behaviours. Since human mothers seem to have a greater inclination to scaffold triadic interactions with their offspring, compared to chimpanzees, I predicted that human mothers would onlook their infants' interaction with the laser more than chimpanzee partners.

Face to face contact

Face to face contacts are also referred to as mutual looks or mutual gaze (Bard et al, 2005) and they constitute a central component of most joint attention interactions (Carpenter & Liebal, 2012). It is during face to face contacts when the minds of two individuals can meet and "share" their common experience about an object of interest. Hence, the mutual awareness of having attended to the same entity becomes manifest during face to face contact and is cemented by communication between the two social partners (see Chapter 1 p.22). Therefore, I investigated the frequencies and durations of face to face contacts and compared them between the three groups.

Since face to face interactions are less common in African cultures (Keller, 2003), I predicted that Ugandans would engage in less mutual gaze than British mother-infant dyads. Mutual gaze has been observed in wild chimpanzees by van Lawick-Goodall (1968) and in captivity (Bard, 1994; Bard et al., 2005). The mutual gaze in chimpanzee mother-infant dyads was shorter compared to human dyads (Bard et al., 2005). The studied subjects, however, were much younger than the chimpanzees of this study. Therefore, no directional hypothesis was made with regard to the frequency and duration of chimpanzee offspring-partner dyads' face to face contacts in comparison to the Ugandan and British dyads.

Detailed analysis of face to face contacts

Since face to face contacts were a vital component of joint attention (p.143), individual face to face contacts of chimpanzee, Ugandan and British offspring-partner dyads were analysed in more detail to identify joint attention skills, the partners' scaffolding behaviours and to investigate whether or not joint attention itself occurred.

Laser related attention getters

Before the dyad engaged in face to face contact, they may have used attention getters *about* the laser. Even if a stimulus is visible to both social partners, one individual may still try to attract the attention of the partner to himself, either to prolong the social interaction about the stimulus or to re-direct the partner's attention back to the laser, if her attention shifted away from it. Attention getters that are contingent with laser engagement may therefore occur before directing the attention of a social partner to the laser or they may indicate the motivation to share attention *about* the laser stimulus.

Since chimpanzees have never been shown to direct others' attention to share interest (Carpenter & Call, in press), I hypothesized that human offspring and well as partners would show more laser related attention getters than chimpanzees. The participants from the two human cultures were not expected to differ in this respect.

Anticipatory Facial Movements

Parlade et al. (2009) contrasted anticipatory smiles, in which infants who were engaged with an object of interest were already smiling before looking into the social partner's face, with reactive smiles that were given in response to seeing a smile on the partner's face. Anticipatory smiles have been described as an important indicator for the motivation to share attention and positive affect about an external object with a social partner (Venezia et al., 2004). Therefore, the display of anticipatory smiles may positively correlate with the participants' frequency of engaging in joint attention. Anticipatory smiles were common in 10 month old Western infants (Jones, Collins & Hong, 1991). Reactive smiles, in contrast, may only be a dyadic response to the adults smile and may be mediated by emotional contagion rather than voluntary affective exchange.

In this thesis, I extended the notions of anticipatory smiles into anticipatory facial movements, because in this cross-species comparison it was necessary to include several different types of facial movements, especially given that chimpanzees do not smile like humans do (Vick, Waller, Parr, Smith-Pasqualini & Bard, 2007).

Although mutual gaze (Bard et al., 2005) and facial movements have been studied in captive chimpanzees (Parr et al., 2007; Vick et al., 2007), there is, to my knowledge, no published study that links the display of facial movements to face to face contacts. Therefore, it is not known whether chimpanzees engage in anticipatory movements during (triadic) interactions with conspecifics. Since anticipatory facial movements during the engagement with the laser stimulus may indicate the motivation to share attention, it is important to establish, whether anticipatory facial movements occur in chimpanzee offspring and their partners at all and if so whether they are displayed as frequently as in Western humans. To my knowledge, there is no published study that indicates that Ugandan infants may show different amounts of anticipatory movements. Therefore, no directional hypothesis was made with regard to culture.

Directing and following attention

Previous research has shown that Western mothers often direct the attention of their offspring to objects whose names the infants should learn and that the offspring then follows the attention of the social partner (Tomasello, 1988; Carpenter et al., 1998). Therefore, I investigated whether the social partners, after having engaged in face to face contact with the offspring, directed their attention back to the laser. I hereby distinguished between the partners' functional (e.g. making contact with the laser stimulus) and intentional (e.g. pointing) attention directing behaviours. In addition, I aimed to investigate how successful both types of attention directing behaviours were by measuring the offspring's tendency to look back at the laser after either functional or intentional attention directing behaviours of their partners.

Since there is no evidence that chimpanzee mothers actively direct the attention of their offspring to objects (Bard & Vauclair, 1983) and African mothers in general engage less in object stimulation with their infants than Western mothers (Keller et al., 2009), it was predicted that British partners would use more intentional attention directing behaviours than either chimpanzee or Ugandan partners. Since both chimpanzees and humans infants follow the gaze of conspecifics, I predicted that they would not differ in their amount of attention following.

Gaze alternation

In several studies, gaze alternation was identified as an indicator for the infants' ability to engage in joint attention (e.g. Bakeman & Adamson, 1984; Carpenter et al., 1998; Parlade et al., 2009). Although the individual coordination of attention alone is not a sufficient indicator for joint attention, because gaze alternation can happen individualistically without sharing attention (Carpenter & Liebal, 2012), it is nevertheless a vital precondition for being able to engage in joint attention. Therefore, I first investigated whether each individual, offspring and partner, was able to coordinate their attention between the laser and the conspecific, before investigating whether joint attention as an event occurred.

Chimpanzees and human infants have been shown to engage in gaze alternation (Carpenter et al., 1998; Leavens et al., 2005), but chimpanzees did not alternate their gaze with their mothers or human experimenters to share attention and interest (Tomonaga et al., 2004, Tomasello & Carpenter, 2005). Therefore, I predicted that chimpanzees would show less gaze alternation than the human infants. I did not predict a difference between Ugandan and British infants.

Joint Attention

The final behaviour studied in this chapter determined whether all the joint attention skills and component parts mentioned above actually culminated in any joint attention events. To recap, a joint attention event was defined as:

“The mutual awareness of having attended to the same entity between two (or more) individuals. Mutual awareness is established through communication by at least one individual during mutual gaze.”

The key component of joint attention was mutual gaze (face to face contact) between the offspring and his social partner and the communication between them during face to face contact. Mutual gaze creates “attention contact” (Gomez, 1995) and communication causes “mutual awareness”.

Since 11 months old Western human infants have been shown to have the skills and the motivation to engage in joint attention (Bakeman & Adamson, 1984; Carpenter et al., 1998, Parlade et al., 2007), I predicted that they would engage in

joint attention, as defined above, even at this early age. Since there is no evidence for chimpanzee offspring to engage in joint attention with either humans or conspecifics during systematic investigations (Tomonaga et al., 2004; Tomasello & Carpenter, 2005), it was predicted that chimpanzees would show either no or very low frequencies of joint attention. African mothers generally engage in less object stimulation, which creates habitual triadic situations, than Western mothers (Keller et al., 2009). Although it is undebated that humans of all cultures engage in joint attention, it is nevertheless possible that the lower rates of maternal object stimulation in African cultures may lead to a slightly later onset of joint attention in Ugandan infants compared to British infants. Therefore, it may be possible that Ugandans would show less joint attention at 11 months than British infants.

Methods

Laser Stimulus

The laser stimulus used for the Social experiment was identical to the laser stimulus used in the Infant Only laser experiment (Chapter 4).

Pilot Studies

The pilot studies were described in Chapter 4 and also applied to the Social Laser Experiment.

Participants

Chimpanzees

The participating chimpanzees originated from the Sonso study group described in chapter 3. The final chimpanzee sample consisted of 8 offspring- partner dyads for the Social laser experiments. The mean age of the chimpanzee offspring during the Social laser experiment was 43.1 months (SD = 36.9). Six of the offspring were infants (4 females, 1 male), one was a juvenile female and one a sub-adult female. The partners were mothers for six focals and siblings for two focals. Including siblings as potential partners enabled me to conduct experiments with offspring

whose mothers avoided the laser and could therefore not be tested in the Social laser experiments. In addition, since the experiments were conducted opportunistically and meeting the preconditions for experiments was challenging in this research environment, including siblings in chimpanzees increased the number of experiments I could complete. If an experiment was conducted with a sibling as the social partner, the sibling was older than the focal, except in one instance (KM, KC). The younger sibling (KC) had already completed an experiment with his mother and in order to avoid repeated sampling of him in the role of the focal, his older sister was analysed as the focal. The age difference for KC and KM was 6 years.

Five out of the 8 offspring (focals) of the final sample and only one of the partners had previously been exposed to the laser prior to the Social laser experiment (see Table 5.1).

Table 5.1: Summary of the focals' and partners' laser exposures prior to the Social laser experiment and number of days that had elapsed between the last laser exposure before the Social laser experiment.

ID Dyad	Focal		Partner	
	Number of laser exposures prior to Social laser Experiment	Duration between last laser exposure and the Social Laser Experiment	Number of laser exposures prior to Social Laser Experiment	Duration between last laser exposure and the Social Laser Experiment
KX, KA	0	n.a.	0	n.a.
KC, KL	1	75 days	0	n.a.
NT, NB	1	28 days	0	n.a.
KB, KW	0	n.a.	0	n.a.
MI, MK	0	n.a.	0	n.a.
KM, KC	1	8 days	3	61 days
KH, KU	3	30 days	0	n.a.
HR, HT	2	9 days	0	n.a.

The mean number of exposures before the Social laser experiment was 1.0 (SD = 1.1) for focals and 0.38 (SD = 1.1) for partners. The mean number of days that had elapsed between the Social laser experiment and the last previous laser exposure was 30 days (SD = 27.2) for focals.

Ugandans and British

In humans, 12 Ugandan and 12 British mother-infant dyads participated in this study. Five of the 12 infants in each group were female and seven infants were male. Their mean age on the day of the Social experiment was 337.25 days (SD = 6.34) for Ugandan infants and 337.33 days (SD = 8.64) in British infants. Based on the counterbalanced design of Infant Only and Social experiment, 6 out of 12 infants of each human group had been exposed to the laser before, but no additional exposures occurred.

For all three study groups, the offspring was defined as the focal during the Infant Only laser experiment. Either the focal's mother or sibling was considered to be the social partner.

Design of Laser Experiments

The design of the laser experiments together with the average time that elapsed between the Infant Only and the Social experiment are explained for all three groups on page 103ff in Chapter 4.

Procedure

Chimpanzees

The chimpanzee Social laser experiments were conducted between March and May 2009 and between May and December 2010.

Preconditions

In chimpanzees, the laser experiments were conducted opportunistically whenever the following conditions were met:

- (1) The partner was less than 2m away from the offspring at the moment the experiment started
- (2) No conspecific other than the partner was present within 5m or they were unable to see the laser.

(3) The offspring and the partner were resting or playing. Feeding was also permitted, if the focal dyad had been feeding for at least 5min to make sure that they were not entirely focused on the food due to hunger.

Experimental Period

When the above-mentioned pre-conditions were met, after 1min of filming, the laser was switched on and presented within the visual field of offspring and partner. When occasionally, it was not possible to project the laser into the visual field of both, the laser was projected preferably into the visual field of the offspring. The recording equipment and the manner and duration of the laser presentation were the same as described in Chapter 4 (p.106-107). I worked with a field assistant (GM) who noted the party composition and alerted her of any individuals entering the presentation area.

Ugandans and British

The data collection for Ugandan infants took place between April 2010 and January 2011 and for the British infants between December 2009 and March 2010. The human Social laser experiment was conducted during one of the two visits to the participants' homes (Chapter 3). The partners in the human experiments were always the mothers of the infants.

Preconditions

Whenever the infant cooperated and was alert in the beginning of a visit, the laser experiments were completed before the other study parts. After both the mother and the infant had become relaxed and comfortable with the experimenters' presence, the mother was asked:

(1) To sit in a comfortable position within 2m of her infant with no body contact

(2) To face her infant

(3) To feel free to play with the infant using a familiar toy and to remove all other toys from within reach of the infant.

(4) when she sees the laser, to “interact with her baby as she would normally do, if something slightly unusual, like the laser dot was present” and that she was free to show the dot to the baby, but not to force the baby to interact with it, if he was not interested. Since the mothers were aware that the laser dot was the central part of the experiment, I wanted to avoid them feeling obliged to make the baby play with the laser as much as possible. Therefore, I explained that I was interested in natural interactions and there was no need to worry if the baby was not interested in playing with the laser.

(5) Not to behave as if she had already seen the laser before.

As in the Infant Only experiment described in Chapter 4, to reduce distractions during the experiment, the research assistant for the British study group invited siblings of the infant to play with her in a different room, before I started filming. Since in Uganda one field assistant was not enough to distract all children present in the compound, she instructed everyone present to stay beyond 5m of the presentation area and not to interfere with the experiment. In addition, she prevented arriving individuals from entering the experimental area.

The mother-infant dyad was filmed for one minute before the laser was presented as in the chimpanzee study group. The duration and laser presentation patterns were also identical to those for chimpanzees (Chapter 4, p.106-107.).

Ethics

The ethical approval obtained for the Social laser experiment were identical to the Infant Only experiment (see p.108-109, Chapter 4).

Two chimpanzee mothers were not comfortable in the presence of the laser, as demonstrated by repeatedly moving away from the laser dot during the experiment, or immediately leaving the area. The laser was not presented to them anymore. None of the chimpanzee offspring showed any signs of fear (i.e. screaming, bared teeth expression, pilo-erection, moving away from the laser) during the Social laser experiment.

Data Analysis

Laser exposure and periods for analysis

As in the Infant Only laser experiment, the aim for the duration of the laser presentation to both, the focal and the partner, was 180s. In chimpanzees, this could not always be achieved (see Table 5.2), because several chimpanzee trials were prematurely aborted when the preconditions were not met anymore (see participants). This happened more in chimpanzee than human trials because of the opportunistic character of the experiments and the lack of experimenter control over movement of the focal dyad and other individuals. Some experiments exceeded the desired maximum exposure of 180s, because my live measurements with the stopwatch were later corrected during the exact video analysis. If the laser exposure was longer than 180s, the video coding was cut off at 180s.

As in the Infant Only laser experiment, I used two different versions of the experimental period for the analysis of the Social laser experiment: the first had to be a standardised experimental period with an equal duration of laser exposure (see Table 5.2; 85.08s), available for all offspring-partner dyads of the three groups) and it was used to compare simultaneous laser engagement, onlooking, frequencies and durations of face to face contact. This period was called '*85 sec experimental period*'.

The second experimental period was of variable duration between 85.08s and 180s and was used to extract specific data during face to face contacts such as laser related attention getters, gaze alternation and joint attention (hereafter: '*entire experimental period*'). In contrast to the Infant Only experiment, there were no control periods analysed in the Social laser experiment although the dyads were filmed for 1min before the laser was presented. This was because the differential instructions for chimpanzees and humans (i.e. humans were asked to play with their offspring, whilst chimpanzees could not be instructed) would not have resulted in a comparable baseline of the behaviours of interest.

Table 5.2: Target and minimum laser exposure for the offspring-partner dyad in each group. The duration of the shortest chimpanzee experiment was used as the duration of the standardised '85 sec experimental periods' for the analysis.

	Target duration of laser exposure for the dyad (s)	Minimum duration of laser exposure for both (s)
Chimpanzees (N = 8)	180	85.08
Ugandans (N = 12)	180	113.40
British (N = 12)	180	158.12

Video coding

All Social laser experiments were coded using The Observer XT 10.5 software (see Chapter 4). The main behaviours coded were:

(1) Laser visible or invisible for offspring and partner

(2) Head direction of offspring and partners. As defined in chapter 4, the head direction of the participants was taken as an indicator for their gaze direction (Emery, 2000). Coded targets of the participants' looking behaviours were:

(a) laser, (b) partner/offspring (depending on who was coded), (c) other conspecific (excluding experimenter) or (d) elsewhere (including experimenter).

For the offspring's look to the partners, it was further distinguished whether he looked at the partner's face, torso, or whether this distinction was not possible.

Whether or not this face/torso distinction was possible depended on the distance and the relative position of offspring and partner.

(3) Laser engagement of offspring and partners. The coded types of laser engagement were: (a) Eye tracking only (i.e. no physical engagement), (b) Silent laser engagement. This was defined as any postural or limb movement in relation to the laser that did not produce a sound. (c) (Potentially) audible laser

engagement. This was defined as any postural or limb movement in relation to the laser that potentially or definitely produced a sound. (d) Pointing. This was defined as extending the arm, hand or any finger in the direction of the laser without closely following its movement or with a distance of 10cm or greater between laser and finger.

(4) Vocalisations and sounds of offspring and partners distinguishing between (a) vocalisations and/or sounds and (b) referential language.

(5) Salient facial movements for offspring and partners. A salient facial movement was defined as any salient movement of the facial muscles whenever at least half the face of the offspring or partner was visible. This included behaviours such as smiles, pouts, pressing lips together, raising eye-brows and clearly opening and closing the mouth.

(6) Distance between offspring and partners ranging from (a) body contact, (b) within reach to (c) beyond reach.

Inter-observer reliability

All videos were coded by the author. 25% of all videos were coded for inter observer reliability by a second independent coder who was blind to the hypotheses. Overall, kappa was good ($\kappa = 0.72$) indicating a sufficiently good inter observer reliability between the first and the second coder (Altman, 1991).

Definitions of Behaviours of Interest

In the following section, I will outline all the behaviours of interest that were analysed in this chapter and explain how they were coded.

Simultaneous laser engagement

There were two types of simultaneous laser engagements: (a) simultaneous visual laser engagement in which the offspring and the partner looked at the laser simultaneously in the absence of physically actions towards the laser, and (b) simultaneous physical laser engagement in which the offspring and the partner directed some physical behaviour at the laser simultaneously. The behaviour of the

offspring did not have to be identical to that of the partner. For example, whilst the offspring was trying to hit the laser, the partner pointed at it.

Onlooking

Onlooking was a measure of the offspring's or the partner's interest in the laser related behaviours of the other. Operationally, onlooking was defined as individual A looking at individual B or the laser whilst individual B was physically engaging with the laser. Individual A could either be the offspring or the partner. The same is true for individual B.

Face to Face Contact

Face to face contact was defined as follows: the offspring's head faced towards the partner's face and the partners head faced in the direction of the offspring's face at some point during the offspring's look to the partner's face. For offspring looking at the laser generally meant looking down and looking to the partner's face meant looking up: these were relatively easy to code. Indeed, for the offspring, I was able in most cases (82.6% for chimpanzees, 97.1% in Ugandans and 92.3% in the British, no group difference GLMM: $z = 1.21$, $p = .227$) to distinguish their looks to the face from their looks to the torso of the partner. Unfortunately, due to the larger body size of the partners, coding their head direction was more challenging. For partners, looking at the laser and the offspring generally required them to look down, therefore, it was not always possible to reliably distinguish between the partners' looks to the offspring's torso and face (Samuelson, Smith, Perry & Spencer, 2011). In these instances I coded whether the partners head direction was congruent with the position of the offspring's face during the offspring's look to the partner's face. I applied the same rules to the offspring's looks in the rare instances in which their exact head direction could not be accurately determined.

Laser Related Attention Getters

Generally, attention getters included the following behaviours:

(A) Producing vocalisations/ sounds

(B) Producing any noise that may function to attract the attention of the other towards to the body and/or face of the individual who produced the noise (e.g. clapping hands, ostensibly touching one's own body, audible laser engagement)

(C) Producing visual signals within the visual field of the focal/partner that may function to attract the attention of the other to look towards the body and/or face of the individual who produced the signal (e.g. scratching, waving arms, overtly tracing the laser).

Merely producing one or more of the three above mentioned behaviours alone, however, would not have indicated whether the attention getter was directed at the social partner. Therefore, looking at the other whilst performing the behaviour was essential for any of those behaviours to be counted as a dyadic attention getter, because otherwise, individualistic laser engagement would have been included in this category. In short, only if the head of the actor was facing the recipient in the 3s before and/or during one of the behaviours defined above, was the behaviour scored a dyadic attention getter.

In order to single out dyadic attention getters from the potentially triadic ones (i.e. that were *about* the laser), I further scored whether the actor looked to the laser within 3s before the attention getter started. Therefore, ***laser-related attention getter*** was scored, (a) if the actor produced any of the above mentioned behaviours (A-C) within 3s before the face to face contact started and (b) if the actor looked to the recipient in the 3s before and/or during the attention getting behaviour. This behaviour was scored in offspring as well as partners.

Anticipatory Facial Movements

The definition of an anticipatory facial movement was as follows: whilst or after an individual looked to the laser she produced a salient facial movement (e.g. a smile) and only then shifts her head to the other individual's face to face. This means that the facial movement was already present at the start of the face to face contact (Parlade et al., 2009).

Directing and Following Attention

The partners' directing of attention was defined as the partner engaging in behaviours that may function to direct the attention of the offspring to the laser either during face to face and/or within 3s after. The offspring, who was not attending to the laser at the moment the attention directing behaviour started, may subsequently orient towards the laser, but this was not a necessary prerequisite for the partner to be scored as engaging in directing attention (as she may have had the intention to direct individual B's attention to the laser, but remained unsuccessful).

The behaviours that were defined as directing attention are as follows:

- (a) Contact visual laser signals (contacting or trying to contact laser)
- (b) Non-contact laser signals which are not used to physically make contact with the laser, e.g. hand >10cm away from the laser or stationary (pointing)
- (c) Referential language about the laser

Contact laser signals were categorised as "**functional attention directing behaviours**", i.e. communicative signals that may function to direct the attention of the offspring, but the partner may not have had the intention to do so. Instead, the partner may shift her attention away from the offspring to engage individualistically with the laser again. As a result of her behaviour, the offspring then may have used the unintentional signal of the partner to shift his attention to the laser.

Non-contact laser signals and referential language *about* the laser, however, may have been used by the partner to intentionally direct the attention of the offspring

to the laser. Therefore, they were categorised as “**intentional attention directing behaviours**”.

The partners’ attention directing behaviours could only be scored, if she looked at the laser before the offspring after the face to face contact. The above defined attention directing behaviours were scored for the brief interval in which the partner already faced the laser and the offspring had not yet shifted his attention back to the laser. The interval was terminated once the recipient re-focused his attention on the laser or 3s had elapsed.

To investigate the offspring’s attention following, I scored for each attention directing event whether the offspring looked back at the laser within 3s after the face to face contact. I further aimed to analyse whether the offspring looked back at the laser more often after the partners’ intentional attention directing behaviours compared to functional attention directing behaviours.

Gaze Alternation

If an individual looked to the laser within 3s before the face to face contact started and looked back at the laser within 3s after the face to face contact ended, this was scored as **gaze alternation** in the absence of any other communicative behaviour (e.g. attention getter, directing attention behaviour).

Joint Attention

The operationalisation of joint attention in this thesis is not just a simple gaze shift pattern, it also tackled the communicative aspect during a stimulus associated face to face contact and, in addition, is mutual, because both individuals are involved in a face to face contact. The operational definition of joint attention, as given in Chapter 1, was:

Individual A and individual B looked at the same stimulus before engaging in face to face contact. During face to face contact, individual A and/or B engaged in communication. Communication consisted of either vocalisations or salient facial movements.

Based on this operationalisation, I first scored whether both individuals, the offspring AND the partner looked to the laser in the 3s before engaging in face to face contact. Second, I investigated whether the following communicative behaviours were present DURING the face to face contact: (a) vocalisations/sounds and (b) salient facial movements. If either of these two communicative behaviours was present in one or both partners, after both had looked to the laser in the 3s before the face to face contact, the interaction was labelled "**joint attention**".

There are some behaviours that are similar to joint attention, but do not fulfil all criteria of its operational definition:

(1) Neither individual looked to the laser within 3s before the face to face contact started. In this case, the face to face contact was not associated with and therefore probably independent of the presence of the laser. Since the two individuals are attending to each other and possibly engaging in a dyadic interaction, this event was scored as "**dyadic attention**"

(2) Only one of the two individuals looked to the laser before the face to face contact. This may show one individual's attempt to engage in joint attention with the social partner, but since the social partner did not look to the laser, no mutual awareness of both having attended to the laser can be established. This event was scored as "**unilateral triadic attention**"

(3) Both individuals looked to the laser within 3s before the face to face contacts, but there was no communication during face to face contact. In this case the face to face contact would be triadic, but since communication is required for "mutual awareness" to be established, it could not be scored as joint attention. Instead, this event was scored as "**triadic attention**"

Statistical Analysis

The statistical methods used in this thesis were outlined in the statistical analysis section in Chapter 4, p.116ff.

Results

Excluded Experiments

In addition to the 8 chimpanzee offspring who were included in the final sample, 4 additional chimpanzee offspring participated in this study and 13 additional experiments were conducted. In the 13 excluded instances, the experiment was aborted at an early stage, because either the partner showed repeated avoidance of the laser (N = 2), or the preconditions for conducting the experiment were no longer met and the resulting laser exposures were too short to meaningfully analyse (N = 11) (see Data Analysis).

None of the sessions in humans had to be prematurely aborted. Therefore, all 24 dyads (12 Ugandan and 12 British) were included in the data analysis.

Activities of Chimpanzee Offspring and Partners

Since human mothers were instructed to play with their infants during the 1min preceding the laser presentation (see below), the human mother-infant dyads were either resting or playing. Since this was not possible with the chimpanzees, it is important to report here, what their main activity was before the start of the laser exposure. All 8 chimpanzee offspring were mainly resting during the 1min preceding the laser presentation, whereas 6 partners were also resting and 2 were feeding for more than 5min.

Laser Exposure

Table 5.3 summarises the mean laser exposures in Social laser experiments of up to 180s duration. In addition, it shows the individual mean laser exposure for the offspring and the partner.

Table 5.3: Mean durations of exposure time with laser for offspring, partner and both during the social laser experiment.

	Chimpanzees (N = 8)	Ugandans (N = 12)	British (N = 12)
Laser visible to both	150.17s SD = 41.91	162.06s SD = 21.69	173.77s SD = 7.20
Laser visible to offspring (visible to both included)	174.39s SD = 44.20	162.43s SD = 21.75	173.77s SD = 7.20
Laser visible to partner (visible to both included)	169.02s SD = 44.97	169.61s SD = 22.30	176.48s SD = 6.25

Interest in the Laser Stimulus

Before conducting any further analysis, it was important to establish whether the participants of the three groups were interested in the laser stimulus.

The offspring of the three groups did not differ in their overall or physical laser engagement in the Social experiment. In contrast, for overall laser engagement, the partners of the three groups differed significantly (see Table 5.4). Chimpanzee partners engaged less with the laser than either Ugandan or British partners. When comparing only the physical engagement of the partners, however, there was no significant difference with respect to the partners' laser engagement between the three groups.

Table 5.4: Summary of average proportions of the '85 sec experimental period' of the Social laser experiment that offspring and partners spent performing laser engagement behaviours. The right column shows the statistical results. *** refers to a p-value < .001.

	Chimpanzees (N = 8)	Ugandans (N = 12)	British (N = 12)	Statistics
Mean proportion (SD) offspring engaged (visually or physically) with laser	0.52 (0.16)	0.67 (0.20)	0.67 (0.18)	One Way ANOVA, F (2,29) = 2.12, p = .138
Mean proportion (SD) partners engaged (visually or physically) with laser	0.42 (0.22)	0.88 (0.09)	0.82 (0.08)	Welch's F (2, 14.9) = 16.39, p < .001 CH <***UG CH <***BR UG = BR
Mean proportion (SD) offspring physically engaged with laser	0.28 (0.23)	0.22 (0.11)	0.32 (0.16)	One Way ANOVA, F (2,29) = .975, p = .389
Median proportion (IQR) partner physically engaged with laser	0.07 (0.19)	0.29 (0.53)	0.09 (0.20)	Kruskal-Wallis, χ^2 (2) = .909, p = .635 (asymptotic)

	Chimpanzees (N = 8)	Ugandans (N = 12)	British (N = 12)	Statistics
Number of offspring who physically engaged with the laser	7/8	12/12	11/12	n.a.
Number of partners who physically engaged with the laser	7/8	8/12	10/12	n.a.

Simultaneous Laser Engagement

In order to calculate the proportions of simultaneous laser engagement, *the '85 sec experimental period'* was used. Since the partners of the three groups engaged with the laser at different rates, I had to examine the proportions of overall engagement each individual spent performing simultaneous laser engagement. Hence, I calculated for offspring and partners separately, the proportions of their total duration of visual/physical laser engagement they dedicated to simultaneous visual/physical laser engagement when the laser was visible to both offspring and partner. The resulting proportions for each group were then compared between the three groups.

The possible sample for simultaneous visual engagement consisted of 8 chimpanzee, 12 Ugandan and 12 British offspring and partners; however, one chimpanzee and one British offspring and one chimpanzee, 4 Ugandan and 2 British partners did not engage with the laser physically during the first 85s of laser exposure. Therefore, the final sample consisted of 7 chimpanzees, 12 Ugandans and 11 British offspring and 7 chimpanzees, 8 Ugandans and 10 British for partners. Table 5.5 shows that there was a significant group difference for the offspring's simultaneous visual laser engagement.

Table 5.5: Summary of the results for the proportions of simultaneous laser engagement in the offspring's overall visual or physical engagement with the laser. IQR = Inter quartile ranges, ** corresponds to a p-value between .001 and .01 and * to a p-value > .01.

OFFSPRING	Chimpanzees	Ugandans	British	Kruskal-Wallis and Mann U post-hocs
Median proportions of simultaneous visual laser engagement (IQR) in all engagement	0.28 (0.68)	0.98 (0.08)	0.92 (0.15)	$\chi^2(2) = 10.95$, p = .004 (asympt.) CH <** UG CH <* BR UG = BR
Median proportions of simultaneous physical laser engagement (IQR) in all engagement	0.00 (0.10)	0.06 (0.22)	0.20 (0.12)	$\chi^2(2) = .782$, p = .687

Post-hoc pair wise comparisons showed that chimpanzees engaged less in simultaneous visual laser engagement than both human groups who did not differ statistically. Chimpanzee and Ugandan offspring both showed very low rates of physical laser engagement with their partners compared to the British. There was no statistical difference, however, between the three groups.

Like offspring, the partners of the three groups differed significantly with respect to their proportions of simultaneous visual laser engagement with a trend for chimpanzee partners to engage less in simultaneous visual laser engagement than the British (Table 5.6). There was no difference between the three groups in terms of simultaneous physical engagement.

Table 5.6: Summary of the results for the proportions of simultaneous laser engagement in the partners' overall visual or physical engagement with the laser. SD = Standard deviation, IQR = Inter quartile ranges,' corresponds to a trend.

PARTNERS	Chimpanzees	Ugandans	British	Statistics
Mean proportions of simultaneous visual laser engagement (SD) in all engagement	0.51 (0.29)	0.68 (0.18)	0.74 (0.20)	One Way ANOVA: F (2,29) = 2.75, p = .081 CH = UG CH < BR UG = BR
Median proportions of simultaneous physical laser engagement (IQR) in all engagement	0.00 (0.38)	0.09 (0.10)	0.20 (0.34)	Kruskal-Wallis: $\chi^2(2) = 1.64,$ p = .457

Onlooking

The rates of onlooking indicate whether an individual was interested in observing the others' laser engagement. As for simultaneous laser engagement, the '*85 sec experimental period*' was used for all groups. Since the opportunities for the offspring's onlooking were limited by the duration of the partners' physical laser engagement (and vice versa), the onlooking durations for the offspring were divided by the total duration of the partners' physical laser engagement during the '*85 sec experimental period*'. The same procedure was applied for the total duration of the partners' onlooking.

Partners' onlooking

As mentioned before in simultaneous laser engagement, there was one chimpanzee and one British offspring who did not engage with the laser physically during the '*85 sec experimental period*'. Their partners therefore had to be excluded

from the analysis. The final sample for onlooking of the partners consisted of 7 chimpanzees, 12 Ugandans and 11 British.

Figure 5.1 shows that, descriptively, chimpanzee partners engaged in onlooking at low rates compared to the Ugandan and British partners.

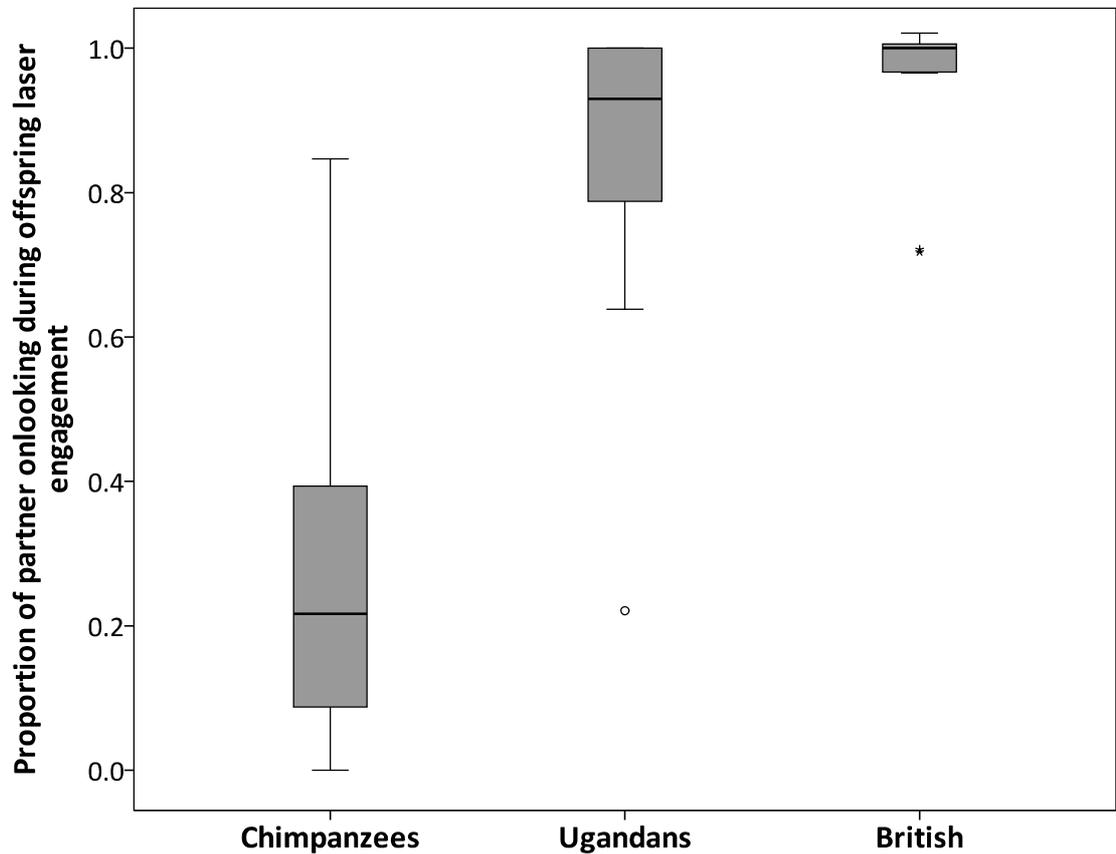


Figure 5.1: Boxplot showing the partners' median proportion of onlooking whilst the offspring was physically engaged with the laser.

A Kruskal-Wallis test showed that the rates of the partners' onlooking of the partners in the three groups differed significantly ($\chi^2(2) = 15.04, p = .001$, asymptotic). Post-hoc Mann Whitney U tests revealed that chimpanzee partners engaged in onlooking significantly less than Ugandan partners ($U = 6.00, p = .001$) and British partners ($U = 2.00, p > .001$). There was no statistical difference in partner onlooking between the British and the Ugandans ($U = 36.00, p = .064$, corrected α). This result shows a clear species difference.

Offspring's onlooking

As mentioned above, there was one chimpanzee, 4 Ugandan and 2 British partners who did not physically engage with the laser in the '85 sec experimental period'.

The offspring of those partners were therefore excluded from the analysis, which resulted in a final sample of 7 chimpanzees, 8 Ugandans and 10 British offspring.

Figure 5.2 shows that, descriptively, the offspring of the two human groups engaged in onlooking at higher rates compared to the chimpanzee offspring.

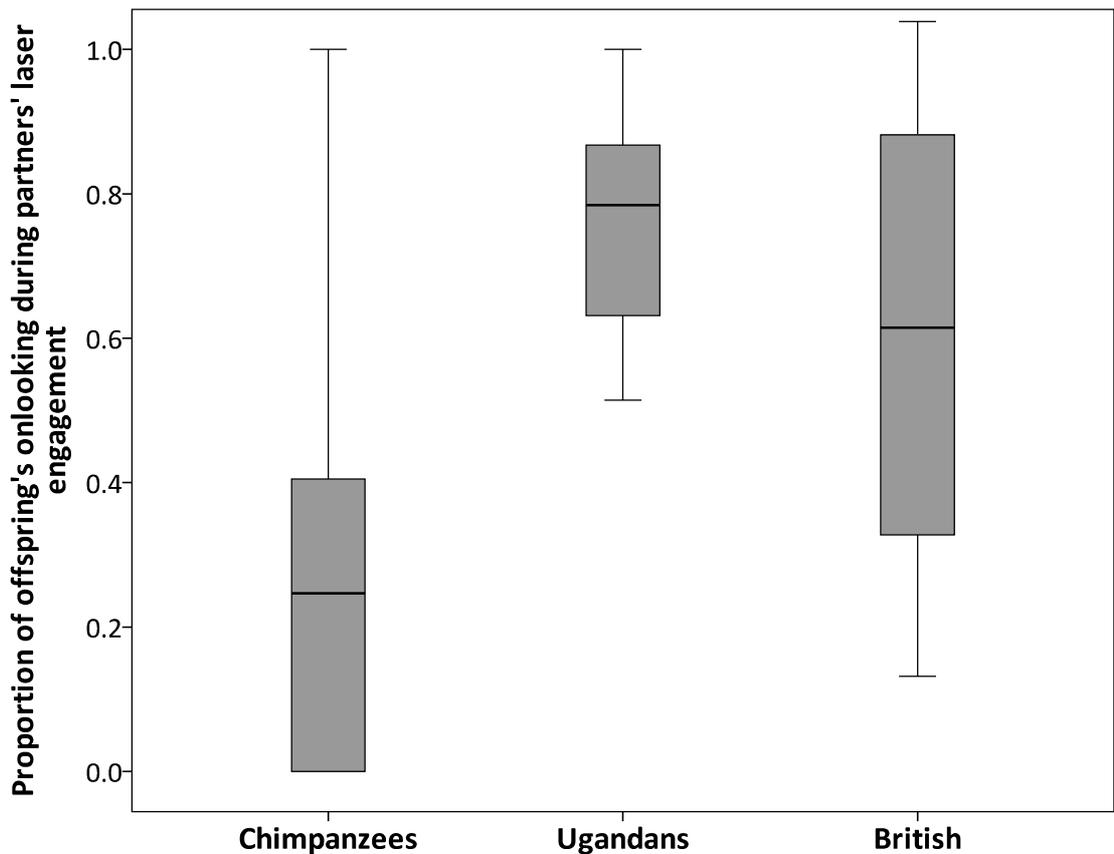


Figure 5.2: Boxplot showing the offspring's median proportion of onlooking whilst the partners were physically engaged with the laser.

A Kruskal-Wallis test revealed a significant group difference ($\chi^2(2) = 6.08, p = .048$, asymptotic). The Mann Whitney U post hoc comparisons showed that there was a trend for Ugandan offspring to engage more in onlooking than chimpanzee offspring ($U = 8.5, p = .021$, Sidak corrected), but chimpanzee and British offspring

did not significantly differ with respect to their onlooking rates ($U = 16.0, p = .070$) nor did Ugandan and British offspring ($U = 30.0, p = .408$).

Face to Face Contacts

As mentioned in the introduction, face to face contacts or mutual looks are central for most non-verbal joint attention bouts. Therefore, face to face contacts are extensively analysed in this chapter. First, the frequencies and durations of face to face contacts were compared between the three groups within the '*85 sec experimental period*' and then the nature of all face to face intervals that occurred within 180s of laser exposure were analysed in more detail.

Frequency and duration of face to face contacts

In order to extract the frequencies of face to face contacts, the '*85 sec experimental period*' was used. The frequencies of face to face contacts in the '*85 sec experimental period*' were relatively low in all three groups and their frequencies of face to face contacts did not differ significantly (Table 5.7). Unfortunately, no inferential statistical tests for the durations of face to face contacts could be performed for all three groups, because only 5 chimpanzee dyads engaged in face to face contacts in the '*85 sec experimental period*'. Ugandans and British, however, did not differ with respect to their durations of face to face contacts.

Table 5.7: This table summarises the number of focal dyads in each group who displayed face to face (ftf) contact during the '85 sec experimental period' in the Social experiment, the median number of looks and the median duration of the face to face contacts. On the right, the results of the statistical test are displayed.

	Chimpanzees	Ugandans	British	Statistics
Number of dyads who engaged in ftf contact	5/8	9/12	12/12	n.a.
			0 variation	
Median number of ftf contacts (IQR)	1.5 (3)	1 (3)	1.5 (2)	Kruskal-Wallis: $\chi^2 (2) = .825, p = .676$
Median duration of ftf contacts (IQR)	0.96s (0.54)	1.58s (0.95)	1.39s (0.97)	Mann- U: UG vs. BR U = 47, p = .651
	small N			

Detailed analysis of face to face contacts

In the following sections, for all face to face contacts that occurred in the Social experiments, specific sequences of behaviours (e.g. gaze alternation) were extracted and analysed for all three groups. The 'entire experimental period' (up to 180s of laser exposure) was considered, as it was the details of behaviour surrounding these key events that were of interest (not the relative frequency of the face to face events themselves) and it was important to sample as many of these as possible to make the results as representative as possible.

All face to face contacts before or after which the offspring was also engaged with an object other than the laser were excluded. This was to make sure that the analysed behaviours were about the laser and not any other object. In addition, for

all behaviours that required a look to the laser in the 3s before or after the face to face contact, face to face contacts in which the subjects did not look to the laser and the laser was switched off less than 2s before or after the face to face contact were excluded from the analysis. This was done to give the subjects enough opportunity to look at the laser. These factors together mean that different analyses have different sample sizes.

Laser Related Attention Getters

Laser related attention getters may reveal whether the offspring and the partners were trying to attract the attention of the social partner either to initiate a triadic interaction about the laser or to prolong an existing interaction about the laser. Eight chimpanzee, 9 Ugandan and 11 British offspring and 8 chimpanzee, 10 Ugandan and 11 British partners contributed data to this analysis.

The offspring of all three groups displayed laser related attention getters at equally low rates (Table 5.8). The total number of the chimpanzee partners' laser related attention getters was equally small. Ugandan and British partners displayed more laser related attention getters which was reflected in an overall difference between the partners of the three groups. The post-hoc analyses, however, showed no significant differences between the partners of the three groups.

Table 5.8: Summary of the results of the offspring's and partners laser related attention getters before engaging in face to face (ftf) contact.

	Chimpanzees	Ugandans	British	GLMM
Total number of ftf contacts in which offspring showed laser related attention getters	5/21	1/24	5/32	$z = .194,$ $p = .846$
Total number of ftf contacts in which partners showed laser related attention getters	5/21	10/31	16/32	$z = 2.01,$ $p = .045$ CH = UG CH = BR UG = BR

Table 5.8 also indicated that whilst chimpanzee offspring and partners engaged in the same number of laser related attention getters, Ugandan and British partners showed more laser related attention getters than the offspring. A binomial GLMM confirmed this observation and shows that the increased use of laser related attention getters in the Ugandan and British partners was significant (Figure 5.3).

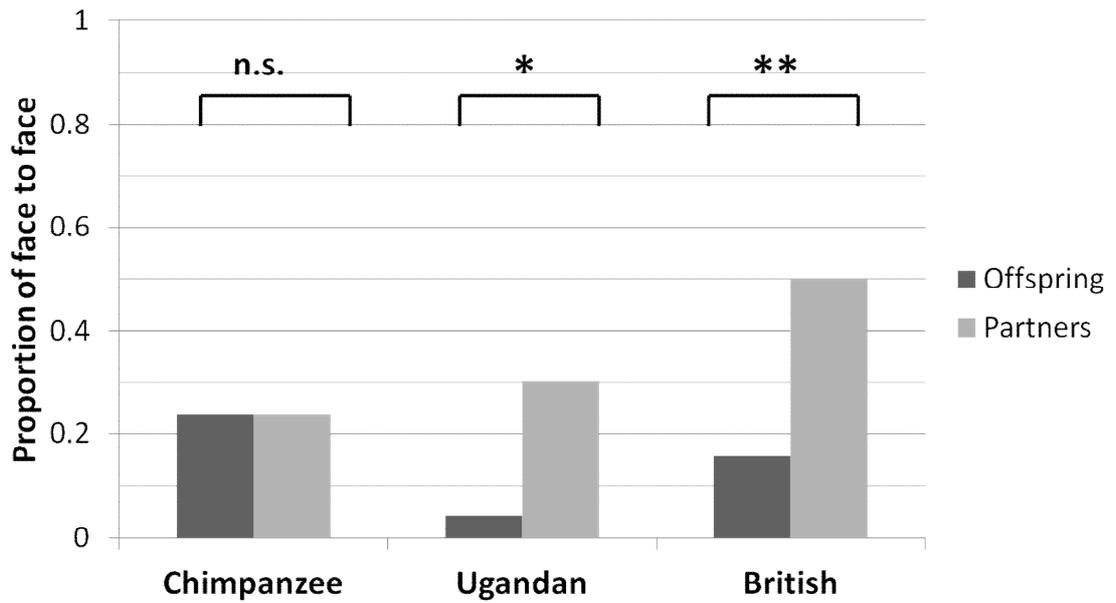


Figure 5.3: Bar graphs showing the proportion of all face to face contacts in which laser related attention getters were present in offspring and partners. A binomial GLMM showed that partners gave more attention getters than offspring in Ugandan ($z = 2.11$, $p = .035$) and British ($z = 2.80$, $p = .005$). Chimpanzee offspring and partners did not statistically differ ($z = .196$, $p = .844$).

Anticipatory Facial Movements

Anticipatory facial movements are linked to an individual's motivation to share attention and interest about an external object or event. Seven chimpanzee, 7 Ugandan and 9 British offspring were included in this analysis. Only 2 chimpanzee partners contributed data to this analysis. This was mainly due to the limited visibility of their face before and during the face to face contact. Therefore, they had to be excluded from the statistical analysis and only the partners of the two human groups were compared.

The offspring of the three groups did not differ with respect to their rates of displaying anticipatory facial movements. In addition, Ugandan and British partners did not differ in their rates of anticipatory facial movements (see Table 5.9).

Table 5.9: Summary of the results of the total number of face to face (ftf) contacts in which the offspring or the partners showed anticipatory facial movements. The right column shows the results of the statistical tests (GLMM).

	Chimpanzees	Ugandans	British	GLMM
Total number of ftf contacts in which offspring displayed anticipatory facial movements	2/13	6/21	4/19	$z = .404,$ $p = .686$
Total number of ftf contacts in which partners displayed anticipatory facial movements	1/4 small N	5/25	4/16	UG vs.BR $z = .377,$ $p = .706$

Directing and Following Attention

In order to investigate potential scaffolding behaviours of the partners, several different attention directing behaviours were examined. Unfortunately, only 4 chimpanzee partners contributed data to this analysis, because in most cases, the offspring looked at the laser first after the face to face contacts. Therefore, inferential statistics were only conducted with the two human groups. Nine Ugandan and 8 British partners contributed data to this analysis.

British and Ugandan partners did not differ with respect to functional attention getters, but Ugandan partners showed a trend for using more intentional attention directing behaviours than British partners (Table 5.10). Chimpanzee partners could not be included in the statistical tests, but they were not observed to engage in any intentional attention directing behaviours.

Table 5.10: Summary of the chimpanzee, Ugandan and British partners' functional and intentional attention directing behaviours after face to face (ftf) contacts. In the right column, the results of the statistical tests are displayed.

	Chimpanzees	Ugandans	British	GLMM
Total number of ftf contacts after which only functional attention directing behaviours to laser were present	5/11 small N	2/18	2/13	UG vs. BR z = .369, p = .712
Total number of ftf contacts after which intentional attention directing behaviours to laser were present	0/11 small N	9/18	4/13	UG vs. BR z = -1.87, p = .062

The offspring's attention following was dependent on the presence of the partners' attention directing behaviours analysed above. Table 5.11 lists the proportion of functional and intentional attention directing behaviours of the partners after which the offspring looked back at the laser. Due to small sample sizes, no inferential statistics on intentional and functional attention directing behaviours could be performed.

Table 5.11 shows that the offspring of all three groups had a high tendency to look back at the laser within 3s after the face to face contact ended. The two human groups looked back at the laser after all intentional and functional attention directing behaviours of the partners which may just reflect their high overall tendency to look back at the laser.

Table 5.11: Summary of the results for the offspring's attention following to the laser after face to face (ftf) contacts after which the partners looked back at the laser first.

	Chimpanzees	Ugandan	British
Total number of ftf contacts after which offspring looked back at laser regardless of whether attention directing behaviour was present or not	7/11 N = 4	17/18 N = 9	11/13 N = 8
Total number of ftf contacts after which any attention directing from partner behaviour was present	5/11 N = 4	11/18 N = 9	6/13 N = 8
Total number of ftf contacts with partners' functional attention directing behaviour after which offspring looked back at laser	4/5 N = 4	2/2 N = 1	2/2 N = 2
Total number of ftf contacts with partners' intentional attention directing behaviour after which offspring looked back at laser	0/0 N = 4	9/9 N = 5	4/4 N = 3

Gaze Alternation

Before revealing whether joint attention has occurred between the offspring – partner dyads, I first investigated whether the offspring and the partners individually coordinated their attention between the laser and the social partner.

8 chimpanzees, 9 Ugandans and 9 British offspring and partners contributed data to this analysis. There was no difference between the offspring or partners of the three groups with regard to the total number of face to face contacts in which gaze alternations were present (see Table 5.12).

Table 5.12: Summary of the results of the offspring's and partners gaze alternation that included a face to face (ftf) contact.

	Chimpanzees	Ugandans	British	GLMM
Total number of ftf contacts in which offspring engaged in gaze alternation	7/16	18/20	14/20	$z = 1.48,$ $p = .139$
Total number of ftf contacts in which partner engaged in gaze alternation	10/16	20/20 0 variation	20/20 0 variation	n.a.

Since chimpanzee offspring engaged in gaze alternation in less than half of their face to face contacts, but the offspring of both human groups in more than half of their face to face contacts, I decided to test whether there was a species difference between the chimpanzee and the human offspring. A binomial GLMM revealed that human offspring engaged significantly more in gaze alternation than chimpanzee offspring ($z = 2.41, p = .016$).

Joint Attention

By investigating gaze alternation, I only looked at offspring and partners individually to see whether they were individually able to coordinate their attention between laser and the conspecific. The following analysis focused on revealing whether joint attention occurred between the offspring and their social partner. At first, I will focus on the behaviours that are similar to joint attention, but do not fulfil the all criteria of the operational definition of joint attention (i.e. dyadic attention, unilateral triadic attention, triadic attention). After that, I will focus on joint attention itself.

(a) Dyadic and unilateral triadic attention

For dyadic and unilateral triadic attention, 8 chimpanzee, 9 Ugandan and 9 British offspring-partner dyads could be included into the analysis. All three groups engaged in dyadic attention (i.e. face to face contacts that were not preceded by a look to the laser from either offspring or partner) at very low rates (see Table 5.13).

The table shows that, descriptively, chimpanzees engaged in a higher number of unilateral triadic attention bouts (i.e. face to face contacts that were preceded by a look to the laser by only the offspring or the partner) than the two human groups. Since the Ugandans had no variability in their data, they had to be excluded from the analysis. The GLMM showed that chimpanzees and the British did not differ with respect to the number of face to face contacts that were classified as unilateral triadic attention (Table 5.13).

Table 5.13: Summary of the results of the total number of face to face (ftf) contacts with dyadic and unilateral triadic attention between the offspring and the partner. The right column shows the results of the statistical tests (GLMM).

	Chimpanzees	Ugandan	British	GLMM
Total number of ftf contacts in which dyadic attention occurred	1/21	0/25	1/22	n.a.
		0 variation		
Total number of ftf contacts in which unilateral triadic attention occurred	5/21	0/25	1/22	CH vs. BR z = -1.64, p = .100
		0 variation		

With regard to the 5 instances of unilateral triadic attention in chimpanzees, in 3 instances, it was the partner who looked to the laser before the face to face contact and in 2 instances it was the offspring. In the British, the one instance of unilateral triadic attention was caused by the partner looking to the laser before the face to

face contact. Face to face contacts that involved dyadic and unilateral triadic attention were excluded from further analysis.

(b) Triadic Attention

For triadic attention (i.e. face to face contacts that were preceded by both individuals' looking to the laser, but during which no communication occurred), the data originated from 8 chimpanzee, 9 Ugandan and 9 British offspring-partner dyads. Only 6 out of 8 chimpanzee dyads engaged in triadic attention, whereas all Ugandan and British offspring – partner dyads engaged in triadic sharing attention. In contrast to dyadic and unilateral triadic attention, triadic attention was relatively common in all three groups (see Figure 5.4).

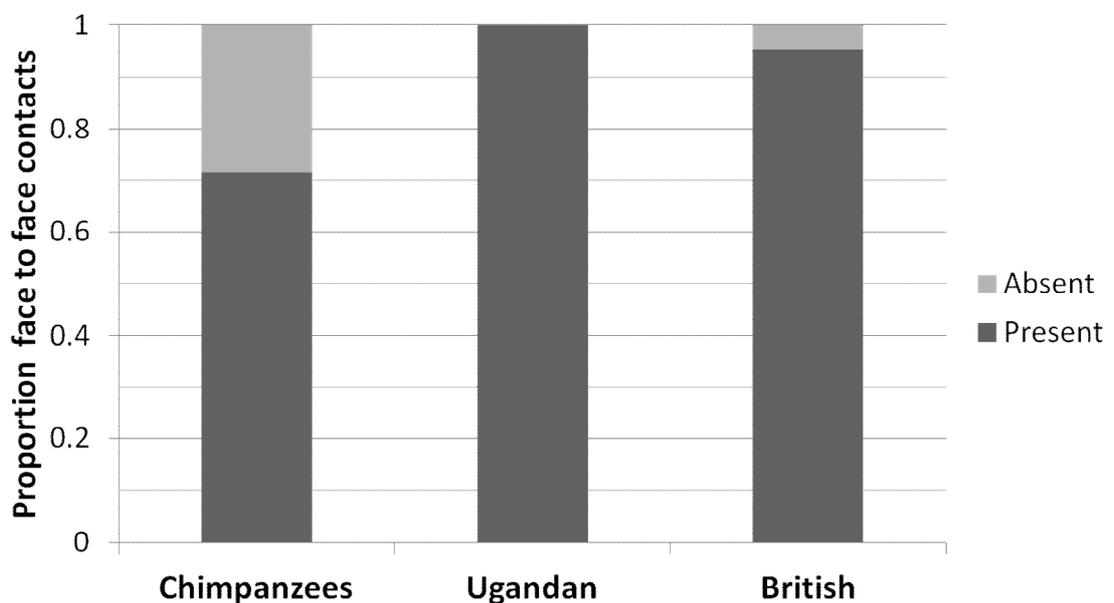


Figure 5.4: Proportions of face to face contacts in which triadic attention was present or absent. The total number of face to face contacts was 21 for chimpanzee, 25 for Ugandan and 22 for British offspring - partner dyads.

Since all face to face contacts in Ugandans were triadic (0 variation), they could not be entered into the GLMM as a group (Zuur, 2012). Therefore, since both human groups showed similar amounts of triadic face to face contacts, they were merged into one human group (N = 18). A binomial GLMM showed that human offspring-partner dyads engaged more in triadic sharing attention than chimpanzee dyads ($z = 2.60, p = .009$).

In order to exclude the possibility that offspring and partners only switched their attention from laser to their social partner instead of possibly engaging in joint attention, I analysed whether the offspring and partners looked back at the laser after triadic attention occurred. In offspring, only 5 different chimpanzees contributed data to this analysis and 9 Ugandans and 9 British. Therefore, no inferential statistics could be performed for the three offspring groups, but the Ugandan and British offspring were compared (see Table 5.14). In partners, 6 chimpanzees, 8 Ugandans and 9 British, contributed to this analysis.

Table 5.14: Summary of the offspring's and partners' results of looking back to the laser after triadic attention. Chimpanzees had to be excluded for offspring from the statistical analysis, because the sample was too small (see text).

	Chimpanzees	Ugandan	British	GLMM
Total number of triadic ftf contacts after which offspring looked back at laser	8/12 small N	22/24	16/19	UG vs. BR z = -.746, p = .456
Total number of triadic ftf contacts after which partners looked back at laser	13/14	25/25 0 variation	20/20 0 variation	n.a.

The results in Table 5.14 show that in most instances, both, offspring and partners looked back at the laser after engaging in triadic attention and that there were no group differences.

(c) Occurrence of Joint Attention

To recap, for joint attention to be scored, both, the offspring and the partner needed to look at the laser within the 3s before the face to face contacts and at least one of them needed to communicate during face to face contact by either vocalising or by displaying salient facial movements. Since joint attention was a special subtype of triadic attention, triadic attention and joint attention were not mutually exclusive (i.e. joint attention was also scored as triadic attention).

Six chimpanzees, 9 Ugandan and 9 British offspring-partner dyads contributed to this analysis. Figure 5.5 shows for each group the proportion of triadic attention bouts in which communication was present.

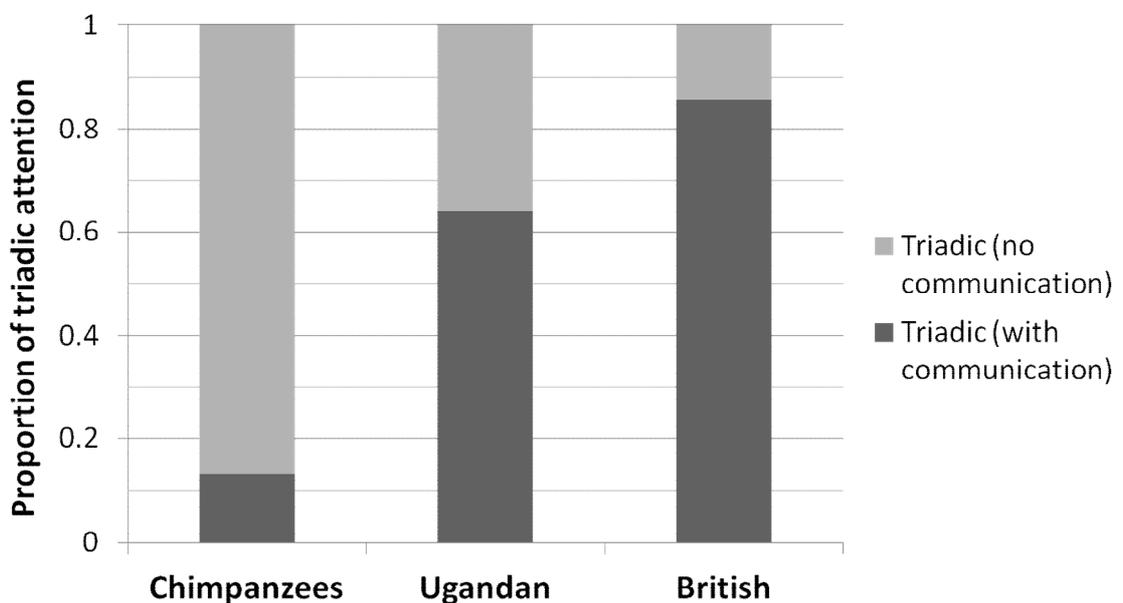


Figure 5.5: Bar graph of the proportions of triadic attention bouts in which communication (i.e. vocalisations or salient facial movements) were either present or absent. If communication was present, this constituted an instance of joint attention.

The two data points for joint attention in chimpanzees originated from the same individual (KB), whereas joint attention was observed in 7 out of 9 Ugandan offspring - partner pairs and in all British dyads. A binomial GLMM revealed that there was a significant difference between the three groups with regard to the frequency of joint attention ($z = 3.61, p < .001$). Post-hoc pair wise GLMMs showed that Ugandan offspring-partner dyads ($z = 2.83, p = .005$) and the British dyads ($z = 3.59, p < .001$) displayed more joint attention than the chimpanzees. In addition,

there was no significant difference between the Ugandan and British offspring – partner dyads ($z = 1.34$, $p = .180$). This result indicated a clear species difference with chimpanzees engaging less in joint attention than either of the human groups. A binomial GLMM confirmed this species difference: the human dyads as a collapsed group engaged more in joint attention than chimpanzee offspring-partner dyads ($z = 3.43$, $p > .001$).

The chimpanzee dyad that showed two instances of joint attention both looked back at the laser after the face to face contact in one of the two bouts. Ugandan offspring and partners both looked back at the laser in 100% of their joint attention bouts and the British offspring and partners both looked back at the laser in 72.2% of the bouts. No inferential statistics were performed between the three groups, because chimpanzees did not contribute enough data.

(d) Who communicated during joint attention?

Whenever joint attention was scored, it could either have been the offspring, the partner or both who showed communicative behaviours. In the following analysis, I investigated whether there were any group differences with respect to who the communicator was.

Figure 5.6 shows that in chimpanzees, only the offspring was observed to communicate. Again, this is only based on two instances from one individual (KB). In both instances, KB was vocalising (whimpering) and in one, she was additionally displaying a pout facial expression. In Ugandans and British, the offspring, the partner and both were observed communicating during joint attention bouts.

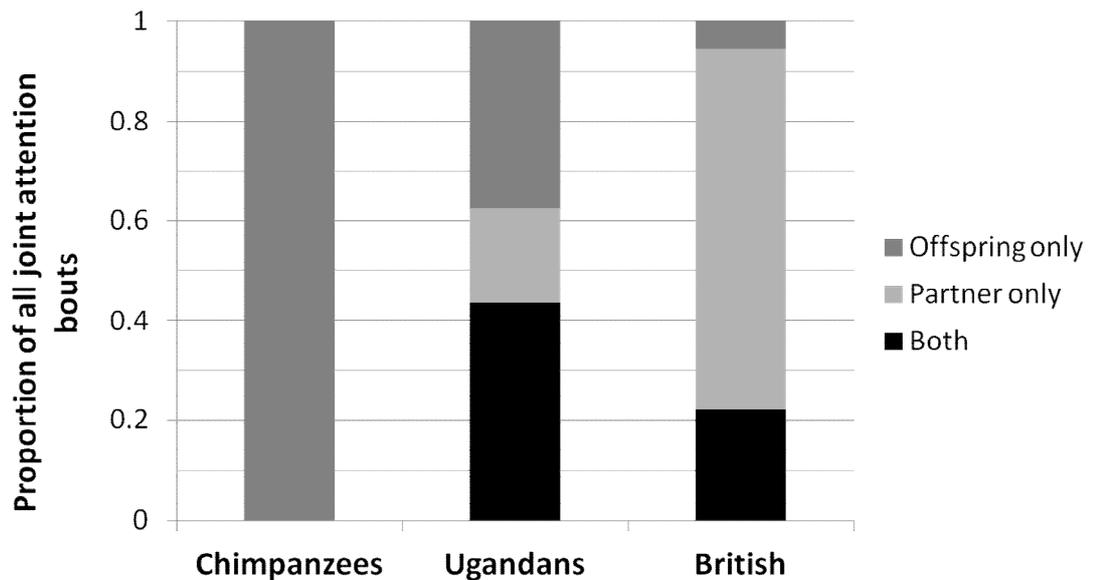


Figure 5.6: Bar graph displaying the proportions of different types of communicators (offspring, partner or both) in all joint attention bouts. Chimpanzees contributed 2 bouts, Ugandans 16 bouts and British 18 bouts.

Chimpanzees had to be excluded from the statistical analysis due to insufficient data ($N = 1, 2$ bouts). Three separate binomial GLMMs were run. The dependent variable for each respective model was whether (1) the ‘offspring only’, (2) ‘both’ and (3) the ‘partners only’ communicated during face to face contact. In all three models, Group was the explanatory variable and ‘Individual’ the random variable. The GLMMs showed that there was no difference between the Ugandan and British with respect to the proportion in which the offspring was the only communicator ($z = -0.622, p = .534$) and in which both communicated ($z = -1.39, p = .165$). There was a trend for British partners, however, to communicate alone more than Ugandan partners ($z = 1.82, p = .070$).

(e) Type of Communication during Joint Attention

As mentioned above, the type of communication that occurred between offspring and partner in a joint attention bout could have been either vocalisations or salient facial movements. Facial movements, however, were not always visible for each individual in each face to face contact. Therefore, I first determined in how many joint attention bouts the facial movements of both individuals were visible.

In chimpanzees, the facial movements in the two instances of joint attention were not visible for both, offspring and partner. In Ugandans, facial movements were visible for both individuals in 15 out of 16 joint attention bouts and in the British in 12 out of 18 bouts. Figure 5.7 shows the proportions of the type of communication used in joint attention bouts, where the face was visible for both, offspring and partners. No inferential statistics on the type of communication used could be conducted due to the small sample sizes for Ugandan and British dyads in which the facial movements were visible for both.

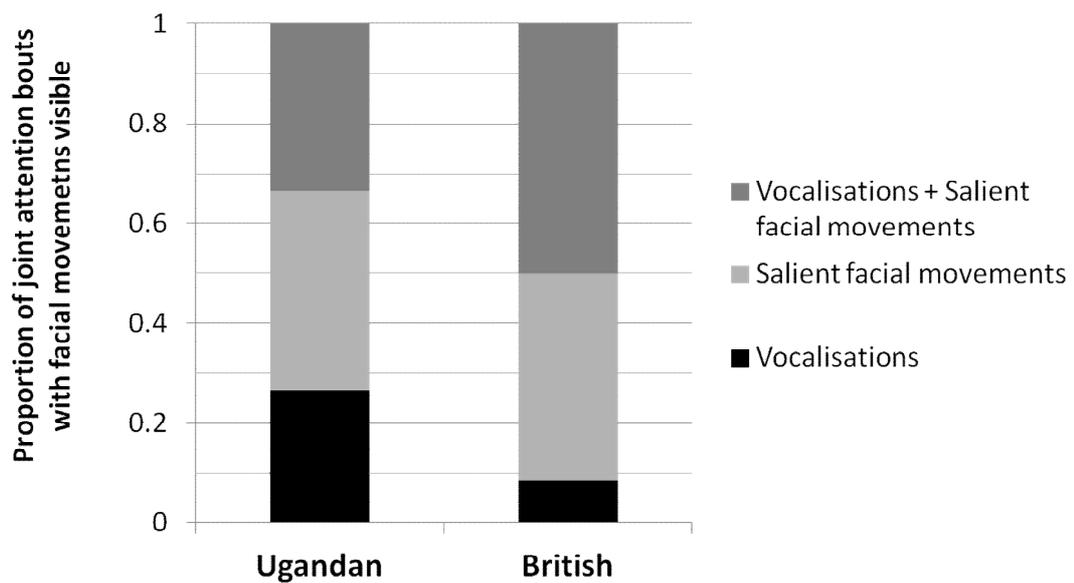


Figure 5.7: Bar graph displaying the proportions of the different types of communication used in the joint attention bouts in which the facial movements were visible for both, offspring and partner. The data originated from 6 Ugandan and 7 British dyads and a total number of 15 and 12 joint attention bouts respectively.

Figure 5.7 shows that more than 70% of all joint attention bouts in humans included facial movements and approximately 40% of the bouts were scored as joint attention based on the facial movements alone. Therefore, if facial movements were not visible at similar rates in all three groups, this could have biased the results. Unlike the participants of the human groups, chimpanzees could not deliberately be positioned so that the faces of both, the offspring and the partner were always visible. Table 5.15 shows that the chimpanzee facial movements were visible from both, offspring and partners, less often in all face to face contacts than for Ugandans and the British.

Table 5.15: Percentage of all face to face (ftf) contacts during which the facial movements were visible for both, offspring and partner. Chimpanzees contributed 21 face to face contacts, Ugandans 35 and British 39.

	Chimpanzees	Ugandans	British	GLMM
% ftf contacts in which facial movements visible both	19.1	85.7	61.5	z = 1.83, p = .067 CH < **UG CH < *BR UG = BR

The clear species difference and the low rates of joint attention in chimpanzees may have been caused by their facial movements not being visible, and therefore not being detected by the coder. Unlike facial movements, vocalisations were equally detectable across species.

(f) Joint Attention through Vocalisations

In order to control for the potential confound of detectability of communicative signals between species in the initial analysis, I further conducted a binomial GLMM on the presence of joint attention that was based solely on the presence of vocalisations. That means I scored joint attention to be present only when a vocalisation was present during the face to face contact (regardless of whether facial movements were also present). 6 chimpanzee and 18 human offspring-partner dyads were included in this analysis.

The GLMM revealed that based on vocalisations only, chimpanzee offspring-partner dyads still engaged less in joint attention during face to face contacts than the human dyads (z = 2.04, p = .042) (Figure 5.8).

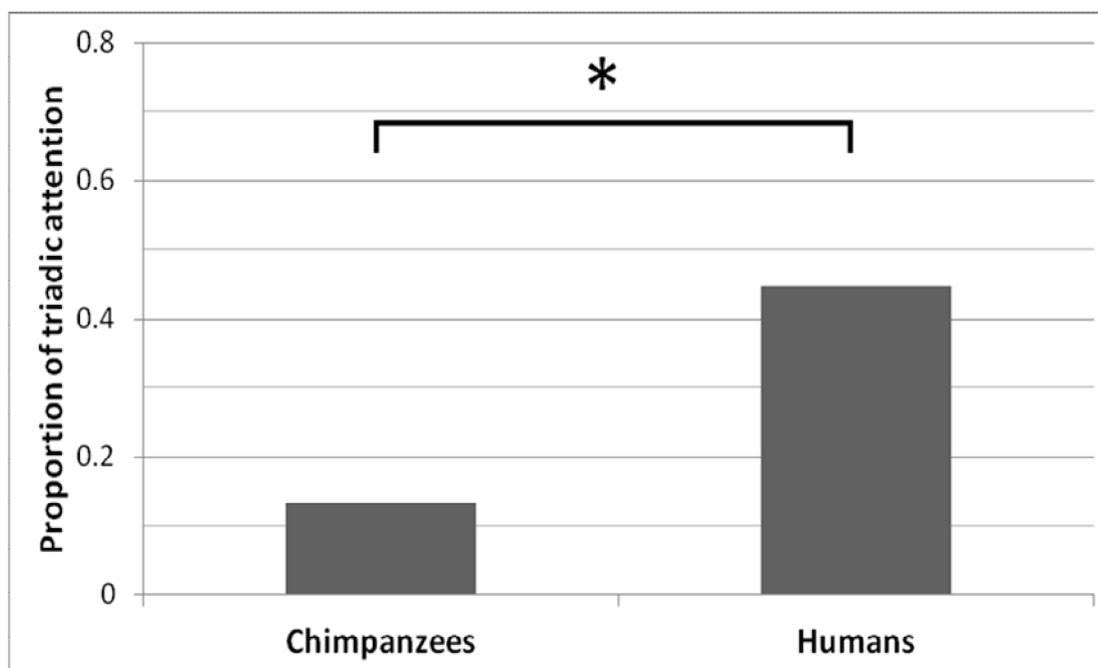


Figure 5.8: Bar graph of the proportions of all vocalisation based joint attention bouts in all triadic attention. The star refers to the significant species difference that resulted from the GLMM (see text).

Discussion

There is currently no evidence for chimpanzees to engage in joint attention as defined in Chapter 1 (p.22) regardless of their rearing history or whether they interacted with humans or conspecifics (Carpenter & Call, in press). Therefore, I sought to investigate whether wild chimpanzees naturally engage in joint attention. In addition, I aimed to compare the chimpanzee offspring's joint attention skills (e.g. gaze alternation) and the chimpanzee mothers' scaffolding behaviours (e.g. onlooking) to those of human mothers.

At 11 months of age, Western human infants are able to coordinate their attention between an object of interest and others (Bakeman & Adamson, Carpenter et al., 1998) and they are motivated to share attention by showing objects to others (Carpenter et al., 1998) and by smiling in anticipation of face to face contact during a joint attention interaction (Parlade et al., 2009). It is still unclear, however, whether there is some cultural variation with regard to the emergence of joint attention and its related skills. Human mothers also play an important role in

scaffolding early joint attention interactions, but African mothers have been shown to engage less in object manipulation than Western mothers (Keller et al., 2009). Therefore, I aimed to confirm the hypothesis that 11 months old Western human infants engage in joint attention and to investigate potential cultural variation of the mother-infant joint attention interaction and of the human infants' joint attention skills.

Before I discuss the results of this chapter, it is important to note that some chimpanzee dyads differed from the human dyads with respect to their composition. Whilst the human offspring were all 11 months old, the chimpanzee offspring varied considerably in age. In addition, although the majority of the chimpanzee dyads were mother-offspring dyads (6/8), two offspring were paired with a sibling, one of which was younger than the focal offspring. Although there was no indication that the offspring or the sibling-partners behaved differently than mother-offspring dyads, it cannot completely be ruled out that using siblings in two experiments may have disadvantaged the chimpanzees. This, however, is unlikely, because one of the siblings was a sub-adult (KA) and almost 10 years older than the focal offspring. KA even started her menstrual cycles in 2012, meaning she was likely to become a mother herself in the next few years.

Most importantly, the advantages of including different ages and sibling-sibling dyads in chimpanzees outweighed the disadvantages. First, there is no evidence to date that chimpanzee offspring engage in joint attention as defined in this thesis with either their mothers or their siblings. Based on the lack of evidence of joint attention in chimpanzees, the potential age of emergence for joint attention is not known. Therefore, by including chimpanzee offspring of all ages and by including siblings, the studied chimpanzees were given the best possible opportunities to show joint attention. In addition, given the limited total number of potential chimpanzee subjects and the difficulty of successfully conducting laser experiments in the wild, I decided to include all possible constellations and ages. As this is the first experimental study on joint attention in wild chimpanzees, this thesis can constitute the basis for developing more specific hypothesis and methods for future studies. As the majority of the dyads were mother – infants

(30/32), for simplicity, from here onwards, I will refer to the mother/sibling – offspring dyads as mother-offspring dyads.

In the following sections, I will first discuss the results of the Social laser experiment and then develop suggestions for future research.

Simultaneous Laser Engagement

Chimpanzee offspring and partners showed low rates of both visual and physical simultaneous laser engagement, whereas the offspring and partners of the two human groups showed high rates of simultaneous visual laser engagement, but, like chimpanzees, low rates of simultaneous physical laser engagement. This means, in contrast to chimpanzees, that the human dyads' visual attention was focused on the laser during the majority of the Social laser experiment, but the dyads of all three groups did not engage much with the laser physically at the same time.

The species difference in the offspring's simultaneous visual engagement cannot be explained by the chimpanzee dyads having had less opportunity to engage with the laser simultaneously, because the calculations were based on the standardised '*85 sec experimental period*' in which the laser was visible to both offspring and partners for identical durations (85.08s) across all three groups. In addition, chimpanzee offspring individually engaged with the laser visually (and physically) at similar rates as the infants of the two human groups did. This means that chimpanzee offspring were equally interested in the laser individually as the human infants, but chimpanzee offspring may have been less motivated to engage with their partners and the laser simultaneously.

There was not such a clear species difference for the partners, but chimpanzees had a tendency to engage less in simultaneous visual laser engagement than the British. Since simultaneous engagement constitutes a triadic situation that is conducive for joint attention to occur, it was therefore to be expected that chimpanzees engaged in joint attention at lower rates than the two human groups.

Onlooking

Monitoring the actions of the offspring is fundamental to scaffolding their behaviours and following into or directing the offspring's attention. The Ugandan and British partners observed their offspring's physical engagement with the laser at very high rates. Ugandan mothers did not differ from the British mothers in this respect. These results show that the human partners, instead of interfering with the offspring's actions, took a physically passive, but visually observant role during their offspring's laser engagement. Chimpanzee partners, however, observed the offspring's physical laser engagement at much lower rates than the human mothers. This may be due to their low rates of overall laser engagement compared to the partners of the two human groups. Mothers across groups, however, showed similarly low rates of physical engagement with the laser, indicating that the laser was not as exciting or stimulating for mothers of all groups as it was for their offspring. Importantly, despite the laser probably not being of great individual interest to mothers, human mothers, in contrast to chimpanzee mothers, seemed to be motivated to stay visually engaged with the laser, because it was of interest to their infant. Chimpanzee partners seemed to have less intrinsic motivation to continuously observe the offspring's engagement with the laser, once they considered the laser stimulus as 'safe' for their offspring to engage with. Therefore, I conclude that, as predicted, human partners were more interested in the offspring's engagement with the laser than chimpanzee partners. This finding is also consistent with studies that show that human mothers often follow into their offspring's focus of attention, thereby supporting the language development of infants (Tomasello & Farrar, 1986; Carpenter et al., 1998).

In the offspring's rates of onlooking, there was no clear-cut species difference between the two human groups and chimpanzees. Descriptively, the human infants of both groups observed their mothers' interaction with the laser at higher rates than chimpanzees. Statistically, only the Ugandan offspring onlooked their mothers' laser engagement more than chimpanzee offspring. Ugandan and British offspring, however, did not differ in their amount of observing their mother's laser engagement.

Face to Face Contacts

Mutual gaze or, as operationalised in this thesis, face to face contact was a key component of joint attention in non-verbal individuals, because during face to face contact two individuals' attention can meet and share attention. Therefore, I investigated the frequencies, durations and communication before, during and after face to face contact to shed light on the question of whether chimpanzees naturally engage in joint attention, and whether joint attention skills (e.g. gaze alternation) and the motivation to share attention (e.g. anticipatory facial movements) varied between species and human cultures. In the following sections, I will first discuss some general parameters of the face to face contacts, then the results concerning joint attention skills (i.e. laser related attention getters, facial movements, partner's attention directing, offspring's attention following and gaze alternation) and finally the results for joint attention as an event.

In contrast to my hypothesis, the two human groups did not display more face to face contacts than chimpanzees and descriptively the durations of face to face contacts were similar across groups. Therefore, with regard to frequencies and durations of face to face contacts, no differences between chimpanzees, Ugandans and British offspring – partner dyads were observed. Since I coded head direction as an indicator of gaze direction (Emery, 2000), it cannot be ruled out that the three groups differed in their frequencies and durations of having looked at each others' eyes. Whilst the offspring's and partners' heads were facing each other's face, it could have been possible that each individual focussed on a different aspect of the other's face and there was no eye contact. Since gaze was not equally visible in all three study groups in this thesis, it was vital to apply equal coding criteria to all three groups by taking head direction as the indicator for the subjects' gaze (Emery, 2000). As a consequence, I obtained a less precise data set that allowed for more errors and noise, but the data set was comparable across the three groups. For future studies, it would be fantastic, if the gaze tracking technology that has already been applied in labs (e.g. Kano & Tomonaga, 2009) could be developed further so that it can be used under field conditions.

Skills and Motivation for Joint Attention

Laser Related Attention Getters

Laser related attention getters were examined as an indicator for the offspring's and the partners' motivation to initiate or prolong their social interaction *about* the laser. When comparing the partners and the offspring of the three groups separately, they did not differ in their use of laser related attention getters.

Therefore, in contrast to my prediction, human offspring and partners did not use more laser related attention getters than chimpanzees in order to initiate or prolong their social interaction *about* the laser.

When comparing the partners to their offspring within each group, however, the partners of the Ugandan and British infants engaged significantly more in laser related attention getters than their offspring. This was not the case for the chimpanzee partners. This indicates that in contrast to the chimpanzee partners, the mothers of the two humans groups were more active than their offspring in initiating a joint interaction *about* the laser or re-directing the infants' attention back to the laser.

This result, however, may be confounded with the differential amount of instructions given to humans and chimpanzees. Whilst chimpanzees were unaware that they were participating in an experiment and they did not know that the laser dot was the central feature of the experiment, it is possible that the partners of the two human groups felt more obliged to focus their child on the laser. Although a strong effort was made to explain to the mothers that we are trying to observe "natural" interactions and that there was no need to force the infant to continue engaging with the laser if he had lost interest, the possibility that human partners were influenced by their knowledge about the experiment cannot be completely excluded. Based on the ethical requirements of studies with humans, this bias could not have been avoided. These results, however, are still consistent with Bard & Vauclair's (1984) finding that humans tried to engage their infants' attention with objects more than chimpanzee mothers.

Anticipatory Facial Movements

The display of anticipatory facial movements (i.e. a facial movement is already present *before* face to face contact) during laser engagement may indicate an individual's motivation to share attention and interest *about* the laser. Therefore, I aimed to investigate whether human infants showed a higher motivation to share attention by comparing the rates of anticipatory facial movements between the three groups.

Anticipatory facial movements were not very common in any of the three groups of offspring. Although human infants younger than 11 months displayed anticipatory smiles in other studies (e.g. Jones & Hong, 2001), the human infants showed low rates to anticipatory facial movements in this study and chimpanzees did not constitute an outlier to any of the human groups. Therefore, contrary to my prediction, the display of anticipatory facial movements (which included smiles) could not be replicated with the human study groups of this thesis and no species difference was found. Therefore, I cannot conclude that based on the human infants' facial expressions, they showed a higher motivation to share attention than chimpanzee offspring.

Ugandan and British partners did not differ in their amount of anticipatory facial movements. Unfortunately, chimpanzee partners could not be included into the analysis of anticipatory facial movements, because of the limited visibility of their faces. This was mainly due to the opportunistic character of the chimpanzee laser experiments which did not allow me to position the participants as I would have wished and the restrictions of filming in the dense Budongo forest which often entailed greater distances to the participants than in humans, different filming angles (chimpanzees in trees) and some limitations of visibility (branches between the subjects and the camera). One way to improve the video quality and the visibility of the wild chimpanzee faces would be to use an HD camera that has a high light sensitivity as well as advanced backlight compensation. In addition, having two additional field assistants who could film the dyad from different angles would also increase the amount and quality of data on facial movements. Replicating the Social laser experiment with captive chimpanzee dyads would

allow the experimenter to film from different angles, to approach the dyad more closely and to reduce the amount of objects that occlude the subjects' facial movements.

Directing and Following Attention

Directing and following attention are both joint attention skills, for which the mothers require the motivation to direct the attention of their offspring and the offspring require the motivation to tune into the communicative attempt of the mother for intentional attention directing behaviours (e.g. pointing) to be successful. Therefore, I investigated whether the partners intentionally tried to direct the offspring's attention back to the laser after having engaged in face to face contact and whether the offspring responded to that by looking back at the laser.

Chimpanzee partners were not observed engaging in any intentional attention directing behaviours and there was a trend for Ugandan partners to display more intentional attention directing behaviours than the British. This was surprising at first, because I predicted, based on higher rates of object stimulation in Western mothers, that the British would show more intentional attention directing behaviours than the Ugandan mothers. This finding, however, is consistent with Dixon et al's (1984) study who have shown that African mothers used more directive communication during a teaching task by repeatedly re-focusing their infants' attention on the task.

Regardless of whether the Ugandan or British mothers engaged in functional or intentional attention directing behaviours, their infants always looked back at the laser. Therefore, it cannot be concluded that intentional attention directing behaviours were more effective in directing the offspring's attention than functional attention directing behaviours. It is more likely that human infants had a generally high tendency to look back at the laser after the face to face contact. It was difficult to fit the chimpanzees into this picture as they did not contribute enough data to the analysis. The chimpanzee offspring, however, looked back at the laser in the majority of cases of functional attention directing behaviours or their partners.

No final conclusions can be drawn about the species differences in the partners' attention directing and the offspring's attention following behaviours, because the small amount of data did not allow any inferential statistics. Further studies are needed to reveal whether intentional attention directing behaviours of the partners are present in chimpanzees and whether they are more effective in re-directing the offspring's attention back to the laser than functional attention directing behaviours.

Gaze Alternation

As mentioned in the introduction, gaze alternation between an object of interest and a social partner is an essential ability in order to share attention with others (Carpenter et al., 1998, Tomasello & Carpenter, 2005). Therefore, I investigated whether chimpanzee, Ugandan and British offspring and their partners differed in their individual abilities of coordinating their attention by alternating their gaze between laser and the social partner.

Chimpanzee offspring showed gaze alternation from the laser to the partner and back to the laser in approximately half of their face to face contacts and the offspring of the three groups did not differ from each other with regard to their rates of gaze alternation. On a species level, however, the findings were consistent with my hypothesis: human infants coordinated their attention more between the laser and their partner than chimpanzee offspring. Since Ugandan and British partners showed a ceiling effect for gaze alternation, they could not be statistically compared to chimpanzees. Descriptively, however, chimpanzee partners seemed to have alternated their gaze at slightly lower rates than the human partners.

Joint Attention

The main question of this chapter was whether there was some evidence for joint attention in wild chimpanzees and whether the three groups differed in the nature of their joint attention interactions.

Firstly, for Ugandan and the British dyads the majority of their face to face contacts were instances of triadic attention in which both partners looked to the laser before they engaged in face to face contact. In contrast, approximately a third of

the chimpanzee face to face contacts were either dyadic or unilateral triadic attention in which either none or only one of the participants looked to the laser before the face to face contact. On a species level, chimpanzees engaged less in triadic attention than human offspring-partner dyads which indicates that chimpanzee offspring and their partners coordinated their attention with each other about the laser less than the human dyads.

It is important to note that the majority of offspring and partners in all three groups looked back at the laser after triadic attention was scored. This means that the participants did not only shift their attention from the laser to each other, but that it is very likely that their face to face contacts were *about* the laser. This line of argument was equally true for all three groups.

During instances of triadic attention, however, we cannot be sure yet that true joint attention occurred in which both individuals were “mutually aware” of having attended to the laser. According to my definition of joint attention (Chapter 1, p.22), mutual awareness is established through communication. Whereas in humans, there was communication present in over half of the dyads’ triadic attention bouts, chimpanzees communicated in less than 20% of their triadic attention bouts. The statistical analysis revealed a clear species difference between chimpanzees and human offspring-partner dyads with regard to joint attention. Altogether, chimpanzees only showed two instances of joint attention. Both instances originated from the same individual (KB), whereas 7 Ugandan and 12 British infants showed joint attention in the majority of their triadic face to face contacts.

Further systematic research is required to find out whether these two instances of joint attention in chimpanzees can be replicated and are representative for chimpanzees in general. Based on these results, it can be concluded that there was little evidence for chimpanzees to engage in joint attention, whereas the majority of Ugandan and British offspring-partner dyads did. In addition, in contrast to my prediction, Ugandan and British mother-infant dyads engaged in joint attention at equally high rates. This result indicates that regardless of the amount of maternal object stimulation and potential other cultural variation in the infants’ social

environment, joint attention is a robust human ability that occurred in both Ugandan and British 11 month old infants and their mothers.

When analysing who the communicator was during joint attention, Ugandan and the British offspring-partner dyads did not differ with respect to the proportion of face to face contacts in which either both or only the offspring communicated. There was a trend for British partners, however, to be the only communicator more often than Ugandan partners. This may indicate that the British partners may have scaffolded the joint attention interactions more than Ugandan partners. Alternatively, it is possible that Ugandan and British partners scaffolded the interactions at equal rates, but the Ugandan infants showed more communicative behaviours than the British which then led to a coding category change from “partner only” to “both”. This is in fact the more likely explanation, because in the remaining category of the offspring being the only communicator, Ugandans and the British did not differ.

Since a considerable percentage of communication was mediated through salient facial movements in the two human groups, and chimpanzee facial movements were less often visible in chimpanzees than for any of the human groups, it was essential to repeat the analysis for joint attention based on a form of communication that could be scored equally well in all three groups: vocalisations. This analysis made sure that the species difference in joint attention discussed above was not driven by the bias of the differential visibility of facial movements. The analysis revealed that chimpanzee offspring-partner dyads still engaged less in joint attention that was based solely on vocalisations as the communicative medium than human mother-infant dyads.

Instead of promoting the sole use of vocalisations as an indicator for joint attention in cross-species research, however, I would strongly suggest to use multiple high definition cameras and to adopt the Facial Action Coding System that allows for identification of specific facial movements and that has already been applied in captive chimpanzees (Parr et al., 2007). This would allow a more sensitive coding of facial expression than was possible within the time constraints of this thesis. Since facial movements were frequently present during joint attention events in

humans, they should be taken into account in future research. If facial movements could be measured equally well in both species, maybe the differences between chimpanzees and humans would melt away.

General Discussion

The results of the Social laser experiment indicate that human partners were more interested in the offspring's interaction with the laser than chimpanzee partners and they actively communicated during joint attention. Chimpanzee partners, however, were never observed to communicate during face to face contacts with their offspring. This indicates that the partners may have played an important role in scaffolding the joint attention interactions in humans which then resulted in higher rates of joint attention events compared to chimpanzees. Since chimpanzee partners may not have a high intrinsic motivation to enhance and support their offspring's object play (Bard & Vaclair, 1983), they may not have scaffolded the joint attention interactions as human mothers did.

The results of this chapter have further shown that chimpanzees possess some joint attention skills as evidenced by alternating their gaze between the laser and their partners. Previous research has shown that chimpanzees alternated their gaze between food and human experimenters when pointing imperatively for food (Leavens et al., 2005), but no evidence is available for chimpanzees gaze alternating with humans (Tomasello & Carpenter, 2005) or their mothers (Tomonaga et al., 2004) when engaging with objects to share attention. This study provides the first evidence of coordination of attention via gaze alternation in chimpanzees outside of a food context. In the absence of communication between partners, it remains unclear whether they did so to share attention or to check the attention of their social partner. Nevertheless, this is the first time that gaze alternation has been recorded in wild chimpanzees in a non-food context.

Leavens and co-workers proposed that captive chimpanzees engage in joint attention (e.g. Bard & Leavens, 2009; Leavens & Racine, 2009; Leavens & Bard, 2011, Leavens, 2012). Leavens and Racine (2009) state that great apes (including chimpanzees) "display every phenomenon described as joint attention in humans" (p. 240). As previously discussed in Chapter 1 (p.10 ff), Leavens and co-workers

use a different, more inclusive definition of joint attention which focuses on the “intentional co-orientation” of two individuals (Leavens & Racine, 2009, p.241). Chimpanzee pointing is regarded as an important indicator of joint attention in chimpanzees. Although pointing can be used to initiate or prolong a joint attention interaction, most instances of chimpanzee pointing are imperative (i.e. with the motivation to obtain food) which does not involve the sharing of attention (Carpenter & Liebal, 2012). Although Leavens and co-workers emphasize the communicative aspect of joint attention (as I do), they refer to communication in order to cause the co-orientation of the individuals to a common focus, whereas I emphasize communication as a way of sharing attention after the co-orientation has taken place. Therefore, Leavens and co-workers do not address the sharing aspect of joint attention and therefore include behaviours into their definition on joint attention which do not constitute joint attention according to the definition of joint attention proposed in this thesis and that of Carpenter and Liebal (2012).

Despite using a stricter definition than Leavens and co-workers, I recorded two instances of joint attention in a chimpanzee mother-infant dyad using a strict definition of joint attention. These are the first cases reported of joint attention in a chimpanzee mother –infant dyad, however, they only occurred on two occasions within a single trial, in a single dyad. I hope that this first finding of joint attention in wild chimpanzees will inspire further research that focuses on gaining a clearer footage and applying chimpFACS coding to facial expressions during potential joint attention episodes in wild chimpanzees.

The two instances of joint attention found in this thesis are inconsistent with the findings of Tomonaga et al (2004) and Tomasello and Carpenter (2005) who did not find any evidence for joint attention in captive chimpanzees. Since Tomasello and Carpenter’s (2005) negative results are based on interactions between humans and chimpanzees, this may indicate that young chimpanzees might not show their natural behavioural repertoire when interacting with humans, using human toys and games which highlights the importance of studies that involve chimpanzee-chimpanzee interactions as implemented in this thesis. Tomonaga et al (2004), is the only previous study investigating joint attention during intra-

species communication, however they focused on interactions between a single captive mother and her infant. Given we only observed joint attention in one out of eight mother-infant dyads studied, it is perhaps not surprising that Tomonaga et al. (2004) failed to find evidence for joint attention in this single dyad. The novelty of our results in comparison to these previous studies highlights the need for further research before we can reject the hypothesis that joint attention is uniquely human.

Although Ugandan and British mother-infant dyads originated from very different cultural backgrounds (See Chapter 3 and Chapter 6), they engaged in similar rates of joint attention. This indicates that although differences in the socio-cultural environment in humans may lead to differences in cognition and self-concepts (Markus & Kitayama, 1991; Henrich et al., 2010), the ability and motivation to engage in joint attention seems to be a very robust phenomenon across different human cultures.

Future Directions

Since in the dense forests of Africa the visual modality may not always be the most effective for communication, I would suggest investigating joint attention by examining other modalities such as auditory or tactile joint attention. Auditory joint attention could be investigated through observation alone by recording the behaviour of resting parties upon hearing a distance call or any other audible stimulus. It could be investigated whether the resting chimpanzees engage in face to face contact and with the use of FACS for objectively recognizing facial expressions (Vick et al., 2007), we could identify specific behaviours that occur between the recipients of such distant calls.

Anecdotally, one behaviour of note in this regard was the production of soft vocalisations of several recipients of a distant call that appeared as if the individuals in the resting party “commented” on the just perceived distant call. These soft vocalisations were definitely not loud enough to be a response to the caller. Since we do not know exactly, however, what the informational content of a distance call is, we could also conduct a controlled experiment, by playing back either chimpanzee calls that have been recorded from a chimpanzee whose activity

context was known or by producing an unusual sound that the chimpanzees have never heard before. Such an experiment together with the corresponding observational data could shed some light on naturally occurring auditory joint attention in chimpanzees.

Conclusion

One important finding of this chapter is that one chimpanzee mother-infant dyad engaged in two instances of joint attention. Although it is possible that these two instances of joint attention could be attributed to a chance co-occurrence of the relevant criteria, they still constitute the first reported instances of joint attention in wild chimpanzees. In addition, remarkably, 2/3 of the chimpanzee face to face contacts occurred during a triadic context. Nevertheless, the human mother-offspring dyads engaged in joint attention at significantly higher rates than the chimpanzee dyads. There was no difference between the Ugandan and British mother-infant dyads with regard to their rates of joint attention, despite their very different cultural backgrounds. Ugandan and British partners engaged more in onlooking than chimpanzee partners and they actively engaged in communication during joint attention. This may indicate the human mothers' higher motivation to scaffold their offspring's joint attention interactions. Future research is needed to reveal whether the two instances of joint attention in chimpanzees found in this experiment are representative for the species. In addition, I hope that the use of the chimpFACS and investigating joint attention in different modalities will help us to answer the question of whether or not joint attention is uniquely human.

Chapter 6 : Time Budget and Social Environment of the Study Groups

Summary

Human and chimpanzee infants are shaped by their social environment from very early on (Keller, 2007; Bard & Leavens, 2011). In order to understand how joint attention develops, it is vital to identify socio-environmental factors in the chimpanzee and human everyday environment that are related to the development of joint attention. In addition, recording cultural variation of socio-environmental factors can help us reveal different developmental pathways for joint attention. To this end, I collected instantaneous scan sampling data on the daily activities of chimpanzee, Ugandan and British mother – offspring dyads.

The results revealed that chimpanzee offspring rarely vocalised and compared to human infants they spent more time in biologically essential activities, and less time in social and play activities. Most importantly, whilst human infants of both cultural groups used objects in at least 50% of their social play, chimpanzee offspring never did so indicating that an important triadic constellation of offspring, object and social partner never occurred naturally in the Sonso chimpanzees. In addition, some cultural differences between the Ugandans and the British were revealed. The modal distance for Ugandan (and chimpanzees) was 'body contact' and for British infants 'within reach'. Ugandan infants, like chimpanzees, mainly played with siblings or other people, whereas British infants mainly played with either their mothers or fathers. In addition, the three groups did not differ in the amount of social activities that were done with their mothers. This indicates that the nature of the infants' social interactions may be more important for the development of joint attention than the amount of time spent in social interactions with the mother.

Introduction

Keller (2007) revealed that human infants are shaped by their cultural environment from as early as 3 months. As a result, people from different cultural backgrounds develop different skill sets and cultural identities (Markus & Kitayama, 1991). The ability and motivation to engage in joint attention, however, seems to be a human universal, like pointing (Kita, 2003). Joint attention seems to develop in all normally developing human beings despite considerable variations in the socio-cultural environments they grow up in. This does not necessarily mean that the development of joint attention is genetically fixed. There may be different developmental trajectories leading to a similar end product. Studying factors of the social environment of different human cultures that are relevant for the development of joint attention may help us identify which of these factors are constant across the different cultural groups and may therefore be a vital supporting factor for the development of joint attention in humans. It will also help identify factors that differ between cultures, where joint attention behaviours are similar and thus are unlikely to play a necessary role in the emergence of this behaviour.

Home-raised or language trained chimpanzees, who had extensive experience with human forms of communication, outperform other captive chimpanzees with limited human contact in joint attention related tasks (e.g. comprehension of human pointing) (Lyn et al., 2010). It is important to note, however, even chimpanzees who had extensive human contact, have never been systematically documented to engage in joint attention, as defined in Chapter 1 (p.22). Although studies with home-raised chimpanzees have revealed how important the social environment is for the development of some socio-cognitive skills, research with captive chimpanzees who habitually engage in communication with humans cannot tell us what chimpanzees naturally do in their species-typical environment. Therefore, it is important to investigate everyday life activities and interactions of wild chimpanzees in order to reveal why they may not naturally engage in joint attention.

This chapter aimed to examine socio-environmental factors that are relevant for the development of joint attention in the chimpanzee, Ugandan and British study group. The methodology of this chapter includes an original approach: the data collection method that has been used by several researchers to establish primate time budgets (e.g. Goodall, 1986, Newton-Fisher, 1999) was applied to humans from two cultural backgrounds. This method enabled me to follow the mother-infant dyads for extended periods (<10hrs) and record their everyday life activities. The data of this chapter were collected with the main aim to link potential differences in the social environment of the participants to the results of the laser experiments (Chapter 4 and 5) in order to reveal which factors may have contributed to the development of joint attention (Chapter 7).

Time budgets

The first objective of this chapter was to establish the general time budgets for chimpanzee and human offspring-mothers dyads to get an overview of the everyday life activities. Although activity budgets have been calculated for chimpanzees before (e.g. Goodall, 1986; Newton-Fisher, 1999), it was preferable to have data available on the same study group where the laser experiments were run. Data on everyday life activities in humans from different cultures have mainly been collected with the “spot observation” method (Munroe & Munroe, 1971), in which the experimenter visits families abruptly at different day times on several days. This method, however, only produces “mental snapshots” and does not result in frequencies of specific behaviours for one family. In addition, it was essential to use the same methods for humans and chimpanzees. Although it may have been possible to abruptly visit families in Uganda without interrupting their activities, because compounds are open and most activities done outside, this would not have been possible for the British families, because it would require entering their (fenced) compound/house without announcement.

Based on these considerations, I decided to take an original approach and to expand the instantaneous scan sampling to human participants over an extended period of time (up to 10hrs). Some of the activities of the time budget that may be important for the development of joint attention were then further analysed to

reveal whether the chimpanzee, Ugandan and British mother – offspring dyads differed with regard to these socio-environmental parameters. In the following sections, I will present those factors and make predictions with regard to potential species and cultural differences.

Vocalisations

Joint attention, the mutual awareness of having attended to an object of interest, is established through communication during mutual gaze. Communication in this thesis was operationalised as either displaying facial movements or vocalisations during mutual gaze. Falk (2004) suggested that a frequent vocal exchange between human mothers and their infants evolved after the hominoid-pan lineages split. Chimpanzees do not seem to engage in frequent affective vocal exchange with their offspring (Falk, 2004). Therefore, since vocalisations are one way of communication to engage in joint attention, it was important to investigate the frequency of vocalisations in each study group to reveal whether chimpanzee mothers and their offspring generally used vocalisations as often as humans did. It was predicted that chimpanzees would engage less in vocalisations than humans and that there would be no difference between the Ugandan and British offspring and mothers with regard to their rates of vocalisations in their time budget.

Essential Activities vs. Leisure Time

Another aim of the general time budget was to identify potential factors that may support or prevent the participants from engaging in social activities that are relevant for the development of joint attention (e.g. play). One factor that may prevent chimpanzees from spending much time in social activities that are conducive for joint attention is the necessity to engage the majority of their time in activities that are essential for their survival such as foraging. Tweheyo et al. (2004) investigated the feeding behaviour of the Sonso chimpanzees and found that the chimpanzees spent 80% of their daytime on feeding. 94% of their diet consisted of fruits that were scattered over different parts of the forest. For this reason, chimpanzees spent much time on foraging related activities. Ugandan families were mainly subsistence farmers (see Chapter 3) and some fields were more than 30min walk away from their homes (personal observation). It is

therefore possible that Ugandan mothers also had to invest much time to procure food for their families. It is relatively easy for Western people to obtain food and thanks to supermarkets, cookers and microwaves it does not take as long to cook a meal as it does in Ugandan homes. Food, however, can only be bought if there is enough money available. Therefore, being employed and earning money is the main way to provide food for families in the British. The processes involved in obtaining food and to assure sustainable survival were very different amongst the study groups. Therefore, different activities that served the same function, namely to assure sustainable survival, were grouped and compared between the three groups. The amount of the time budget that was taken up by these “essential activities” determined how much time remained for relaxed social activities (i.e. playing and grooming). These relaxed social activities or “leisure activities” constitute an important context in which mothers and their offspring had the opportunity to devote time to playful interactions with their infants. Therefore, after initially documenting the general time budget of the participants, the chimpanzee, Ugandan and British mothers and offspring were compared with respect to the amount of time spent in essential or leisure activities.

Since essential activities were composed of different activities in the three groups, it was difficult to predict which group may have engaged more in essential activities than others. Therefore, this analysis was exploratory and no directional hypothesis was made.

Social Activities

Although leisure activities are important for the development of joint attention, any social interaction, essential or leisure, with the mothers plays a crucial role, because it provides offspring with a patterned input through familiar interaction routines (Deák & Triesch, 2006). Some essential activities were also social, including care giving activities such as feeding or bathing and they also constituted an important context for joint attention (Deák & Triesch, 2006). Therefore, I first established the amount of social activities in the offspring's and mothers' time budget and then analysed whether the chimpanzee, Ugandan and the British differed in this respect. By doing this, the general tendency of chimpanzees and

humans to engage in social activities was measured and compared. In addition, since previous studies suggest that the mothers are a very important social partner for human infants (e.g. Bakeman & Adamson, 1984, Tomasello & Farrar, 1986), I examined how many of the offspring's social activities were done with the mother.

If the amount of time spent in social activities is an important factor for the development of joint attention, human infants who develop this ability may engage more in social activities than chimpanzee infants who seem not to develop this ability (Call & Carpenter, in press). Since human mothers play an important role in scaffolding joint attention interactions (Deák & Triesch, 2006), I predicted, that human infants would spend more time in social activities with their mothers than chimpanzee offspring do. There was no directional hypothesis made with regard to the mothers' amount of social activities in the time budget.

Play

Playing is a particularly important activity for the development of joint attention as it establishes playful interaction routines between the infant and their social partners and is therefore a good context in which infants can learn from older conspecifics (Tomasello & Farrar 1986; Charman et al., 2000; Deák & Triesch, 2006). Therefore, in order to investigate the offspring's overall tendency and opportunities for play, I compared the frequencies of all play and social play in the total time budget between the three groups. If the amount of play is important for the development of joint attention, I predicted that chimpanzee offspring would play less than human offspring. Since the human infants from both cultures were expected to engage in joint attention, I expected them to play at similar rates.

In addition, I analysed the mothers' proportion of play in the time budget as an indicator of how much time she may have exclusively spent in infant-centred activities. This may indicate the mothers' motivation to tune into the activities of infants and create more contexts for joint attention to develop. Chimpanzee mothers habitually engage in play with their offspring (Goodall, 1986). Whether they play more than human mothers and whether Ugandan and British mothers differ in their amounts of play also depends on how much leisure time they have

available. Therefore, no directional hypothesis was made with regard to the mothers' amount of play in the time budget.

In order for joint attention to occur, at least three things have to be present: two interactants and an object of interest. Therefore, during playing interactions, I systematically analysed the presence of two things in relation to the offspring: an object and a social partner.

Object Play

Since joint attention includes an external object in addition to a social partner, I investigated how often the chimpanzee and human offspring used objects during play. The frequency of object use in individual play indicated the strength of the offspring's tendency to manipulate objects in general. The frequency of object use in social play showed us how often all three preconditions relevant for joint attention co-occurred.

If a correlation between general object use during play and the development of joint attention was assumed, I predicted that Ugandan and British infants would use objects more in play, and especially in social play, than chimpanzee offspring.

Play partners

I investigated whether there were any differences between the groups with regard to who their main playing partner was. Tomasello and Farrar (1986) highlighted the importance of mothers scaffolding in early joint attention interactions and Deák & Triesch (2006) argued that mothers played a vital role in the development of joint attention in human infants. In addition, the majority of the laser experiments were conducted with mothers (66/68). Therefore, I first investigated how much of the social playing interactions were carried out with the offspring's mothers. In addition, I compared the offspring's social play with siblings or other peers.

Bakeman and Adamson (1984) have shown that Western infants showed less joint attention with peers compared to mothers. Therefore, mothers may have been more competent social partners in scaffolding joint attention. Based on this, if we

assume a correlation between joint attention and the proportions of play with their mothers, human infants should play more with their mothers than chimpanzees.

Distance Mother - Offspring

In order to be able to engage in joint attention with one's mother, it is important to spend enough time near her. Therefore, I first investigated the modal distances from the mother for the offspring of the three groups and then analysed in more detail whether there were any group differences in terms of the amount of time spent within 5m of their mothers. It is likely that offspring who stayed mostly within 5m of the mother were most likely to engage in regular joint attention interactions with her compared to offspring who spent a significant amount of time away from the mother. No directional hypotheses were made.

Opportunity for Social Interaction

Although the mothers are an important social partner for infants (Deák & Triesch, 2006), infants also interact with other social partners such as siblings and peers. These interactions also impact on the offspring's social development and may contribute to the development of joint attention. In general, it is likely that individuals who spend much time with conspecifics are more adept in social skills than individuals who had little chance for social interaction (Müller & Brenner, 1977). Therefore, I investigated how many different individuals were present within 5m of the offspring and whether the chimpanzee, Ugandan and British offspring differed in this respect. Due to their large family sizes (UBOS, 2007), I hypothesized that Ugandans had the largest number of conspecifics around them whilst the British infants whose families are usually smaller had the least individuals within 5m. Chimpanzees should fall in between Ugandans and the British.

Methods

Participants

Chimpanzees

The participating chimpanzees originated from the Sonso study group described in chapter 3. According to the age groups defined by Reynolds (2005) and modified for this thesis (see Chapter 3, p.71), the study sample consisted of 13 infants (9 females, 4 males) and 12 dependent non-infant offspring (9 females, 3 males) from 14 different mothers. In total, 16 mothers and 28 offspring were followed during the study period, however, 2 females and 3 offspring had to be excluded because they contributed less than the minimum amount of data (see minimum criteria, p.217). The mean age of the chimpanzees during the study periods was 73.9 months (SD = 43.6).

Ugandans and British

The final Ugandan sample consisted of 20 mother-infant dyads. Eight infants were male, 12 were female. Initially, 23 Ugandan infants participated in this study, however, two dyads had to be excluded because the infants' ages did not fall into the required 320-350-day period and one infant was excluded because we could not obtain enough data. Eighteen of the final 20 families were visited once for a whole day and two families had to be visited on two different days, because the data collection was interrupted by external events. The Ugandan infants were an average of 338 days (SD = 8.5) old during their first visit.

Eleven British mother– infant pairs participated in this study. Five infants were female, six were male. The mean age of the British infants on the day of the visit was 335 days (SD = 5.7). All British infants were visited only once and no dyad had to be excluded.

Procedure

Chimpanzees

The data were collected from March 2010 until January 2011 by either my field assistant Geresomu Muhumuza (GM) and I or by GM alone. During that time period, GM and I spent approximately 220 days in the forest altogether. This equalled approximately 1980 hrs of either following chimpanzees or looking for them. We usually followed chimpanzee females and their offspring from 07:00 hrs to 16:30 hrs and collected data whenever both mother and offspring were visible. The offspring was defined as the focal animal and the data were collected on both the focal and her mother. Focal animals were chosen opportunistically by following the offspring of a female we saw first in a day unless we had already obtained sufficient data from the offspring within the same month.

For each focal and her mother we collected instantaneous scan samples in predefined intervals of 5min (Altmann, 1974). The duration of the scan sampling period was variable, but usually a total of 75min per day were collected for offspring of females who were mainly found in the central part of the study area and as many minutes as possible for peripheral females as they were much harder to encounter and to follow. The observation was stopped whenever the focal and her mother were out of sight or when we found another individual that we needed more data on than the current focal. In addition, we tried to follow each focal during different daytimes to avoid daytime biases.

The focal scan sampling data were either noted on a data sheet and later transferred into an excel sheet or entered directly into an excel sheet on a handheld computer (HP iPAQ H2200). To determine when exactly 5min had elapsed, a Casio watch (CASIO Dual Time, 5 alarm countdown timer 2925, W-752) which repeatedly beeped in 5min intervals was used. Each scan sample consisted of an instantaneous description of the behaviour and environment of the focal offspring and his mother including: (1) the time of the scan; (2) the activity of the offspring as defined in Table 6.1; (3) the activity of the mother as defined in Table 6.1; (4) the distance between the focal and the mother with either (a) body contact or (b) the distance estimate in metres; (5) the identity of individuals within 5m

and (6) the identity of the individuals beyond 5m, but still within 30m. Previous research in this forest has defined individuals within thirty metres of each other as belonging to the same party (Newton-Fisher, Reynolds & Plumptre 2000) thus if mother and offspring were within 30m they were considered in the same party.

Ugandans

The study took place between May 2010 and January 2011. Like in the chimpanzees, instantaneous focal scan sampling was used and the infant was defined as the focal. The data were collected on the focal infant and his mother in 15min intervals. Since humans were usually sampled only for one day, it was not possible to collect 5 min scans continuously for 10 hours without compromising the quality of the data, thus 15 min intervals were used.

Since we were interested in every-day life activities in the natural environment of the participants, the human families were visited at their home. Keeping the impact of our presence as minimal as possible was our highest priority. Therefore, the 15min scan data were collected exclusively by my field assistant Helen Biroch (HB), because my presence as a European would have caused too much attention in the village which in turn would have strongly affected the family's behaviour. Although I was not present during the scan sampling, I was able to visit most families before HB collected the 15min scan sample data. I introduced myself and the overall study and gave the mothers the opportunity to ask questions.

When the infant was approaching 11 months, HB arranged a day for the visit by suggesting 2 days and the mother could either accept or reject the proposed dates in which case HB would suggest another 2 days. By doing this, the choice of days was kept as random as possible, thereby trying to avoid a bias towards days when mothers would not leave their compounds. When arranging a visit, HB requested that the mother should not change her plans for that day, but to do everything she was originally planning to do.

Before HB started visiting families on her own, I trained her extensively by visiting one family together and practicing the focal sampling method in situ. Whilst HB

was collecting data on her own, I closely supervised her data collection, meeting with her to review the data sheets after every 1-3 visits.

On the day of the visit, HB started with a briefing of the mother about the planned procedure. HB explained: (1) the importance of not changing her plans for the day due to HB's presence; (2) HB (the observer) was not allowed to interact with the child nor help with child care activities; (3) the mother was free to stop participating at any time; (4) the mother should ignore the beep of the watch. After that, informed consent was obtained from the mother and HB started with the data collection.

Data were collected between 08:00 hrs and 18:30 hrs. Each scan sample consisted of an instantaneous description of the behaviour and environment of the focal infant and his mother including: (1) the time of the scan; (2) a brief description of the activity of the offspring; (3) a brief description of the activity of the mother; (4) the distance between the focal and the mother with (a) body contact (b) mother within reach of the infant (c) distance estimate in metres or (d) more than 5 metres away; (5) whether or not the infant could see the mother and (6) other individuals within 5m.

After the visits, I converted HB's description of the activities of offspring and mother into the activity codes defined in Table 6.1. Subsequently, the data were entered into an excel sheet. At the end of the study, the mother was given 1kg of sugar and the baby was given a toy to thank them for their participation. The mothers did not receive cash payments in line with BCFS guidelines.

British

The data collection with the British families took place between April 2011 and January 2012. Like in the chimpanzees and Ugandans, instantaneous focal scan sampling was used and the infant was defined as the focal. The data were collected on the focal infant and his mother in 15min intervals. The British infants were also visited at their homes.

The visits were undertaken by the two student research assistants Kate Brook (KB) and Stephanie Burchill (SB) from the University of York. Both assistants were

trained in the procedure of the data collection by me. A practice home visit with both of the assistants was conducted to ensure that the data collection was as similar as possible to the data collection conducted with Ugandans and chimpanzees and to give them the opportunity to familiarise themselves with the procedure.

The British families were either contacted by me, my supervisor (Dr. Katie Slocombe) or one of my research assistants. If the mothers were interested, I entered into personal contact with them. I provided them with an information sheet explaining the purpose and the procedure of the study and answered all open questions. As in the Ugandan infants the dates of visits were arranged by my research assistants depending on their availabilities, but we used the same method of suggesting two random days to the mother as close as possible to the 11 month anniversary of the infant.

Upon arrival on the day of the visit, the research assistant explained the procedure of the study to the mothers and present family members, which was identical to the information presented to Ugandan families (see p.214). After that, informed consent was obtained from the mother and the assistant started with the data collection. Data were collected between 8:00 hrs and 18:00 hrs and the data sheet was identical to that of the Ugandans study group. After 1-3 visits, I met with my research assistants and provided continuous feedback on the procedure and answered any open questions. Subsequently, the data were transcribed into an excel sheet. The British mothers were compensated with £30 for their participation in the study.

Ethics

Approval for this study was obtained from the Departmental Ethics Committee from the University of York, from the Ugandan National Counsel for Science and Technology (UNCST) and the Ugandan Wildlife Authority (UWA).

My field assistants and I made sure to keep the impact of our presence as small as possible during data collection. The chimpanzee study group was already well-acquainted with research equipment. Therefore, only chimpanzee infants initially reacted to the beep of the stopwatch by orienting towards it. After repeated

exposure, they quickly lost interest in the beep and subsequently appeared undisturbed by it.

Definitions of Activities

The behaviours that were scored during the scan sampling procedure outlined above and their definitions are summarised in Table 6.1.

Table 6.1: Overview of the definitions for the scored activities in chimpanzee and human mother-offspring dyads. Working was only scored in human mothers as there was no comparable activity in chimpanzees.

Scored Activity	Definition	scored in
feeding	Individual feeding, manipulating food, foraging, drinking, being (breast-)fed	All
resting	Being stationary; either standing, sitting or lying, sleeping, sunbathing, watching TV, reading, listening to radio, resting on conspecific whilst he/she is locomoting	All
play alone	Play does not involve other individual	All
play social	Play with another individual or attempt to play with another individual (i.e. mother, offspring, father, sibling, other)	All
locomotion	Going from A to B in tree or ground (crawling, climbing, travelling, walking, driving, public transport, sitting on passenger seat), for the offspring only self-induced locomotion is counted here	All
vocalising	Producing a vocalisation (crying, singing, talking, chimpanzee vocalisation)	All

Scored Activity	Definition	scored in
Other	<i>other-leisure social</i> (e.g. texting, arranging burial, swimming lesson with baby, taking pictures) <i>other- leisure individual</i> (e.g. exercise) <i>other- essential social</i> (e.g. begging, aggression, copulation) <i>other-essential individual</i> (e.g. nesting, doctor's appointment)	All
Self- care	Self-grooming, bathing, dressing, toilet	All
Give-care	social grooming , bathing other, dressing other, (breast-) feeding other, changing nappy	All
Receive-care	Being bathed, being dressed, being groomed, having nappy changed	All
Working	Individual work such as preparing food, cooking, drawing water, collecting firewood, tending crops, cleaning, tidying, selling products, animal husbandry, washing dishes, paper work, computer work	Human mothers

Data Analysis

Minimum Criteria for Inclusion of Scans

In order to have a comparable dataset across species, the chimpanzee 5min scans were converted into 15min scans by only using the first of each three scans. Each human and chimpanzee mother and offspring had to contribute a minimum of 28

15-minute scans (7 hours) in total to be included in the analysis. Seven hours were regarded as the best compromise between having a large enough sample and a reasonable amount of scan data. The human scan samples originated from either one or two days of data collection and the chimpanzee scan samples originated from at least five different days with a minimum of at least two scans per day and at least four different months within the ten month study period. This made sure that I obtained a representative sample in chimpanzees.

Behaviours of Interest

Essential and Leisure Activities

Essential activities were defined as activities that are necessary to insure sustainable survival (survival not just for the day, but to stay healthy and to reach adulthood or to stay alive in the long run). The following activities were classified as essential in this study:

Feeding (including being [breast] fed), locomotion, self-care, give care to either offspring, mother or sibling, receive-care from either offspring, mother or sibling, other-essential (individual and social) and working.

Leisure activities were defined as activities that did not ensure direct survival and that were usually carried out after all essential activities had been done sufficiently and there was some “spare-time” or “leisure-time” available. The following activities were classified as non-essential in this study:

Resting, play alone, play social, give care to individuals except the mother, offspring or sibling, receive-care from individuals other than the mother, offspring or sibling and other-leisure (individual and social).

Receiving or giving care to kin was regarded as essential because infants need to receive care from their mothers/ siblings in order to be kept clean and well-fed: aspects essential for survival. The same activities (e.g. grooming, providing drinks) are also directed at non-kin in both species, however, although these activities have an important social function, they are not fulfilling basic survival needs in these non-kin individuals, so are counted as ‘other-leisure’ activities. Vocalisations

were excluded from this analysis as they could be done during both essential and leisure activities.

Individual and Social Activities

A social activity was defined as an activity that involved another individual and could not be done without another individual. The following activities were scored to be social:

Play social, give- care, receive- care (including being [breast] fed), other-leisure-social, other-essential-social and vocalisations.

Vocalisations constituted an exception to the above mentioned definition, as they could be produced when alone. When perceived, however, vocalisations always have a social meaning. In addition, there is some evidence that vocalisations in humans have some degree of functional similarity to grooming in chimpanzees in that they serve to maintain social relationships (Dunbar, 1991). Based on this similarity and the fact that vocalisations usually have a communicative function with conspecifics, they were included as a social activity.

An individual activity was defined as an activity that did not involve another individual and could be carried out alone. The following activities were categorised as individual activities:

Feeding (excluding breastfeeding or being fed), resting, play alone, locomotion, self-care, other-leisure-individual, other essential –individual and working.

Statistical analysis

The statistical tests used in this chapter were identical to those outlined in more detail in Chapter 4 (p.116ff). Whenever the sample size was big enough to analyse chimpanzee infants and chimpanzee non-infants separately, I tested a priori, whether the two chimpanzee groups differed statistically. This was done, because although the chimpanzees in each group belong to different age classes, they were treated as one group in the laser experiments (Chapter 4 & 5). Therefore, to make the results more comparable between the laser experiment and the time budget and social environment study, the data of both groups were collapsed, whenever

possible. The statistical comparison of activities between the three (chimpanzees collapsed, Ugandans and British) or four (chimpanzee infants, chimpanzee non-infants, Ugandans and British) was considered the main test and the subsequent pair wise comparisons between the groups were post-hoc tests for which Sidak corrections were applied (see Chapter 4, Table 4.3, p.117).

Results

For the final 14 chimpanzee mothers and their 25 offspring, I obtained 365 hrs of focal scan sampling data during the study period. The mean number of 15min scans obtained from the chimpanzee offspring were 55.7 scans (SD = 16.0). The data collection for Ugandans resulted in a mean of 38 scans per individual (SD=9.6) and a total number of 201 hours of focal scan sampling. From the British study group, I obtained a mean number of scans of 38.5 (SD = 1.4) and a total number of 106 hours of focal scan sampling.

Time budgets

In order to get an overview of the daily activities of the chimpanzee infants, non-infants, Ugandan and British infants, the general time budget was calculated. The data originated from 13 chimpanzee infants, 12 chimpanzee non-infants, 20 Ugandan and 11 British infants and from 14 chimpanzee, 20 Ugandan and 11 British mothers.

Time budget offspring

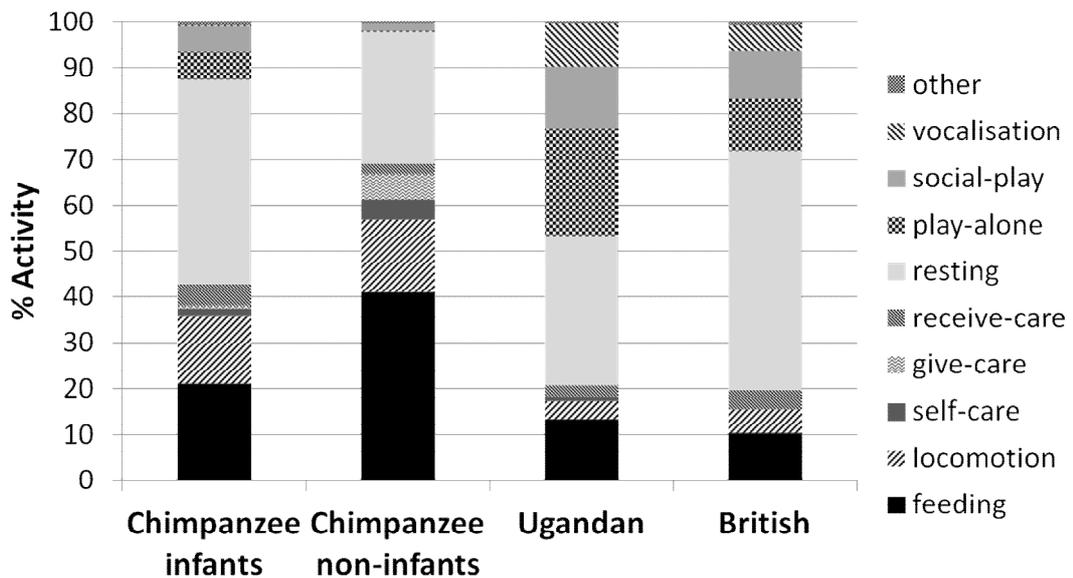


Figure 6.1: Bar Graph illustrating the time budgets of offspring, based on 15 minute-scan data of their everyday activities.

Figure 6.1 illustrates that the modal activity of all infant groups was resting, with British infants resting the most (more than half of their total time budget). Feeding was the modal activity for chimpanzee non-infants and compared to chimpanzee mothers their amount of time feeding was similar (Figure 6.1; 6.3). Therefore, it seems that as chimpanzees get older, resting time is reduced and feeding time is increased. Descriptively, human infants, however, spent less time feeding than either chimpanzee group. The proportion of scans spent in locomotion was nearly constant between the two chimpanzee age groups, but locomotion rates in the two human groups were lower than in the chimpanzee groups.

Chimpanzee infants played considerably more than chimpanzee non-infants, but compared to both human groups, chimpanzee infants played less. Playing behaviour will be analysed in more detail below as it is an important context for the development of joint attention. Chimpanzee and British infants received care at similar rates, and both of those groups received more care than chimpanzee non-infants and Ugandan infants. All three infant groups gave care at low rates. Only chimpanzee non-infants spent more than 5% of their time budget with providing care for others. Vocalisations were very rare in both chimpanzee groups. This

confirms the observation made in the laser experiments. Therefore, statistical tests were performed to see whether chimpanzee offspring significantly differed in their use of vocalisations from the two human groups. Chimpanzee infants did not statistically differ in their percentage of vocalisation from chimpanzee non-infants ($U = 66, p = .480$). The median for vocalisations for the collapsed chimpanzee groups was 0% (IQR = 0) (Figure 6.2).

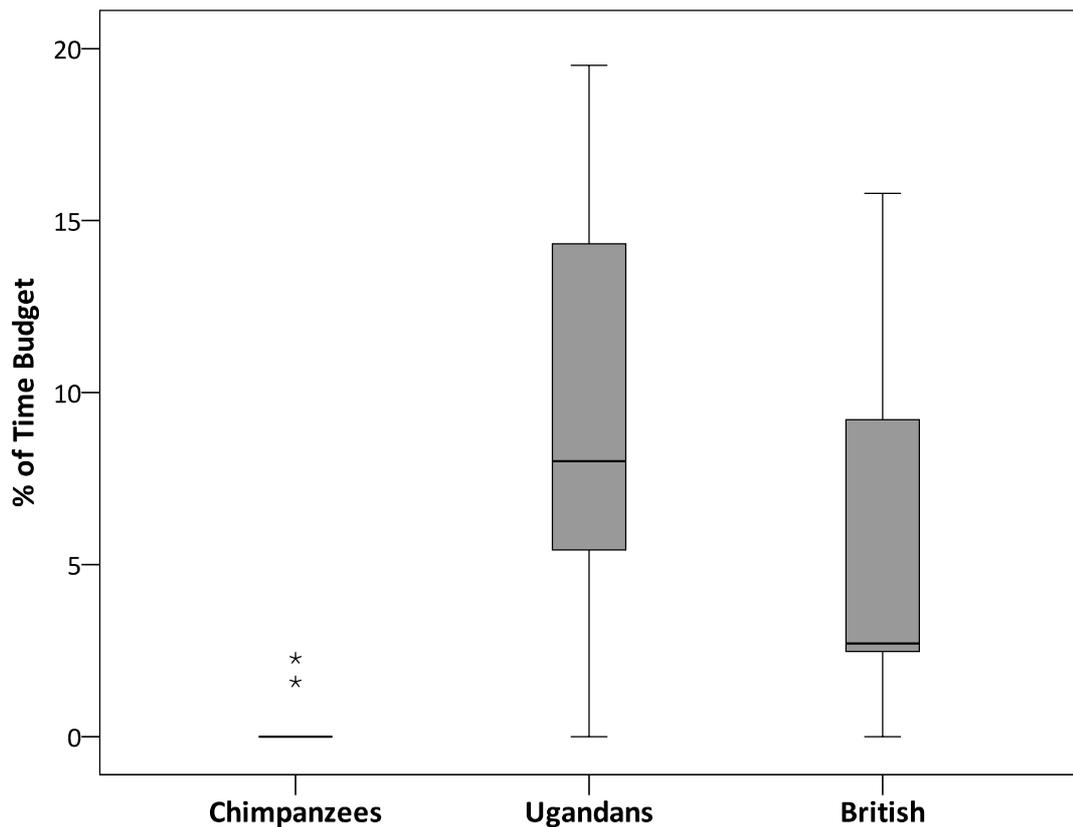


Figure 6.2: Box plots of the offspring's median percentage of vocalisations in their total time budget.

A Kruskal-Wallis test revealed that there was a significant group difference ($\chi^2 (2) = 40.14, p < .001, \text{asymptotic}$). Post-hoc pair wise comparisons showed that chimpanzees vocalised significantly less than both Ugandans ($U = 13.4, p < .001$) and British ($U = 13.5, p < .001$). There was no significant difference, however, in the median proportions of vocalisations between Ugandan and British infants ($t (29) = 1.83, p = .078, \text{Sidak corrected}$).

Time budget mothers

Fourteen chimpanzee mothers, 20 Ugandan mothers and 11 British mothers participated in this study. Since some chimpanzee mothers had more than one offspring who entered into the offspring-analysis above, there is a large variability on the number of scans that entered the mother-analysis, because I collected more data on mothers who had three offspring than on mothers with only one dependent offspring. The mean number of scans for mothers was 102.3 (SD = 46.38).

Figure 6.3 illustrates that chimpanzee mothers' modal activity was feeding and descriptively they spent more time feeding than Ugandan and British mothers.

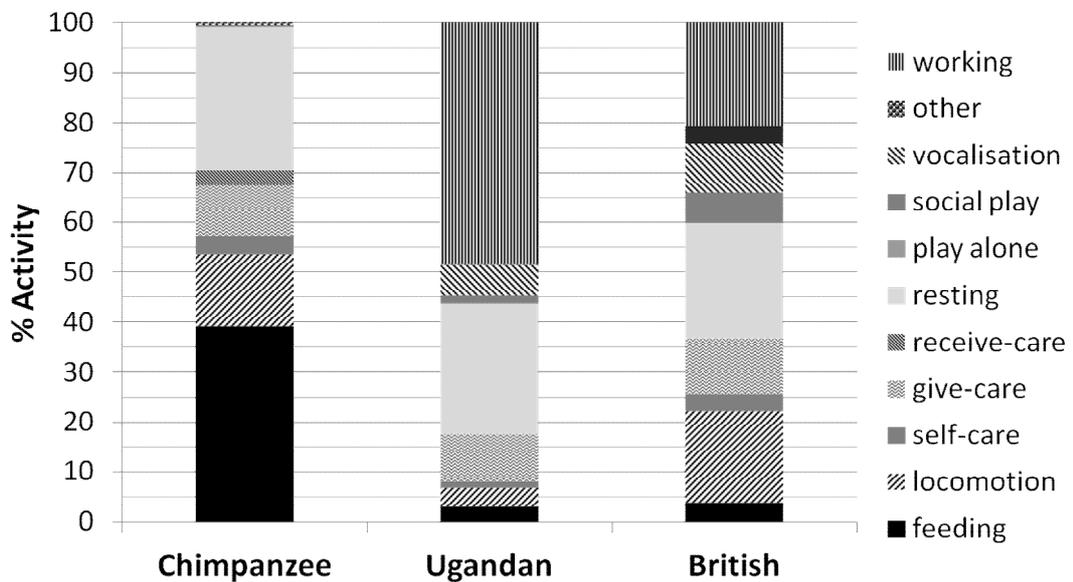


Figure 6.3: Bar Graph illustrating the time budgets of mothers, based on 15 minute-scan data of their everyday activities.

Working took almost half of the Ugandan mothers' time budget and was therefore their modal activity. The modal activity of British mothers was resting followed closely by working. The mothers of all three groups gave care at similar rates, but only chimpanzee mothers also received some care. Only British mothers spent more than 5% of their total time budget with social play (Figure 6.3). Playing behaviour of mothers will also be analysed in more detail below. The mothers of the three groups rested at similar rates. Like chimpanzee offspring, chimpanzee mothers were also rarely seen to vocalise (Figure 6.4).

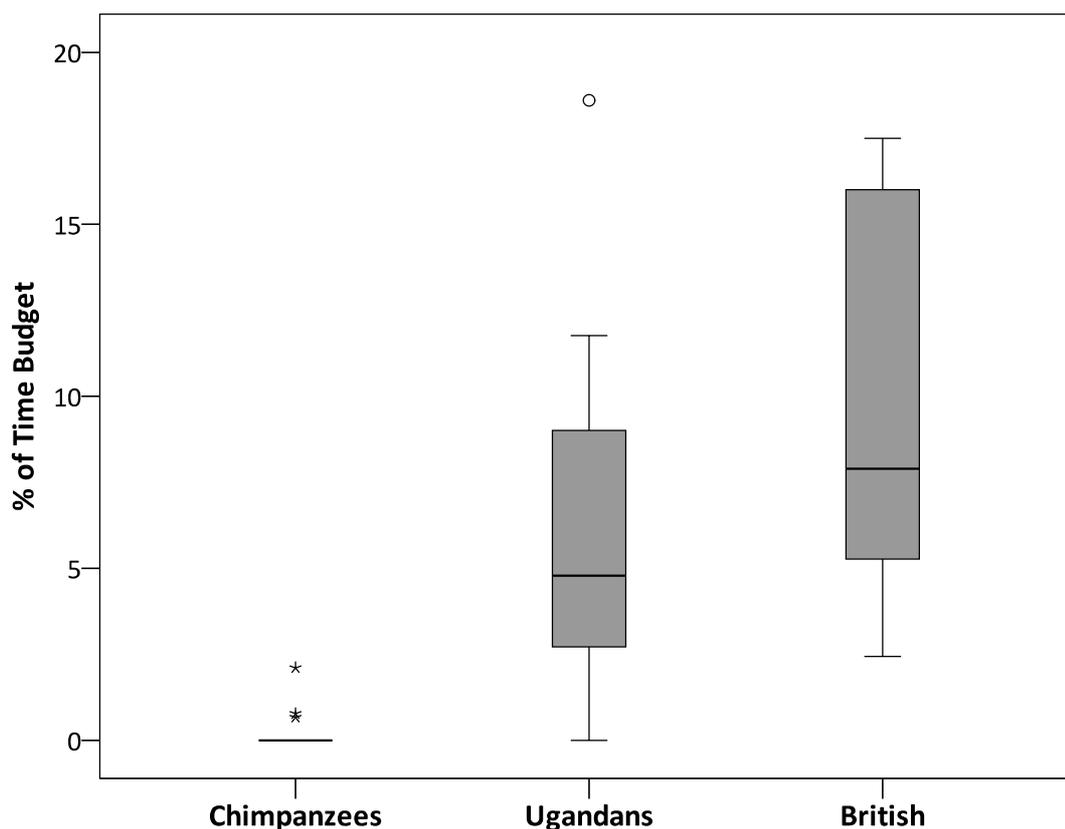


Figure 6.4: Box plots of the mother's median percentage of vocalisations in their total time budget.

A Kruskal-Wallis test revealed that the three groups differed significantly in terms of the percentage of their time budget they were observed vocalising ($\chi^2 (2) = 24.68, p < .001$, asymptotic). Chimpanzee mothers vocalised less than British mothers ($U = 0, p < .001$) and Ugandans mothers ($U = 25.5, p < .001$). There was no significant difference in vocalisation between British and Ugandan mothers ($U = 71.00, p = .110$). This result shows a clear species difference.

Essential vs. Leisure Activities

The analysis of the amount of essential activities will reveal how much 'leisure time' the offspring and the mothers from each group have to dedicate to relaxed social interactions that are relevant for the development of joint attention. Based on the definition of essential activities, vocalisation scans were excluded from the analysis. After that, the proportions for essential and leisure activities were calculated for each group: chimpanzee infants, chimpanzee non-infants, Ugandan infants and British infants. Since essential and leisure activities were mutually

exclusive and exhaustive categories in this analysis, only the percentage of essential activities was entered into statistical analysis.

Essential vs. Leisure Activities: Offspring

Thirteen chimpanzee infants, 12 chimpanzee non-infants, 20 Ugandan infants and 11 British infants contributed to this analysis. Figure 6.5 shows chimpanzee non-infants engaged more than half of their time budget in essential activities.

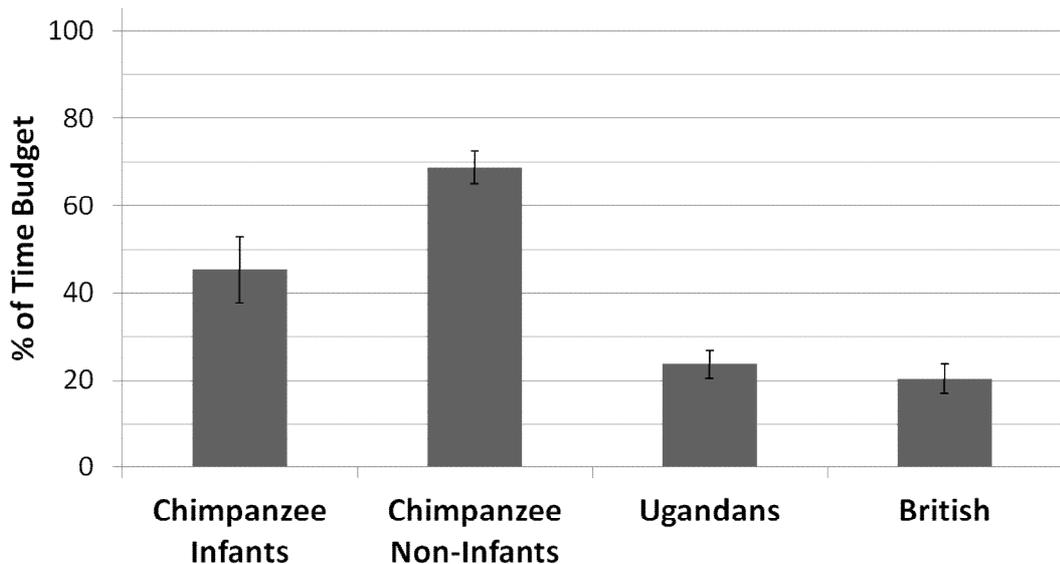


Figure 6.5: Bar graph showing the mean percentage of the offspring's essential activities within the total time budget. The error bars represent 1 standard deviation from the means.

A paired-sample t-test showed that chimpanzee non-infants engaged more in essential activities than chimpanzee infants ($t(17.65) = -5.04, p < .001$). Therefore, they were analysed as two different groups for the following analysis.

The four groups engaged in essential activities at different rates (*Welch's F* (3, 24.9) = 120.66, $p > .001$). Games-Howell pair wise comparisons revealed that chimpanzee infants engaged significantly more in essential activities than Ugandan infants ($p = .001$) and British infants ($p < .001$). Chimpanzee non-infants engaged significantly more in essential activities than Ugandan infants ($p < .001$) and British infants ($p < .001$), but there was no difference between Ugandan and British infants ($p = .527$). This result shows a clear species difference.

Essential vs. Leisure Activities: Mothers

Fourteen chimpanzee, 20 Ugandan and 11 British mothers contributed data to this analysis. Chimpanzee mothers engaged in essential activities 69.83% (SD = 7.35) of their time budget, Ugandan mothers 70.05% (SD = 10.77) and British mothers 63.61% (SD = 10.74). A One Way ANOVA revealed that there was no significant difference between the three groups ($F(2, 42) = 1.73, p = .189$) in terms of percentage of all time budget scans spent with essential activities.

To sum up, there was a clear species difference between the offspring of the three groups: chimpanzee offspring spent significantly more time with essential activities than the infants of the two human groups. In addition, there was an age difference between chimpanzee infants and chimpanzee non-infants with the latter engaging more in essential activities. The mothers of the three groups spend more than 60% of their time budget in essential activities and the three groups did not differ.

Social vs. Individual Activities

Since joint attention is a social activity, the amount of time that offspring engage in social activities indicates the opportunity offspring have for joint attention to occur. The amount of social activities in mothers may reflect their general tendency to engage socially with their offspring. According to the definitions (p.219), the proportions of social and individual activities were calculated for each group: chimpanzee infants, chimpanzee non-infants, Ugandan infants and British infants. Since social and individual activities were mutually exclusive and exhaustive categories in this analysis, only the percentage of social activities was entered into statistical analysis.

Social vs. Individual Activities: Offspring

Thirteen chimpanzee infants, 12 chimpanzee non-infants, 20 Ugandan infants and 11 British infants contributed to this analysis. Interestingly, the offspring of all three groups engaged in social activities in less than 50% of their total time budget (Figure 6.6). A paired samples t-test showed that there was no significant difference between chimpanzee infants and non-infants in terms of the percentage

spent in social activities ($t(23) = 1.42, p = .170$). Therefore, the two chimpanzee groups were collapsed in the further analysis.

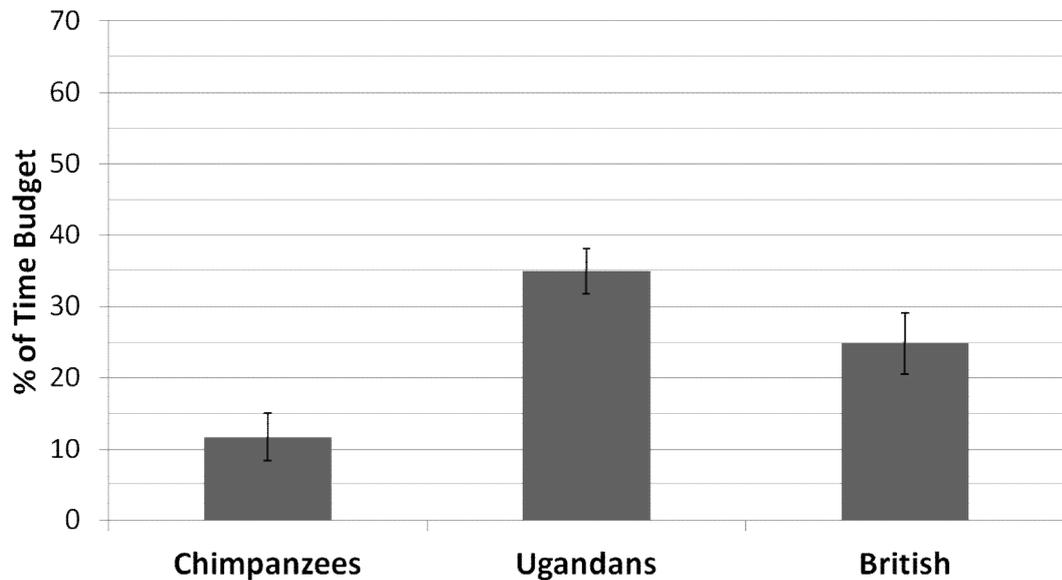


Figure 6.6: Bar graph showing the mean percentages of the offspring's social activities in their total time budget. The error bars represent 1 standard deviation from the mean.

A One Way ANOVA showed that the three groups differed significantly with regard to the total time spent in social activities ($F(2, 53) = 61.96, p > .001$). Post-hoc pairwise comparisons revealed that Ugandan infants engaged significantly more in social activities than either chimpanzees ($p < .001$) or British infants ($p = .001$). British infants spent more time with social activities than chimpanzees ($p < .001$).

Social vs. individual Activities: Mothers

Fourteen chimpanzee, 20 Ugandan and 11 British mothers contributed data to this analysis. The mothers of the three groups spent less than 30% of their time budgets with social activities (Figure 6.7).

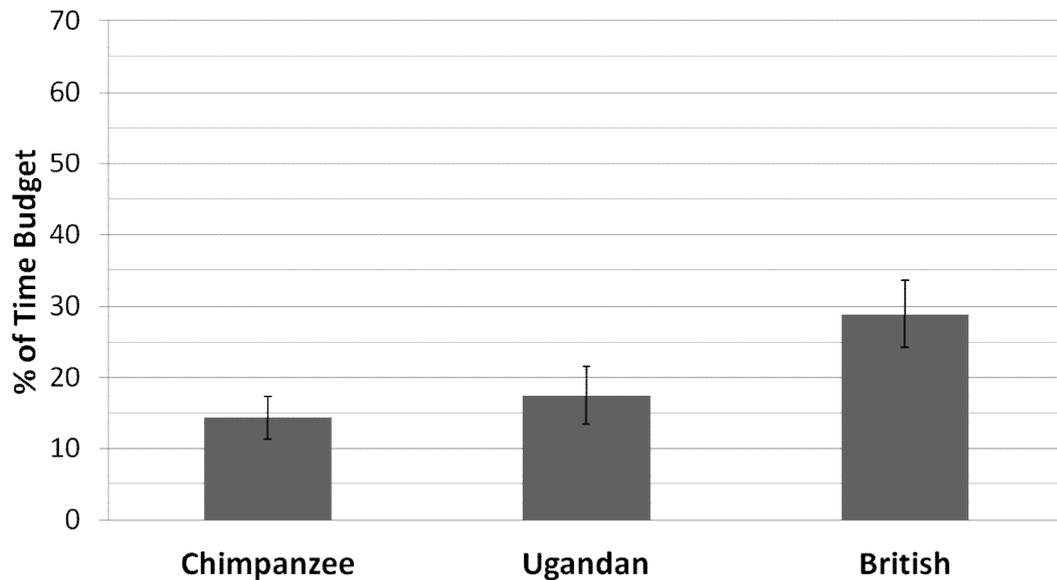


Figure 6.7: Bar graph showing the mean percentages of the mother's social activities in their total time budget. The error bars represent 1 standard deviation from the mean.

A One Way ANOVA revealed that the three groups differed significantly ($F(2, 42) = 11.26, p < .001$) in their social activity rates. Sidak post-hoc comparisons showed that there was no significant difference between chimpanzee and Ugandan mothers in terms of the percentage of their social engagement ($p = .607$), but chimpanzee mothers ($p < .001$) and Ugandan mothers ($p = .001$) engaged significantly less in social activities than British mothers. This result indicates a cultural difference between Ugandan and British mothers.

Offspring's social activities with mothers

Thirteen chimpanzee infants, 12 chimpanzee non-infants, 20 Ugandan infants and 11 British infants contributed data to this analysis. For each individual, the percentage of social scans in which the mother was the offspring's social partner was calculated. Chimpanzee infants engaged in social activities with their mothers 33.33% (IQR = 58.00) of all social activity scans, chimpanzee non-infants 67.95% (IQR = 40.00), Ugandan infants 33.97% (IQR = 27.00) and British infants 55.67%

(IQR = 46.00). A paired samples t-test showed that there was a trend for chimpanzee non-infants to engage more in social activities with their mothers than chimpanzee infants ($t(23) = -1.90, p = .070$). Therefore, chimpanzee infants and chimpanzee non-infants were treated as separate groups.

A Kruskal-Wallis test showed that there was a trend for differential engagement in social activities with their mothers between the four groups ($\chi^2(3) = 7.52, p = .057$, asymptotic). Based on this trend, the data were further investigated, but none of the pair wise comparisons yielded any significant results. Thus there were no significant group differences in the amount of social activities offspring engaged in with the mother.

Play

Play is an important context for joint attention to develop. Therefore, first, the amount of play for offspring and partners of the four groups was analysed followed by a more detailed examination of object play and play partners.

Offspring's Overall Play

The first question was how prevalent play was in the total time budget regardless of whether it was social or individual play. Figure 6.8 illustrates the median proportions of the offspring's play.

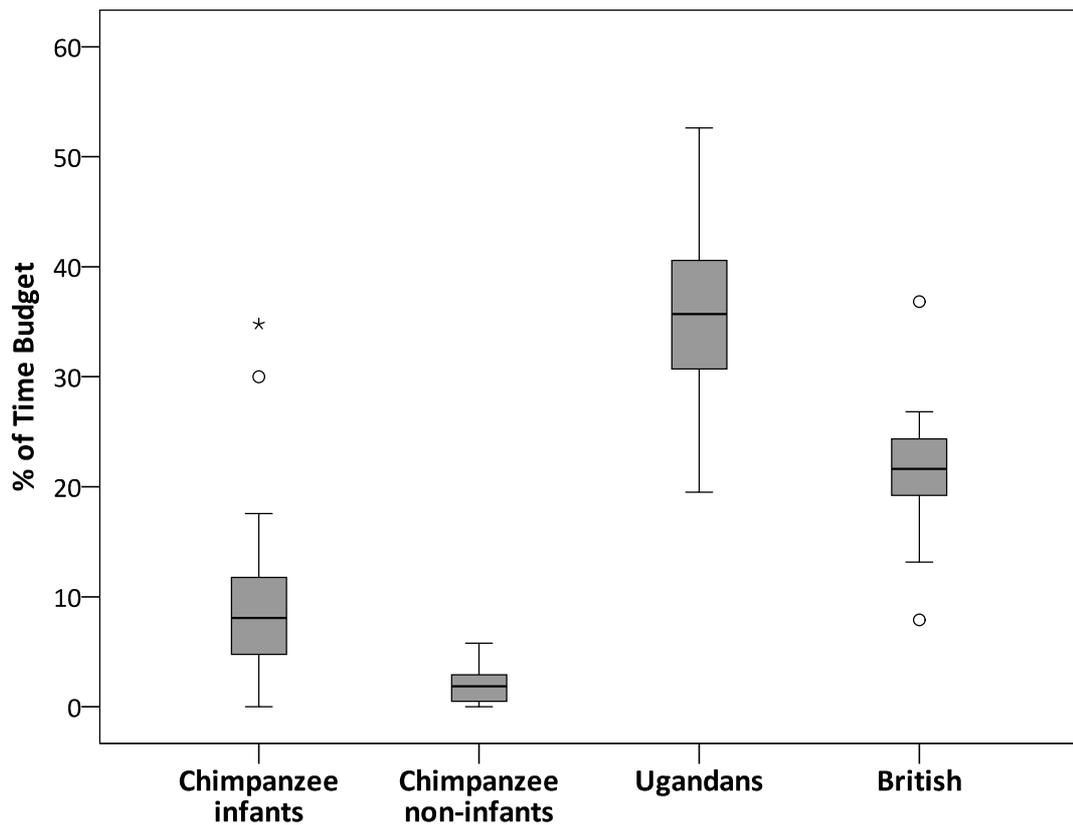


Figure 6.8: Boxplots illustrating the proportions of the offspring's individual and social play in the total time budget.

Chimpanzee infants engaged in play significantly more than chimpanzee non-infants ($U = 22.5$, $p = .002$). Therefore, they were treated as two separate groups in the subsequent analyses.

A Kruskal-Wallis test showed that the four groups differed significantly in their rates of play in their time budget ($\chi^2(3) = 41.46$, $p > .001$, asymptotic). Post-hoc pair wise comparisons revealed that Ugandan infants played more than offspring of all other groups: chimpanzee infants ($U = 14.00$, $p > .001$), chimpanzee non-infants ($t(21.6) = -17.36$, $p > .001$), and British infants ($t(29) = 4.85$, $p > .001$). British infants played significantly more than chimpanzee infants ($U = 26.00$, $p = .007$) and chimpanzee non-infants ($t(11) = -8.58$, $p > .001$). To sum up, Ugandan infants played the most, followed by the British and then the chimpanzee infants. Chimpanzee non-infants played the least.

Offspring's Social Play

Just because Ugandans played the most in general does not necessarily mean that they also played the most socially. Therefore, after having investigated the offspring's general tendency to engage in play, the next step was to test for a difference in social play. A paired samples t-test showed that chimpanzee infants spent significantly more time in social play than chimpanzee non-infants ($t(14.41) = 2.30, p = .037$). Therefore, the two chimpanzee groups were analysed separately (Figure 6.9).

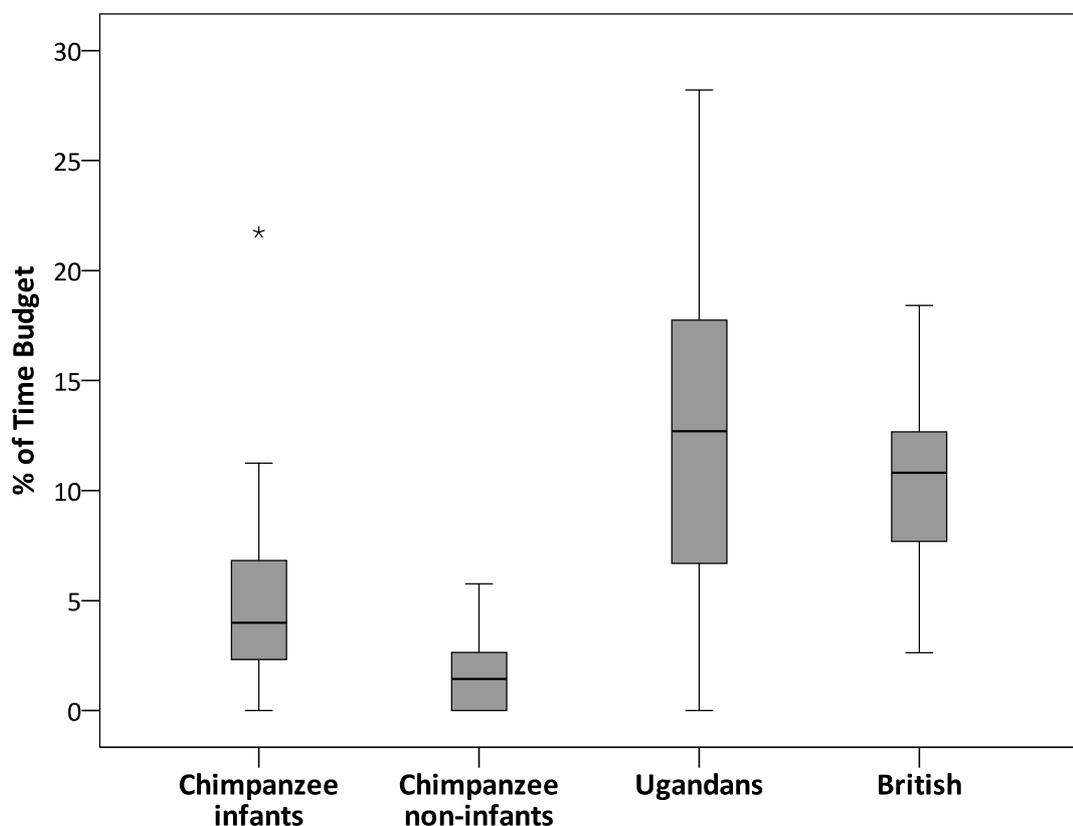


Figure 6.9: Boxplots illustrating the proportions of the offspring's social play in the total time budget.

A Kruskal-Wallis test revealed that the four groups significantly differed with regard to their social play ($\chi^2(3) = 26.50, p < .001$, asymptotic). Post-hoc pair wise comparisons showed that chimpanzee infants engaged less in social play than Ugandan infants ($U = 49.5, p = .002$), but not less than British infants ($U = 32.00, p = .021$, Sidak corrected). Chimpanzee non-infants played less socially than

Ugandan infants ($t(22.6) = -6.68, p < .001$) and British infants ($t(12.9) = -5.79, p < .001$). There was no significant difference in the amount of social playing scans between Ugandan and British infants ($t(29) = 1.29, p = .209$).

In summary, Ugandan infants played more socially than both chimpanzee groups. The two human groups did not differ in their rates of social play. British infants did not differ in their social play to chimpanzee infants. Chimpanzee non-infants, however, played socially less than every other group.

Mothers' Overall Play and Social Play

None of the mothers of any group was observed playing alone during the observation period. Therefore, the frequency of general play was identical to the frequency of social play which was analysed below. The medians and inter-quartile ranges for mothers' social play are illustrated in Figure 6.10.

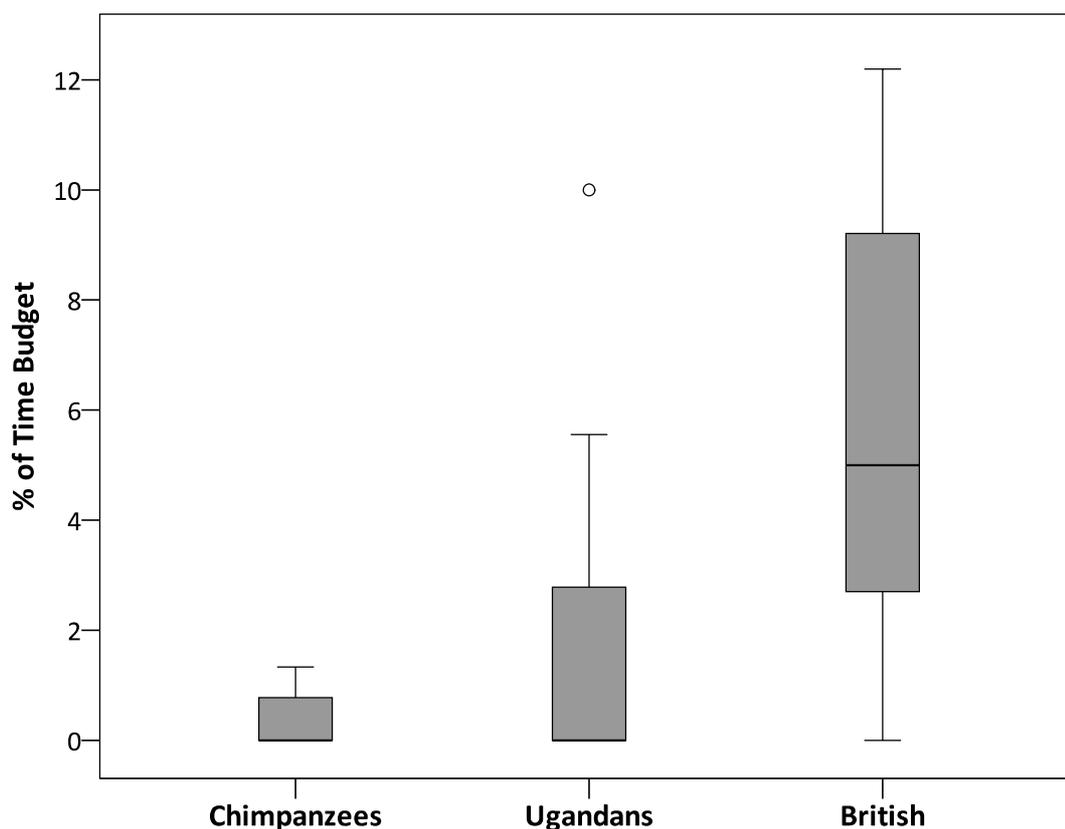


Figure 6.10: Boxplots illustrating the proportions of the mother's social play in the total time budget.

A Kruskal-Wallis test showed that there was a significant difference between the three groups in terms of the percentage of social play in their total time budget ($\chi^2(2) = 17.55, p < .001, \text{asymptotic}$). Mann-Whitney U pair wise comparisons showed that British mothers played more socially than the mothers of any other group: chimpanzee mothers ($U = 9.0, p < .001$) and Ugandan mothers ($U = 36.5, p = .001$). There was no difference, however, between chimpanzee and Ugandan mothers in their percentage of social play ($U = 108, p = .199$).

Detailed Analysis of Play

So far, the percentages of play and social play have only been examined in the context of the total time budget. In the following analyses, the play behaviours themselves will be investigated. Since playing only represents a small proportion of the total time budget and chimpanzee play was not as frequent as human play, the additional 5 min scans that were initially excluded to match the 15min scan sampling of the human groups were considered for the following play analyses.

Otherwise, the data for chimpanzees would have been insufficient for further analysis.

Object play

Proportion of object play in all play

Out of all participants, two chimpanzee offspring were never observed to use an object in their play, whereas all 20 Ugandan and ten British infants used an object in their play. In order to calculate how often chimpanzee and human offspring used objects in their play regardless of whether it was play alone or social play, I selected all individuals with at least four playing scans (Table 6.2).

Table 6.2: Table showing the number of individuals with at least 4 playing scans.

	Chimpanzees	Ugandans	British
Total number of individuals	25	20	11
Number of individuals with at least 4 playing scans	8 (infants)	20	10

The proportion of object play was calculated by dividing the number of playing scans in which an object was used by the total number of play scans. Water, faeces and soil were counted as objects, whereas body parts, urine and saliva did not count as an object. Since “object used” and “no object used” were mutually exclusive and exhaustive categories, only “object used” was entered into the analysis (Figure 6.11).

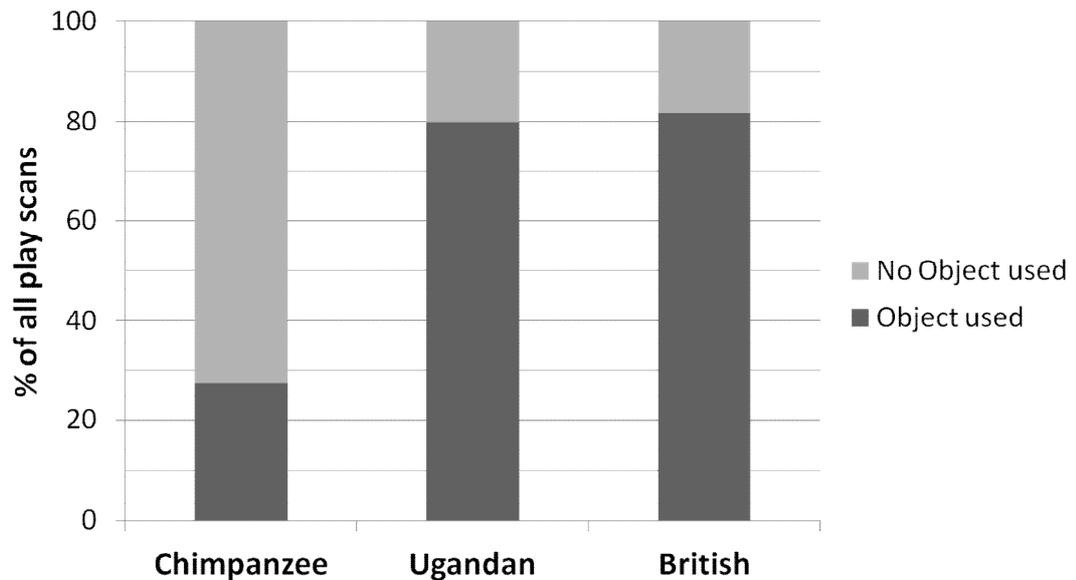


Figure 6.11: Bar graph illustrating the offspring's object use in all play. The standard deviations for object used were: chimpanzee (SD = 11.42), Ugandans (SD = 12.07) and British (SD = 18.38).

Whereas the two human groups used objects in nearly 80% of their playing scans, chimpanzees only used an object in a quarter of all playing scans (Figure 6.11). A One Way ANOVA revealed that the three groups were statistically different in terms of the percentage of objects used in play ($F(2, 35) = 46.24, p < .001$). Sidak post-hoc comparisons showed that British infants ($p < .001$) and Ugandans ($p < .001$) used more objects than chimpanzee offspring, but there was no significant difference between Ugandans and British ($p = .984$). This results shows a clear species difference.

Object play in individual play

So far, we know that the two human groups used more objects during play, but it is not yet clear whether the three groups also show the same pattern if social and individual play are analysed separately. Therefore, I first compared the offspring's object use in individual play and finally their object use in social play which was the central category for joint attention, because a social partner and an object of interest were involved in this type of interaction.

Since individual play was a sub-category of play and therefore less scans available, the minimum number of individual play scans that were included were three individual playing scans. This resulted in a sample of six chimpanzee infants, 20

Ugandan and nine British infants. To calculate the proportion of object play in play alone scans, the number of scans in which an object was used was divided by the total number of play alone scans. The medians and inter-quartile ranges for object use in individual play is shown in Figure 6.12:

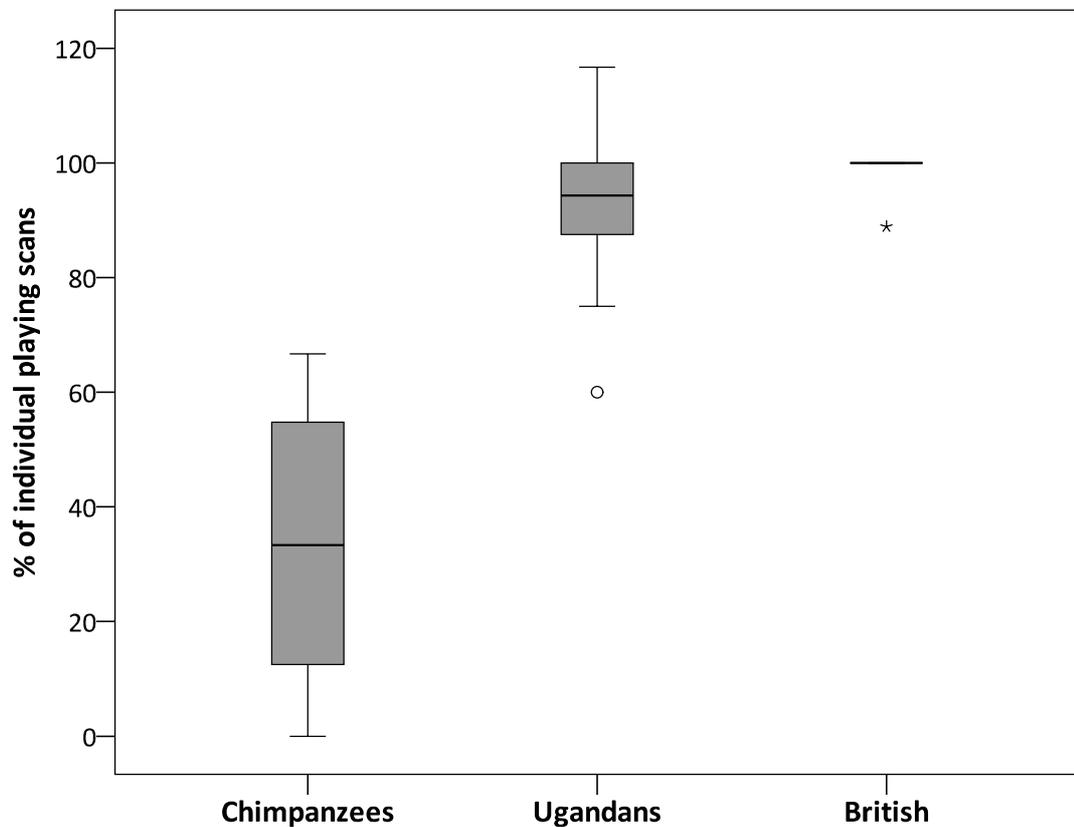


Figure 6.12: Boxplots showing the offspring's use of objects during individual play.

A Kruskal-Wallis test showed that the three groups statistically differed ($\chi^2(2) = 21.32, p < .001, \text{asymptotic}$). British infants ($U = 0, p < .001$) and Ugandan infants ($U = 2.00, p < .001$) used objects more during individual play than chimpanzees, but there was no significant difference in object use between British and Ugandan infants ($U = 53.5, p = .062, \text{Sidak corrected}$). The species difference of object use in all play above remains valid also for object use in individual play.

Object play in social play

Secondly, all chimpanzee and human offspring who contributed at least three social play scans were selected. This process resulted in six chimpanzee offspring, 15 Ugandan and nine British infants. The resulting sample is summarised in Table 6.3.

Table 6.3: Table illustrating the sample sizes for the offspring's social play.

	Chimpanzees	Ugandans	British
Total number of individuals	25	20	11
Number of individuals with at least 3 social playing scans	6 (5 infants, 1 non-infant)	15	9

To calculate the proportion of object play in social play scans, the number of scans in which an object was used was divided by the total number of social play scans. Interestingly, the chimpanzees were never observed using an object during their social playing scans (Figure 6.13).

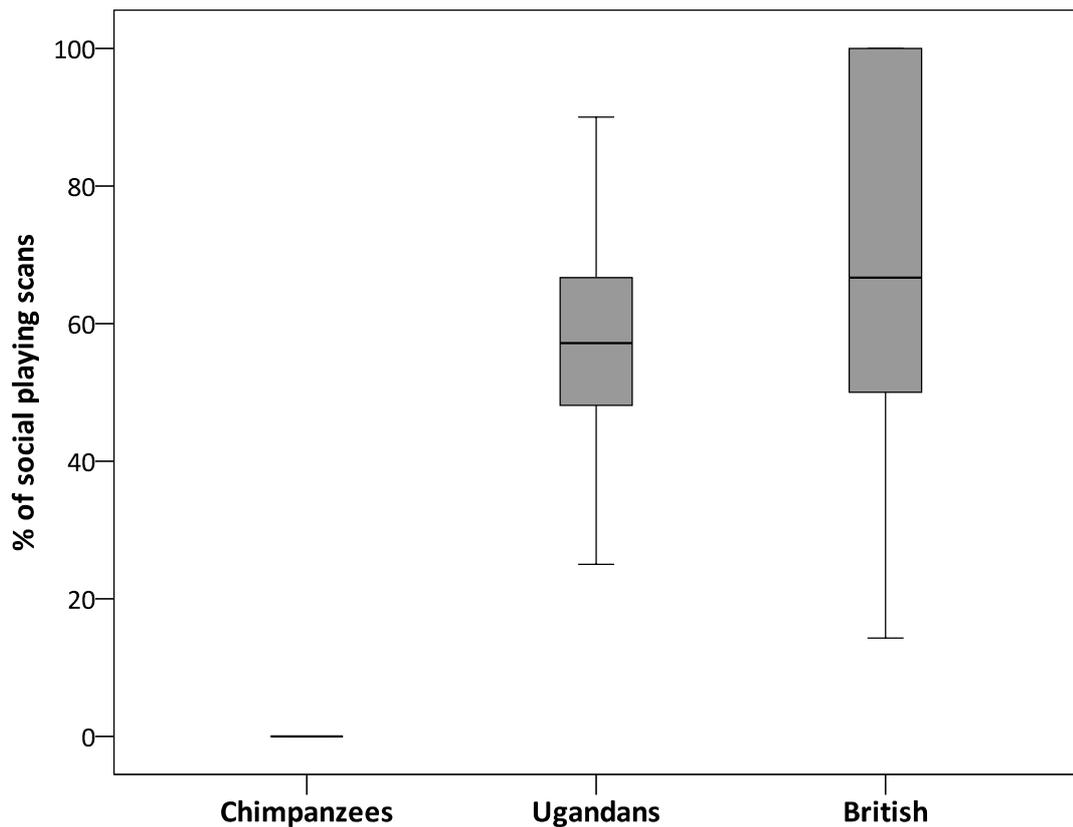


Figure 6.13: Boxplot illustrating the offspring's use of objects in social play.

A Kruskal-Wallis test revealed that the three groups were significantly different ($\chi^2(2) = 14.91, p < .001$). The two human groups did not differ statistically ($U = 49.5, p = .293$), but chimpanzees engaged significantly less in social object play than Ugandans ($U = .00, p < .001$) and British infants ($U = .00, p < .001$). Also for social play, there was a clear species difference for object use.

Social play partners

Infants could play with different individuals during social play: the mother, the father, siblings and other related or unrelated individuals. In Ugandans, the infants' playing with their fathers was observed, but it was very rare. In the British, the infants played with their fathers (41.53%, $SD = 40.0$) and mothers (41.80%, $SD = 37.0$) at similar rates. This is probably based on the different roles that mothers and fathers play in the Ugandan and British culture. Whilst it is common to share parenting in British families, it is the sole responsibility of the mothers (and other female family members) to look after the infants in Uganda (Keller, 2007). Since

the laser experiments were only conducted with mothers and not fathers, fathers as playing partners constituted their own category and they were excluded from the analysis. In addition, siblings and other individuals were also collapsed, because not every offspring had a sibling.

For all offspring who were able to contribute at least three social playing scans, the proportion for play with either mothers or siblings/others was calculated by dividing the number of social playing scans in which the respective partner was involved by the total number of social playing scans.

Play with mothers

The medians and inter-quartile ranges for the mothers as the playing partners of the offspring are illustrated in Figure 6.14:

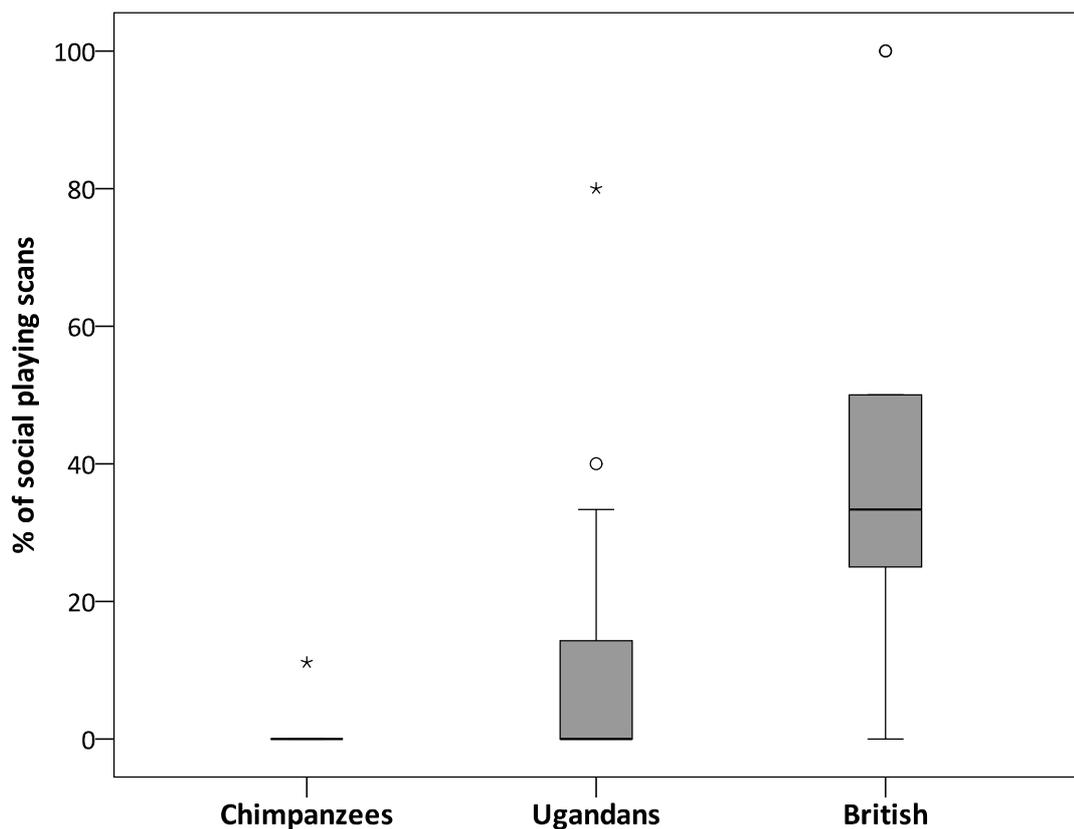


Figure 6.14: Boxplots for median percentage of the offspring's playing bouts that were done with the mothers.

The three groups differed with respect to social play with their mothers (Kruskal-Wallis: $\chi^2 (2) = 8.11, p = .012$). Mann-Whitney U pair wise comparisons showed that British infants played more with their mothers than chimpanzees ($U = 7.0, p = .011$), and that there was no difference between chimpanzee and Ugandan infants ($U = 30.0, p = .273$). In contrast to the social play with parents, Ugandan and British infants did not differ in their social play with mothers ($U = 30.5, p = .032$, Sidak corrected).

Play with siblings/others

Figure 6.15 shows that with the exception of two outliers, British infants played with their sibling/others at very low rates compared to chimpanzee and Ugandan offspring.

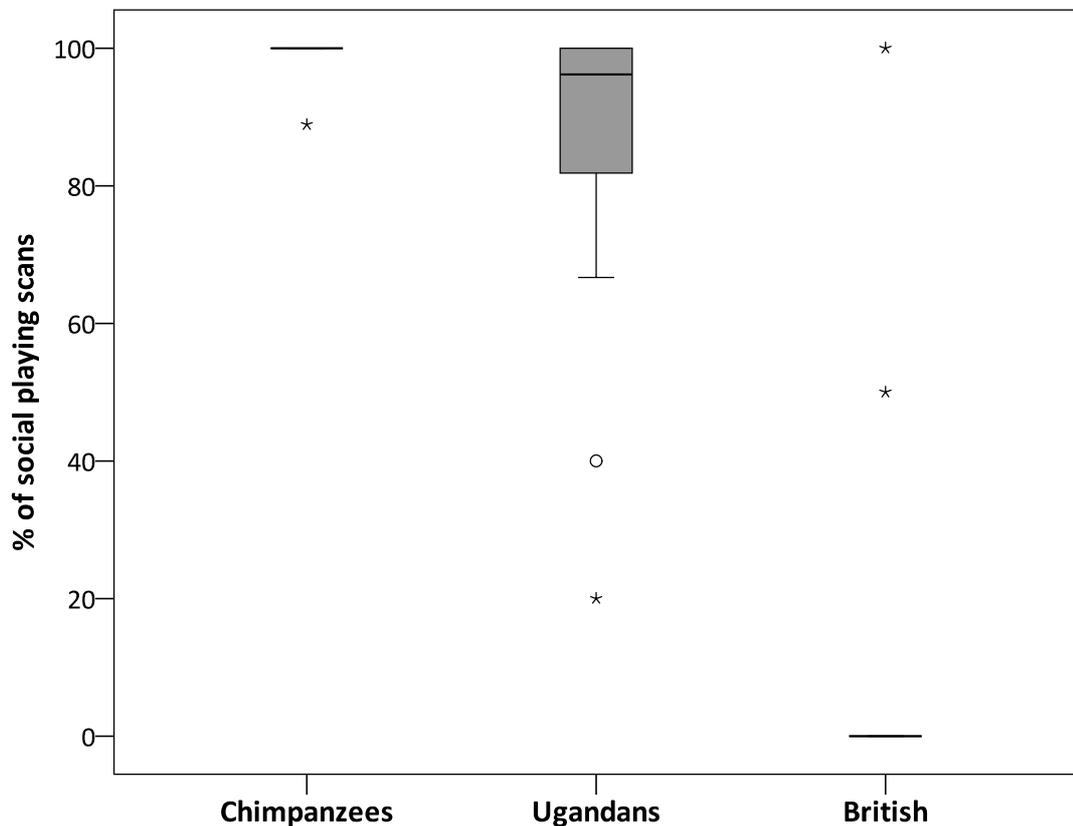


Figure 6.15: Boxplots for median percentage of the offspring’s playing bouts that were done with siblings/others.

A Kruskal-Wallis test showed that there was a significant group difference ($\chi^2 (2) = 14.61, p < .001$). Post-hoc pair wise Mann-Whitney U comparisons revealed a clear

cultural difference: Ugandan infants engaged significantly more with siblings/others than British infants ($U = 12.50, p < .001$). Chimpanzee offspring did not differ from Ugandan infants ($U = 26.50, p = .170$), but chimpanzees played more with their siblings/others than British infants ($U = 3.50, p = .003$).

Distance Mother-Offspring

To homogenize the datasets of the chimpanzees and humans, the following distance categories were used for the analysis: (a) body contact, (b) within reach = <1m, (c) beyond reach, but within 5m, (d) 5m+, but mother present and (e) 5m+ and the mother was absent (outside of the party). In order to decide whether a human mother who was more than 5m away from her offspring was absent, I checked whether mother and offspring were in the same area (e.g. home and field). If they were in different areas, the mother was scored as being absent. If the mother was in the same area or the area was very big (e.g. public place), the mother was scored as absent, if the offspring was scored not to be able to see the mother. Since for chimpanzees, it is difficult to distinguish areas and I had exact distance estimates beyond 5m for chimpanzees, a mother was also scored as absent, if she was beyond the defined party range of 30m (Newton-Fisher et al., 2000). As for the time budget above, 13 chimpanzee infants, 12 chimpanzee non-infants, 20 Ugandan infants and 11 British infants contributed their data to this analysis.

Descriptives

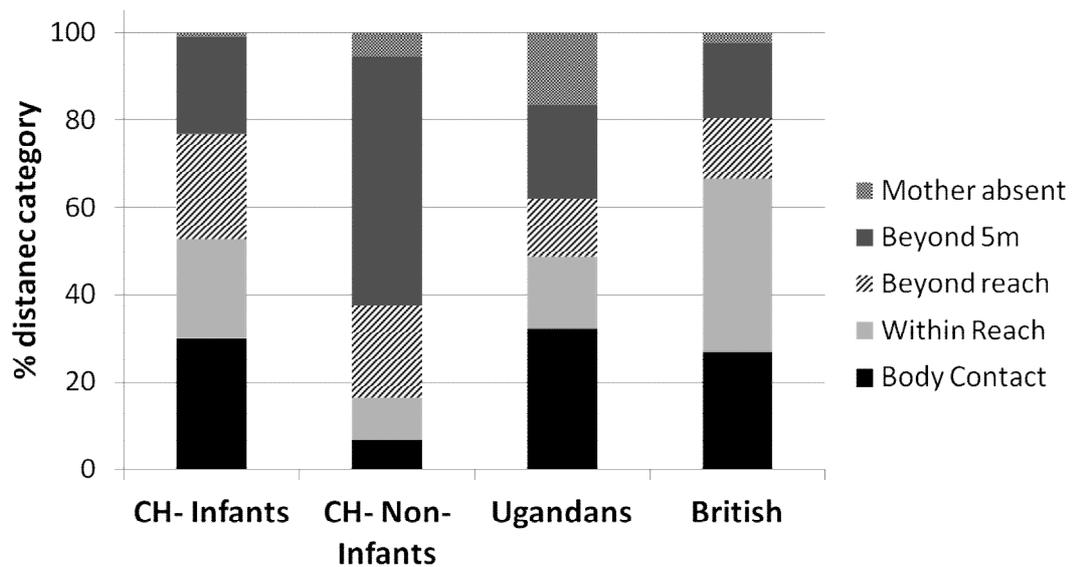


Figure 6.16: Bar graph illustrating the mean distances between offspring and mothers.

The chimpanzee infants' modal distance was "body contact" (Figure 6.16) and the modal distance for chimpanzee non-infants was "beyond 5m" of their mothers. Like chimpanzee infants, Ugandans also spent more scans in "body contact" than in any other category, but British infants modal distance was "within reach" of their mother.

Offspring within 5m of their mothers

For joint attention to occur between mothers and their offspring, it is important that the infants spend time in proximity of the mothers. When they are within 5m of their mothers, face to face contact was still possible in most cases. Figure 6.17 shows that chimpanzee and British infants spend most time within 5m of their mothers.

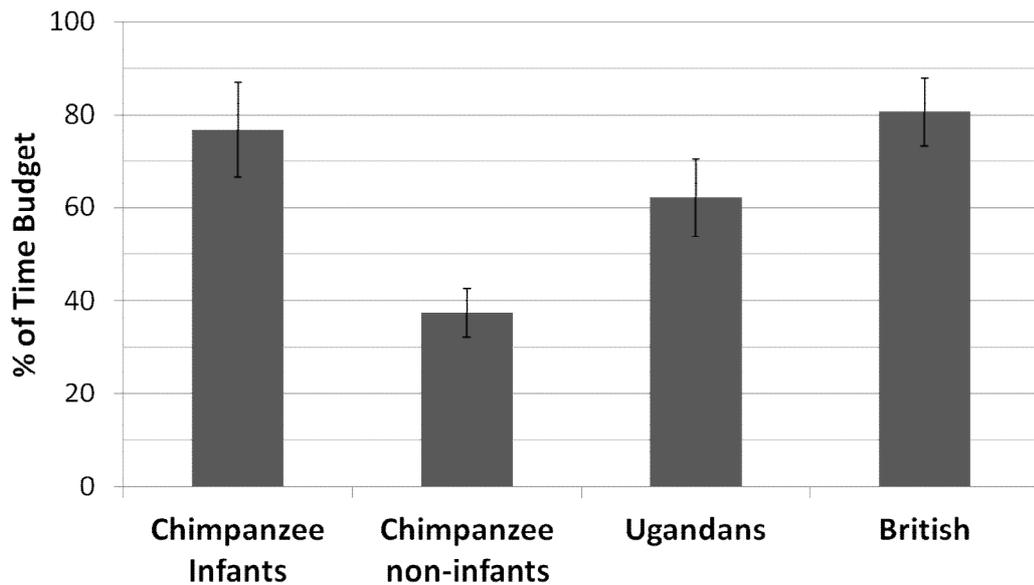


Figure 6.17: Bar graph illustrating the mean percentages of the offspring having been within 5m of their mothers. The error bars represent 1 standard deviation from the mean.

An independent samples t-test revealed that chimpanzee infants spent significantly more time within 5m of their mothers than chimpanzee non-infants ($t(23) = 6.02$, $p < .001$). Therefore, the two chimpanzee age groups were analysed separately for the following analysis.

A One-Way ANOVA revealed that the four groups were significantly different with respect to how many scans the offspring spent within 5m of their mothers ($F(3, 52) = 17.65$, $p < .001$). Sidak post-hoc pair wise comparisons showed that chimpanzee non-infants spent less time within 5m of their mothers than any other group: Ugandans ($p = .001$) and British ($p > .001$). There was a trend for chimpanzee infants to be within 5m of their mothers more often than Ugandan infants ($p = .075$), but there was no difference between chimpanzee and British infants ($p = .993$). British, infants, however, spent more time within 5m of their mother than Ugandan infants ($p = .020$).

To sum up, these results show a clear age difference in chimpanzees. There was little difference between chimpanzee and British infants, but Ugandan infants spend slightly less time within 5m of their mothers than chimpanzee or British infants.

Number of individuals within 5m

The number of individuals within 5m determines the offspring's opportunities to engage in joint attention with individuals other than the mother. The purpose of the following categories was to describe the opportunities that the offspring had to interact with other individuals. I did not differentiate between adults and children, because this was beyond the scope of the study. The mother and the research assistant were not counted. The categories were: (a) no other conspecific present, (b) 1-4 other conspecifics present and (c) 5+ other conspecifics present. The rationale behind this categorisation was the idea that no other conspecific represented an opportunity for a one-to-one interaction with the mother, 1-4 other conspecifics present represented an opportunity for interaction with a small group of conspecifics and 5+ other conspecifics present represented an opportunity for interaction with a big group of conspecifics and possibly the opportunity for choosing a preferred interaction partner.

From the total of 13 chimpanzee infants, three had to be excluded, because their mother's level of habituation meant that they were impossible to follow when they were on their own, which may have biased the average number of conspecifics within 5m, because these females were usually only seen in bigger groups. Therefore, the sample for this analysis consisted of ten chimpanzee infants, 12 chimpanzee non-infants, 20 Ugandan infants and 11 British infants.

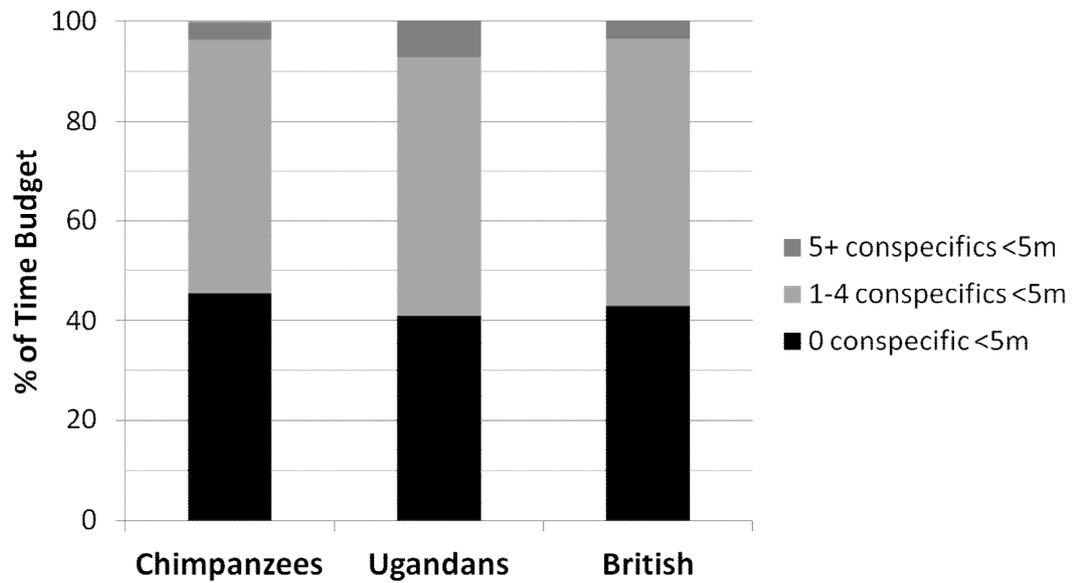


Figure 6.18: Bar graph showing the mean percentages of the number of conspecifics within 5m of the offspring.

Figure 6.18 shows that all three groups were very similar with regard to the percentages of how many conspecifics were present within 5m of the offspring.

Table 6.4 lists the analyses that were conducted to test whether the three groups were similar in every respect.

Table 6.4: This table shows the mean and median percentages of other individuals being within 5m of the offspring. Numbers with IQR (Inter Quartile Ranges) are medians, and numbers with SD (Standard Deviation) are means. In the right column, the statistical tests are listed. ‘ indicates a trend.

	Chimpanzee infants and Chimpanzee non-infants	Ugandans	British	Statistics
0	43.68 (IQR = 12.00)	42.46 (IQR = 29.00)	45.00 (IQR = 32.00)	Kruskal-Wallis: $\chi^2 (2) = .483,$ p = .785, asympt.
1-4	50.92 (SD = 10.33)	51.81 (SD = 17.66)	53.43 (SD = 24.70).	Welch's F (2, 21.6) = .062, p = .940
5+	2.41 (IQR = 5.00)	5.48 (IQR = 8.00)	2.63 (IQR = 5.00)	Kruskal-Wallis: $\chi^2 (2) = 6.49,$ p = .039 CH < UG CH = BR UG = BR

For the categories of 0 and 1-4 individuals within 5m of the offspring, the three groups did not differ. There was a trend, however, for Ugandan offspring to be exposed to bigger numbers of people (Table 6.4).

Discussion

It was the aim of this chapter to investigate differences and similarities in the social environment and the everyday life activities of chimpanzee, Ugandan and British mothers and their offspring. In the following sections, I will summarise and discuss the results of the time budget study relevant to the development of joint attention. The results of this chapter will then be linked to the results of the Infant Only and Social laser experiment in Chapter 7 in order to identify which factors of the social environment of the participants may have played a crucial role for the development of joint attention.

Vocalisations

The first striking difference was the near absence of vocalisations in chimpanzee offspring as well as chimpanzee mothers. It could be argued that the instantaneous scan sampling method was not a suitable method to investigate vocalisations in general, because vocalisations may be rather short and can therefore not reliably be picked up during a single short instance in a 15min interval. The data of the Ugandan and British participants, however, were collected with exactly the same method. Therefore, chimpanzees either vocalised less or their vocalisations were shorter. In order to disentangle the two possibilities, it would be necessary to collect all occurrence vocal data. Based on the current results, however, it seems that chimpanzees, as predicted, were indeed rather silent compared to their human counterparts and this was equally true for offspring and their mothers.

Essential Activities vs. Leisure Time

The analysis of essential and leisure activities revealed that both chimpanzee infants and non-infants had less time available for leisure activities than Ugandan and British infants. Older chimpanzee offspring spent more than 50% of the time budget with essential activities. This may have been due to the increased necessity for older chimpanzee offspring to engage in foraging activities like their mothers, as they cannot rely on their mothers' nutritious breast milk anymore.

Interestingly, the mothers of the three groups did not differ with respect to the amount they engaged in essential activities. The mothers of all three groups had

less than a third of their time available to rest or to engage in leisure activities. The amount of feeding in chimpanzee was less than reported by Tweheyo et al. (2004), because the 70% of essential activities also included locomotion. Since Tweheyo et al. (2004) followed the chimpanzees from “dawn to dusk” (p.269) and I had to stop data collection at 16:30 hrs, they may have obtained more feeding in the chimpanzee time budgets, because chimpanzees usually resumed feeding in the late afternoon when it was cooler (personal observation).

Social Activities

Social activities included essential social activities (e.g. breastfeeding, dressing) and ‘leisure’ social activities (e.g. playing). Social activities can be done with mothers or other social partners and constitute an important context for the development of joint attention (Deák & Triesch, 2006).

Human infants engaged in social activities more than twice as much as chimpanzee offspring. As predicted, human infants spent more time in social activities than chimpanzee offspring. The offspring of all three groups, however, spent less than half of their time budget in social activities. Ugandan infants spent more time in social activities than any other group and chimpanzee offspring less time than any other group. The Ugandan infants’ high social engagement rate may be linked with having had the most scans with more than 5 people within 5m of themselves. This may have increased their chances of social interactions. In contrast to my prediction, there was no species-difference with respect to the proportion of social activities in which the mothers were the infants’ social partners. Thus, mothers played an important and central role in the offspring’s lives across the three groups.

The results for the social activities of the mothers revealed that in contrast to my prediction, there was no species difference between chimpanzees and both human groups when considered together. When the three groups were considered separately, however, British mothers spent most time in social activities compared to the chimpanzee and Ugandan mothers. It would have been ideal, if I could have determined the interaction partner of the social activities in order to reveal whom the mothers were interacting with. Unfortunately, the current data set did not

allow this analysis, because the social partner for vocalisations in mothers was not consistently recorded. Therefore, I suggest that for future studies, all interaction partners of the mothers and who the mothers were addressing their vocalisations to should be recorded.

Play

Play is an important context for joint attention to develop, because it naturally provides opportunities for emotional exchange and triadic constellations (e.g. object play) (Deák & Triesch, 2006). Play of both types, individual and social, made up less than 10% of the time budget for chimpanzee infants and non-infants, whereas for Ugandans, playing made up a third of and for the British more than 20% of their time budget. There was a clear species difference in play, with humans playing more than chimpanzees, but also a cultural difference with Ugandans playing the most. This finding is consistent with the hypothesis that human infants who are likely to engage in joint attention (Carpenter et al., 1998) also played more than chimpanzees who most likely do not engage in joint attention.

There are several possible reasons for the low rates of play in chimpanzee offspring. First, they may not have the energy to play more. Since chimpanzee diet is raw, unprocessed and less rich in energy than human food, they may have spent more time resting than the two human groups. Second, chimpanzee infants may have had less intrinsic motivation to play. Third, since their mothers spent a large amount of her time with either feeding or foraging, the infants may have been in the ventral position for a significant amount of time in which play was not possible.

Chimpanzee and Ugandan mothers engaged in social play at low rates and did not differ from each other. British mothers played more socially than both, chimpanzee and Ugandan mothers, but their median rate of social play did not exceed 5% of their time budgets. This cultural difference is consistent with the finding of Keller et al. (2009) which shows that Western mothers dedicate more time to exclusive mother-infant interactions.

Object Play

As previously indicated, there can be no joint attention without an external object that both social partners co-orient to. Regardless of the type of play, social or individual, there was a clear species difference in terms of how often the offspring used objects during play. Chimpanzees used objects in approximately a third of their individual play, whereas the offspring of the two human groups used objects in nearly all of their individual playing scans. This result reveals a great difference in the chimpanzee and human infants' play practices.

Why did chimpanzees engage with objects at such low frequencies compared to human infants? Chimpanzee individual play without an object consisted mainly of swinging on a branch or physical movement that did not function as locomotion from A to B. Chimpanzee infants physically develop much faster than human infants (Bard & Gardner, 1996). In addition, the human sample consisted of 11 month old babies, whereas chimpanzee individuals of up to the end of their 4th year were classified as infants (Reynolds, 2005). Therefore, human infants were physically much less able to engage in play behaviour that involved locomotion than chimpanzee infants. This difference in physical ability and strength reveals an interesting point: if human infants are physically constrained, it may promote them to engage more with objects. Whilst chimpanzee infants had the choice between swinging in the tree, running around and picking up a twig, human infants could not physically move in such sophisticated ways and may therefore have been more likely to focus their attention on objects. Could this be the first step of how joint attention may have evolved? As the cognitive abilities of our human ancestors increased disproportionately to their physical development in infancy (Bjorklund & Pellegrini, 2002), they may have started to be more and more interested in objects around them in addition to their high motivation of engaging with others in affective dyadic interactions. This situation depicted here could be the first context in which infants had to switch their attention between the object they were interacting with and other people present. With increasing brain capacities, this could then have resulted in coordinating attention in a meaningful way.

For joint attention to occur, however, the presence of an object alone is not enough. At the same time, the infant needs a social partner to interact with. The analysis revealed that during the instantaneous scan data collection chimpanzees were never observed playing with another individual and an object at the same time. That means that the essential things for joint attention (offspring, partner, object) never co-occurred for chimpanzees in natural interactions during the study period. Hobaiter (2010) also found that although objects were occasionally used to initiate play in the Sonso chimpanzee offspring of the Budongo forest, they were hardly ever included in the subsequent social playing bout. Furthermore, in those instances in which offspring simultaneously focused on one object, it was mainly a competitive interaction about the possession of the object rather than mutual play. Kahlenberg and Wrangham (2010) reported that chimpanzee offspring at Kibale forest used sticks during social play. The Kibale chimpanzees also use sticks as probing tools and for food acquisition which has never been observed in the Sonso chimpanzees of the Budongo forest (Whiten, 1999; Gruber et al., 2009). It is possible that this cultural difference with regard to object use in different contexts between the two chimpanzee communities is mirrored in the offspring's tendency to use objects during social play.

A very interesting future study could be the systematic comparison of the offspring's object use in different contexts between the chimpanzees of the Budongo and Kibale forest. It could be revealed whether the frequencies of object use, the types of engagement with the objects and the contexts in which objects are used differ between the offspring of the two chimpanzee communities. This suggested observational study combined with replicating the laser experiments with the Kibale chimpanzee community in which the all preconditions for joint attention (2 individuals and an object) co-occur, could reveal whether the low rates of social object play correlate with the presence of joint attention.

In this study, however, chimpanzees have not been observed engaging in social object play. Human infants, however, used objects in more than half of their social playing interactions. Does this result mean that chimpanzee offspring lack the ability or the motivation to coordinate their attention between a social partner and

an object? It is unlikely that chimpanzees are generally unable to coordinate attention between another individual and an object, because captive chimpanzees have been shown to engage in gaze alternation during communicative interactions (Leavens & Hopkins, 1998). It is important to note, however, that there is no evidence from wild chimpanzees that they naturally coordinate their attention between conspecifics and events in a communicative context. Therefore, future studies that aim at identifying the coordination of attention in communicative contexts are needed for wild chimpanzees.

Alternatively, it is possible that chimpanzee offspring prefer playing dyadically rather than including an object into the interaction. This could have two reasons: first, as mentioned above, chimpanzee infants physically develop much faster than human infants. As a consequence, they have the choice between dyadic play (chasing, rough-tumble play) and triadic play. It is possible that chimpanzee offspring find dyadic play more rewarding than triadic play.

Second, chimpanzee infants may not usually get much attention from other individuals as others are busy with foraging activities or they spend much time in very small parties with few opportunities for social interaction. Therefore, when they play with an object individually, the moment someone attends to them, they may switch activity from object play to social play without combining the two.

The finding that chimpanzees used less objects during play and social play is consistent with my hypothesis. Therefore, the habitual occurrence of social object play may be an important factor in the development of joint attention. It is still necessary, however, to find out whether the lack of social object play in the Sonso chimpanzees is representative for the majority of wild chimpanzee populations. Therefore, more research on cultural variation of object engagement is needed from other chimpanzee field sites.

Play Partners

Mothers have been reported to be a very important play partner for Western human infants, because they are motivated to scaffold early joint attention interactions (Tomasello, 1988; Deák & Triesch, 2006). In addition, Western human infants aged 9-15 months spent more time in joint attention with their mothers

than with peers (Bakeman & Adamson, 1984). Therefore, it was important to establish whether the three groups differed with respect to their main playing partners to reveal whether the development of joint attention depends on having the mothers as playing partners for the majority of the time.

Whilst Ugandan and the chimpanzee offspring mainly played with siblings or other individuals (peers or other relatives), mothers (and fathers) were the main playing partners for British infants. In contrast to my prediction, there was a clear cultural difference with Ugandans playing more with siblings/others than British. If only considering the proportion of play where the mother was the social playing partner, however, there was no difference between the two human groups. Chimpanzee infants did not differ from Ugandans in terms of their percentage of social play with mothers or siblings/others.

Number of individuals within 5m

The number of the offspring's potential playing partners depends on the number of individuals that were present within 5m of the infant. Therefore, joint attention may occur more, if the infants have frequent opportunities to interact with others. This does not only include peers, but also other adult relatives. Therefore, I analysed whether there were any species or cultural difference with regard to the infants' having no other conspecifics, 1-4 conspecifics or more than 5 within 5m (excluding the mothers).

The analysis revealed that chimpanzee, Ugandan and British offspring did not differ with respect to having either no conspecific other than the mother or 1-4 additional conspecifics present within 5m. Ugandan infants, however, were in the presence of more than 5 individuals within 5m more often than chimpanzee offspring, but there was no difference between the Ugandans and the British. This is surprising, because Ugandan families were much bigger than British families (UBOS, 2007), and I expected the Ugandans to be more similar to the chimpanzees. In addition, I expected the British infants to have the least number of people within 5m. When taking a closer look at the data of the British infants, however, it became evident that British mother-infant dyads spent a considerable amount of time in public places and play groups where many people were present. Therefore, the

small number of family members was compensated by frequent excursions into popular public areas.

Summary

The time budget study aimed at revealing potential species and cultural differences in the social environment of individuals from the same overall study group of the laser experiments (Chapter 4, 5). To this end, the instantaneous scan sampling method was applied to all three study groups and their general time budget established.

For potential factors that may contribute to the development of joint attention, I obtained the following species differences: chimpanzee offspring had less leisure time available to engage in activities that support the development of joint attention than human infants. Chimpanzees in general vocalised less, their offspring engaged less in social activities, showed less in play and used less objects during play than both human groups. In addition, the following cultural differences were revealed: Ugandan mothers engaged less in social activities and played less than British mothers.

Ugandan (and chimpanzee) infants' modal distance from the mother was 'body contact', for British infants it was 'within reach'. Nevertheless, British infants spent more time overall within 5m of their mothers. In addition, Ugandan and chimpanzee offspring played more with their siblings/others than British infants almost exclusively played with either their mothers or fathers. There was no clear-cut species or cultural difference between the offspring of the three groups in terms of how often the offspring's social activities were done with their mothers and how many conspecifics were present within 5m. In addition, the mothers of the three groups did not differ with respect to the amount of leisure time they had available.

Future studies are needed to reveal whether the low rates of object play observed in chimpanzee offspring are representative for all wild chimpanzees. In the next and last chapter, the results from the time budgets will be linked with the results from the Infant Only and Social laser experiments in order to reveal which socio-

environmental factors may have played an important role in the development of joint attention.

Chapter 7 : Joint Attention and the Social Environment

Summary

This final chapter aimed to link the findings of the laser experiments (Chapter 4, 5) to the patterns found in the time budgets of the three study groups (Chapter 6). I first explain the rationale and limitations of considering everyday activities and socio-environmental factors as potential explanatory factors for the results of the laser experiments. I then summarise the main findings of the laser experiments in terms of species and cultural differences and discuss them in light of differences and similarities in socio-environmental factors and everyday activities between the three study groups.

The relatively high rates of vocalisations, large amounts of infant 'leisure' time dedicated to social activities and play and the high rates of object play that were found in the two human groups but not the chimpanzees, were identified as potentially important factors in the development of joint attention behaviours. Conversely, there was no evidence that the low levels of joint attention shown by the chimpanzees were related to mothers having insufficient leisure time to engage with their infants, or a lack of a strong social bond between mother and infant, as these factors were very similar across the three groups. Finally I found no evidence for the identity of the main play partner being related to joint attention behaviours, as the British and Ugandans differed on this factor, despite showing similar joint attention behaviours.

Given the important species differences found in mother behaviour in the laser experiments and the lack of corresponding differences in their everyday activities, I also examine the potential role of the mother's intrinsic tendency to cooperate in explaining the pattern of data obtained in the laser experiments. This is followed by a general discussion of the principal findings of the thesis. Finally, I make suggestions for future studies and finish this thesis with an overall conclusion.

Linking Joint Attention to the Social Environment

Rationale

The aim of this chapter was to combine the outcome of the two laser experiments (Chapter 4, 5) with the results of the time budget study (Chapter 6). The logic behind this approach can be explained as follows: since human and chimpanzee infants are shaped by their social environment as they develop (Keller, 2007), it is important to take variations of the participants' social environment into account in order to explain differences found in their abilities and motivation to engage in joint attention. In addition, in order to explain differences in the mothers' scaffolding behaviours during joint attention interactions, considering their time budget and habitual activities may help us explain why this is so.

Including two human cultural groups added an important advantage to this approach: in addition to providing a more representative view of human behaviour, the inclusion of two human groups was critical for interpreting species differences found in the laser experiments. For example, to explain why chimpanzees displayed less of behaviour X than the two human groups in the laser experiment, I considered different parameters of the social environments of the participants (for instance parameter Y). If chimpanzees engaged significantly less in parameter Y of the social environment than the British, this may at first indicate that parameter Y may be linked to the species difference found in the laser experiment and may therefore be key for the development of joint attention in humans, not chimpanzees. If, however, the Ugandans also engaged significantly less in parameter Y than the British (and are no different from chimpanzees), this indicates that parameter Y is unlikely to be linked to the species difference in performance on the laser experiments. Therefore, including two different human groups in the study design enables me to reach a more valid conclusion about which factors of the social environment may be potential explanatory factors of the results of the laser experiments than relying on data from a single culture. To conclude, species differences in parameters of the social environment that are mirrored by the results of the laser experiments indicate that this particular socio-

environmental parameter may play an important role in the development of joint attention.

It is important to note that by linking the social environment and everyday activities of the study groups to the patterns found in the laser experiments, I was not attempting to make any causal inferences about the relationship between socio-environmental factors and the participants' behaviour in the laser experiment. It is only possible to extract potential correlational relationships from my observational data. These relationships may indicate which specific factors of participants' respective social environment might have influenced and shaped the development of joint attention (skills). In order to reliably identify any causal relationships between socio-environmental factors and joint attention skills, controlled experimental studies would be required which, however, may be ethically problematic.

In the following sections, I will first summarise the main patterns found in the laser experiments, then link these results to the time budgets of the three study groups and conclude which factors may be important for the development of joint attention. I will then discuss other factors that may have contributed to the patterns found in the laser experiments. This will be followed by a general discussion and a final conclusion.

Summary of the Main Findings in the Laser Experiments

Cultural Differences

Overall, Ugandan and British mothers and their infants behaved very similarly during the laser experiments and no significant cultural differences were found with regard to their rates of engaging in joint attention or the infants' joint attention skills. Therefore, I conclude that 11 months old Ugandan and British infants were equally able and motivated to engage in joint attention with their mothers and it is likely that the developmental trajectory of joint attention in Ugandans infants was similar to that of British infants. Based on that, the ability to engage in joint attention seems to be a robust human ability.

There was a trend, however, for British mothers to more often be the only communicator during joint attention compared to Ugandan mothers (Chapter 5, p.186, Figure 5.6). In addition, there was a trend for Ugandan mothers to use more intentional attention directing behaviours after face to face contact than British mothers (Chapter 5, p.178, Table 5.10). Although the mothers of both cultures tended to exhibit these behaviours at different frequencies, they still engaged in similar rates of joint attention. This further supports the hypothesis that joint attention is a robust human ability despite some cultural variations in the way mothers interact with their infants.

Species Differences

The most important species difference found in this thesis was that Ugandan and British mother- offspring dyads showed significantly more joint attention than chimpanzee mother (sibling)- offspring dyads when exposed to a laser stimulus (Chapter 5, p.184, Figure 5.5). This species difference remained stable regardless of which type of communication was examined: either vocalisations and facial movements or vocalisations alone (Chapter 5, p.189, Figure 5.8).

In chimpanzees, the partners were never observed to communicate during laser related mutual gaze (face to face contacts). In contrast, Ugandan partners communicated in over 60% of such face to face contacts and British partners in more than 90% of triadic face to face contacts (Chapter 5, p.186, Figure 5.6). This means that in the two human groups, the partners played a very active role in the joint attention interaction. In addition, the mothers of the two human groups looked at their infants' laser engagement significantly more than chimpanzee partners (Chapter 5, p.170, Figure 5.1) and, in contrast to chimpanzees, used more laser related attention getters than their infants (Chapter 5, p.176, Table 5.3).

Although the offspring of the three groups did not differ in their attempts to communicate with their mothers/siblings when discovering a laser dot nearby (Chapter 4, p.127, Figure 4.7), young chimpanzees looked at the laser simultaneously with their partners at lower rates (Chapter 5, p.168, Table 5.5) and showed less gaze alternations than both human groups (Chapter 5, p.180, Table 5.12).

Overall Similarities

The 'Infant Only' laser experiment revealed that when the offspring encountered a novel stimulus, and their mothers were not attending to them, the chimpanzee, Ugandan and British offspring did not attempt to communicate with their mothers or siblings *about* the laser stimulus (Chapter 4, p.126ff). This result is of particular interest, especially given that there was a clear species difference in joint attention when both, the mothers and the offspring were attending to the laser stimulus (see above). This finding highlights that the mothers may have played an important role in scaffolding joint attention interactions in humans, but not chimpanzees.

Joint Attention, Everyday Life Activities and the Social Environment

In the following sections, I will summarise some parameters of the social environment and of the general time budgets of the chimpanzee, Ugandan and British study groups that were analysed in Chapter 6 and discuss whether or not they may explain the species differences found in the laser experiments. I will consider the following parameters: vocalisations, the participants' availability of leisure time, engagement in social activities and offspring play.

Vocalisations

One reason why chimpanzees may have engaged in lower rates of joint attention than the human dyads is that they showed less communicative behaviours in the face to face interaction than humans. Whilst the unavoidable differences in video quality meant that lower rates of facial expressions were confounded by lower rates of facial visibility, vocalisations were equally detectable across groups. Therefore, one factor that is linked to the chimpanzee dyads' low rates of joint attention is that the chimpanzee mothers and offspring vocalised at very low rates in the laser experiments as well as the time budgets (Chapter 6, p.223-225, Figure 6.2, 6.3). In addition, only one chimpanzee infant and none of the chimpanzee partners were observed to vocalise during laser related face to face contacts in the Social laser experiment (Chapter 5, p.184).

Why do chimpanzee mother – offspring dyads vocalise at such low frequencies? There may be three explanations for this: first, it may be more adaptive in the

chimpanzee habitat for an offspring to be quiet unless he is in danger and a vocalisation becomes necessary to survive (Plooij, 1984). If chimpanzee offspring vocalised as much as human infants, it may expose the whole chimpanzee party to danger by revealing the location of the group to potential rival communities.

Second, vocal communication may not be the primary mode of mother-infant communication in chimpanzees. The increased use of the vocal communicative channel in humans may be explained by the differential evolutionary pathways related to foraging that emerged after the hominoid-pan lineages split: whilst the chimpanzee ancestors continued to forage in the forest environment, the human ancestors adapted to a foraging style in the savannah which entailed the evolution of bipedalism (Falk, 2004). The anatomic consequence of bipedalism was the re-shaping of the birth canal which, in combination of increased brain sizes, led to the birth of underdeveloped neonates. These neonates were no longer able to cling to their mothers. This, in addition to the stark reduction of body hair and the vertical orientation of the mothers' backs meant that the infants were no longer able to cling to their mothers and ride effortlessly on their backs (Falk, 2004). As a consequence, constantly carrying the infant whilst foraging was no longer an energy efficient strategy. Therefore, Falk (2004) suggested that the human ancestors responded to this challenge by "putting the baby down" (p.500) and using vocalisations to "keep in touch" (p.500). Based on the vulnerability of underdeveloped infants and the physical separation from their mothers, it was more adaptive for these infants to express their needs by using different vocalisations.

In contrast, chimpanzee infants spend a considerable amount of time in body contact with their mothers and are soon physically developed enough to stay in visual contact with their mothers even when they are physically separated. Therefore, they may be more likely to communicate through the tactile modality or through facial expressions rather than through the use of vocalisations (Bard & Vauclair, 1984). Based on this evidence, it is plausible that an increased use of vocalisations evolved as a function of giving birth to premature infants and increased physical separation from the mothers.

Third, another explanation for the different use of the vocal channel in humans compared to chimpanzees is that chimpanzees may not have voluntary control over their vocal behaviour as humans do (Tomasello, 2008). Although chimpanzees were found to modify their vocalisations as a function of the composition of the audience (Slocombe & Zuberbühler, 2007; Townsend, Deschner & Zuberbühler, 2008; Laporte & Zuberbühler, 2010), the type of vocalisations chimpanzees produce seems to be tightly linked to the respective emotional context and therefore cannot be produced flexibly in a different context (Goodall, 1986; Tomasello, 2008). In addition, the chimpanzee vocal repertoire seems to be fixed and there is very little evidence for vocal plasticity and vocal learning in chimpanzees (Tomasello, 2008).

Based on these three potential explanations of why chimpanzees vocalise at low frequencies, chimpanzees may have been unable to use vocalisations during face to face contacts in the Social laser experiment to share attention with each other about the laser. In humans, however, vocalisations were an important mode of communication during face to face contact and were therefore a driving force of the species difference found in joint attention. It can be concluded that the low rates of vocalisations in chimpanzees in general may be an important factor that explained why chimpanzees engaged less in joint attention than humans.

Availability of Leisure Time

Offspring

Is having large amounts of 'leisure time' available for engaging in relaxed social activities (e.g. play) an important factor that influences the development of joint attention and may therefore be linked to the species differences in the Social laser experiment? The results of the time budget revealed that chimpanzee offspring engaged significantly more in essential activities (e.g. feeding, locomotion) than the infants of the two human groups (Chapter 6, p.226, Figure 6.5). As a consequence, Ugandan and British infants had more 'leisure' time available to engage in play than chimpanzee offspring. In addition, chimpanzees spent a significant amount of time resting when they were not engaged in essential activities (Chapter 5, p.222, Figure 6.1). It may be that their raw, largely vegetarian diet and physical exertions

to complete essential activities means they do not have the energy to use their 'leisure' time to engage in play. Therefore, the chimpanzee offspring's high rates of essential activities together with high rates of resting may not have been conducive for engaging in activities that are important for the development of joint attention such as play which may explain their lower rates of joint attention in the laser experiments.

Mothers

Is the amount of 'leisure' time that mothers had available a potential explanatory factor for the human mother-offspring's higher rates of joint attention compared to chimpanzees? As mentioned above, the lack of species differences found in offspring's behaviour in the 'Infant Only' experiment highlighted the important role that mothers may play in early joint attention interactions. In order to frequently scaffold these interactions, mothers may regularly require some leisure time to devote to their infants and to develop playing routines.

The results of the time budget study revealed that the mothers of all three groups spent more than 60% of their time budgets in essential activities and did not differ from each other in this respect (Chapter 6, p.227). That means that they would have had a similar amount of time available to engage with their infants in play. Therefore, it is not the case that chimpanzee mothers, in contrast to human mothers, had prohibitively high levels of essential activities that left them with no opportunities to engage with their infants. Across species and groups, mothers had equal and sufficient opportunities to engage in relaxed social interactions with their infants. Alternatively, it seems likely that although the mothers of all three groups had 'leisure' time available to engage with their offspring in activities that support the development of joint attention, chimpanzees may have used their 'leisure' time differently to humans. It is possible that chimpanzees more frequently chose to interact with individuals other than their infants. Future research should examine this possibility.

In addition, even when the mothers chose to interact with their infants, the *type* of interaction the mothers had with their infants during their 'leisure time' may have varied. Whilst chimpanzees may have engaged mainly in dyadic interactions (i.e.

without including an object) with their offspring (e.g. dyadic play, grooming), human mothers may have engaged in triadic play (i.e. with objects) which has been identified to support the development of joint attention (Deák & Triesch, 2006).

Social Activities

Are high proportions of social activities in infant everyday life related to joint attention development and a potential explanatory factor for the higher rates of joint attention in human mother-infant dyads compared to chimpanzees? Deák and Triesch (2006) suggested that joint attention first emerges in habitual social activities (e.g. play, care giving). The results of the time budget study revealed that Ugandan and British infants engaged in significantly more social activities than chimpanzee offspring (Chapter 6, p.228, Figure 6.6). As a consequence, the infants of the two human groups had more exposure to social interactions with conspecifics and therefore more opportunities to establish social routines during every day interactions.

Social activities not only included play which will be discussed in more detail below. Other social activities were for example: care giving activities in humans and grooming in chimpanzees. Whilst chimpanzee grooming is a dyadic activity, human care giving activities often involve an external object (e.g. feeding solid food, dressing the infant, brushing the infants hair etc.) and therefore constitute habitual opportunities for the infants to learn to coordinate their attention between the caregiver and objects. The only triadic social activity that I observed in chimpanzee mother-offspring dyads was begging for valued food and this was very rare.

In humans, these habitual and frequent social routines form a structured social environment that provided the infants with patterned input from their caregivers (Deák & Triesch, 2006). Based on learned contingencies within the structured social environment, Ugandan and British infants may have become more competent in engaging in joint attention with a social partner than the chimpanzees who lacked the opportunity to develop such adept social skills based on a more limited amount of social interaction with conspecifics in their time budget.

Once joint attention becomes habitually established in the social routines of human infants, this ability to coordinate attention and to become mutually aware of having attended to a common focus through communication can then be generalised to novel situations like encountering a moving laser dot. Therefore, the chimpanzee offspring's lower rates of social activities in the time budget may explain their lower rates of coordinating attention between the laser and a social partner (i.e. gaze alternation) in the Social laser experiment compared to the infants of the two human groups. In addition, human infants may have focused on the laser simultaneously with their mothers longer than chimpanzee offspring, because they were familiar with triadic interactions from their everyday life.

Given the potential importance of habitual activities and routines in joint attention development (Deák & Triesch, 2006), is the emergence of this ability related to an infant having a strong central social relationship with the mother? It could be that infants have to develop joint attention behaviours with one central individual, before being able to coordinate their behaviour with less familiar individuals. I examined whether mothers were the main interaction partner during the infants' social activities as an indicator of such a central relationship. Interestingly, the proportion of the offspring's social activities that were carried out with their mothers did not significantly differ between the groups (Chapter 6, p.229-230). This indicates that the offspring of all three groups had similarly strong central relationships with their mothers. Thus the lower levels of joint attention shown in the chimpanzees are unlikely to be related to the strength of the social bond between infant and mother.

Consistently and regularly performing social activities with the mother may be important in joint attention development in infants, but it does not seem to be sufficient, as evidenced by the low levels of joint attention shown by chimpanzees. Further systematic studies are needed to establish whether or not this factor is important in the emergence of joint attention. Studying Western infants, who enter full time child care at a very early age and thus lack a consistent dominant social partner, may reveal the relevance of this factor for joint attention development.

Play

Play is a very important social activity for the development of joint attention, because it constitutes a relaxed context for affective social interaction and infant learning (Deák & Triesch, 2006). In addition, during playing interactions, the opportunity for joint attention may naturally occur: during individual object play, a social partner may join the play or during social play, objects may spontaneously be included. In the following sections I will try and identify which parameters of the offspring's play may be likely to be linked to the humans' higher rates of joint attention than chimpanzees in the Social laser experiment.

Prevalence of Overall Play

Are high rates of offspring play and particularly social play important in the development of joint attention behaviours and are these factors linked to the chimpanzees' lower engagement in joint attention compared to Ugandan and British mother-infant dyads? There was indeed a species difference with regard to overall play in the time budgets: Ugandan and British infants showed higher rates of overall play in their time budgets compared to chimpanzee offspring (Chapter 6, p.231, Figure 6.8). This indicates that based on lower rates of play in general, chimpanzee offspring had less opportunities for spontaneous triadic constellations to arise during playful activities.

Object Play

As mentioned above, joint attention by definition involves an external object. Therefore, it is important to relate the rates of object use during play to the outcome of the laser experiments. Are high rates of object play important for the development of joint attention and can the amount of objects the offspring used during play explain why chimpanzees engaged less in joint attention in the Social laser experiments than human infants?

The time budget study revealed that Ugandan and British infants used significantly more objects during individual and social play than chimpanzees (Chapter 6, p.236, Figure 6.11). Therefore, since the participants of all three groups had objects available in their everyday life environment, the human infants' frequent use of

objects during both individual and social play at 11 months may indicate that human infants were more interested in using objects in general during play.

Most important, however, is the observation that chimpanzee offspring were never observed to use an object during social play in the whole study period. Whilst for humans, playing with objects and other individuals was an everyday life activity at 11 months, individual object play was infrequent in chimpanzee offspring (at least in the Sonso chimpanzees) and social object play was absent (Chapter 6, p.239, Figure 6.13). Therefore, the human dyads higher rates of joint attention in the Social laser experiment compared to the chimpanzees', was mirrored in the offspring's object use during general play, but especially during social play. This indicates that using objects during play with others in everyday life may be an important factor for the development of joint attention in human infants. This seems plausible, because it creates countless opportunities for the infants to coordinate their attention between the object and a social partner and habitual social playing routines with an object can be established. It is likely that triadic situations similar to that created by the laser paradigm are part of the everyday lives for 11 months old infants, but not for wild chimpanzees. The human infants' higher rates of social object play found in the time budgets may therefore be a very likely explanatory factor for the, higher rates of gaze alternation and joint attention shown by human infants in comparison to chimpanzee offspring in the Social laser experiment.

Why did chimpanzee offspring engage in object play at such low frequencies? As mentioned before, chimpanzee infants physically develop much faster than human infants (Bard & Gardner, 1996). Therefore, since in contrast to human infants at 11 months, their movement was less restricted, they had a choice between swinging in a branch and interacting with objects. Chimpanzees may find physical, locomotive play more rewarding than more sedentary object play. The slow physical development of human infants may explain why they have evolved such a strong focus on objects: when they were physically separated from their mothers (Falk, 2004), there was just not much else to do than to inspect the objects of the immediate environment. In addition, as the human ancestors started to create

more sophisticated tools, they may have become more eye-catching for a curious developing infant. Therefore, the presence of salient man-made objects and an increasing number of social partners to engage with (see cooperative breeding below, Hrdy, 2006) together with the infants' limited mobility may have been the first context in which infants had to switch their attention between the object they were interacting with and other people present.

Play partners

As mentioned above, human mothers play an important role for their infants' development of joint attention by scaffolding the infants' early joint attention interactions (Tomasello & Farrar, 1986, Carpenter et al., 1998). To recap, in the social laser experiment human mothers observed their offspring's interaction with the laser at significantly higher rates than chimpanzee partners. This indicates that human mothers carefully monitored their infants' interaction with the laser, possibly to engage with them jointly with the visible laser dot in a triadic way (e.g. by commenting on the infants' behaviour, initiating joint attention). In addition, in contrast to the chimpanzee partners, human mothers actively participated in the joint attention interactions by communicating with the offspring during the majority of the laser-related face to face contacts.

Based on the importance of the mothers' scaffolding for the development of joint attention and the results of the Social laser experiment the following question arises: Is the development of joint attention related to high levels of play with the mother in everyday life? Interestingly, the identity of the offspring's main playing partner during everyday life did not seem to relate to which groups engaged in joint attention at higher rates in the Social laser experiment. Chimpanzee and Ugandan offspring played more with siblings or others than British infants, whereas British infants mainly played with either their mothers or their fathers (Chapter 6, p.239ff). Whilst chimpanzee and Ugandans were more similar with regard to their playing partners, Ugandans were more similar to British infants in joint attention behaviours and thus engaged more in joint attention than chimpanzees. This highlights the importance of including two different human cultures into the study design: if I had only included the British study group, I may

have concluded that having the mothers as the main playing partners in everyday life related to the outcome of the Social experiment and may therefore be an important socio-environmental factor for joint attention to develop. The fact that Ugandan infants mainly played with siblings or other individuals, yet still engaged in joint attention with the mother highlights that the identity of the most frequent play partners is unlikely to be an important factor in the development of joint attention.

It is important to note that in chimpanzees, the mother is the only main caregiver for the chimpanzee offspring (Goodall, 1986). This is not necessarily the case in humans. From an evolutionary perspective, after the hominoid-pan lineages split and as the human ancestors became more cooperative, foraged together and shared their resources with each other, they also started to divide child-care with a wider range of family members, also known as cooperative breeding (Hrdy, 2006, Whiten & Erdal, 2012). Since more individuals were responsible for child care and therefore responsive to the infants, the infants' opportunities for social interaction increased in comparison to chimpanzee infants. Since Ugandan infants lived in large, extended families (UBOS, 2007), their reduced amount of interaction with their mothers was compensated by interactions with older siblings and other adult family members who cared for them and were also able to provide a scaffold for joint attention interactions. This is supported by the finding that Ugandan infants showed higher social play rates than any other group in their time budgets. In contrast, chimpanzee offspring mainly played with unrelated same-aged peers and very rarely with other adult chimpanzees, so opportunities for receiving scaffolding from more experienced individuals was limited. Given the cultural difference with regard to the infants' main playing partner found in Chapter 6, it can be concluded that what is important for the development of joint attention is to interact with social partners that are motivated and able to scaffold the infants' early joint attention interactions, but it is less important whether the mothers or other family members play this role. Despite the differences in their main playing partners, the infants from both cultural backgrounds showed similar competence in joint attention with their mothers in the Social laser experiment. Since chimpanzee partners displayed far less scaffolding behaviours than human

mothers, it can be concluded that chimpanzee mothers and possibly siblings and other chimpanzee play mates were either not motivated or unable to encourage the chimpanzee offspring to engage in joint attention (see mothers' cooperativeness below).

Summary of Potential Explanatory Factors

In the following section, I will briefly summarise potential explanatory factors for the chimpanzees' lower rates of joint attention that were discussed above by first presenting the factors that mirrored the species differences found in the laser experiments and followed by those that were not mirrored by the results of the laser experiments:

- (1) Frequencies of vocalisations. Chimpanzees generally vocalised very little in the time budget study and also showed lower rates of vocalisations during triadic face to face contacts which was an essential operational component of joint attention. Vocalisations may not be the primary mode of mother-infant communication in chimpanzees and they may lack voluntary control over their vocalisations
- (2) Offspring's availability of leisure time. Chimpanzee offspring spent more time with essential activities than human infants which may reflect a lack of opportunity to engage in leisure activities that are important to the development of joint attention (e.g. play)
- (3) Offspring's proportion of time spent in social activities. Human infants spent more time in social activities than chimpanzee offspring which may have allowed human infants to develop habitual social routines with their caregivers that include objects. Therefore, they may have had more opportunities to habitually engage in naturally occurring triadic interactions than chimpanzees.
- (4) Offspring's proportion of time spent with play. Chimpanzee offspring engaged significantly less in play than human infants. This is related to having less 'leisure' time available in their time budget (see (2)), but it may also be caused by chimpanzee infants lower levels of energy

- (5) Proportions of object play in individual and social play. Chimpanzee offspring used less objects during play in general and they were never observed to use objects during social play. This indicates that in their everyday life, chimpanzees face very little opportunities for triadic interactions.

Factors that were identified as being unlikely to have contributed to the species differences found in the laser experiments.

- (1) The mothers' availability of leisure time. The mothers of all three groups had equal amounts of leisure time available to dedicate to their infants, but chimpanzee mother showed less joint attention related scaffolding behaviours in the laser experiment and the chimpanzee dyads less joint attention. Therefore, the species difference in joint attention is not related to chimpanzee mothers simply having less opportunity to engage with their infants. It may not be the amount of time that mothers have available for their infants that play a key role in the development of joint attention, but whether the mothers chose to dedicate their leisure time to activities that support the development of joint attention and the quality of the mother-infant interaction
- (2) A strong central social relationship with the mother. Across all three groups the mothers were the main interaction partner during the infants' social activities, indicating the presence of a central relationship between mother and offspring in both species. The lower levels of joint attention shown in the chimpanzees compared to humans are thus unlikely related to the strength of social bond between infant and mother.
- (3) Mother being the main play partner. There was a clear cultural difference between Ugandan and British infants with regard to who the infants' main playing partner was. Ugandan and chimpanzee infants both played more with individuals other than the mother, yet both human groups showed similar rates of joint attention. Therefore, playing with other individuals can also support the development of joint attention and this is not reliant on high levels of play with the mother alone.

Joint Attention and the Mothers' Cooperativeness

Since the chimpanzee and human offspring seemed equally unable or unmotivated to attract the attention of a social partner during the 'Infant Only' experiment, their partners may have played a vital role in establishing joint attention and driving the species differences we see in the mother-offspring interactions in the social laser experiment. Indeed I found important species differences in the mothers' behaviour in supporting and participating in joint attention events during the laser experiments. However, despite these differences in joint attention behaviours, remarkably few relevant differences in the mothers' time budget and everyday activities were found. My results indicate that chimpanzee mothers have comparable opportunities compared to human mothers to engage with their infants during 'leisure time' and to be the main partner in their infants' social activities. Yet despite these similarities, the chimpanzee mothers are not scaffolding attention sharing with their infants. This suggests that a key difference between species may be the motivation to engage in sharing activities and thus may be related to the overall levels of cooperative and 'other-regarding' tendencies present in the humans and chimpanzees. In contrast to humans, chimpanzees have a highly competitive and individualistic nature (Hare & Tomasello, 2004, Jensen, Hare, Call & Tomasello, 2006) and demonstrate low level of 'other-regarding' or pro-social behaviour (Silk, Brosnan et al., 2005). Matsuzawa (2007) reported that chimpanzee mothers do not actively teach their offspring how to crack nuts, but the chimpanzee offspring responds to this by having a very high intrinsic motivation to observe the actions of their mothers. In addition, although there is some evidence for chimpanzees to cooperate with conspecifics, they only do so mutualistically, if they obtain an immediate pay-off (Melis et al., 2006). Therefore, although chimpanzee mothers are very tolerant of their offspring (Goodall, 1986), their less cooperative nature may mean chimpanzee social partners lacked the motivation to attend to and scaffold the offspring's interaction with the laser. In contrast to the chimpanzees' high levels of egocentrism, humans are very cooperative in several different contexts and engage in collaborative activities with shared goals (Tomasello et al., 2005; Tomasello, 2008).

As mentioned above, by changing their foraging strategies, human ancestors adapted to their new lifestyles in several ways. As they began to adopt a hunter-gatherer lifestyle, they started to become more cooperative and to share labour as well as food (Whiten & Erdal, 2012). These higher-level forms of organisation of activities made cooperation and joint attention evolutionary stable strategies. It is possible that in a society without a cooperative framework, joint attention behaviours could be exploited and they would therefore not constitute an evolutionary stable strategy to follow. In contrast, since chimpanzees usually forage individualistically, some argue even during hunting (Tomasello, 2008), sharing and cooperation are not adaptive strategies unless the food source is big enough to share without significant cost to the individual (Slocombe et al., 2010).

To conclude, human mothers may have been more motivated to scaffold their offspring into joint attention, because they are more cooperative than chimpanzees in general. This was reflected in the chimpanzee partners' lack of scaffolding related behaviours such as monitoring the offspring's interaction with the laser and laser related attention getters. Therefore, the mothers' (or social partners') level of cooperativeness and motivation to scaffold social interactions may be an important factor for joint attention to develop and may also explain why chimpanzees showed lower rates of joint attention in the Social laser experiment.

General Discussion

The research conducted in this thesis was inspired by the importance of joint attention during human development and the unresolved debate concerning its phylogenetic origins. Since joint attention plays an important role in language development in humans, understanding the origins of this fundamental ability may help us understand the evolution of language. The existence of joint attention in chimpanzees would indicate that communicative abilities that are pivotal to human language were present in the last common chimpanzee-human ancestor.

Joint attention has been studied in captive chimpanzees, but the methodology used made valid comparisons with human infants problematic (e.g. Tomasello & Carpenter, 2005). Whilst human infants interacted with a member of their own

species, chimpanzees were investigated during inter-species interactions with humans (e.g. Carpenter & Tomasello, 2005; Herrmann et al., 2007). In addition, research on captive chimpanzees, who have to adapt to a species-untypical social and physical environment, cannot reveal whether chimpanzees naturally engage in joint attention in an environment they have adapted to.

To date, joint attention has only been studied in Western human cultures. Given the considerable differences in parenting practices and socio-cultural environments of human infants across the globe together with the impact the social environment has on developing infants (Deák & Triesch, 2006; Keller, 2007), examining early joint attention in different human cultures is necessary to test how robust this ability is in humans and to potentially reveal different developmental pathways of joint attention. In addition, identifying which factors of the infants' social environment are constant and which factors vary across cultures, could reveal which factors are an important contributor to the development of joint attention.

The methodological difficulties of previous comparative research and the lack of cross-cultural data were addressed in this thesis by using an original cross-species and cross-cultural design. The study had high ecological validity as all participants grew up with their biological mothers and were tested with familiar conspecifics in the environment they grew up in. The stimulus used for the experiments was novel to all participants and the same experimental procedures were applied to all study groups. Therefore, the results obtained with the research of this thesis constitute the first directly comparable results in comparative joint attention research.

Using a strict definition of joint attention, I report with this thesis the first two instances of joint attention in wild chimpanzees. In light of the previous negative finding of joint attention in captive chimpanzees (e.g. Tomasello & Carpenter, 2005), this finding highlights the importance of studying chimpanzees in their species-typical environment in which they display their natural behavioural repertoire. Nevertheless, two instances of joint attention from a single trial in a single dyad do not indicate chimpanzees habitually engage in joint attention. Therefore, future research is required to reveal whether the results found in this

thesis can replicated and are representative of the wider wild chimpanzee population.

The laser experiments revealed that without the influence of the mothers, chimpanzee and human offspring behaved in remarkably similar ways. They mainly engaged with the experimental laser stimulus individualistically and did not show a high tendency to actively and purposefully attract the attention of their inattentive mothers to the laser stimulus. In contrast, when both, the offspring and the mother, attended to the experimental laser stimulus, the human mother-offspring dyads engaged in significantly higher rates of joint attention than the chimpanzee dyads. These two findings combined indicate that human mothers seemed to have scaffolded the joint attention interactions, whereas chimpanzee mothers did not do so, suggesting the human mothers' important role for joint attention events to occur. Chimpanzee mothers, however, may not have the intrinsic motivation to share attention and to scaffold joint attention interactions (Tomasello, 2008). This possibility was supported by the findings of the Social laser experiment: human mothers observed their offspring's interaction with the laser at higher rates than chimpanzee social partners and human mothers actively communicated during laser-related mutual gaze whilst this was absent in chimpanzee partners. In addition, the time budget study revealed that chimpanzee and human mothers did not differ in many important aspects of their everyday activities. This supports the suggestion that the low rates of scaffolding behaviours in the Social experiment may more likely be linked to the chimpanzee mothers' lack of intrinsic motivation to scaffold such interactions than limited opportunities for triadic social activities during everyday life.

The time budget study revealed that human infants of both cultures had more opportunities in daily life than chimpanzee offspring to engage in social activities that are relevant for scaffolding joint attention interactions (e.g. social play with objects). Repeated interactions with social partners and objects may have enabled the human infants to discover triadic contingencies and to develop relevant joint attention skills (Deák & Triesch, 2006). Although the human infants at 11 months may not have yet been able to initiate joint attention with their mothers when she

was inattentive in the 'Infant Only' experiment, the habitual opportunities to engage in joint attention relevant activities may have given human infants the necessary skills to be able to follow the lead of their mothers and to engage in joint attention with her during the Social laser experiment.

Having investigated a considerable range of behaviours during the laser experiments, the Ugandan and the British participants generally behaved very similarly despite considerable variations of their non-social and social environment (for more details, see Chapter 3 and 6). Although there was some cultural variation in the mothers' scaffolding behaviours, such as the frequencies of intentional attention directing behaviours and communication during mutual gaze, this did not lead to different rates of joint attention between the two human cultural groups. Therefore, the ability and the motivation to engage in joint attention seem to be a robust phenomenon in the human species.

Future Directions

Longitudinal Studies

It is important to note that, for human infants, the laser experiments (Chapter 4, 5) and the observational data (Chapter 6) were conducted within the same time periods when the infants were 11 months old. Therefore, the approach of comparing parameters of the everyday life and socio-environmental factors of the two cultures rests on the assumption that these parameters were representative of the first 11 months of the infants' lives. Although mother-infant interactions change as the infant matures, and the behaviour of an 11 month old infant is the product of the preceding months of life, I had to assume that the relative group differences and similarities observed at 11 months were likely to be representative of the earlier months. Given the time constraints of a PhD, I had to follow this assumption, however, future research should extend these cross-sectional findings with systematic longitudinal studies. Longitudinal studies may be able to identify important factors in the earlier months of the infant's life that lay vital foundations for the emergence of joint attention. I hope that the conclusions drawn in this chapter will inspire some longitudinal studies on the link between joint attention

in different primate species and human cultures and factors of the social environment.

The chimpanzee offspring in the studies of this thesis varied considerably in age. In addition to testing a group that is more homogenous in age, I would also suggest to conduct a longitudinal or cross-sectional study with wild chimpanzees to examine joint attention relevant behaviours at different ages. In particular, I would suggest following the development of joint attention skills (e.g. gaze alternation, object related attention getters, any forms of directing attention, communication during face to face contact) from birth to 12 months of age. This would enable us to reveal the developmental trajectory of these skills and compare the development of communicative skills between wild chimpanzees and human infants.

Since most of the tested chimpanzees were older than 2 years, I could not detect whether chimpanzee infants might show joint attention skills that are similar to those of humans before 12 months which then disappear later on, because they are not reinforced by their mothers. This possibility should be explored because other aspects of mother-infant communication change with the age of infant: As chimpanzees get older, mutual gaze reduced (Bard et al., 2005). In addition, Ferrari, Paukner, Ionica and Suomi (2009) have shown that mutual gaze between mothers and their infants in rhesus macaques peaked at the infants' age of 2-3 weeks, but significantly reduced after the infants was 2 months old. Ferrari et al. (2009) suggested that early mother-infant interactions are vital for regulating emotions and developing more sophisticated social interactions at a later age. Therefore, investigating the chimpanzee mothers' interactions with small infants (0-12 months) in the wild, will help us understand more about the affective exchanges between mother and their infants and the mothers contingencies to the infants behaviours when the infants are still spending the majority of their time in body contact with their mothers.

The importance of the mothers' scaffolding

In order to test the hypothesis that 11 months old human infants require scaffolding to engage in joint attention, I would suggest replicating the Social laser experiment with siblings or peers as the social partner of 11 months old infants. It

would be essential to choose an age of the social partners in which the mothers' scaffolding behaviours found in this thesis are significantly lower or absent (e.g. onlooking, directing attention). If the 11 months old infants show the same rates of joint attention with social partners who do not scaffold the joint attention interaction, it can be concluded that 11 months old infants do not require the social partners' scaffolding at this age. If the infants show low rates of joint attention with a younger social partner, this indicates that the mothers' scaffolding behaviours were vital for 11 months old infants to engage in joint attention.

Facial Expressions in Wild Chimpanzees

Unfortunately, the video quality did not allow me to reliably code facial expressions in the wild chimpanzees' habitat. It is important to note that the two instances of joint attention in wild chimpanzees that were recorded in this thesis included vocalisations as communication. No instances of joint attention that were based on facial expressions only could be found in this thesis due to the limited visibility of the chimpanzees' faces. Several human joint attention events, however, included facial expressions. Therefore, further studies with an enhanced video quality are needed to reveal potential joint attention events in chimpanzees that are mediated through facial expressions. A good quality video in combination with applying the chimpFACS (Parr et al., 2007; Vick et al., 2007) could reveal more instances of joint attention in wild chimpanzees. This would be a very important finding, because it would challenge the hypothesis that joint attention is uniquely human (Tomasello, 1995; Carpenter & Tomasello, 2005; Tomasello, 2008; Carpenter & Liebal, 2012; Carpenter & Call, in press).

'Cultural' Variation of Joint Attention in Wild Chimpanzees

Finally, in contrast to other chimpanzee populations, the chimpanzees of the Budongo forest do not habitually use tools (Whiten et al., 1999; Kahlenberg & Wrangham, 2010) and in the Sonso chimpanzees offspring rarely used objects during play. As a consequence, it is likely that the social environment with regard to the amount of triadic constellations in their everyday life varies between different chimpanzee populations. In order to test whether joint attention abilities vary as a function of tool and object use in social and non-social activities, the laser

experiments and the time budget study could be replicated with different chimpanzee populations who show different levels of tool and object use.

Conclusions

Finally, I would like to address the question posed in the introduction of this thesis: is joint attention a uniquely human ability? The studies in this PhD thesis have revealed the presence of relevant joint attention skills in chimpanzee offspring (e.g. coordinating attention through gaze alternation) and behaviour that was indistinguishable to that of human infants when the mother was inattentive. Crucially, two instances of joint attention between one chimpanzee mother and her infant were identified. Based on these results, should we conclude that humans and chimpanzees share the ability and the motivation to engage in joint attention?

Given that the two instances of joint attention originate from a single dyad within a single trial, this conclusion would seem premature. Future replication of this result is vital. This study has shown wild chimpanzees may be capable of joint attention and with the implementation of reliable and detailed facial expression coding, future research may reveal stronger, more robust evidence for this ability and therefore challenge the current assumption that joint attention is unique to humans. Whilst this is possible, the results of this study would indicate that joint attention is likely to occur at lower rates in chimpanzees than humans and that this is in part due to the very different roles chimpanzee and human mothers play in joint attention interactions. In contrast to the human mothers, chimpanzee mothers showed very little evidence for actively scaffolding joint attention interactions and encouraging their offspring to engage in joint attention.

This thesis revealed that the very low levels of joint attention in wild chimpanzees could be related to socio-ecological factors that varied between humans and chimpanzees: triadic constellations between offspring, object and another individual rarely occur in chimpanzee everyday life. In addition, since chimpanzees are generally less cooperative than humans, chimpanzee mothers may not have the intrinsic motivation to actively support the development of joint attention in their infants.

To conclude, the design of this thesis has made an original contribution to the research into joint attention by using a paradigm that is directly comparable between chimpanzees and humans. In addition, by systematically examining everyday activities I was able to identify socio-environmental factors that may play an important role in the development of joint attention. The inclusion of two human cultural groups that differ considerably in parenting practices and the infants' social environments, revealed that joint attention is a robust human ability. The first valid comparison of chimpanzee and human joint attention behaviour, made possible by the methods used, revealed joint attention skills in both species, the first two reported instances of joint attention in wild chimpanzees and some important species differences, particularly in the behaviour of the mothers.

Appendix

The Items of the Bayley Scale for Infant Development

Since the Bayley Scale for Infant Development (Bayley, 2006) can be administered with infants younger than 11 months, I only listed the items from the start point for the youngest infants of this thesis. This is the reason why the numbers of the items do not start at “1.” The exact age of the infants on the first day of the administration of the Bayley’s test battery determined the start number in the items list. The items are arranged by difficulty. The easiest items are in the beginning, the most difficult ones at the end. If the infants passed the first three items from the start point of their respective age, they obtained all points from the items before their age-start point. Depending on the individual performance of the infants, some infant did not complete all items. The last item listed in each category (cognitive, receptive language, expressive language, gross motor skills) could not be solved by any of the tested infants. The administration of item 11 from the receptive language sub-scale was discontinued, because it could not be delivered uniformly in all participants.

Cognitive Sub-Scale

Table A.1: Items of the cognitive sub-scale from the Bayley Scale for Infant Development that have been scored for Ugandan and British infants. The items are arranged by difficulty, starting with the easiest. No infant was able yet to score on the last item (55.)

Item	Object used	Description
25. Searches for fallen object	Squeeze toy (duck)	When the attention of the infant was on the toy, the toy was dropped from the side of the table. It was recorded whether infant looked into the direction of where the toy had fallen
26. Bell Series: Manipulates	Bell	The experimenter showed and rang the bell for the infant. Then the bell was handed to the infant. It was recorded whether the infant showed interest in and inspected the bell

Item	Object used	Description
27. Picks up block series: Reaches for second block	3 Blocks without holes	The infant was presented with 3 blocks one at a time. After she picked up the first, it was recorded whether she reached for the second block without dropping the first
28. Pulls Cloth to Obtain Object	Washcloth Object of interest	After the object of interest was placed out of reach on the washcloth, it was recorded whether the infant pulled the cloth towards himself to obtain the object
29. Pulls string adaptively	Ring with string	The ring with string was shown to the infant, suspended on its string and then placed on the table with the ring out of reach and the string within reach of the infant. It was recorded whether the infant pulled the string towards her to obtain the ring
30. Retains both blocks	2 blocks without holes	It was recorded whether infant held both blocks simultaneously for at least 3s
31. Bell Series: Rings Purposely	Bell	After showing the infant how to ring the bell, it was handed to the infant and recorded whether she rang it to make the sound
32. Looks at pictures	Picture Book	The infant was presented with the picture book and it was recorded whether she looked at one or more pictures with interest or recognition
33. Picks up block series: Retains 2 of 3 blocks	3 blocks without holes	See 27. When the third block was presented it was recorded whether the infant retained the first two blocks after seeing the third

Item	Object used	Description
34. Searches for missing objects	3 blocks without holes, Cup with handle	The three blocks were placed one by one into the cup by the experimenter whilst the infant was watching. Then, the experimenter shook the cup with the blocks and tipped the cup over so that the blocks fell out of the cup on the table. The same procedure was repeated once. After the blocks were placed inside the cup for the third time, the experimenter quickly and quietly unloaded the blocks out of sight of the infant and gave her the empty cup. It was then recorded whether the infant looked inside the cup in expectation to find the blocks.
35. Takes blocks out of cup	3 blocks without holes Cup with handle Stopwatch: 2min	The 3 blocks were placed into the cup one by one by the experimenter. The cup was then moved close to the infant and the experimenter asked her to remove the blocks from the cup. It was recorded whether the infant intentionally removed the blocks within 2 min
36. Block Series: 1 Block	9 blocks Cup with handle	The experimenter verbally asked the infant to put the blocks into the cup and pointed from the blocks to the cup. It was recorded whether the infant placed at least one block in or over the cup.
37. Picks up block series: 3 blocks	3 blocks without holes	See 27. And 33. It was recorded whether the infant tried to pick up the third block whilst retaining the first two blocks either in one or two hands
38. Explores holes in Pegboard	Pegboard	The infant was shown the pegboard (which has 6 holes). The experimenter then pointed out the holes to the infant. It was recorded whether the infant intentionally poked her fingers into at least one hole

Item	Object used	Description
39. Pushes Car	Small toy car	The experimenter pushed the toy car across the table. It was recorded whether the infant intentionally pushed the car in some way with all 4 wheels staying on the table
40. Finds hidden object	Glitter bracelet 2 washcloths	One washcloth was placed on the right and the left side of the infant. Her attention was drawn to the glitter bracelet and it was hidden under one of the washcloths. It was recorded whether the infant looked under the correct washcloth. This was tested for both sides
41. Suspends Ring	Ring with string	See 29. After pulling the ring on the string towards her, it was recorded whether the infant suspended it on her own without the ring touching the table
42. Removes Pellet	Food Pellets Bottle (without lid)	The infant was given one food pellet to eat. Then the experimenter placed another pellet into a small plastic bottle and rattled it whilst the infant was watching. Then the experimenter handed the bottle to the infant and asked her to remove the pellet. It was recorded whether the infant intentionally removed the pellet from the bottle
43. Clear Box: Front	Clear Box Object of interest Stopwatch: 20s	A clear box that was open on the bottom and on one side was placed in front of the infant with the open end towards the infant. Whilst the box was placed, the object of interest was simultaneously put under the box at the opposite end of the infant. It was recorded whether the infant retrieved the object through the open end within 20s
44. Squeezes Object	Squeeze toy (duck)	The experimenter demonstrated to the infant how to make the sounds by squeezing the duck. The duck was then handed to the infant and it was recorded whether she tried to squeeze the duck to make the sound

Item	Object used	Description
45. Finds Hidden Object (Reversed)	Glitter bracelet 2 washcloths	See 40. After hiding the bracelet under one of the washcloths, the experimenter reversed the washcloths. It was recorded whether the infant looked under the correct washcloth. This was done for both sides.
46. Removed lid from bottle	Bottle with lid	The experimenter slowly screwed the lid onto the bottle whilst the infant was watching. The bottle was handed to the infant with the verbal request to open the bottle. It was recorded whether the infant successfully unscrewed the lid.
47. Pegboard Series: 2 holes	Pegboard 6 yellow pegs Stopwatch: 70s	The infant was presented with the pegboard with the 6 pegs already sticking in the 6 holes of the board. Whilst the infant was watching, the experimenter removed all 6 pegs one by one. She then asked the infant to place the pegs back onto the board whilst making a gesture from the pegs to the board (not at the holes). It was recorded whether the infant placed one peg two or more times in the same or different holes.
48. Relational Play Series: Self	Doll, bear, plastic cups, spoons, small ball, washcloths, several blocks	It was recorded whether the infant demonstrated spontaneous play with the given objects to herself
50. Finds Hidden Object (Visible Displacement)	Glitter bracelet 2 washcloths	See 40. and 45. After hiding the bracelet, the experimenter retrieved it and hid it again under the washcloth of the opposite side. It was recorded whether the infant looked under the correct washcloth. This was done form both sides.

Item	Object used	Description
51. Blue Board Series: 1 piece	Blue board 9 blue shapes (5 square, 4 round) Stopwatch: 150s	The infant was presented with the blue board and all shapes in place. Whilst the infant was watching, the experimenter removed all 9 shapes and asked the infant to place them back onto the board by saying: "Put them where they belong" and using no complimentary gestures
52. Clear Box Sides	Clear box object of interest Stopwatch: 20s per side	See 43. The object of interest is put under the box, but this time the open end is not facing the infant, but instead facing to the right or the left side. It was recorded on each side whether the infant successfully removed the object from under the box within 20s.
53. Relational Play Series: Others	Doll, bear, plastic cups, spoons, small ball, washcloths, several blocks	It was recorded whether the infant demonstrated spontaneous play with the given objects to others (e.g. mother or doll)
54. Block Series: 9 Blocks	9 blocks cup with handle	The experimenter verbally asked the infant to put the blocks into the cup and pointed from the blocks to the cup. It was recorded whether the infant placed all 9 blocks into the cup.
55. Pegboard Series: 6 Pegs	Pegboard 6 yellow pegs Stopwatch: 70 s	See 47. It was recorded whether the infant placed all six pegs into the holes within 70s

Receptive Language Sub-Scale

Table A.2: Items of the receptive language sub-scale from the Bayley Scale for Infant Development that have been scored for Ugandan and British infants. The items are arranged by difficulty. No infant was able yet to score on the last item (24.)

Item	Object used	Description
6. Searches with head turn	Bell Rattle	The experimenter stood behind the infant (approximately at 50cm distance) slightly to the right or left, but outside the visual field of the infant. She then made a sound with either the bell or the rattle and it was recorded whether the infant oriented towards the sound.
7 Discriminates Sounds	Paper Rattle	Whilst standing behind the infant, the experimenter continuously scrunched up a paper approximately 20cm from the ear of the infant. When he habituated to it by no longer orienting towards it, the experimenter shook the rattle. It was recorded whether the infant oriented towards the rattle.
8. Sustained Play With Objects	Objects of Interest Stopwatch: 60s	It was recorded whether the infants played continuously (with only short lapses of attention) with one or more objects of interest for at least 60 s
9. Responds to Name	None	The experimenter called the infant with a name other than his own, then with his real name and then again with another name. It was recorded whether the infant responded differentially only to his name.
10. Interrupts activity	Objects of interest	Whilst the infant was playing with objects, the experimenter called the infants' name. It was recorded whether the infant interrupted the play briefly in response to hearing his name
11. Recognizes 2 Familiar Words	None	The experimenter talked to the infant using non-familiar and familiar words. It was recorded whether the infant reacted differently to at least two familiar words as opposed to unfamiliar ones

Item	Object used	Description
12. Responds to No-No	Objects of interest	An object that the infant was known to be interested was placed in front of him. When the infant started reaching for it, either the experimenter or the mother said "No, No!" in a firm voice. It was recorded whether the infant hesitated or stopped reaching for the object
13. Attends to other's play routine	Stopwatch: 60s	The mother was asked to engage in a play routine with her infant. It was recorded whether the infant attended to the play routine for at least 60s with only short lapses of attention
14. Responds to request for social routines	none	The mother was asked to which social routines the infant knew. Then she was asked to ask the infant to perform a social routine (e.g. waving bye-bye) without modelling it. It was recorded whether the infant responded to the spoken request for the social routine requested.
15. Identifies Object Series: 1 Correct	British: Story Book Plastic cup Spoon Small ball Doll Ugandans: Soap Plate Plastic Cup Money Doll	The experimenter or the mother asked the child: "Give me the..." or "Where is the...". It was recorded whether the infant identified at least one object correctly.
16. Identifies Object in the Environment	none	The mother was asked the infant to identify a familiar object in the environment. It was recorded whether the infant oriented to or retrieved the object requested.

Item	Object used	Description
17. Identifies Picture Series: 1 Correct	Picture Book	The picture book was shown to the infant. The experimenter or the mother asked the infant “Where is the ...?” or “Show me the...?”. It was recorded whether the infant correctly identified the requested object by either touching it or clearly looking at the correct picture
18. Understands Inhibitory Words	6 blocks (2 cm edge)	The experimenter built a tower with the 6 blocks and collapsed it to establish a play routine. Later, when the infant reached for the tower to collapse it, the experimenter said “Wait!”. It was recorded whether the infant hesitated as a reaction to this inhibitory word.
19. Identifies Object Series: 3 Correct	See 15.	See 15. It was recorded whether the infant identified three objects correctly.
20. Follows One-Part Directions	Doll Spoon, Comb, Facial Tissue	The mother asked the infant to either feed the doll with the spoon, comb the hair of the doll with the comb or wipe the doll’s face with the tissue. It was recorded whether the infant correctly responded to at least two of the requests.
21. Identifies Picture Series: 3 Correct	Picture book	See 17. It was recorded whether the infant correctly identified at least three items in the book.
22. Identifies 3 Clothing Items	None	The infant was asked by his mother to identify three clothing items that either the infant was wearing or the mother was wearing
23. Identifies Action Picture Series: 1 Correct	Picture Book	The mother or the experimenter asked the infant “Show me the boy and girl x-ing”. It was scored whether the infant correctly identified at least 3 actions pictures
24. Identifies 5 Parts of the Body	Doll	The infant was asked to show the experimenter his own body parts or the body parts of the doll. It was recorded whether the infants correctly identified at least 5 body parts.

Expressive Language Sub-Scale

Table A.3: Items of the expressive language sub-scale from the Bayley Scale for Infant Development that have been scored for Ugandan and British infants. The items are arranged by difficulty. No infant was able yet to score on the last item (23.)

Item	Object used	Description
3. Vocalises Mood	None	I was recorded whether or not the infant expressed at least one mood with her vocalisations
4. Undifferentiated Nasal Sounds	None	It was recorded whether the infant produced nasal vocalisations
5. Social Vocalising or Laughing	none	It was recorded whether the infant vocalised socially or laughed when a person interacted with her
6. Two Vowel Sounds	None	It was recorded whether the infant produced at least 2 distinct vowel sounds
7. Gets Attention	None	It was recorded whether the infant attempted to get the attention from others, for example by pulling the cloths of another individual
8. Two Consonant Sounds	Object of interest	It was recorded whether the infant produced at least two different consonant sounds
9. Uses Gestures	None	It was recorded whether the infant used any gesture to get her wants known (e.g. raising arms when wanting to be lifted) or to share attention (e.g. showing)
10. Consonant-Vowel Combination Series: 1 Combination	None	It was recorded whether the infant produced at least one repetitive consonant-vowel combination
11. Participates in Play Routine	Objects of Interest	It was recorded whether the infant participated in at least one playing routine with the mother
12. Jabbers Expressively	None	It was recorded whether the infant used intonation in his vocalisations and whether his vocalisations were expressive

Item	Object used	Description
13. Consonant-Vowel Combination Series: 4 Combinations	None	It was recorded whether the infant produced at least 4 consonant-vowel combinations
14. Uses One-word Approximations	None	It was recorded whether the infant uses a specific vocalisation for one specific item that resembled the actual word for this item
15. Directs Attention of Others	Objects of Interest	It was recorded whether the infant pointed at and object or showed an object to either the mother or the experimenter
16. Imitates Word	None	It was recorded whether the infant imitated at least one word even if the imitation consisted of vowels only
17. Initiates Play Interaction	Objects of interest	It was recorded whether the infant initiated at least one playing interaction with either the experimenter or the mother
18. Uses Words Appropriately Series: 2 Words	Object of interest	It was recorded whether the infant used at least two different words appropriately
19. Uses Words to Make Wants Known	None	It was recorded whether the infant used at least one word to make her wants known (e.g. "food" or "give")
20. Names Object Series: 1 Object	<p>British: Story Book Plastic cup Spoon, Small ball, Doll</p> <p>Ugandans: Soap, Plate Plastic Cup Money, Doll</p>	It was recorded whether the infant spontaneously named one of the objects without anyone having mentioned the name of the object before. If the infant did not name the objects spontaneously, either the experimenter or the mother asked her: "What is this?"

Item	Object used	Description
21. Combines Word and Gesture	None	It was recorded whether the infant combined a word with a gesture
22. Names Picture Series: 1 Picture	Picture Book	The infant was given the picture book and the experimenter opened the book for the infant. It was recorded whether the infant named at least one object in the book either spontaneously or when asked by the experimenter or the mother: "What is this?"
23. Uses 8 Words Appropriately	Objects of interest	It was recorded whether the infant used 8 different words appropriately for each respective object.

Gross Motor Skills Sub-Scale

Table A.4: Items of the gross motor skills sub-scale from the Bayley Scale for Infant Development that have been scored for Ugandan and British infants. The items are arranged by difficulty. No infant was able yet to score on the last item (46.)

Item	Object used	Description
22. Sits Without Support Series: 5 Seconds	Stopwatch: 5s	It was recorded whether the infant was able to sit for at least 5s without support
23. Pulls Up to Sit	None	Either the experimenter or the mother kneeled at the feet of the baby who was lying on his back. She offered him one finger on each side to hold on. Without pulling the baby up, it was recorded whether the baby pulled himself up to reach the sitting position
24. Grasps Foot With Hands	Facial tissue	Whilst the infant was lying on her back, a piece of tissue was placed on one of her feet. It was recorded whether the infant grasped the foot where the tissue was with her hand
25. Rolls from Back to Stomach	Object of interest	Whilst the infant was lying on her back, an object of interest was shown to the infant and then placed next to her but out of reach as long as she remained in her current position. It was recorded whether the infant rolled from the back to her stomach to retrieve the object
26. Sits Without Support Series: 30 Seconds	Stopwatch: 30 Seconds	It was recorded whether the infant was able to sit for at least 30s without support
27. Sits Without Support and Holds Object	Object of Interest Stopwatch: 60s	During play it was observed whether the infant was sitting without support and simultaneously holding an object for at least 60s

Item	Object used	Description
28. Rotates Trunk Whilst Seated	Object of interest	Whilst the infant was sitting without support, the experimenter/mother went to the side of the infant and offered him a toy. It was recorded whether the infant whilst staying seated turned to the adult to retrieve the toy
29. Makes Stepping Movements	None	The mother/experimenter was holding the infant in a standing position, supporting her weight. It was recorded whether the infant when moved forward made stepping movements
30. Crawls Series: On Stomach	Object of interest	If the infant had not yet been able to crawl, an object of interest was placed 1m in front of the infant who was lying on the stomach. It was recorded whether she was able to reach the object by using her arms and legs to propel her forward
31. Crawls Series: Crawl Position	Object of interest	It was recorded whether the infant moved from lying on her belly to being up on her hands and knees
32. Moves From Sitting to Hands and Knees	Object of interest	Whilst the infant was sitting without support, an object of interest was placed out of reach. It was recorded whether the infant changed her position from sitting to the crawl position
33. Supports Weight	None	The experimenter/ mother held the infant in the standing position and then held the infant without supporting her weight (only giving stability to stand). It was recorded whether the infant was able to support her own weight for at least 2 s
34. Crawls Series: Crawl Movement	Object of Interest	An object of interest was placed 1m away from the infant. It was recorded whether the infant crawled either on his hands and knees or his hands and feet to the object

Item	Object used	Description
35. Raises Self to Standing Position	Object of interest	Whilst the infant was sitting on the floor, an object of interest was shown to him and placed onto a chair (or anything that was of similar height). It was recorded whether the infant pulled himself up to reach the object of interest
36. Bounces Whilst Standing	None	Whilst standing with support, it was recorded whether the infant bounced up and down at least twice by bending and straightening her knees
37. Walks Series: With Support	None	Without supporting the infant's weight, the experimenter/mother guides the infant to walk. It was recorded whether the infant made coordinated alternating stepping movements
38. Walks Sideways With Support	Object of interest	Whilst the infant stood and held on to a piece of furniture, the experimenter placed an object of interest out of reach of the infant, but still on the same piece of furniture. It was examined whether the infant walked sideways along the furniture to retrieve the object
39. Sits Down With Control	None	It was recorded whether the infant lowered himself purposefully from the standing into the sitting position
40. Stands Alone	None	It was recorded whether the infant stood alone for at least 3 s after the experimenter/mother released his hand
41. Stands Up Series: Alone	None	It was recorded whether the infant moved from the sitting into the standing position without support
42. Walks Series: Alone	None	It was recorded whether the infant took at least 3 steps without support even if gait and stiff legged and wobbly

Item	Object used	Description
44. Throws Ball	Small Ball	During a throwing game, the infant was asked to throw the ball towards a play partner. It was examined whether the infant purposely threw the ball forward. This could be clumsy and the ball did not have to reach the play partner
45. Squats Without Support	Object of Interest	It was recorded whether the child moved from a standing into the squatting position while staying balanced and without using any support
46. Stands Up Series: Mature	None	It was recorded whether when getting up, the infant used the technique of rolling to the side and then standing up without using any support

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