Origins of Intentional and Referential Communication

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List of original publications

1. This dissertation is based on the following original research articles:

Study 1

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition, 14*(3), 433-439.

Study 2

Tempelmann, S., & Liebal, K. (2012). The emergence of gesture sequences in orangutans. A case for strategy? *Gesture studies, 6,* 72-93.

Study 3

Tempelmann, S., Kaminski, J., & Liebal, K. (*in press*)**.** When apes point the finger – Three great ape species fail to use a conspecific's imperative pointing gesture. *Interaction Studies.*

2. Further presentations and publications based upon this dissertation:

Tempelmann, S., & Liebal, K. (2009). The use of gesture sequences in orang-utans [Conference Abstract]. *Folia Primatologica, 80,* 144-145.

Tempelmann, S., & Liebal, K. (2009, August). *The use of gesture sequences in orang-utans.* Paper presented at the 3rd Congress of the European Federation for Primatology, Zurich, Switzerland.

Tempelmann, S., & Liebal, K. (2010, July). *Apes' assessment of a human's adequacy as food giver and the role of the attentional state.* Paper presented at the Workshop "Current developments in primate gesture research", 4th Conference of the International Society for Gesture Studies, Freie Universität Berlin, European University Viadrina Frankfurt (Oder), Germany.

Zusammenfassung

Wesentliche Merkmale von menschlicher Sprache sind ihre willentliche Steuerung durch den Produzenten und ihr referentieller Charakter. Dementsprechend ist es eines der Hauptanliegen der vergleichenden Forschung die Kommunikation von Menschenaffen hinsichtlich dieser Aspekte zu untersuchen, um Gemeinsamkeiten und Unterschiede mit menschlicher Kommunikation zu identifizieren. Bezüglich beider Merkmale gibt es eine Fülle an Forschungsarbeiten, jedoch sind viele Fragen noch nicht beantwortet. Im Rahmen der hier vorliegenden Arbeit wurden drei verschiedene Studien zu diesen Themen durchgeführt. Zwei von Ihnen widmen sich offenen Fragen bezüglich der Intentionalität, also der willentlichen Steuerung von Menschenaffenkommunikation und eine der Studien hat die referentielle Kommunikation, namentlich die Zeigegeste als Archetyp der präverbalen Referenz, zum Thema.

Bei der Messung von intentionaler Kommunikation bei nicht menschlichen Primaten steht deren Abgrenzung von nicht willentlich gesteuerter Kommunikation im Hauptfokus. Zentrale Dimensionen von Indikatoren, die in diesem Zusammenhang untersucht werden, sind 1. die Beachtung des Aufmerksamkeitszustandes des Rezipienten durch den Sender, 2. die Zielgerichtetheit der kommunikativen Handlung und 3. die Flexibilität bezüglich des Gebrauches der Signale. Zwei der hier vorgestellten Studien zielen auf wichtige, bisher ungeklärte Aspekte bezüglich dieser Kriterien ab.

Studie 1 (Visual Attention-Studie) untersuchte die Kommunikation von Menschenaffen mit einem Menschen hinsichtlich der erstgenannten Dimension. Hier wurde die Fähigkeit von Menschenaffen den visuellen Aufmerksamkeitszustand eines Gegenübers einzuschätzen und diese Einschätzung in ihre Handlung zu implementieren untersucht. In vorhergehenden Studien hatte sich gezeigt, dass alle Menschenaffenspezies beim Futterbetteln sensibel für den Aufmerksamkeitszustand des menschlichen Futtergebers sind. Aus den

vorliegenden Studien wurden sich teilweise widersprechende Annahmen über die Art der von Menschenaffen für diese Einschätzung genutzten Hinweise abgeleitet. Einerseits suggerieren einige Arbeiten, dass Schimpansen den Aufmerksamkeitszustand eines Menschen nicht anhand der Gesichts- oder Augenausrichtung einschätzen können, sondern ausschliesslich auf die Körperausrichtung fokussieren. Andere Studien wiederum lassen vermuten, dass Informationen über die Körper- und Gesichtsausrichtung getrennt verarbeitetet werden. Dabei dient allein die Gesichtsausrichtung der Einschätzung des Aufmerksamkeitszustandes, während die Körperorientierung ausschliesslich über die Fähigkeit des Experimentators Futter geben zu können informiert.

In der Visual Attention-Studie wurde die Gültigkeit dieser beiden sich widersprechenden Annahmen bei allen vier Menschenaffen-Arten untersucht. Die Ergebnisse zeigen, dass alle Menschenaffenarten nur auf die Gesichtsausrichtung des futtergebenden Menschen achten, sobald die Futterabgabe nicht mehr von dessen Körperausrichtung abhängig ist. Damit können wir als erste nachweisen, dass alle Menschenaffen-Arten den Aufmerksamkeitszustand eines Rezipienten anhand dessen Gesichtsausrichtung erkennen. Des Weiteren zeigen die Ergebnisse, dass bei der bisherigen Interpretation von solchen Futterbettel-Kontexten der triadische Aspekt der Situation vernachlässigt wurde.

Studie 2 (Sequenzen-Studie) befasste sich mit der Produktion von Gestensequenzen bei der innerartlichen Kommunikation von in Gefangenschaft lebenden Orangutans und stützte sich auf Verhaltensbeobachtung. Ziel war es zu untersuchen, ob die Produktion von Gestensequenzen, (d.h. von aufeinander folgenden Gesten) bei der innerartlichen Kommunikation das Resultat des zielgerichteten Einsatzes von kommunikativen Mitteln ist (zweite Dimension). Zielgerichtete Kommunikation könnte angenommen werden, wenn Gesten kombiniert werden, um deren Effektivität zu erhöhen. Beispiele dafür wären a) der vorausplanende Gebrauch einer Geste um die Aufmerksamkeit eines kommunikativen

Partners auf sich und das nachfolgende (die eigentliche Botschaft transportierende) Signal zu lenken (Attention-Getting Gesture) und b) das Weiterkommunizieren wenn vorausgehende Gesten nicht erfolgreich waren (Persistence). Beide Formen des Effektivität steigernden Gebrauchs von Gestensequenzen gelten als wichtige Indikatoren für intentionale Kommunikation. Auch hier ist die Befundlage widersprüchlich, und es wird kontrovers diskutiert, ob die Verwendung von Gestensequenzen bei Menschenaffen als zielgerichtete und intentional eingesetzte Strategie gelten kann. Die vorliegende Studie möchte zu dieser Diskussion beitragen, indem sie die gestische Kommunikation von in Gefangenschaft lebenden Orangutans systematisch untersucht. Tatsächlich kamen Gestensequenzen eher selten vor und generell konnte der Gebrauch von Gestensequenzen auf keine intentionale Strategie zurückgeführt werden. Die Ergebnisse sprechen also gegen die Hypothese, dass die Produktion von Gestensequenzen bei Orangutans aus einem zielgerichteten Umgang mit diesen Signalen resultiert. Hingegen konnte festgestellt werden, dass überdurchschnittlich viele Gestenabfolgen im Spielkontext gebraucht wurden und somit die Produktion von Gestensequenzen wahrscheinlich hauptsächlich von der kontextuellen Aufgeregtheit des Individuums abhängig war.

Studie 3 (Conspecific Pointing-Studie) befasste sich mit dem Verständnis von Menschenaffen für referentielle Kommunikation im Allgemeinen und der indexiellen Referenz im Besonderen. Die präverbale Zeigegeste als ein Beispiel für indexielle Referenz ist aus ontogenetischer Sicht von grosser Bedeutung für die Entstehung eines arbiträren, symbolischen Systems wie der menschlichen Sprache. Viele Forscher sehen die Zeigegeste als eine Art *missing link* zwischen der Kommunikation von Menschenaffen und Menschen. In letzter Zeit mehren sich die Zeichen dafür, dass Menschenaffen Zeigegesten tatsächlich intentional und referentiell produzieren. Im Gegensatz dazu sind die Befunde zum

Verständnis der Zeigegeste noch sehr widersprüchlich, diesem Umstand widmete sich die Conspecific Pointing-Studie.

Die Diskrepanz zwischen den Forschungsergebnissen zur Produktion und dem Verständnis von Zeigegesten mag an der jeweils verwendeten Forschungsmethodik liegen. Untersuchungen der Produktion befassten sich fast ausschliesslich mit der imperativen Zeigegeste, wenn beispielsweise das Tier Futter vom Menschen einfordert. Im Gegensatz dazu fokussierten Studien, die das Verständnis von Zeigegesten untersuchten, mehrheitlich auf deklarative, also hinweisende, kooperative Zeigegesten. In der vorliegenden Studie wurde zur Untersuchung des Verständnisses für die Zeigegeste das spiegelbildliche Abbild des experimentellen Designs verwendet, welches normalerweise in Untersuchungen zur Produktion der Zeigegeste genutzt wird. Dabei konfrontierte ich Menschenaffen (Bonobos, Schimpansen und Orangutans) mit einem Individuum der gleichen Art, welches mittels imperativer Zeigegeste Futter von einem Menschen forderte. Im Anschluss wurde untersucht, ob das Subjekt durch das Beobachten dieser Szene die durch die Zeiggeste dargebotene räumliche Information nutzen konnte, um ein verstecktes Futterstück zu lokalisieren. Die Ergebnisse zeigen, dass die getesteten Subjekte nicht in der Lage waren, die Zeigegeste als räumlichen Hinweis zu nutzen. Da Menschenaffen grundsätzlich fähig sind, indexielle räumliche Informationen aus den nicht-kommunikativen Handlungen anderer herauszulesen, stellt die vorliegende Studie in Frage, ob Menschenaffen, die Zeigegeste tatsächlich als intentional auf eine bestimmte Entität verweisende Referenz verstehen.

Bezüglich der Intentionalität von Menschenaffen-Kommunikation lässt sich also feststellen, dass sie viele der Kriterien erfüllt, welche herangezogen wurden um eine Kommunikationsform hinsichtlich ihrer Intentionalität zu evaluieren. Die im Rahmen dieser Arbeit durchgeführte Visual Attention-Studie konnte zudem zeigen, dass Menschenaffen tatsächlich die Ausrichtung des Gesichtes eines Menschen nutzen um dessen visuelle

Aufmerksamkeit einzuschätzen. Dies ist von grosser Bedeutung, besonders hinsichtlich der weiteren Erforschung der Fähigkeit von Menschenaffen den Aufmerksamkeitszustand anderer auf mentaler Ebene einzuschätzen. Die Ergebnisse der Sequenzen-Studie lassen jedoch darauf schliessen, dass sich zumindest bei der innerartlichen Orangutan-Kommunikation keine kommunikative Persistence oder gar ein antizipatorischer Gebrauch von Attention-Getter-Gesten systematisch manifestiert. Der Vergleich mit Studien welche den selben Gegenstand bei anderen Menschenaffen-Arten untersuchten und solchen die zwischenartliche Menschenaffen-Mensch Kommunikation zum Gegenstand hatten, lässt den Schluss zu, dass Menschenaffen, gemäss den hierfür genutzten Indikatoren, mit Menschen *zielgerichteter* kommunizieren als mit Artgenossen. Dieser Befund lädt ein zu weiteren systematischen Untersuchungen der Ursachen, welche evtl. wichtige Einblicke in die motivationalen Hintergründe der Entstehung von menschlicher Kommunikation geben.

Hinsichtlich der referentiellen Kommunikation zeigen die vorliegenden Ergebnisse, dass Menschenaffen Schwierigkeiten bei der Nutzung von indexieller, diskreter Referenz haben. Zum einen konnten die Subjekte in der Conspecific Pointing-Studie die Zeigegeste eines Individuums der gleichen Art nicht nutzen, um das Versteck von Futter zu identifizieren. Da Menschenaffen sonst sehr begabt sind, die Absichten und Handlungen anderer zu interpretieren, liegt der Schluss nahe, dass Menschenaffen, wenn sie auf etwas zeigen, dies nicht tun, um einen konkreten Gegenstand zu bezeichnen, sondern, dass es sich z.B. eher um eine entsprechend erfahrungsbasierter Heuristiken genutzte holistische Futterbettel-Geste handelt.

Zum anderen lassen sich die scheinbaren Probleme von Menschenaffen in Vorgängerstudien der Visual Attention-Studie den Aufmerksamkeitszustand von Menschen anhand der Ausrichtung des Gesichtes bzw. der Augen einzuschätzen, mit ihren Problemen mit diskreter, indexieller Referenz begründen. Im Gegensatz zu früheren Studien erlaubte ihnen das vorliegende experimentelle Setting dyadisch zu kommunizieren. Das heisst, sie mussten in dem eigentlich triadischen Futterbettel-Kontext nicht mehr auf das Futter verweisen, da die direkte Verbindung von Mensch und Futter suggerierte, dass die Gewinnung der Aufmerksamkeit des Menschen automatisch die Freigabe des Futters bedeutet. Durch die fehlende Notwendigkeit *über* etwas zu kommunizieren, konnte dem Aufmerksamkeitszustand des Menschen Rechnung getragen werden. Somit suggerieren sowohl die Ergebnisse der Conspecific Pointing-Studie als auch der Visual Attention-Studie, dass ein entscheidender phylogenetischer Unterschied zwischen Menschenaffen- und Menschen-Kommunikation in der Verwendung von diskreter, indexieller Referenz liegt.

Summary

The human language is essentially characterized by being (i) referential and (ii) under the sender's voluntary control. Accordingly, comparative research on great ape communication has focused on these aspects in order to identify similarities and differences between human and great ape communication. Despite much research addressing both aspects of communication (i.e. referentiality and voluntary control), many questions have not yet been answered. In this work, I have conducted three studies on these topics. Two of these studies have addressed the topic of intentionality (i.e. the degree of voluntary control) in great ape communication, and the other study has addressed the topic of referentiality, focusing on the pointing gesture as the archetype of preverbal referentiality.

When studying intentional communication in non-human primates, it is essential to differentiate it from unintentional communication. For this reason, special dimensions of indicators are used, including (i) whether the sender takes into consideration the receiver's attentional state; (ii) whether the communicative act is goal-directed and (iii) whether the signals are used in a flexible way. Two of my studies aimed to investigate important aspects of these criteria that have not yet been addressed.

Study 1 (Visual Attention Study) explored communication between great apes and humans in the frame of the first indicator. In this study I investigated great apes' ability to evaluate the receiver's attentional state and to use this evaluation to implement communication. Previous studies have shown that all great ape species are sensitive to the human's attentional state when begging for food from a human. In these studies, different cues have been proposed to be used by great apes to evaluate the receiver's attentional state. Some studies have proposed that chimpanzees only evaluate the human's attentional state according to his body-orientation, but not to his face- or eye-orientation. Other studies have

instead suggested that information on the body- and face-orientation is processed separately. In particular, face-orientation would be used to evaluate the attentional state, and body-orientation to only evaluate the human's ability to provide food. In the Visual Attention Study, I tested the validity of these two hypotheses. The results showed that all great ape species only pay attention to the face-orientation of the human experimenter, as soon as the provision of food is independent from the human body-orientation. This suggests that all great ape species understand the receiver's attentional state from the orientation of his face. Moreover, results suggest that previous studies failed to address the triadic aspect of the begging paradigm when interpreting great apes performance.

Study 2 (Sequence Study) used behavioural observations to investigate the production of gestural sequences (i.e. gestures) in intra-specific communication by captive orangutans. The aim of this study was to understand whether the production of gesture sequences in intra-specific communication results from a goal-directed use of communicative means. Communication can be considered goal-directed when i.e. gestures are combined in order to enhance their effectiveness. This includes for example (i) an anticipatory use of gestures to direct the communicative partner's attention to a forthcoming signal, which is carrying the real information (attention-getting gestures), and (ii) continued communication when the previous gesture is not successful (persistence). The use of attention-getting behaviours and persistent communication both enhance the effectiveness of gestural communication and are important indicators of intentional communication (second dimension, see above). Scientific evidence is again contrasting and it is still debated whether the use of gesture sequences by great apes can be considered a form of intentional and goal-directed strategy. My second study aims to contribute to this discussion by systematically investigating gestural communication in captive orangutans. In my study, gestural sequences were seldom and their use could not be defined as being intentionally strategic. The results did not therefore confirm the hypothesis that orangutans produce gestural sequences in a goal-directed way. On the contrary, most gestural sequences were used in play-contexts, suggesting that the production of gestural sequences is probably dependent on the individual’s contextual arousal.

In **Study 3** (Conspecific Pointing Study) I investigated whether great apes understand referential communication and specifically indexical communication. Preverbal pointing gestures are an example of indexical reference and they are ontogenetically fundamental for the development of an arbitrary and symbolic system like the human language. The pointing gesture is often considered as the *missing link* between great ape and human communication. Recently, more positive evidence has been collected on the intentional and referential production of pointing gestures by great apes. On the contrary, there is contrasting evidence on the understanding of pointing gestures by great apes and my third study aims to specifically investigate this topic. The different results on production and understanding of pointing gestures in great apes might depend on the methodology used. Studies on the production of pointing gestures usually deal with imperative pointing, e.g. when the animal requires food from humans. On the contrary, studies on the understanding of pointing gestures mainly focus on declarative pointing, i.e. indicative, cooperative pointing gestures. In this study I investigated whether the understanding of pointing gestures depends on the experimental design. For this reason, great apes (bonobos, chimpanzees and orangutans) were tested after observing a conspecific using imperative pointing to obtain food from a human. I investigated whether subjects observing conspecifics’ pointing could use the spatial information provided by the pointing gesture to locate hidden food. The results showed that subjects were not able to use the pointing gesture as a spatial cue. Since great apes are able to read out indexical spatial information in non-communicative contexts, my study suggests that great apes might not be able to understand the pointing gesture as intentionally referring to a specific entity.

Great ape communication therefore appears to satisfy many of the criteria commonly used to evaluate intentionality in communication. Moreover, the Visual Attention Study also showed that great apes use the human face-orientation (and not his body-orientation) to evaluate his attentional state. This is especially meaningful in terms of great apes' ability to evaluate others' attentional state at a mental level. The results of the Sequence Study suggest that at least in intra-specific communication, orangutans do not systematically show communicative persistence or an anticipatory use of attention-getting behaviours. The comparison with similar studies on intra-specific communication in other great ape species and on communication with humans suggests that great apes rather communicate in a goal-directed way with humans than with conspecifics. These findings call for further investigations, which could provide us with important insights into the motivational background regarding the evolution of human communication.

In terms of referential communication, my results show that great apes have problems at using indexical, discrete reference. First of all, subjects in the Conspecific Pointing Study could not use the pointing gesture of a conspecific to locate hidden food. Since great apes are usually very skilled at evaluating other individuals' behaviours and motives, it seems probable that great apes do not use the pointing gesture to indicate concrete objects, but rather as a holistic gesture to beg for food which has been learned through experience. Secondly, our results suggest that great apes' problems with discrete indexical reference might explain why great apes in other studies seemingly had problems to evaluate a human's attentional state from his face- or eye-orientation. In contrast to these studies, my experimental set-up allowed great apes to communicate in a dyadic way. Consequently, great apes did not have to refer to the food in the triadic context of a food-begging paradigm, since the connection between human and food suggested that obtaining the human's attention would automatically lead to obtain food. Without the need to communicate about something, great apes managed to take into consideration the human attentional state. Both the results of the Conspecific Pointing Study and the Visual Attention Study suggest that a decisive phylogenetic difference between great ape and human communication lays in the use of discrete indexical reference.

1. General Introduction - On Communication

Recently, much attention has been devoted to the topic of communication in great apes. Researchers from different areas have addressed this topic from various perspectives. Two main reasons seem to explain the increasing interest in the study of communication in great apes. First of all, investigating communicative patterns in great apes might provide us with interesting information on the great ape species themselves. Secondly, the study of our closest relatives allows us to better understand the evolutionary origins of human communication.

A better understanding of the communicative structures and processes in great apes plays of course a central role in enhancing our general knowledge on these species. Since all great apes live at least occasionally in groups, inter-individual interactions constitute an essential part of their behaviour and communication is thus essential to maintain the social structure of the group. Consequently, more information on the different forms, aims and contents of their communication might help to better understand the behavioural, social and ecological characteristics of these species. On the other hand, different social structures can explain different phenomena related to communication. For example, the lack of pointing gestures in free-ranging great apes is often explained in terms of their competitive social structure, which rarely allows individuals to cooperatively interact when external objects are involved (e.g. food sharing; see Tomasello, 2008). Moreover, communication in primates, and especially in great apes, is often considered a “window into primate social mind” (Cartmill & Maestripieri, *in press*, n.p.). The study of communication in great apes is therefore essential to investigate their socio-cognitive skills. These are for example basic socio-cognitive skills that could be associated with the ability to represent other group members’ mental states (like e.g. the capacity to consider other individuals’ state of audience and to communicate accordingly). Finally, research on communication also provides us with important information on how signals are learned, produced and understood (Cartmill & Maestripieri, *in press*).

Research on communication in great apes is also an essential tool to better understand the evolution of human language and communication. Human communication (and especially human language) is unique among animals. As far as we know, only human language allows the unlimited production of different expressions. Tecumseh Fitch (2005) put it in the following words:

“While other animals communicate meaningfully… only humans can communicate virtually any concept that they can entertain. Chimpanzees can certainly know about leopards, fruit, caves and much more besides …, but are unable to communicate this propositional knowledge to others” (Fitch, 2005, p.195).

This attribute of human language is *inter alia* thought to be due to two hierarchical levels of combinatory rules within the human linguistic system. According to the first rule, a limited number of meaningless phonemes (i.e. basic speech sounds) is combined to an unlimited number of meaningful morphemes and, according to the second rule, these morphemes are combined to an unlimited number of words and sentences (duality of patterning; Hocket, 1960).

The American ethnologist and linguist Edward Sapir described the uniqueness of human communication from another direction. He described the fundamental difference between human and non-human communication with the following words: “Language is a purely human and non-instinctive method of communicating ideas, emotions and desires by means of voluntarily produced symbols” (Sapir, 1921, p.8).

Edward Sapir drew attention on two of the most fundamental characteristics of human language. Firstly, human language is mainly under the voluntary control of the sender. Secondly, human language is symbolic and therefore referential. One question is therefore whether only humans possess the cognitive skills allowing the production and understanding of such a complex communicative system. Are there direct precursors of the human language in other animals, or has the human language no equivalent across the other species? This problem is highly discussed in the scientific community and known as the continuity/discontinuity debate (e.g. Knight, Studdert-Kennedy, & Hurford, 2000). In particular, some authors claim that the evolution of language happened as a sum of different, discrete events, thus saltationally (e.g. Bickerton, 1990; Chomsky, 1957, 1965, 1972; Lenneberg, 1967), whereas others propose that the human linguistic system has continuously evolved (e.g. Cheney & Seyfarth, 2005; de Ruiter & Levinson, 2008; King, 1999; Pinker & Bloom, 1990; Tomasello, 2008). However, scholars following the continuous line of language evolution depart in different fractions, e.g. proposing gestural or vocal roots of human communication or more generally localising these roots of human communication in the ability to intentionally use communicative means (e.g. Tomasello, 2008). Nevertheless, following either the arguments of the continuous or the discontinuous evolution of human language, comparative studies are essential to better understand the evolutionary roots of human communication and to disentangle the relevant socio-cognitive skills involved. Great apes are indeed the closest living relatives to humans. Investigating the way they communicate and identifying differences and similarities to humans are therefore crucial aspects for a better understanding of the evolution of human communication. On the one hand, it is extremely interesting whether communication in great apes is also characterized by intentionality and a symbolic-referential nature, which according to Edward Sapir are both peculiar to human language. On the other hand, it is important to analyse whether the socio-cognitive skills necessary for human language are also to be found in great apes.

The following two chapters address these issues by focusing on two main characteristics of human language, i.e. voluntary controlled production and symbolic-referential nature. To do that, I will briefly introduce these concepts theoretically and present empirical evidence from human ontogenetic development whenever needed. Importantly, I will discuss the extent of voluntary controlled action and symbolic-referential nature in communication, as having so far been evidenced in great apes.

2. Intentional Communication

Paul Watzlawick indirectly addresses the issue of intentionality in communication in his first axiom (meta-communicative axiom): “One cannot not communicate” (Watzlawick, Beavin, & Jackson, 1967, p. 49). Communication is therefore not necessarily performed voluntarily by the sender. Therefore, to identify voluntarily controlled communication, it needs to be clearly differentiated from communication which is involuntary. Involuntary communication includes, for example, genetically determined signals of strictly physiological nature (like aposematic coloration in several insects), or conditioned and/or innate behavioural responses to external or internal stimuli (i.e. involuntary stimulus-response relationships). A typical example for such a stimulus-response reaction is the piloerection, i.e. the mammals’ erection of hair as an involuntary reaction to a stimulus. This involuntary response to the stimulus by a specific individual is nonetheless perceived and interpreted by external observers. In these forms of communication, the sender is not voluntary “communicating” and he is not aiming to perform a voluntary communicative manipulation of the recipient, but he rather communicates without any cognitive involvement and almost unwillingly. However, it is often difficult to decide whether animal communication follows a stimulus-response relationship or is rather a voluntary act. Call and Tomasello (2007) propose to extend the term “intentional communication” to communicative voluntarily controlled signals in animals:

> *… the signals we are interested in are not signals that are invariably elicited by particular external or internal stimuli, but rather they are signals that the individual chooses to produce, or not to produce, in particular situations for particular social goals. Although the term sometimes creates confusion, we know of no better way to*

> *designate these strategically used signals than with the term intentional communication*. (Call & Tomasello, 2007, p. 3)

According to this definition, in these studies I will use the term “intentional” for all the forms of communication which are voluntary and not mere predetermined responses to specific stimuli.

In literature, different criteria have been proposed to differentiate intentional and unintentional communication. The first criterion to measure intentionality in communication was proposed by Bates, Camaioni and Volterra (1975) and Bates, Benigni, Bretherton, Camaioni and Volterra (1979) in their studies on preverbal communication in children. In the same line, Ploij (1978, 1984) was the first one to explicitly differentiate between intentional and unintentional signals and gestures in great apes (see Cartmill & Maestripieri, *in press*). In particular, he defined gestures as being intentional when they were used flexibly in terms of means-end dissociation and/or when they were accompanied by gaze alternation (see section 2.3 for more detailed information). Ploij’s definition was later improved by other authors who introduced other criteria. Intentionality, for example, would be linked to waiting for a response from the recipient (i.e. response waiting) or to paying attention to and manipulating the attentional state of the communicative partner (Tomasello, George, Kruger, Farrar, & Evans, 1985; Tomasello, Gust, & Frost, 1989). In the years, more criteria have been introduced and the concept of “intentional communication” has very often been theoretically extended. However, the three following main dimensions, including different criteria, are usually recognized as crucial to identify acts of intentional communication:

1 attention of the sender to the attentional state of the communicative partner (i.e. audience effect)

2 goal-directedness in communicative interaction

3 flexibility in the use of signals

These three dimensions are not always easy to disentangle. For example, purposely influencing the attentional state of a partner is an indicator of goal-directed communication, but it also indicates understanding of the attentional state of a partner. By some authors, the audience effect is not considered a dimension on its own, but rather a sub-criterion to evaluate flexibility (Pika, Liebal, & Tomasello, 2005). Occasionally, flexibility has been considered a synonym for intentional communication (Call & Tomasello, 2007). About these issues, more details will be provided in section 2.3.

The following classification attempts to organize the concepts and criteria which are commonly linked to the concept of intentional communication. These criteria do not claim to be exhaustive.

2.1. Audience effect

Intentional communication requires one sender and at least one receiver. The production of signals in the absence of receivers, for example, clearly suggests a form of communication that is not voluntarily aimed to influence a recipient. On the contrary, an adapted use of signals is suggested by communication taking into account the receiver’s attentional state (i.e. visual gestures being only used when the receiver is looking at the sender, and auditory signals being only used when the partner is in range of audibility; e.g. Hostetter, Cantero, & Hopkins, 2001; Leavens, Hostetter, Wesley, & Hopkins, 2004; Leavens, Russell, & Hopkins, 2010). Moreover, the way in which communication varies depending on the receiver’s attentional state provides important information about the sender’s understanding of signal processing in the receiver. The extent to which the sender takes into account the receiver’s attentional state during the communicative interaction is also highly debated and crucial in understanding whether primates (and especially great apes), aim to manipulate others on a mental level when communicating (e.g. Emery, 2000; Povinelli & Eddy, 1996; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

2.2. Goal-directedness in communication

The criterion of goal-directedness is especially important to consider communicative interactions as being intentional. Pursuing a goal in a communicative interaction, having expectations and making efforts to reach this goal, for example, are usually considered evidence against an automatic stimulus-response relationship. Below, I will briefly outline the most widely used criteria for identifying goal-directedness in communication.

1. **Response waiting**: the sender expects a reaction from the receiver. This expectation becomes evident, for example, when the sender stares at the receiver until the receiver reacts (see e.g. Cartmill & Byrne, 2010; Sarimski, 2002; Tomasello et al., 1985, 1989).
2. **Eye-contact:** the sender accompanies the communicative interaction with eye-contact. Eye-contact is especially important to consider communication as being referential. In this case, “gaze alternation” takes place, meaning that sender alternates gaze between the receiver and the entity on which communication is focused (see e.g. Bates et al., 1975; Franco & Butterworth, 1996; Gomez, 2004; Plooij, 1978, 1984; Sarimski, 2002).
3. **Persistence:** if the communicative goal is not reached, the sender keeps on communicating and only stops when the goal has been reached. Persistence therefore consists

in **repetition** and **elaboration** of the communicative acts (see e.g. Bates et al., 1975, 1979; Leavens et al., 2005; Liebal et al., 2004a; Sarimski, 2002).

4. Attention-getting behaviour: the sender uses communicative means to gain attention from the potential receiver and direct it toward another communicative signal (Bates et al., 1975). In other words, the sender attempts to direct the potential receiver’s attention directly to another signal or to the sender himself, so that the receiver can pay attention to the forthcoming signal (see e.g. Bates et al., 1975, 1979; Nishida, 1980; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994).

The criteria used to detect goal-directedness in communication are very heterogeneous. They differ, for example, in terms of their cognitive complexity, allowing a further rough classification into (a) *simple* goal-directedness and (b) *more elaborated* goal-directedness. Simple goal-directedness includes actions in which the sender clearly expresses the intention to reach a specific goal. In this case, it is possible to talk about intentional behaviour instead of intentional communication (Bard, 1992; Bruner, 1982). Examples of simple goal-directedness include response waiting and repetition of the signal until a satisfactory response (i.e. the offering of food) is produced by the recipient. However, simple goal-directedness is often problematic in that it does not always clearly hint to whether communication is intentional. For example, it is possible that, in the presence of an eliciting stimulus, signals are produced until the stimulus has disappeared or the triggered desire has been satisfied (e.g. an animal unsuccessfully tries to reach for a banana and keeps on producing signals until the goal has been reached).

However, a clear example of more elaborated goal-directedness is the anticipatory use of attention-getting behaviours. These behaviours very probably suggest a strategic goal-directed form of communication, as prearranging and flexibly adjusting communication to different conditions appear to be impossible through simple automatic responses to specific stimuli. The sender has indeed to make a communicative detour, and such a form of signalling cannot be directly linked to an eliciting stimulus. On the contrary, persistence and response waiting rather suggest the intention to reach a specific goal, without *necessarily* implying any intentional use of communicative means.

2.3. Flexibility

A fundamental dimension of intentional communication is the flexible use of signals, although the concept of flexibility has been used in several different ways (Call & Tomasello, 2007; Liebal, Call, & Tomasello, 2004a; Pika et al., 2005). Below, I will stick to the two most widely used definitions of flexibility (and its criteria). Firstly, flexibility concerns the relationship between the signal and the information conveyed by the signal. When the same signal has different meanings and different signals can have the same meaning, then gestures cannot probably constitute automatic responses to specific internal or external stimuli. This form of signal use is also known as means-end dissociation (Bruner, 1981; Plooij, 1978, 1984).

Secondly, flexibility is used to describe the diverse use of signals either between or within groups of the same great ape species, suggesting again that communication goes beyond stimulus-response relationships. Differences in the use of gestures at the group level or at the individual level would indeed suggest that the use of signals is not innate, as a genetically determined use of gestures would lead to a much broader homogeneity in signal use (e.g. Liebal, Pika, & Tomasello, 2006; Pika, Liebal, & Tomasello, 2003, 2005; Tomasello et al., 1997b).

Both these forms of flexibility hint to an ontogenetic learning process to acquire gestures, deeply challenging the hypothesis that communication is an innate stimulus-response relationship. However, both these indicators of flexibility do not alone suffice to evaluate communication as being intentional. If means-end dissociation can provide some information as to whether the signal is a mere response to a stimulus, the risk is that only signals with no clear meaning be considered as intentional. This criterion is especially problematic with regard to human language, which allows very discrete communication. Similarly, researchers do not agree as to whether the heterogeneous use of signals within and between great ape groups of the same species can be a real indicator of intentional communication. Firstly, this heterogeneity in gesture repertoire could simply be due to insufficient data, as Byrne and colleagues suggested (e.g. Genty & Byrne, 2010). Secondly, if the use of certain signals is innate, this does not necessarily mean that they cannot be used intentionally. Tanner and Byrne (1993), for example, showed that captive gorillas can intentionally use their “playface”, which is commonly used in inter-individual play and is considered an innate signal being under emotional (and not voluntary) control. For example, gorillas tried to deliberately conceal their “playface” from their partners to deceive them about their current emotional state. Tanner and Byrne interpreted this behaviour as being intentional, since the sender would intentionally try to conceal information about its emotional state to the receiver. Therefore, also signals that are not under voluntary control can be used intentionally when communicating.

In conclusion, although being widely used in literature, these two different types of flexible communication must be carefully used because of their limits as indicators for intentional communication. Moreover, the concept of flexibility is itself very heterogeneously discussed in the literature. For example, in addition to the afore mentioned two forms of flexibility, the term “flexible” can also be used to simply define the use of signals that varies according to the circumstances, like different use of signals depending on the attentional state of the potential receiver, or pursuing a communicative goal notwithstanding initial failures. Such a broad use of this concept makes “flexibility” coincide with the concept of “intentionality” as used in this work (Call & Tomasello, 2007). On the contrary, flexibility differs from intentionality in that flexibility varies along a *continuum*, while behaviours can seemingly only be dichotomously classified into intentional or unintentional.

3. Referential Communication

Referential communication also plays a major role in the study of the evolution of human language. In contrast to dyadic signals, which require an exchange between sender and receiver and should direct the receiver's attention to the sender, referential and thus triadic signals also involve external objects or events (i.e. third entities). This referential communication therefore enables partners to communicate about "third entities". This is a key aspect in the evolution of human language, which is a system of arbitrary symbols whose meaning is purely conventional.

3.1. Types of referential communication

Experts usually recognize three different forms of referential communication during human ontogenetic development, from a less to a higher degree of abstraction: (a) indexical reference, (b) iconic reference and (c) symbolic reference (e.g. Csibra & Gergely, 2006; Tomasello, 2008).

In **indexical reference**, sense and meaning are provided by the context of the expression. Non-verbal indexical reference has often been investigated in comparative research. One example of indexical reference is the spatial reference to a third entity through a gesture performed with the hand or the finger (i.e. pointing).

Iconic reference is characterized by referential signals abstractly referring to an external entity. In contrast, **symbolic reference** is characterized by a completely arbitrary relationship between referent and entity. Moreover, symbolic reference is not innate and must be learned. The completely developed human language is the best example of symbolic reference, due to the completely arbitrary relationship between symbols (referents) and entities.

3.2. *Indexical reference*

In Study 3 (Conspecific Pointing Study), I will focus my attention on pointing gestures, an example of indexical reference. Pointing is considered the archetype of *non-verbal* referential communication (Bates, O'Connell, & Shore, 1987) and it is widespread across human cultures, with little variation (e.g. lip-pointing or chin-pointing; for an overview see Kita, 2003). In this kind of referential communication, the context in which communication takes place plays a major role. One extended pointing finger is not a communicative message on its own. The gesture must also be clearly produced in a communicative effort and not, for example, as a stretching exercise. Moreover, in order to understand the gesture, the receiver must clearly understand 1) the discrete relation between the entity and the gesture and 2) the communicative context in which it was produced. If somebody is pointing to the sun, without the receiver knowing the communicative intent and the context of the pointing gesture, the receiver can only guess the meaning of the gesture (e.g. was the sender expressing that it was hot or that the sun was beautiful, or did he expect the receiver to take the sun from the sky?).

In order to understand this form of indexical reference, it is therefore essential to understand the intention of the sender during communication (i.e. mental state attribution; e.g. Pika & Liebal, 2006; Tomasello, 2008), and to correctly interpret the spatial relationship between referential activity and external entity.

The pointing gesture is especially interesting because it clearly demarcates the shift from dyadic to triadic communication. In contrast to communication via symbolic and iconic reference, communication by spatially indexing a concrete entity has no need for prior learning about the referent (Csibra & Gergely, 2006). Consequently, pointing behaviour plays a decisive role in the study of the ontogenetic and evolutionary development of human language (e.g. Baldwin, 1995; Bates et al., 1979; Butterworth, 2003; Csibra & Gergely, 2006; Tomasello, 2008). Some researchers have even proposed that, during evolution, humans have acquired an innate sensitivity to use and understand this form of indexical reference (Gergely, Egyed, & Király, 2007).

However, many recent studies investigated great apes pointing behaviour and many of them could show that when great apes communicate with humans they do use the pointing gesture very effectively to i.e. obtain hidden food (e.g. Call & Tomasello, 1994; de Waal, 2001; Krause & Fouts, 1997; Menzel, 1999). Indeed, there is strong evidence that chimpanzees point referentially and intentionally. Thus, some scientists suggest that apes' pointing behaviour might be comparable with that of human infants' (e.g. Leavens & Hopkins, 1998; Leavens, Hopkins, & Bard, 2005; Leavens, Hopkins, & Thomas, 2004; Leavens, Russel, & Hopkins, 2005).

As raised above, non-verbal indexical reference is thought to be a determining step in human ontogenetic development. The transition from dyadic to triadic communication marks an important step in the development of learning and teaching and it mediates the development of the capacity to communicate iconic and symbolic reference (Baldwin, 1995; Bates et al., 1979; Butterworth, 2003; Csibra & Gergely, 2006; Tomasello, 2008). The pointing gesture is considered as the archetype of *non-verbal* indexical and referential communication (Bates et al., 1987). Ontogenetically the use of pointing gestures in human infants directly correlates with the development of language (Colonnesi, Stams, Koster, & Noom, 2010). In order to understand the evolution of human communication it is therefore essential to understand the extent to which pointing in great apes resembles pointing in humans and to resolve in detail which cognitive processes are involved.

In the third study included in the present thesis (Conspecific Pointing Study; Tempelmann, Kaminski, & Liebal, 2012), I will further address this topic and provide more detailed information on our actual knowledge about pointing.

4. Forms of Communication in Primates

Research on communication in primates, and especially in great apes, is usually focused on three different forms of communication: vocal, gestural and facial communication (see Slocombe, Waller, & Liebal, 2011). Below, I will briefly define these forms of communication and analyze to what extent they can be considered intentional, according to the criteria presented above. Since facial communication is often considered to be a component of gestural and /or vocal communication (see Slocombe et al., 2011, for a review), I will focus my analysis on vocal and gestural communication in primates and great apes.

Both these forms of communication are separately analyzed in literature and evolutionary theories on the development of human language have usually focused on only one of these two forms.

4.1. Vocal communication

The study of vocal communication in primates has always played a central role, due to its links with the human spoken language.

Some researchers trace back the origins of human language directly to vocal communication in primates (e.g. Zuberbühler, 2005). However, only few researchers have studied vocalizations in great apes, as also evidenced by a meta-analysis from Slocombe et al. (2011). Indeed, only 8.5% of the 352 included studies on primate vocalization were focused on great apes. Below, I will briefly highlight the most important aspects of vocal communication in primates, presenting data as an excursus on primate vocalization.

The common evolutionary origins of human language and primate vocalization seem supported by some referential aspects of primate vocalizations. The best example in this sense probably consists in alarm calls. Alarm calls are predator-specific and are typically produced by e.g. vervet monkeys (*Chlorocebus pygerythrus*) and Diana monkeys *(Cercopithecus diana)*, for example when potential predators have been spotted (Seyfarth & Cheney, 1997; Seyfarth, Cheney, & Marler, 1980; Zuberbühler, 2000a, b). Alarm calls are usually produced depending on the presence or absence of receivers (e.g. in vervet monkeys: Cheney & Seyfarth, 1985), but they are produced independently of whether the receiver is already informed or not (e.g. in *Macaca*: Cheney & Seyfarth, 1990). Recently, it has been claimed that some primate species produce regular sound sequences, which could be interpreted as syntactic structures and would provide evidence for anticipatory communication (Ouattara, Lemasson, & Zuberbühler, 2009a, b). However, some aspects of vocal production are innate (e.g. Seyfarth & Cheney, 1997; Seyfarth et al., 1980), and the vocal repertoire in non-human primates is not flexible. This is also true for individuals having been raised by members of another species (e.g. Owren, Dieter, Seyfarth, & Cheney, 1992). To summarize, in terms of referentiality, vocal communication in primates is partly context-dependent and thus discretely referencing concrete entities and processes. In terms of perception, signals in primates can elicit specific responses from the receivers, even when receivers do not perceive the stimulus eliciting the vocalization by the sender. Therefore, signals can function in a "referential manner" (Liebal, Waller, Slocombe, & Burrows, *in press*, n.p.). However, due to the above mentioned limitations of monkey communication, especially with respect to the production, this kind of reference has to be distinguished from human referential communication. For example, one still open question is whether primates communicate to intentionally inform or at least manipulate other individuals. Assuming the sender's intention to inform receivers about something, it is also unknown whether the information provided by the sender is congruent with what receivers understand. Consequently, this kind of reference is referred to with the term "functional reference", to distinguish it from human referential communication (e.g. Evans, 1997; Macedonia & Evans, 1993; see Liebal et al., *in press*, for an overview).

In conclusion, vocal production in non-human primates varies according to the audience, but according to the criteria for an intentional communication it is neither flexible nor goal-directed. On the contrary, the ability to understand vocalizations (even from other species) appears to be very flexible (Arnold & Zuberbühler, 2008; Cheney & Seyfarth, 2005; Seyfarth & Cheney, 1997; Seyfarth et al., 1980; Zuberbühler, 2000a, b). Consequently, some researchers consider the understanding of vocalizations to be more relevant for the evolution of human language, as compared to the production of vocalizations (e.g. Call & Tomasello, 2007; Slocombe et al., 2011).

The studies reported so far focus on vocalizations in monkeys. In great apes, very few studies have specifically addressed the topic of vocalizations. Concerning the audience effect, travelling female chimpanzees were found to produce more pant hoots when their partner was in proximity (Mitani & Nishida, 1993). Concerning the referential nature of communication, chimpanzees were found to produce food grunts differently depending on whether food was dividable (Crockford, Herbinger, Vigilant, & Boesch, 2004). Despite not being exclusively focused on vocal signals, other researchers suggest from their studies that captive chimpanzees use sounds, including vocalizations, as attention-getters (i.e. Hopkins, Tagliatella, & Leavens, 2007; Leavens et al., 2004b).

Although the production of sounds in great apes appear to be intentional, according to several of the criteria previously reported, more data is needed to draw definitive conclusions. Moreover, the use of vocal communication in great apes does not appear to be more complex than in other primates, excluding the possibility of an evolutionary trend at this level (for an overview, see Cartmill & Maestripieri, *in press*).

4.2. Gestural communication

Gestural communication has been often proposed as the evolutionary precursor of human language (Arbib, 2004; Arbib, Liebal, & Pika, 2008; Armstrong, 2008; Cartmill & Maestripieri, *in press*; Corballis, 2002; King, 2004; Tomasello, 2008). Supporting evidence for this hypothesis usually highlights the following three facts:

(1) New studies have evidenced the importance of gestures in human language and during its development (e.g. Arbib, 2004; Armstrong, 2008; Corballis, 2002; King, 2004). Gestures play a major role in pre-linguistic communication and in children's acquisition of language (e.g. Bates et al., 1975). A special role is played by the so-called pointing gestures, which will be treated below in more details. Moreover, when gestures accompany languages, they are used as a non-redundant mean of communication (e.g. Goldin-Meadow, 2002; Iverson & Goldin-Meadow, 2001; Kendon, 2004; McNeill, 2002).

(2) Experimental evidence hints to functional and structural neurological similarities between language in humans and gestures in great apes. In primates, for example Rizzolatti and Arbib (1998) discovered a system of mirror neurons, which are activated in the same way either when performing a hand grasping action or when observing it being performed. Several authors have hypothesized that this mirror-neuron system (Area F5) is analogue to the Broca's area in humans (see Rizzolatti & Arbib, 1998, for an overview). The Broca's area is an area in the human frontal cortex playing a crucial role in processing language and especially concerning syntactical integration- and access-activities when producing or understanding language. Consequently, some authors have suggested that gestural communication played a major role in the evolution of human language (Arbib, Pika, & Liebal, 2008; Arbib & Rizzolatti, 1997; Rizzolatti & Arbib, 1998).

Other studies have evidenced functional similarities in the laterality of brain functions between human and non-human primates. Some authors suggest for example that great apes, like humans, preferentially use the right hand to perform gestures. Moreover, right-hand-using appears to be influenced by the production of vocal behaviour also in non-human primates, which is also true for humans (Hopkins & Cantero, 2003). However, evidence of hand preference in non-human primates is so far contrasting (see Liebal & Call, 2012, for a detailed review).

(3) In contrast to vocal communication, gestural communication in great apes fulfills several of the criteria for intentional communication. Below, I will briefly report on the actual knowledge on gestural communication in great apes and on the degree of intentionality in this form of communication, according to the criteria of intentionality presented above.

Apes use gestures in very flexible ways. For example, one gesture can be used to achieve different social goals or, vice versa, several gestures can be used to obtain a specific social goal (means-end dissociation; Bruner, 1981; Call & Tomasello, 2007). There is also a considerable degree of variability among individual gestural repertoires, both within and between groups. This is partly due to the fact that individuals can invent and incorporate new gestures into their repertoires through their lifetime (e.g. for bonobos: Pika et al., 2005; for chimpanzees: Tomasello et al., 1997b; for gorillas: Pika et al., 2003; for orangutans: Liebal et al., 2006). Furthermore, all great ape species appear to be sensitive to the attentional state of communicative partners, selecting the appropriate gesture modality according to the attentional state of the recipient. Compelling evidence for this comes from observational studies focusing on intra-specific communication (for bonobos: Pika et al., 2005; for chimpanzees: Liebal et al., 2004; Tomasello et al., 1994, 1997b; for gorillas: Genty, Breuer, Hobaiter, & Byrne, 2009; Pika et al., 2003; Tanner & Byrne, 1993; for orangutans: Liebal et al., 2006). Other evidence comes from experimental studies in which humans were used as communicative partners (for all great ape species: Kaminski, Call, & Tomasello, 2004; for chimpanzees: Hostetter et al., 2001; Hostetter, Russell, Freeman, & Hopkins, 2007; Leavens et al., 2004b; for orangutans: Call & Tomasello, 1994; Shillito, Shumaker, Gallup, & Beck, 1998, 2005).

It has therefore been proposed that great apes use gestures intentionally. According to the criteria for intentional communication, however, there is still much research to be done on this topic. For example, it is still not clear which parameters are considered by great apes when they use gestures. In particular, it is unclear whether senders use information about the receivers' eyes or about the receivers' face-orientation in order to evaluate the receiver's attentional state (e.g. Kaminski et al., 2004). I will focus on this topic in more details in the first study included in the present thesis (Tempelmann, Kaminski, & Liebal, 2011).

Contrasting results have been reported about the goal-directed use of gestures by great apes, possibly depending on the different research methods that have been used (observations of spontaneous behaviour versus observations within a task context, captive versus free-ranging subjects, inter- or intra-specific communication). Liebal et al. (2004a), for example, found no evidence of complex forms of inter-specific communication in great apes (e.g. anticipatory attention-getting behaviour). In contrast, Leavens et al. (2005) found that chimpanzees beg to a human experimenter within a task context, providing evidence for communicative complexity. This topic will be addressed in more details in the second study included in the present thesis (Tempelmann & Liebal, 2012).

In conclusion, the ability to use different vocalizations is widely recognized as a necessary precursor for the evolution of the complex human language. Slocombe et al. (2011) also evidenced the risks of addressing single modalities of communication when investigating the evolutionary roots of human communication. Such a narrow approach would indeed wrongly underestimate the importance that other more general cognitive skills also play in the development of human language, both as a source and as an engine of evolution. Consequently, my work will address *different* modalities of communication as potential evolutionary precursors of human language. Moreover, I will focus on different aspects of communication in great apes, with a special interest in the cognitive skills linked to them.

5. Dissertation Projects: Aims and Objectives

The proximal aim of the present work is to fill evident gaps of knowledge regarding the intentionality and referentiality (i.e. indexical reference) in great apes' communication. The distal aim is to deduce potential evolutionary traits of the human communicative system from the more detailed description of great apes' skills in these areas.

The present thesis consists of three different studies which are all published or accepted for publication in peer-reviewed scientific publications. These articles are attached as separate copies (see Appendix). Each article contains a detailed introduction summarizing the state of research in the investigated domain as well as a detailed discussion of the findings. In the present thesis these articles are supplemented by introductive chapters and a general discussion section which provide additional in-depth information pertaining the theoretical background and the embedding of the existing literature. In the following I will briefly present the three studies I have conducted. They all focus on different aspects of communication, addressing the topic of intentionality and referentiality in great ape communication from different perspectives.

5.1. *Study 1: Focus on the essential: all great apes know when others are being attentive.* (Tempelmann, Kaminski, & Liebal, 2011)

In Study 1 (in the following called Visual Attention Study), I have addressed an essential and still open question regarding the audience effect. When begging for food, all great ape species are sensitive to a human's attentional state. However, studies investigating which cues are relevant for chimpanzees to assess the attentional state of others have produced highly inconsistent results. Some authors have suggested that chimpanzees assess attentional states based on the status of the face or the eyes, while others have indicated that body posture alone is the relevant cue (e.g. Povinelli & Eddy, 1996). Kaminski et al. (2004) compared the behaviour of chimpanzees, bonobos and orangutans while begging for food from a human experimenter who systematically varied his face and body orientation. Their results indicated that both factors (face and body orientation) affect apes' begging behaviour. The authors claimed that while body orientation provides information about the experimenter's general disposition to offer food, the visibility of the face provides information about the human's attentional state. In the current study, we tested this hypothesis with all four great apes species. However, unlike Kaminski et al. (2004), the experimenter was able to hand over food regardless of body orientation.

5.2. *Study 2: Spontaneous use of gesture sequences in orangutans - A case for strategy?* (Tempelmann & Liebal, 2012)

In Study 2 (in the following called Sequence Study), I have addressed the question of whether orangutans use gestures during intra-specific communication in a way that provides evidence for goal-directedness, i.e. whether combinations of gestures are used in the sense of a communicative strategy. Great apes use gestures flexibly across different contexts and with a considerable degree of individual variability. However, little is still known about whether great apes combine gestures to increase the efficacy of their communicative attempts, either by anticipatorily attracting the attention of the recipient toward themselves or by continuing to gesture in case the recipient does not respond. Both anticipatory use and persistence are characteristics of intentional communication. Thus, the use of sequences of gestures can be investigated as a means for gaining additional information about intentionality in apes' gestural communication.

However, existing studies on the great apes' use of gesture sequences are not consistent in their conclusions. The present study aims to contribute to this discussion by systematically investigating gesture sequences in 16 captive orangutans. This species is especially interesting in this context as it differs from the other great apes due to its peculiar social life. This peculiarity appears to importantly affect orangutans' communication, and the comparison with the other great apes provides interesting information on the potential factors influencing the evolution of gestural communication.

5.3. Study 3: When apes point the finger – Three great ape species fail to use a conspecific's imperative pointing gesture.

(Tempelmann, Kaminski, & Liebal, *in press*)

In Study 3 (in the following called Conspecific Pointing Study), I have addressed the question of whether great apes can use deictic, indexical references. Due to the outstanding role of indexical reference for the ontogenetic and phylogenetic development of human communication, it is necessary to thoroughly investigate the skills of great apes in this domain, in order to draw back the evolutionary pathway of human communication.

However, in contrast to great apes' seemingly sophisticated skills at producing pointing gestures referentially, the comprehension of other individual's pointing gestures as a source of indexical information seems to be less pronounced.

One reason for great apes' difficulty at comprehending pointing gestures might be the experimental set-up. In former studies, great apes were mainly confronted with human declarative pointing gestures, whereas apes have largely been shown to point imperatively and towards humans. In the present study, bonobos, chimpanzees and orangutans were confronted with a conspecific's imperative pointing gesture in a competitive context, therefore mirroring former studies that have investigated great apes' skills at producing these gestures.

6. General Discussion

6.1. Synopsis

The research presented in this work essentially contributes to the debate on intentionality and referentiality in great ape communication. In the first study (Visual Attention Study), I investigated how great apes assess the attentional state of others. Here I present the first evidence that all great ape species are able to assess the attentional state of a recipient based on the orientation of the face and to use visual signals accordingly. In the second study (Sequence Study), I examined orangutans' use of gesture sequences in conspecific communication, and found no evidence that they strategically use signals in order to increase communicative effectiveness. On the contrary, results suggest that orangutans' production of gesture sequences depends on their individual arousal in particular contexts, such as play. In the third study (Conspecific Pointing Study), I investigated bonobos, chimpanzees and orangutans' ability to use an imperative conspecific pointing gesture to locate hidden food. In previous studies, great apes and especially chimpanzees were found to referentially and intentionally produce pointing gestures (e.g. Leavens et al., 2004a). However, apes in the present study did not use their conspecifics' pointing gesture as source of spatial information. As apes have been shown to use indexical spatial information if provided non-communicatively and to interpret other individuals' actions in terms of motives, these results challenge the assumption of many researchers that great apes (at least chimpanzees) really produce those gestures, as human children do, to index a specific location or entity.

The studies presented here aimed to investigate communication in great apes, in order to gather information on the evolution of human communication. For this purpose, special attention was given to decisive aspects of human communication, i.e. intentionality and referentiality. When studying intentionality in great ape communication, it is crucial to distinguish between those forms of communication which follow the stimulus-response schema and those which do not. In order to make this distinction, several criteria can be used (see the Chapter 2 for details). In this work, I have only focused on some of these criteria and indicators of intentional communication. The same is true for referential communication. In this domain, special attention was given to the indexical pointing gesture, which is considered a milestone for the ontogenetic and probably phylogenetic development of human language.

Of course, my studies alone cannot provide a definitive answer to the general questions on intentionality and referentiality in great ape communication. In all the three studies, the research questions were addressed using different methods and samples. Therefore, all these studies should be considered as fragments of information gathered to fill in some of the missing pieces of our actual knowledge, although much more research needs of course to be done. In the discussion sections of each study (see Appendix) I have examined how my findings relate to the already existing literature on the topic. The limits of this work having been already highlighted there, in this chapter I will instead describe the general picture that we can draw from the results of my three studies.

In the first part of this Discussion, I will discuss the results in relation to the existing literature on intentional communication. In the second part, I will discuss how these studies contribute to the knowledge on referential communication in great apes and I will propose possible reasons for the results I obtained and for the fundamental differences between human and great ape communication.

6.2. Intentional communication

In this work I have focused on two dimensions of intentionality in communication: *audience effect* and *goal-directedness*. Below, I will briefly resume the results obtained and I will discuss them in a more general framework.

6.2.1. Audience effect

In the Visual Attention Study, I have investigated whether great apes are able to assess human visual attention and consequently adjust their communication and communicative means. The results showed that all great ape species adjust to the visual direction of a human receiver in non-auditory communication. Therefore, this study provided clear evidence that great apes effectively take into account the human visual attentional state when communicating. In this sense, these results contrast with the hypothesis that great apes only focus on general cues like body-orientation (e.g. Povinelli & Eddy, 1996). Importantly, when producing signals, this ability is an essential prerequisite to anticipate the receiver's mental processing of signals (e.g. Call & Tomasello, 2007).

Our results, however, could not prove that great apes use *auditory* signals differentially, i.e. depending on the receiver's attentional state. Although pure visual signals were used less frequently when the receiver was not looking compared to when he was looking, auditory signals were used independently of the receiver's attentional state. These results are in contrast to what other studies have found (e.g. Hostetter et al., 2001, 2007; Leavens et al., 2004b). Possible reasons for this undifferentiated use of auditory signals are discussed in section 6.2.2, in the context of the triadic aspects of food-begging paradigms.

In the Sequence Study, however, orangutans only used visual gestures when the receiver was facing the sender. On the contrary, tactile gestures (which do not require a visual attentive recipient) were used independently of the receiver's attentional state. Altogether, these results suggest that great apes are at least able to infer the attentional state of a human from the orientation of his face and to take into account the human receiver's visual attentional state by adjusting their use of pure visual signals. For all the other signal modalities, the results are less clear. These findings will be discussed below in more details (section 6.1.2.2), for example by addressing the use of auditory signals as attention-getters.

6.2.2. Communicative goal-directedness

The Sequence Study specifically addressed the topic of the criteria to detect communicative goal-directedness. These criteria include *communicative persistence* (when the goal of the preceding communicative act has not been reached), and *elaboration* of the communicative tool (in order to subsequently reach the communicative goal). I have also investigated whether orangutans systematically use attention-getting gestures to direct the receiver's attention on the forthcoming communicative act, but results showed no evidence of this behaviour. In the following sections, the results are discussed together with the existing literature, providing interesting insights into the phylogenetic and ontogenetic development and developmental potential of goal-directedness in communication.

6.2.2.1. Persistence and elaboration

When taking into account previous studies on great ape communication, my studies clearly show that results on persistence and elaboration are dependent on the methodology used and, especially, on whether great apes communicate with conspecifics or with humans. In contrast to my Sequence Study, for example, Cartmill and Byrne (2007) found evidence that orangutans begging for food from a human persisted to communicate when their communicative goal was not achieved, and even elaborated their communication when being misunderstood, by avoiding repetitions of the previously failed signals (see the Discussion in the Sequence Study). Similarly, Liebal et al. (2004a) found that chimpanzees showed persistence, but not elaboration, in intra-specific communication. On the contrary, Leavens et al. (2005) found evidence of both communicative persistence and elaboration when chimpanzees had to obtain food from a human. Despite important methodological differences across studies, different patterns of communication are clearly used by great apes, depending on whether communication takes place between conspecifics or with humans.

Notably, great apes appear to show more goal-directedness when communicating with humans than in intra-specific communication. This suggests that captive life and dependence on humans might have caused important changes in great ape communicative behaviour. Communication with humans usually concerns food, conferring a special urgency and relevance to communication. Spatial separation from humans, moreover, pushes great apes to communicate with humans in order to obtain food. In conclusion, despite differences among great ape species, a comparison between studies on intra-specific communication (Sequence Study; Liebal et al., 2004a) and studies on inter-specific communication (Cartmill & Byrne, 2007; Leavens et al., 2005) suggests that communication between great apes and humans is “more” goal-directed than intra-specific communication, according to both criteria of persistence and elaboration. This means that, when the communicative goal is not reached, great apes are more likely to continue signalling and even to improve their communicative means when they communicate with humans as compared to when they communicate with conspecifics.

6.2.2.2. Attention-getting behaviours

Different conclusions have to be drawn on the use of attention-getting behaviours (i.e. signals used to direct the receiver’s attention on the sender or on another signal). In the present work, attention-getting behaviours (i.e. gestures) were investigated especially with regard to their function to direct attention to another communicative signal (following Bates et al., 1975). However, recent studies, including the Sequence Study, suggest that great apes do not use these attention-getting behaviours systematically (Genty, Breuer, & Byrne, 2009; Genty & Byrne, 2010; Hobaiter & Byrne, 2011; Liebal et al., 2004a,b, 2006).

These findings appear in contrast with the Visual Attention Study, in which all great apes were able to use visual signals depending on the (visual) attentional state of the receiver.

Also in the Sequence Study, pure visual signals were only directed to attentive receivers. Great apes surely understand the importance of gaining the human's attention to obtain food from him. Liebal et al. (2004b), for example, found that all great ape species tried to enter the human's visual field to gain attention and obtain food. Why orangutans are able to understand the receiver's attentional state, but at the same time fail to use attention-getting gestures with conspecifics in order to drive the inattentive receiver's attention to the forthcoming visual gesture? Why is knowledge on the receiver's attentional state not used to make communication more effective?

Furthermore, the negative findings of my study appear in contrast to other studies, in which some kinds of attention-getting behaviours were used to direct the attention towards the sender's involuntary display of specific moods (e.g. piloerection or sexual erection; Nishida, 1980; Tomasello & Call, 2007; Tomasello et al., 1989, 1994).

These findings, however, are only superficially contradictory. Attention-getting behaviours are often understood as dyadic signals that direct the recipient's attention on the sender of the signal (e.g. Liebal & Call, 2012; Tomasello, 2006). Nevertheless, if the goal is to drive the receiver's attention on the sender in order to enhance the chance that e.g. a forthcoming signal is received, dyadic communication becomes a sort of triadic communication by actually referring to an entity different from the self. Attention-getting behaviours can indeed be used in a quasi-triadic way. This happens, for example, when the sender intentionally uses a tactile or auditory attention-getting behaviour to direct the inattentive partner's visual attention to a forthcoming pure visual signal. On the contrary, the use of attention-getting behaviours which only aims to direct the receiver's attention towards the self is strictly dyadic.

The fact that great apes in my study were not found to systematically use attention-getting signals in order to drive a recipients' attention to another (i.e. intentional) signal indicates that great apes might simply lack a strategic use of attention-getting behaviours, because this “triadic” interaction might be cognitively too demanding.

Consequently, the distinction between dyadic and quasi triadic use of attention-getting behaviours might also explain the seemingly heterogeneity of the results obtained so far. As stated above, some authors found that at least chimpanzees use some kind of attention-getting behaviour when they involuntary display specific moods (Nishida, 1980; Tomasello et al., 1989, 1994). This use of attention-getting behaviours directs the recipient’s attention toward the mood-displaying signal (e.g. piloerection), thus superficially appearing to have a quasi-triadic character. In these cases, however, great apes might use these attention-getting signals only to direct the attention to the self and the accompanied mood, but not explicitly to the expressions of the mood (e.g. the actual piloerection). Consequently, the attention-getting behaviour has a dyadic, not triadic character.

To resume, goal-directedness in great ape communication is characterized by the ability to pursue concrete communicative goals, i.e. according to the criteria of persistence and elaboration. However, these abilities strictly depend on whether communication is intra-specific or with human partners. Possible reasons for these differences are that communication with humans usually concerns food and that alternative strategies to communication (like violent withdrawal of food) cannot be successfully used with humans. Dependency on humans as food-providers and physical separation from humans because of captivity could therefore push great apes to continue signalling even when a previous communicative act failed and, when completely misunderstood, to increase signal frequency and to use other signals than those which previously failed. However, as the Sequence Study and other recent studies also indicate goal-directed communication in great apes might find its limits in the anticipatory use of attention-getting behaviours. Despite their ability to take into account the others' visual attentional state, great apes could indeed lack the complex cognitive skills required to deal with triadic communicative acts.

6.2.3. Intentional communication in great apes: conclusive remarks

In the Introduction, I have highlighted the differences between intentional communication and communication following a stimulus-response schema. Moreover, I have presented numerous criteria to evaluate whether communication can be considered intentional. Many of these criteria are satisfied by great apes when communicating, as my studies also confirm. Great apes, for example, clearly link human attentional state with human face-orientation, and they communicate accordingly. Therefore, there are many reasons to expect that great apes communicate intentionally. However, my studies could not evidence any form of strategic use of communication, i.e. the use of communicative means to direct the attention toward another communicative signal.

To sum up, intentional communication in great apes cannot be discussed without taking into account the relevant cognitive requirements linked to it. Certainly, great ape communication cannot be reduced to a stimulus-response relationship. However, this does not mean that great ape communication must be strategic. One difficulty arises from the multiplicity of criteria used to interpret communication, which are mostly the same ones used to describe and evaluate human communication (e.g. Bates et al., 1975, 1979). Each of these criteria can be used as indicator of intentional communication. However, these criteria are very heterogeneous and refer to different levels of communication that also vary in the underlying cognitive complexity. Satisfying one of these criteria (especially if the criterion requires low cognitive skills), does not necessarily imply that all the other criteria for intentional communication will be also satisfied. The other way around, not satisfying some criteria does not automatically imply that communication is not intentional, given the different levels existing within the category of intentional communication. Similarly, when studying tool use, early hominids' ability to manufacture arrows cannot be compared to modern space flights. However, early hominids still prepared and used tools, marking a significant step in the evolution of skills which would have later allowed modern space flights. It is therefore crucial to critically evaluate and differentiate the criteria used to define intentional communication.

6.2.3.1. The teleological understanding of communicative means

In the following I will introduce an alternative, complementary approach to describe and investigate communicative systems. Human communication is a very powerful tool to describe the world and to interact socially. Indeed, communication via signals can be perceived as a form of (social) tool use. Tomasello (1990) quotes:

"…these two behaviours [tool and signal use] seem to involve analogous, if not homologous cognitive structures: in both cases the organism uses an outside element (tool or social signal) as instrument to attain an otherwise unattainable goal" (p. 275).

Human language exemplifies a sophisticated and strategic use of these communicative "tools", by meaningfully combining them according to specific combinatory rules (e.g. Hocket, 1961) and thus allowing communicating complex information. However, it is essential for such a tactic use of communicative "tools" to be aware of their impact and to use them accordingly to reach specific goals.

Insight into the degree of strategic and goal-directed use of communicative "tools" by great apes might therefore provide us with a better understanding of the evolutionary origins of human communication. Below, I will consequently examine the level of goal-directedness and strategy in great ape communication. In order to quantify how strategically signals are used, I will compare communicative signals with physical tools, using the same teleological approach proposed by Csibra and Gergely (2006). In particular, Csibra and Gergely (2006) proposed three hierarchical stages for the teleological understanding of tools and objects, evolutionarily leading to the tool use of modern humans.

The first stage is characterized by a relatively simple teleological understanding of tools and objects, and it would be typical for great apes' physical tool use (Csibra & Gergely, 2006). In this stage, tools are selected to achieve temporary and specific goals. The choice of tools is therefore activated by the pursued goal, and tools can be modified according to the goal. However, tools acquire no permanent function. The second stage is instead characterized by an inverse teleological understanding of objects and tools, which become independent of a specific goal and acquire a permanent function. Consequently, it is possible to think about the tool and its possible functions. In the third stage (i.e. recursive use of tools), tools can be even used to produce other tools (mediated tool use). According to Csibra and Gergely (2006), this stage has been decisive for the evolution of human learning and it has been possibly responsible for human cognitive uniqueness. Below, I briefly apply this same classification to signals as communicative tools.

If signals are considered communicative tools, it is crucial to distinguish between signals being only used in specific situations (i.e. always in relation with a concrete goal to be attained) and signals on whose function it is possible to think of (at least second stage). Examples of the second kind might be attention-getting behaviours being used in a quasi-triadic way (i.e. to indirectly reach the concrete goal of communication, by directing the receiver's attention to the forthcoming signal which carries the real communicative information). Such an indirect use of signals might require insight into the concrete function of signals.

According to Csibra and Gergely (2006), great apes' teleological understanding of physical tools is "simple" (first stage). Great apes' use of communicative means also appears to be “simple”, as also shown by the examples I have provided on *persistent communication* and *elaboration*. Evidence of a strategic use of communicative means by great apes (comparable to inverse teleology, or second stage), in contrast, is seldom and contrasting. It is possible that the shift from the first to the second stage marks the difference between great ape and human communication. Testing this hypothesis (and the reasons why great apes have not managed to perform this shift) is a question surely deserving future systematic investigation.

6.3. Referential communication

The present studies reveal great apes’ consistent difficulties to use indexical reference. Most striking are the results in the Conspecific Pointing Study, which evidence great apes’ inability to use conspecifics’ pointing gestures as a source of spatial information. Moreover, the Visual Attention Study indicates that former findings suggesting great apes’ inability to infer a human’s attentional state from the state of his face were significantly influenced by great apes’ inability to cope with the cognitive demands of a triadic food-begging context.

Great apes’ use of pointing gestures and the involved cognitive mechanisms are still controversially discussed in literature. However, great apes undeniably produce pointing gestures to obtain food. What is not clear is whether they do it to intentionally and communicatively refer to an entity or whether they use them as a learned strategy implying no understanding of the relationship between pointing gesture and entity. As already discussed, evidence of understanding the relationship pointing-entity is very seldom and many studies suggest no understanding of this relationship by great apes. Similarly, my Conspecific Pointing Study suggests that the understanding of this form of indexical communication is at least a great challenge for great apes and that pointing gestures are not understood as an intentional act of a deictic and discrete reference.

Furthermore, the contrasting results of previous studies investigating how much great apes pay attention to the human attentional state when communicating to obtain food may be explained by the fact that the triadic context of these paradigms is cognitively too demanding for great apes. Some of these studies have indeed emphasized the triadic context (e.g. creating a strong spatial separation between the human giver and the food, when the human turned away from the food), making the task harder for great apes (e.g. Povinelli & Eddy, 1996; see the Discussion in the Visual Attention Study for more detailed information). In the Visual Attention Study, on the contrary, different orientations of the human body relative to the subjects did not alter the bond between food and experimenter, enabling apes to communicate dyadically even when the human's body was averted and thus making the task easier for them.

Below, I will discuss in details the results of my studies with regard to referential communication in great apes. I will discuss the results with regard to the role of pointing gestures in great ape communication and subsequently I will generally address the topic of communication in a triadic context.

6.3.1. Pointing

In the Conspecific Pointing Study, great apes were not able to use pointing gestures as an indexical font of information. These results are especially impressing, considering the abundant evidence of related complex cognitive skills in great apes.

Chimpanzees, for example, visually follow pointing gestures and are consequently able to perceive them (e.g. Itakura, 1996; Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997). They are also able to locate hidden food in one out of several boxes, after a competitor's unsuccessful attempt to reach for one of them (Hare & Tomasello, 2004). Chimpanzees can therefore extract indexical and spatial information from a movement which superficially corresponds to the pointing gesture. Furthermore, great apes (or at least chimpanzees) take into account other individuals' motives when evaluating their actions (Call, Hare, Carpenter, & Tomasello, 2004; Call & Tomasello, 1998) and use their knowledge about other individuals' intention to adjust their own behaviour (Buttelmann, Carpenter, Call, & Tomasello, 2007; Tomasello & Carpenter, 2005; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006). Consequently, the problem in the use of pointing gestures does not lay in the perception or use of the information, but rather in great apes' inability to interpret this information in a communicative context (i.e. as an intentionally produced gesture containing indexical information).

What does this all mean when interpreting the production of pointing gestures? As already discussed, great apes appear to produce pointing gestures quiet flexibly. When confronted with out-of-reach food, for example, great apes only produce gestures if a potential receiver is present (Call & Tomasello, 1994; Kaminski et al., 2004; Leavens et al., 2004; Tomasello et al., 1994). Moreover, great apes also take into account the receiver's attentional state, at least to some degree (Kaminski et al., 2004; Liebal et al., 2004a, b). Leavens and colleagues also reported that great apes point to the location of preferred food, when confronted with different types of food (Leavens et al., 2004a). Furthermore, great apes show persistence and elaboration in their pointing behaviour, when human receivers offer the not-chosen food or only a part of it (Cartmill & Byrne, 2007; Leavens et al., 2005). Do these findings really suggest a truly referential and intentional use of pointing gestures? The fact that great apes fail at using these gestures in order to infer a specific location/entity, however, draws another picture. Great apes (or at least chimpanzees) are able to interpret other individuals' action in terms of their motives. However, it is conceivable that when pointing to the food they want to receive, great apes do not index it discretely and intentionally (i.e. they might not communicate "here is the banana, the food I would like to receive"). On the contrary, great apes might use pointing gestures to manipulate human behaviour in the desired way and according to experience based heuristics (i.e. “if I place my finger next to the banana, I will get it”). The spatial relationship between the pointing gesture and the desired food might not be used for communicational purposes. The reference behind the gesture therefore lies in the apes’ motivation to receive the food, and great apes act according to their previous experience to reach their goal. In this sense, it is an indirect form of reference, triggering the apes’ gesture without being intentionally communicated through the gesture itself. Despite being used intentionally and for referential purposes, gestures do not intentionally index a specific location.

In conclusion, it appears possible that great apes neither are able to interpret nor to produce pointing gestures as a source of deictic spatial information. Probably, pointing gestures are used by great apes as a form of learned dyadic attention-getting behaviours, in which humans are used as “social tools” in order to obtain hidden food (e.g. Leavens, Hopkins, & Bard, 1996, p. 352).

6.3.2. Communication in a triadic context

In contrast to previous studies (e.g. Povinelli & Eddy, 1996), the Visual Attention Study provided evidence that, in some conditions, all great ape species can differentially use visual signals depending on the receiver’s face-orientation. Contrary to other studies, great apes therefore appear able to evaluate the partner’s visual state of attention. As already discussed, however, previous studies have investigated great apes’ ability to evaluate the partner’s attentional state when begging for food, without adequately considering the triadic context of the set-up (but see Gomez, 2005). In my study, all great ape species evaluated the human’s attentional state, regardless of the human body-orientation. When the human’s behaviour indicated that food was deliverable, great apes did indeed pay attention to the human's attentional state. Therefore, when the connection between the food-giver (the human) and the food is given and the great ape does not need to establish this relation, the great ape's action is only influenced by the human's attentional state. Interestingly, recent studies following the begging paradigm have led to comparable results. Hattori, Kuroshima and Fujita (2010), for example, have shown that even capuchin monkeys are sensitive to the state of the human eyes in a begging paradigm, but only when the desired food is in the human's hands and not when it is next to him on a table. Similarly, Hostetter et al. (2007) found that chimpanzees differentiate between the state of the human eyes (occluded or not), when the food has been placed in the human's hands.

Altogether, these findings suggest that great apes might be able to manipulate on-going actions in a food-begging context, but they do not initiate them. This would explain why the partner's ability/ disposition to give food has a superior but not gradual influence on the apes' behaviour (Kaminski et al., 2004). This also suggests that great apes are not able to adequately deal with communication in triadic contexts in which reference to a third entity (the food) is needed. In other words, humans and food have to be linked so close that communication with humans automatically implies the delivery of food. This would reduce the communicative situation to a mainly dyadic context in which it is sufficient to direct the human's attention to the sender, as the human's behavioural spectrum is reduced to food delivery.

However, following this way of interpretation, the question arises why auditory signals were not used differentially in the Visual Attention Study. Following the interpretation, great apes used dyadic signals to obtain food by possibly considering the food and the human food-provider as a single entity. However, why did apes not simply use dyadic auditory signals when the humans face was averted? A possible explanation is that by turning his face, the experimenter broke this unit, disrupted the dyadic context and created a highly triadic context, which could be cognitively too demanding. This interpretation seems supported by other studies, which found that great apes might indeed differently use auditory signals to obtain food in such a requesting context, depending on the experimenter’s visual attentional state (Hostetter et al., 2007; Leavens et al., 2004b). Contrary to our experimental setting, in those studies the food was placed in the hands of the human food-provider, so that the relation between human and food was even straighter than in our study and not easily disrupted (e.g. if the experimenter closed his eyes). Therefore, in order to obtain the food, the communicative context still allowed a dyadic use of non-visual signals.

However, when conducting and interpreting studies on great apes’ ability to account for humans’ attentional state in this paradigm, special attention should be always given to the question of whether subjects are forced to communicate referentially or whether they are allowed to employ alternative strategies.

6.3.3. Referential communication in great apes: conclusive remarks

The results of my studies suggest that indexical referential communication is cognitively demanding for great apes. In other words, great apes have problems to communicate *about* something concrete. Indeed, great apes only use pointing gestures in captivity and only to communicate with humans (but see Vea & Sabater-Pi, 1998, for a possible stipulation). In the wild or with conspecifics, great apes probably lack the urgency and motivation to use triadic referential communication. On the contrary, dependence on humans for feeding and lack of alternative strategies might provide this motivation to captive great apes. Leavens et al. (2005, p. 188) have referred to this phenomenon as to the "referential problem space": spatial distance enhances the need to use pointing gestures, as it possibly happens to human children during ontogeny. Similarly to captive great apes, indeed, human children experience a long period in which objects are often out of their reach, although they can be obtained from other people.

The findings of my studies indicate that great apes can only indirectly communicate with a partner about objects, in contrast to human children. In the Visual Attention Study, great apes only begged for food when it was sufficient to catch human attention, but there was no need to communicate about food itself. The Conspecific Pointing Study also suggests that pointing gestures are used to obtain food, but not to communicate about it. Here, pointing gestures were probably used as a learned behavioural pattern, without any insight into their spatial deictic meaning. The goal of great ape communication is indeed referential (because the partner's behaviour must be directed to a specific goal), but the tools used to communicate are not (because great apes do not use gestures to refer discretely to external entities). This can be seen as an indirect form of reference, because the underlying motivation (but not the form of communication) refers to something.

Crucially, we must distinguish such an indirect, purely motivational form of reference from a form of reference which is intentionally chosen by a sender in order to communicate about concrete entities. As already mentioned, pointing gestures are considered a critical step in the development of human communicative skills (both general and linguistic; Baldwin, 1995; Csibra & Gergely, 2006; Tomasello, 2008). Indeed, (preverbal) indexical reference in human infants is ontogenetically the first communicative act intentionally referring to an external entity and therefore allowing a communication about entities other than the self. Therefore, indexical reference provides a new quality in terms of learning and teaching and probably crucially contributes to the development of iconic and symbolic reference.

However, great apes' indirect referential communication (i.e. their motivation to manipulate another individual's behaviour to make her act in a desired way upon an external entity) may at least be seen as a motivational precursor of indexical reference. Importantly, the reasons why great apes have problems to communicate referentially are still an open question. Some authors assume that great apes, in contrast to humans, are not motivated to share information and attitudes with others (e.g. Tomasello, 2008). Therefore, great apes would not create a common ground based on shared intentionality. Moreover, it has been proposed that a general lack of motivation to cooperate might be the reason why great apes fail at using pointing in comprehension tasks (e.g. Tomasello & Carpenter, 2007; Tomasello, Carpenter, & Liskowski, 2007). However, this might be the crucial difference between humans and great apes in the development of pointing skills. Motivation to share experiences and attitudes requires tools to communicate about external entities. Regardless of whether other cognitive skills being potentially involved, motivation may therefore work as a sort of catalyser to communicate referentially (e.g. forming a deeper understanding of external entities by sharing attitudes and mediating through declarative pointing). The link between motivation to cooperate and the development of referential communication appears quite evident when comparing dogs to wolves. Through domestication, dogs have been probably directly or indirectly selected to cooperate with humans (Hare & Tomasello, 2005). In contrast to wolves (and great apes), dogs are able to quiet flexibly use human referential acts, like pointing gestures, as a source of information (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare, Brown, Williamson, & Tomasello, 2002; Miklosi et al., 2003; Pettersson, Kaminski, Herrmann, & Tomasello, 2011; for an overview, see Miklosi & Soproni, 2006). For example, dogs differentiate the meaning of pointing gestures according to the intentional framework of the communicative situation (Kaminski, Schulz, & Tomasello, 2011). Moreover, in contrast to great apes (e.g. Hermann, Melis, & Tomasello, 2006; Tomasello, Call, & Gluckman, 1997a) dogs can use iconic references as social cues in a communicative context (Kaminski, Tempelmann, Call, & Tomasello, 2009). Dogs' sophisticated social-communicative skills can hardly be explained in terms of a general enhancement of their cognitive skills (Bräuer et al., 2006). These findings therefore highlight the role of motivation to cooperate with other individuals in a communicative context. Although motivation seems a crucial factor to explain inter-specific differences in communication, great apes' little motivation (as compared to dogs and humans) cannot alone exclude the existence of complex communicative skills. It is indeed possible that specific ontogenetic experience might cause a qualitatively different communication system in great apes (Tomasello & Call, 1997, p. 393).

Nevertheless, regarding symbolic reference, it is unknown whether great apes' problems at using indexical reference are due to a general difficulty with referential communication, or whether great apes' poor performance at the level of indexical reference exacerbates the acquisition of symbolic reference. However, fact is that apes were not found to be very skilful at any other kind of communicative reference. For example, although much endeavour has been made to train ape individuals to use symbols (e.g. gestures or lexigrams), the outcome is rather limited. Despite having been explicitly and intensively trained (but see Lyn & Savage-Rumbaugh, 2000), great apes learned only a small amount of symbols (e.g. Gardner & Gardner, 1969; Patterson, 1978; Premack, 1971; Savage-Rumbaugh et al., 1993; Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert, 1986). Moreover, these symbols were not used in a very flexible way, indicating that the comprehension of these symbols is different from that of children (e.g. Kaminski et al., 2009; Terrace, Petitto, Sanders, & Bever, 1979; Tomasello, 2006).

In the section 6.2.3.1. a model of the evolution of tool use proposed by Csibra and Gergely (2006) was introduced as an additional approach to describe communicative systems. There it was discussed in terms of how it can be adapted to describe the aspect of strategic use of communicative means in great apes' communication. In my view, this model also offers important insights when discussing referentiality in great apes' communication. As already explained above, the use of communicative means may be compared to the use of physical tools. The teleological understanding of tools can be divided in three developmental stages (simple, inverse and recursive teleological understanding; Csibra & Gergely, 2006). However, here I expand this approach to compare the use of physical tools with the use of communicative means in apes' referential communication.

The use of pointing gestures by great apes is imperative (i.e. it is used to push a human to perform an action that the subject alone cannot perform, e.g. because of a spatial separation). Consequently, the use of pointing gestures in great apes is often seen as a "social tool use", in which humans are treated like tools to reach a specific goal. If communicative means are treated like physical tools, the use of pointing gestures is therefore a "mediated tool use", as the tool *pointing gesture* is used to manipulate the tool *human*. This form of tool use is especially challenging from the perspective of teleological understanding, in that the function and goal of the tool do not correspond to the ultimate goal of the whole action, but they are used in order to produce another tool which is aimed to reach the goal. Interestingly, a declarative pointing (not using the partner as a mere tool) is the simplest form of understanding of communicative means, by only requiring a simple teleological understanding. In this sense, imperative pointing is much more cognitively demanding than declarative pointing. This explains the possibly important differences between great apes and humans: because of the special human interest to share information and emotional states with others, humans manage to use indexical, referential communication more easily than other species. Importantly, evidence has also been found of a correlation between the use of declarative, but not imperative, pointing gestures with the ontogenetic development of language in human infants (Colonnesi et al., 2010).

7. General Conclusions and Future Directions

The main focus of the present thesis was the intentionality and referentiality of great ape communication. Regarding intentionality my results clearly support the view that a relevant part of great ape communication is intentional, not following a simple stimulus-response schema. However, it is still not clear to what extent great ape use intentional strategies in communication. Human language is characterized by clear rules which relate language units to specific meanings, thereby qualifying human language as a highly strategic form of communication. In order to evolutionary frame great ape communication and propose the proximal and distal forces that might have led to the development of human communication, it is therefore crucial to understand whether and to what extent great ape communication is strategically used. This way of thinking opens new perspectives when comparing human and ape communication and might evidence critical aspects regarding the evolution of human language and the cognitive skills related to it.

Moreover, I proposed to compare the use of communicative means with the use of physical tools and interpret it in terms of the teleological thinking involved in it, following the approach of Csibra and Gergely (2006). As already discussed, it is not clear whether great apes' use of communicative means is limited to the simple stage of teleological understanding. This would imply that great apes can assign a function to their communicative means only when they have situative goals. Consequently, great apes could not think about the function of their communicative means independently of the specific goal, and they could not attribute a permanent function to them. On the contrary, human language attributes a permanent meaning to arbitrary symbols in order to purposefully communicate about entities and processes.

In order to ontogenetically develop such a symbolic understanding, it is not only necessary to be able to strategically use communicative means, but evidently also to communicate referentially. The most basic form of communicative reference is the use of non-verbal indexical reference, the second topic investigated in the scope of the present thesis. The studied pointing gesture is the most thoroughly investigated exponent of this type of reference. In contrast to previous studies suggesting intentional referential pointing in great apes, my studies indicate that great apes have general problems with this form of reference. The reason for this is probably tied to the fact that great apes, in contrast to humans, lack the motivation and the urgency to communicate about external entities. However, even when dependency on human food-givers might push captive great apes to communicate about food as an external entity, they only indirectly do so, showing no complete understanding of the referential and indexical use of communication. Great apes’ evident problems with this archetype of preverbal, indexical reference might point out a *still* missing link between human and great ape communication.

Nevertheless, future research should further investigate the critical differences between great ape and human communication, and the ontogenetic and phylogenetic variables which differentiate great ape and human communication. The insights deriving from the present thesis suggest that the critical shift between human and great ape communication consists in referential communication *per se* and in the strategic use of communicative means in conformity with an inverse teleological understanding. The aim of future studies should therefore be to more precisely define this shift.

References

Arbib, M. A. (2004). How far is language beyond our grasp? A response to Hurford. In K. Oller & U. Griebel (Eds.), *Evolution of communication systems: A comparative approach* (pp 315–322). Cambridge, MA: MIT Press.

Arbib M. A., Liebal, K., & Pika, S. (2008). Primate vocalization, gesture, and the evolution of human language. *Current Anthropology, 49*, 1053-1076.

Armstrong, D. (2008). The Gestural Theory of Language Origins. *Sign Language Studies, 8* (3), 289-314.

Arnold, .K., & Zuberbühler, K.(2008.) Meaningful call combinations in a non-human primate. *Current Biology, 18*, 202–203.

Baldwin, D. A. (1995). Understanding the link between joint attention and language. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 131 – 158). Hillsdale, NJ: Erlbaum.

Bard, K. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development, 63*, 1186-1197.

Bates, E., Benigni, L., Bretherton, I., Camaioni, L., & Volterra, V. (1979). *The emergence of symbols: Cognition and communication in infancy*. New York: Academic Press.

Bates, E., Camaioni, L., & Volterra, V. (1975). The acquisition of performatives prior to speech. *Merrill-Palmer Quarterly, 21*, 205–224.

Bates, E., O'Connell, B., & Shore, C. (1987). Language and communication in infancy. In J. Osofsky (Ed.), *Handbook of infant development* (2nd ed., pp. 149-203). New York: Wiley

Bickerton, D. (1990). *Language and Species*. Chicago: University of Chicago Press.

Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making Inferences About the Location of Hidden Food: Social Dog, Causal Ape. *Journal of Comparative Psychology, 120,* 38-47.

Bruner, J.(1981). Intention in the structure of action and interaction. In L. Lipsitt (Ed.), *Advances in Infancy Research* (Vol. 1, pp. 41-56). New Jersey: Ablex, Norwood.

Bruner, J. S. (1982). The organization of action and the nature of the adult-infant transaction. In E. Z. Tronick (Ed.), *Social interchange in infancy* (pp. 23-35). Baltimore: University Park Press.

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated apes imitate rationally. *Developmental Science, 10,* 31-38.

Butterworth, G. (2003). Pointing is the royal road to language for babies. In S. Kita (Ed.), *Pointing: Where language, culture, and cognition meet* (pp. 9-33). Mahwah, NJ: Lawrence Erlbaum Associates Publishers.

Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). Unwilling or unable? Chimpanzees' understanding of intentional action. *Developmental Science, 7,* 488-498.

Call, J., & Tomasello, M. (1994). The production and comprehension of referential pointing by orangutans. *Journal of Comparative Psychology, 108,* 307-317.

Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*) and human children (Homo sapiens). *Journal of Comparative Psychology, 112,* 192-206.

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

Cartmill, E.A., Byrne R.W. (2007). Orangutans modify their gestural signalling according to their audience’s comprehension. *Current Biology*, *17*, 1345–1348.

Cartmill, E., & Maestripieri, D. (*in press*). Socio-Cognitive Specializations in Nonhuman Primates: Evidence from Gestural Communication. In J. Vonk & T. K. Shackelford (Eds.), *The Oxford Handbook of Comparative Evolutionary Psychology.* Oxford: Oxford University Press.

Cheney, D.L., & Seyfarth, R. M. (1985). Vervet monkey alarm calls—manipulation through shared information. *Behaviour, 94,*150–166.

Cheney, D. L., & Seyfarth, R. M. (1990). Attending to behaviour versus attending to knowledge: examining monkeys' attribution of mental states. *Animal Behaviour*, 40, 742-753.

Cheney, D. L., & Seyfarth, R. M. (2005). Constraints and preadaptations in the earliest stages of language evolution. *Linguistic Review, 22,* 135-159.

Chomsky, N. (1957). *Syntactic Structures.* The Hague: Mouton.

Chomsky, N. (1965). *Aspects of the Theory of Syntax*. Cambridge, MA: MIT Press.

Chomsky, N. (1972). *Language and Mind*. New York: Harcourt, Brace and World.

Colonnesi, C., Stams, G. J. J. M., Koster, I., & Noom, M. J. (2010). The relation between pointing and language development: A meta-analysis. *Developmental Review, 30*(4), 352-366.

Corballis, M. C. (2002). *From hand to mouth: The origins of language.* Princeton: Princeton University Press.

Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology, 110,* 221–243.

Csibra, G., & Gergely, G. (2006). Social learning and social cognition: The case for pedagogy. In Y. Munakata & M. H. Johnson (Eds.), *Processes of Change in Brain and Cognitive Development. Attention and Performance XXI* (pp. 249-274). Oxford: Oxford University Press.

De Ruiter, J. P., & Levinson, S. C. (2008). A biological infrastructure for communication underlies the cultural evolution of language. *Behavioral and Brain Sciences, 31*, 518.

De Waal, F. (2001). Pointing primates: Sharing knowledge without language. *The Chronicle of Higher Education*, B7–B9.

Emery, N.J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, *24*, 581–604.

Evans, C. S. (1997). Referential signals. In D. H. Owings, M. D. Beecher & N. S. Thompson (Eds.), *Perspectives in ethology* (Vol. 12, pp. 99–133). New York: Plenum Press.

Fitch, W. T. (2005). The evolution of language: A comparative review. *Biology and Philosophy, 20*, 193–200.

Franco, F., & Butterworth, G. (1996). Pointing and social awareness: Declaring and requesting in the second year. *Journal of Child Language 23,* 307–336.

Gardner, R. A., & Gardner, B. T. (1969). Teaching sign language to a chimpanzee. *Science, 165*, 664-672.

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

Genty, E., & Byrne, R.W. (2010). Why do gorillas make sequences of gestures? *Animal Cognition, 13*(2), 287-301.

Gergely, G., Egyed, K., & Kiraly, I. (2007). On pedagogy. *Developmental Science, 10*, 139–146.

Goldin-Meadow, S. (2002). Constructing communication by hand. *Cognitive Development, 17*, 1385-1405.

Gómez, J. C. (2004). *Apes monkeys, children, and the growth of mind.* Cambridge: Harvard University Press.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*, 1634-1636.

Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in co-operative cognitive tasks. *Animal Behaviour, 68*, 571 – 581. *Cognitive Sciences, 9*, 439-444.

Hattori, Y., Kuroshima, H., & Fujita, K. (2010). Tufted capuchin monkeys (*Cebus apella*) show understanding of human attentional states when requesting food held by a human. *Animal Cognition, 13*(1), 87-92.

Herrmann, E., Melis, A., & Tomasello, M. (2006). Apes' use of iconic cues in the object choice task. *Animal Behavior, 9*, 118-130.

Hobaiter, C., & Byrne, R. W. (2011). Serial gesturing by wild chimpanzees: its nature and function for communication. *Animal Cognition, 14(6*), 827-836.

Hockett, C. F. (1960). The Origin of Speech. *Scientific American*, 203 (3), 89-96.

Hopkins, W. D., & Cantero, M. (2003). From hand to mouth in the evolution of language: the influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Developmental Science*,6, 55-61.

Hopkins,W. D., Taglialatela, J. P., & Leavens, D. (2007). Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour, 73*, 281–286.

Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional state of a human (*Homo sapiens*). *Journal of Comparative Psychology, 115*, 337–343.

Hostetter, A. B., Russell, J., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition, 10* (1), 55-62.

Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. *Japanese Psychological Research, 38*, 174–180.

Iverson, J. M., & Goldin-Meadow, S. (2001). The resilience of gesture in talk: gesture in blind speakers and listeners. *Developmental Science, 4,* 416–422.

Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' requesting behavior from humans. *Animal Cognition, 7,* 216-223.

Kaminski, J., Schulz, L., & Tomasello, M. (2011). How dogs know when communication is intended for them. *Developmental Science, 15,* 222-232.

Kaminski, J., Tempelmann, S., Call, J., & Tomasello, M. (2009). Domestic dogs comprehend human communication with iconic signs. *Developmental Science, 12*, 831–837.

Kendon, A. (2004). *Gesture: Visible action as utterance*. Cambridge: Cambridge University Press.

King, B. (1999). *The evolution of language: Assessing the evidence from nonhuman primates*. Santa Fe: School of American Research.

King, B. (2004). *The dynamic dance. Nonvocal communication in African Great Apes*. Cambridge, Massachusetts, London: Harvard University Press.

Kita, S. (Ed.). (2003) *Pointing: Where language, culture and cognition meet*. Mahwah, NJ: Erlbaum.

Knight, C., Studdert-Kennedy, M., & Hurford, J.R. (2000). Language: A Darwinian Adaptation? In C. Knight, M. Studdert-Kennedy & J. R. Hurford (Eds.), *The Evolutionary Emergence of Language:Social Function and the Origins of Linguistic Form (*pp. 1-15). Cambridge: Cambridge University Press.

Krause, M. A., & Fouts, R. S. (1997). Chimpanzee (Pan troglodytes) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology, 111*, 330 – 336.

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology, 34*, 813 – 822.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 110*, 346 – 353.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: epigenesis and ecological validity. *Current Directions in Psychological Science, 14*, 185-189.

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004a). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 118*, 48 – 57.

Leavens, D. A., Hostetter, A. B., Wesley, M. J., & Hopkins, W. D. (2004b). Tactical use of unimodal and bimodal communication by chimpanzees (*Pan troglodytes*). *Animal Behaviour, 67*, 467 – 476.

Leavens, D. A., Russell, J. L. & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development*, *76*, 291-306.

Leavens, D. A., Russell, J.L., & Hopkins, W. D. (2009). Multimodal communication by captive chimpanzees (*Pan troglodytes*). *Animal Cognition*, *13*, 33-40.

Lenneberg, E. H. (1967). *Biological Foundations of Language.* New York: Wiley.

Liebal, K., & Call, J. (2012). The origins of nonhuman primates’ manual gestures. *Philosophical Transactions of the Royal Society B, 367, 118-128.*

Liebal, K., Call, J., & Tomasello, M. (2004a). Use of gesture sequences in chimpanzees.*American Journal of Primatology*, *64(4),* 377–396.

Liebal, K., Pika, S., & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture, 6*, 1–38.

Liebal, K., Waller, B., Slocombe, K., & Burrows, A. (*in press*). *Primate Communication*. Cambridge: Cambridge University Press. To appear in 2013.

Lyn, H., & Savage-Rumbaugh, S. (2000). Observational word learning in two bonobos (*Pan paniscus*): Ostensive and non-ostensive contexts. Language *and Communication, 20,* 255–273.

Macedonia, J. M., & Evans, C. S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology, 93,* 177-197.

McNeill, D. (2002) Gesture and language dialectic. *International Journal of Linguistics Acta Linguistica Hafniensia, 34,* 7–37.

Menzel, C. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee after extended delays. *Journal of Comparative Psychology, 113,* 426-434.

Miklosi, A., Kubinyi, E., Topal, J., Gacsi, M., Viranyi, Z., & Csanyi, V. (2003). A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology, 13(*9), 763–766.

Miklosi, A., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition, 9*(2), 81–93.

Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour, 45,* 735–746.

Nishida, T. (1980). The leaf-clipping display: a newly discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution*, *9,* 117-128.

Ouattara, K., Lemasson, A. & Zuberbühler, K. (2009a). Campbell's monkeys use affixation to alter call meaning. *PLoS One,* 4 e7808.

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009b). Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences, 106*, 22026-22031.

Owren, M. J., Dieter, J. A., Seyfarth, R. M., & Cheney, D. L. (1992). Evidence of limited modification in the vocalizations of cross-fostered rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques (pp. 257-270). In T. Nishida, W. C. M. Grew, P. Marler, M. Pickford & F. B. M. de Waal (Eds.), *Topics in primatology*. Tokyo: University of Tokyo Press.

Patterson, F. G. (1978). The gestures of a gorilla: language acquisition in another pongid. *Brain and Language, 5,* 72-97.

Pettersson, H., Kaminski, J., Herrmann, E., & Tomasello, M. (2011). Understanding of human communicative motives in domestic dogs. *Applied Animal Behaviour Science, 133,* 235– 245.

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): Gestural repertoire, learning, and use. *American Journal of Primatology, 60* (3), 95–111.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (*Pan paniscus*): Repertoire and use. *American Journal of Primatology, 65 (1),* 39–61.

Pika, S., & Liebal, K. (2006). Differences and similarities between the natural gestural communication of the great apes and human children. In A. Cangelosi, A. D. M. Smith & K. Smith (Eds.), *The Evolution of language: Proceedings of the 6th International Conference (Evolang6)* (pp. 267—274). London: World Scientific Publishing.

Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences, 13,* 707-784.

Plooij, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture, and symbol: The emergence of language* (pp. 111-131). London: Academic Press.

Plooij, F.X. (1984). *The behavioral development of free-living chimpanzee babies and infants*. Norwood, NJ: Ablex.

Povinelli, D.J., & Eddy, T.J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development, 61,* 1-152.

Povinelli, D.J., Reaux, J.E., Bierschwale, D.T., Allain, A.D., & Simon, B.B. (1997). Exploitation of pointing as a referential gesture in children, but not adolescent chimpanzees. *Cognitive Development, 12,* 423–461.

Premack, D. (1971). Language in chimpanzee? *Science, 172,* 808–822.

Rizzolatti, G., & Arbib, M. A. (1998) Language within our grasp. *Trends in Neuroscience, 21,* 188-194.

Sapir, E. (1921). *Language. An Introduction to the Study of Speech*. New York: Harcourt Brace.

Sarimski, K. (2002). Analysis of intentional communication in severely handicapped children with Cornelia-de-Lange syndrome. *Journal of Communication Disorders, 35,* 483–500.

Savage-Rumbaugh, S., McDonald, K., Sevcik, R. A., Hopkins, W. D., & Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees *(Pan paniscus). Journal of Experimental Psychology: General, 115,* 211-235.

Savage-Rumbaugh, E., Murphy, J., Sevcik, R.A., Brakke, K.E., Williams, S., & Rumbaugh, D. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development, 58* (3–4, Serial No. 233).

Seyfarth, R. M., & Cheney, D. L. (1997). Some general features of vocal development in nonhuman primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 249-274). Cambridge: Cambridge University Press.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour, 28*, 1070-1094.

Shillito, D., Shumaker, R., Gallup, G., & Beck, B. (1998). Visual-perspective taking by an orang-utan. *American Journal of Primatology, 45* (2), 207.

Shillito, D., Shumaker, R., Gallup, G., & Beck, B. (2005). Understanding visual barriers: Evidence for Level 1 perspective taking in an orang-utan, *Pongo pygmaeus*. *Animal Behaviour,* 69, 679–687.

Slocombe K., Waller B., & Liebal K. (2011). The language void: the need for multimodality. *Animal Behaviour, 81(5), 919-924.*

Tanner, J. E., & Byrne, R. W. (1993). Concealing facial evidence of mood: Perspective-taking in a captive gorilla. *Primates, 34*, 451–457.

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition, 14*(3), 433-439.

Tempelmann, S., Kaminski, J., & Liebal, K. (*in press*). When apes point the finger – Three great ape species fail to use a conspecific’s imperative pointing gesture. *Interaction Studies.*

Tempelmann, S., & Liebal, K. (2009). The use of gesture sequences in orang-utans. *Folia Primatologica, 80*, 144-145.

Tempelmann, S., & Liebal, K. (2012). The emergence of gesture sequences in orangutans. A case for strategy? *Gesture studies, 6,* 72-93.

Terrace, H., Petitto, L., Sanders, R., & Bever, T. (1979). Can an ape create a sentence? *Science, 206*, 891–902.

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signaling of chimpanzees? In S. Parker & K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 274-311). Cambridge, UK: Cambridge University Press.

Tomasello, M. (2006). Why Don’t Apes Point? In N. J. Enfield & S. C. Levinson (Eds.), *Roots of Human Sociality: Culture, Cognition and Interaction* (pp. 506–524). Oxford & New York: Berg.

Tomasello, M. (2008). *Origins of human communication*. Boston: MIT Press.

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

Tomasello, M., Call, J., & Gluckman, A. (1997a). The comprehension of novel communicative signs by apes and human children. *Child Development, 68*, 1067-1081.

Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and the use of gestural signals by young chimpanzees: A transgenerational study. *Primates, 35*, 137–154.

Tomasello, M., Call, J., Warren, J., Frost, T., Carpenter, M., & Nagell, K. (1997b). The ontogeny of chimpanzee gestural signals: A comparison across groups and generations. *Evolution of Communication, 1*, 223–253.

Tomasello, M., & Carpenter, M. (2005). The emergence of social cognition in three young chimpanzees. *Monographs of the Society for Research in Child Development, 70,* (1, Serial No. 279).

Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science, 10,* 121–125.

Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A new look at infant pointing. *Child Development, 78,* 705–722.

Tomasello, M., George, B. L., Kruger, A. C., Farrar, M. J., & Evans, A. (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution, 14,* 175–186.

Tomasello, M., Gust, D., & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates, 30,* 35–50.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences, 28,* 675-735.

Vea, J., & Sabater-Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatologica, 69,* 289 – 290.

Warneken, F., Hare, B., Melis, A., Hanus, D., & Tomasello, M. (2007). Roots of human altruism in chimpanzees. *PLOS Biology, 5 (7),* e184.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science, 31,* 1301-1303.

Watzlawick, P., Beavin, J. H., & Jackson, D. D. (1967). *Pragmatics of human communication. A study of interactional patterns, pathologies, and paradoxes*. New York: Norton.

Zuberbühler, K. (2000a). Referential labeling in wild Diana monkeys. *Animal Behaviour, 59,* 917-927.

Zuberbühler, K. (2000b). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London B, 267,* 713-718.

Zuberbühler, K. (2005). The phylogenetic roots of language: evidence from primate communication and cognition. *Current Directions in Psychological Science, 14*, 126-130.

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Mein Lebenslauf wird aus Gründen des Datenschutzes in der elektronischen Fassung meiner Arbeit nicht veröffentlicht.

Eigenständigkeitserklärung

Studie 1 (Tempelmann, Kaminski, & Liebal, 2011): Entwicklung und Durchführung der experimentellen Studie durch Sebastian Tempelmann; Entwicklung des Kodierschemas und Analyse der kodierten Daten durch S. Tempelmann; Anwendung des Kodierschemas in Absprache mit S. Tempelmann durch Martina Neumann. Schreiben der Publikation durch S. Tempelmann. Dr. Juliane Kaminski und Prof. Dr. Katja Liebal hatten im gesamten Prozess eine beratende Funktion.

Studie 2 (Tempelmann & Liebal, 2012): Diese Studie beruht auf Rohdaten, welche durch Prof. Dr. Katja Liebal erhoben wurden. Aufbereitung, Bereinigung und Analyse der Rohdaten durch S. Tempelmann . Schreiben der Publikation durch S. Tempelmann. Prof. Dr. Katja Liebal hatte im gesamten Prozess eine beratende Funktion.

Studie 3 (Tempelmann, Kaminski, & Liebal, *in press*): Entwicklung und Durchführung der experimentellen Studie durch Sebastian Tempelmann. Auswertung und Schreiben der Publikation durch S. Tempelmann. Dr. Juliane Kaminski und Prof. Dr. Katja Liebal hatten im gesamten Prozess eine beratende Funktion.

Hiermit versichere ich, die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Hilfsmittel verwendet zu haben. Die Dissertation wurde in keinem früheren Promotionsverfahren angenommen oder abgelehnt.

Ort, Datum *Unterschrift*

Appendix

- **Study 1: Copy of the published article (not included in online document)**

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition, 14*(3), 433-439. doi: 10.1007/s10071-011-0378-5

- **Study 2: Copy of the published article (not included in online document)**

Tempelmann, S., & Liebal, K. (2012*).* The emergence of gesture sequences in orangutans. A case for strategy? *Gesture studies, 6,* 72-93.

- **Study 3: Copy of the original manuscript** (tables and figures included)

Tempelmann, S., Kaminski, J., & Liebal, K. (*in press*)**.** When apes point the finger – Three great ape species fail to use a conspecific's imperative pointing gesture. *Interaction Studies.*

Study 1

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition*, *14*(3), 433-439. doi: 10.1007/s10071-011-0378-5

The original article is online available at

http://dx.doi.org/10.1007/s10071-011-0378-5

Study 2

Tempelmann, S., & Liebal, K. (2012). The emergence of gesture sequences in orangutans. A case for strategy? *Gesture studies, 6*, 72-93.

The original article is online available at

http://benjamins.com/#catalog/books/gs.6.05tem/details

Original Manuscript of Study 3:

Tempelmann, S., Kaminski, J., & Liebal, K. (2012). When apes point the finger – Three great ape species fail to use a conspecific's imperative pointing gesture. To appear in *Interaction Studies, 13(2)*.

Running head: Pointing the finger

When apes point the finger –
Three great ape species fail to use a conspecific's imperative pointing gesture

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Abstract

In contrast to apes' seemingly sophisticated skill at producing pointing gestures referentially, the comprehension of other individual's pointing gestures as a source of indexical information seems to be less pronounced.

One reason for apes' difficulty at comprehending pointing gestures might be that in former studies they were mainly confronted with human declarative pointing gestures, whereas apes have largely been shown to point imperatively and towards humans. In the present study bonobos, chimpanzees and orangutans were confronted with a conspecific's imperative pointing gesture in a competitive context, therefore mirroring former studies that have investigated apes' skills at producing these gestures.

However, apes in the present study did not use their conspecific's pointing gestures. Apes have been shown to use indexical information when provided non-communicatively and to interpret other individuals' actions in terms of motives. Thus, it is discussed whether apes treat a pointing gesture as intentional act of indexical reference.

Keywords: pointing, referential communication, great apes, triadic communication, indexical reference, evolution of communication

Introduction

In the last two decades there has been much interest in apes’ engagement in pointing behaviour (e.g. Call & Tomasello, 1994; Krause & Fouts, 1997; Menzel, 1999; de Waal, 2001). Indeed, a growing body of evidence suggests that chimpanzees do point referentially and intentionally, which in many ways seems to resemble human infants’ pointing behaviour (e.g. Leavens & Hopkins, 1998; Leavens, Hopkins, & Thomas, 2004; Leavens, Hopkins, & Bard, 1996, 2005; Leavens, Russel, & Hopkins, 2005). The importance of trying to ascertain the detailed cognitive processes underlying apes’ pointing derives from the fact that pointing, and therefore the ability to communicate about entities beyond the ‘self’ by referencing them, is thought to mediate the ontogenetic development of the capacity to communicate iconic and symbolic reference (Baldwin, 1995; Bates, Benigni, Bretherton, Camaioni, & Volterra, 1979; Butterworth, 2003; Csibra & Gergely, 2006; Tomasello, 2008). This transition from dyadic to triadic communication enables a new quality in terms of learning and teaching, and effects the development of the human linguistic system. Therefore, apes’ pointing behaviour might constitute some kind of evolutionary missing link between apes’ natural communication with conspecifics and humans’ communication via arbitrary symbols (Leavens et al., 2004).

However, in sharp contrast to apes’ seemingly sophisticated skills at producing pointing gestures referentially and following them visually (e.g., Itakura, 1996; Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997), they seem to comprehend a pointing gesture only in exceptional cases (e.g., Call & Tomasello, 1994; Lyn, Russel, & Hopkins, 2010; Mulcahy & Call, 2009) as a source for indexical information, e.g. to locate hidden food (e.g., Hare, Brown, Williamson, & Tomasello, 2002; Itakura, Agnetta, Hare, & Tomasello, 1999; Tomasello, Call, & Gluckman, 1997).

This is puzzling as apes have shown in several independent studies that they assign intentional motives to the actions of other individuals (e.g., Call & Tomasello, 1998; Call, Hare, Carpenter, & Tomasello, 2004). Therefore, apes' intentional and flexible use of pointing gestures and their obvious consideration of other individuals as intentional beings should lead one to predict the ability to use those gestures for their own benefit when perceiving them. As a consequence, when apes do not comprehend the indexical information of a pointing gesture, this could suggest that when they produce this gesture themselves they do not intentionally index a specific location. However, the discrepancy between production and comprehension skills could be due to differences in the methodological approach of former studies investigating apes' comprehension skills. Indeed, studies which have examined the comprehension of pointing gestures did not accurately mirror those studies which investigated their production skills.

There are different types of pointing gestures known in the literature. The two basic types are imperative and declaratives pointing gestures. Pointing behaviour is called imperative when it used to request actions from other individuals, whereas declarative points are used to share attitudes on some outside entity or to cooperatively inform a communicative partner. However, the majority of previous studies, which preferentially investigated chimpanzees' ability to understand other individuals' pointing gestures, used declarative pointing gestures, whereas apes have only in exceptional cases (e.g., Greenfield & Savage-Rumbaugh, 1991) been reported to produce those gestures declaratively. On the other hand, those studies investigating apes' pointing behaviour in terms of intention and reference (e.g., Leavens et al., 2005) focus on apes' imperative pointing behaviour (Tomasello, 2006). Declarative pointing needs a highly cooperative context, in which the producer provides information to the *receiver*. Apes are shown to be more skilful at using others' behaviour for their own benefit in competitive rather than in cooperative social tasks (Hare & Tomasello, 2004), which might be explained by their more competitive group structure or a lack of cooperative motives in communication. Therefore, it is likely that apes in highly cooperative contexts do not understand the intention of the social partner, as they do not subscribe those cooperative motives to a social partner's behaviour and therefore do not care at all about the counterpart's pointing gesture (Tomasello, 2008). For example, although they do not use a cooperative pointing gesture, they are able to use a human's unsuccessful reaching behaviour in a competitive task, which superficially resembles a pointing gesture (Hare & Tomasello, 2004).

Another aspect is that most studies have used a human experimenter to indicate the food location to the ape. One exception was a study by Itakura et al. (1999) who investigated the comprehension of conspecific pointing gestures in chimpanzees. The chimpanzees in that study performed no better with a conspecific than with a human, which may suggest that the identity of the other individual does not affect apes' behaviour. However, in that study a chimpanzee was trained to produce a declarative gesture in order to indicate the location of food to a conspecific (Itakura et al., 1999). Here we modified this study in order to investigate chimpanzees', bonobos' and orangutans' comprehension of *imperative* conspecific pointing gestures.

The apes in our study did not communicate directly with each other, but with the human experimenter and therefore competed for the support of the human. The *demonstrator* ape observed the food being hidden, while the other ape (the *receiver*) was naive to the location, but aware of the fact that the other ape had witnessed the baiting. This has three main advantages over the standard design of comprehension studies. First, apes are confronted with the same contextual background in which they themselves point (imperative pointing directed to a human). Second, due to the third party context there is no need to establish a joint attentional and intentional communicative framework. Third and related, as in all former comprehension studies, the situation established in the Itakura et al. (1999) study is highly cooperative, as the *demonstrator* displays a behaviour that seemingly has no personal benefit. The present study used a competitive setup by establishing a situation in which superficially both individuals had to compete for the human's support.

Furthermore, the "pointing gesture" of the *demonstrator* in our study is not artificial and not trained to resemble the human way of pointing but is the ape's regular pointing behaviour, which is used in countless experiments. Also, we reduced the distance between *demonstrator* and *receiver*. This may increase the motivation for competition between individuals (as has been shown in other contexts, see Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006) and it may also make it easier for the *receiver* to perceive the gestures of the *demonstrator*.

However, a positive performance of the subjects in the present study would strongly support the assumption that apes do treat pointing gestures in general as intentional acts of referential communication.

Method

As mentioned in the introduction the goal of the following study is to test whether apes do use a pointing gesture of a conspecific to infer the location of hidden food and more specifically, we are interested if apes really understand the referential, deictic character of the gesture. Nevertheless the successful use of such a gesture may also be the result of local enhancement, which is caused by the low distance between the demonstrator’s fingers and the target. To control for local enhancement effects in addition to a communicative pointing condition apes were tested in a non-communicative pointing condition. For details see below.

Subjects

Four individuals from each species (chimpanzees, orang-utans and bonobos) were tested. For each species, an additional individual was selected to function as *demonstrator* (see table 1). The *demonstrator* was the same for all four subjects of each species. The *demonstrator* was also of a high or middle rank in the respective group hierarchy.

Table 1: Subject Info; Demonstrators in bold

	Subject	**Gender**	**Age**	**Rearing History**	**1st Condition**
Chimpanzee	Gertruida	female	15 years	parental rearing	Communicative
	Annett	female	9 years	hand reared	Communicative
	Alexander	male	7 years	hand reared	Non-communicative
	Alexandra	female	9 years	hand reared	Non-communicative
	Jahaga	**female**	**15 years**	**parental rearing**	**-**
Bonobo	Ulindi	female	15 years	parental rearing	Communicative
	Limbuko	male	13 years	hand reared	Communicative
	Kuno	male	12 years	hand reared	Non-communicative
	Joey	male	26 years	hand reared	Non-communicative
	Yasa	**female**	**11 years**	**parental rearing**	**-**
Orang Utan	Dunja	female	35 years	parental rearing	Communicative
	Padana	female	11 years	parental rearing	Communicative
	Bimbo	male	28 years	hand reared	Non-communicative
	Pini	female	20 years	parental rearing	Non-communicative
	Dokana	**female**	**19 years**	**parental rearing**	**-**

Apparatus

A platform (79.5 cm x 88 cm) was placed between two Plexiglas panels of two separated cages in a testing booth (80cm x 97cm), which was located just outside the enclosure. A sliding board (94cm x 16,5cm) with three angled cups (12 cm x 7.5 cm) on it was attached to the platform (see fig. 1). The apparatus allowed the three cups to move back and forth between the two opposite panels without removing them from the table. At the bottom of each Plexiglas panel were three holes (each 3.6 cm in diameter) arranged in a straight line. The holes were 29 cm apart, as measured from the centre of one hole to the centre of the next.

Each cup had two separate compartments. One was solid and closed to all sides; the other was open to one side such that the *demonstrator* could see a piece of food hidden within. The cups were positioned in such a way that if both compartments were baited, one subject (the *receiver*) could not see the food whereas the other subject (the *demonstrator*) could see the food in the open compartment. A clamping system for a removable opaque barrier (50 cm x 79 cm) was fixed on the sliding table (see fig. 1). This allowed baiting the cups while being blocked from the *receiver*'s view. An occluder made of rubber was fixed to one side of the barrier and could be pulled over the cups. This allowed the cups to be baited beyond the view of the *receiver* and *demonstrator* (see fig. 1c).

The food rewards were grapes, or food-pellets depending on the individuals' preference and diet.

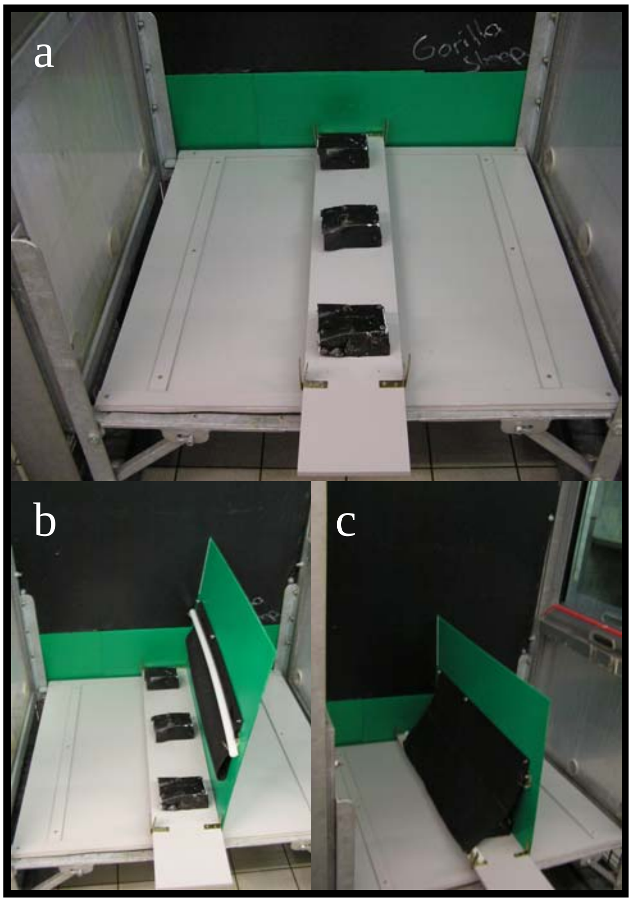

Figure 1:
Apparatus and experimental setting; (a) barrier removed, sliding table with cups in middle position, (b) barrier as used in communicative pointing condition, (c) barrier as used in non-communicative pointing condition

Procedure

Pre-training

At the beginning of each testing day, each subject received a pre-training session to ensure they understood that they were required to indicate a specific cup to receive the food. The procedure was as follows: the sliding table always remained in the starting position in the middle of the platform. In full view of the subject, the Experimenter (E) baited the closed compartment of one of the cups. Then E waited until the subject indicated the correct cup by inserting one ore more fingers through the corresponding hole in the Plexiglas panel. If the subject indicated the correct cup, s/he received the food. If the subject indicated an incorrect cup, E first showed the subject the empty cup and then the baited one, but the subject received no food. If the subject needed more than two attempts to indicate the correct cup, the trial was repeated. If the subject's fingers were inserted into more than one hole at a time, E waited until the subject's fingers were inserted into just one hole. The pre-training consisted of six trials (in the event of failure up to three repetitions were allowed). The order in which the cups were baited was counterbalanced and semi-randomized such that each cup was baited two times. A session was considered successful if the subject had pointed correctly to each of the containers twice.

Warm up

Subsequent to the pre-training, each subject received a warm up session. The function of the warm up was to establish a competitive situation between the *demonstrator* and the *receiver*. The procedure was similar to that in the pre-training phase except that now the *demonstrator* was positioned opposite the subject such that both individuals were facing each other. E then baited one of the three cups in full view of both individuals and then waited for both individuals to indicate the location by inserting one or more fingers through the corresponding hole in the Plexiglas panel. If only one individual indicated the correct cup, E shifted the table in front of this individual and offered the content of the cup to it. If both individuals indicated the correct cup, E chose that ape to whom he had offered the reward based on a fixed testing scheme. The *receiver* ought to get the reward at least three times. The warm up consisted of six trials; each cup was baited twice. After the warm up phase, subjects entered the experimental phase in which they received one of two possible conditions:

Experimental Design

The experiment consisted of two different conditions (communicative- and non-communicative pointing condition). Half of the subjects started with the communicative pointing condition, while the other half started with the non-communicative pointing condition (see figure 1). Each individual received 18 trials in each condition (presented over at least two different days, depending on the motivation of the participants) creating a total of 36 experimental trials altogether. The pre-training and the warm up were the same for both conditions. In addition to the experimental trials, subjects received 12 filler trials per session, creating a total of 24 filler trials altogether. These served as a motivation for the *demonstrator* and to enhance the competitive context. The food location was counterbalanced and semi-randomized across trials, with the stipulation that food could not be in the same location over more than two consecutive trials. Also the order of filler and experimental trials was semi-randomized, with the stipulation that there were no more than two consecutive filler trials.

Communicative pointing condition:

The table with the three empty cups was positioned in the middle of the sliding platform. E obscured the *receiver*’s view by placing an opaque barrier in front of her, so that only the *demonstrator* could see the baiting. Then E baited (both compartments of) one of the cups with food such that the *demonstrator* could see a piece of food (the one in the visible compartment) throughout the entire trial, ensuring that she would point reliably to the corresponding cup. E waited until the *demonstrator* indicated the correct cup before he removed the barrier for the subject to see the *demonstrator* and the cups. E waited approximately 5-10 seconds for the *demonstrator* to indicate the correct cup. If the *demonstrator* switched her choice during this period, and did not directly move her finger(s) back to the correct location, the trial was repeated. The same was also true if the ape kept indicating the correct cup simultaneously with another cup or stopped indicating. After successful demonstration E shifted the table to its position in front of the subject’s cage and let her choose. A choice was considered as made if one or more fingers were inserted through one of the holes in the panel after the sliding table came to rest. If fingers were inserted through more than one hole, E waited until one hand (or finger) had been taken back. If this was not the case for up to 10 seconds the trial was repeated. After the subject had made a choice, E lifted the cup that had been indicated. If the choice was correct, E offered the food to the subject; if the choice was incorrect, E tilted the correct cup in such a way that the subject could see the food in the closed compartment. Then E slid the table to its starting position, replaced the barrier on the sliding table and then offered the content of the open compartment to the *demonstrator*.

Filler trials were conducted between the experimental trials. They were used to motivate the *demonstrator* and to boost the competitive context. The procedure was similar to that of the experimental trials except that the table was moved to the *demonstrator* not the *receiver* and she was allowed to choose subsequently.

Non-communicative pointing condition:

The general procedure was the same as in the communicative pointing condition apart from the following aspects:

After setting up the barrier, E covered the cups and then just baited the closed compartment of one of the cups with food. Therefore neither individual witnessed the baiting process and the *demonstrator* stayed naïve to the food location the entire time. Then the *demonstrator* witnessed E smear peanut butter or a banana-honey cream around one of the holes in the Plexiglas panel (the one in front of the baited cup). To obtain the food the *demonstrator* had to produce an action resembling the pointing gesture (the insertion of one or more fingers through the hole), but with no intent toward any food other than the peanut butter. From observing the demonstrator’s behaviour this could clearly be differentiated from the communicative condition as in contrast to the communicative pointing condition, there was unambiguously peanut butter around the hole and the demonstrators whole behavior targeted on getting this peanut butter. The demonstrator inserted her finger through the hole, brushed aside the peanut butter, retracted the respective finger towards her mouth and licked away the peanut butter.

Results

Due to the relative small number of individuals we used non-parametric statistics throughout. P-values are exact values and unless stated differently they are two-tailed.

The order in which the individuals were assigned to the conditions (non-communicative pointing condition first vs. communicative pointing condition first) did not affect their performance. This is true for the non-communicative pointing condition (correct choices when communicative pointing condition first: MEAN 32.41% (SD ± 6.49) and when non-communicative pointing condition first: MEAN 41.67 % (SD ± 16.39), Mann-Whitney U-test: z = -1.63, *p* = .103) and for the communicative pointing condition (correct choices when communicative pointing condition first: MEAN 38.89% (SD ± 16.48) and when non-communicative pointing condition first: MEAN 37.04 % (SD ± 6.73), Mann-Whitney U-test: z = -.736, *p* = .462). Therefore we pooled the results of the respective conditions for further analyses.

Furthermore, the correct performance in the respective conditions did not differ between species, neither for the communicative pointing condition (correct choices: bonobos MEAN 37.5% (SD ± 8.3), chimpanzees MEAN 41.67% (SD ± 9.62), orangutans MEAN 34.72% (SD ± 18.36); Kruskal-Wallis test: χ^2 = .612, *p* = .733), nor for non-communicative pointing condition (correct choices: bonobos MEAN 44.44% (SD ± 9.08), chimpanzees MEAN 26.39% (SD ± 11.45), orangutans MEAN 40.28% (SD ± 12.32); Kruskal-Wallis test: χ^2 = 4.663, *p* = .103). In addition, there were no differences in performance based on the participants' rearing history (for communicative pointing condition: Mann-Whitney test, z = 0, *p* = 1.0; for non-communicative pointing condition: Mann-Whitney test, z = -.83, *p* = 1.0), based on gender (for communicative pointing condition: Mann-Whitney test, z = -.332, $p = .755$; for non-communicative pointing condition: Mann-Whitney test, z = -.579, $p = .639$) or based on individual performance (for communicative pointing condition: Kruskal-Wallis test: $\chi^2 = 11.0$, $p = 1.0$; for non-communicative pointing condition: Kruskal-Wallis test: $\chi^2 = 11.0$, $p = 1.0$). As a consequence, we grouped the data of the different species for the respective conditions for further analyses.

The performance of the apes in both conditions did not significantly differ from chance (for the communicative pointing condition: MEAN 36.96% (SD ± 12.04), Wilcoxon test, z = -1.591, $p = .115$; for the non-communicative pointing condition: MEAN 37.04% (SD ± 12.83), Wilcoxon test, z = -1.384, $p = .203$). Furthermore, if tested against each other, the apes performance did not differ significantly between conditions (Wilcoxon test: z = -0.236, $p = .836$) (see fig. 2). Overall, the apes did not prefer to choose one position over another in a significant manner (for the communicative pointing condition: Friedman test: $\chi^2 = .044$, df = 2, $p = .995$, N = 12; for the non-communicative pointing condition: Friedman test: $\chi^2 = .174$, df = 2, $p = .931$, N = 12). Therefore, the apes had no bias toward a specific container.

When considering only the first trial of the respective conditions, the apes chose at random in both conditions (communicative pointing condition: in 6 out of 12 times subjects chose the baited cup, binomial test, $p =. 177$, one-tailed; non-communicative pointing condition: in 3 out of 12 times subjects chose the baited cup, binomial test, $p =. 393$, one-tailed). Further, there is no significant difference regarding the first trial performance between conditions (Fisher’s exact test, $p = .400$).

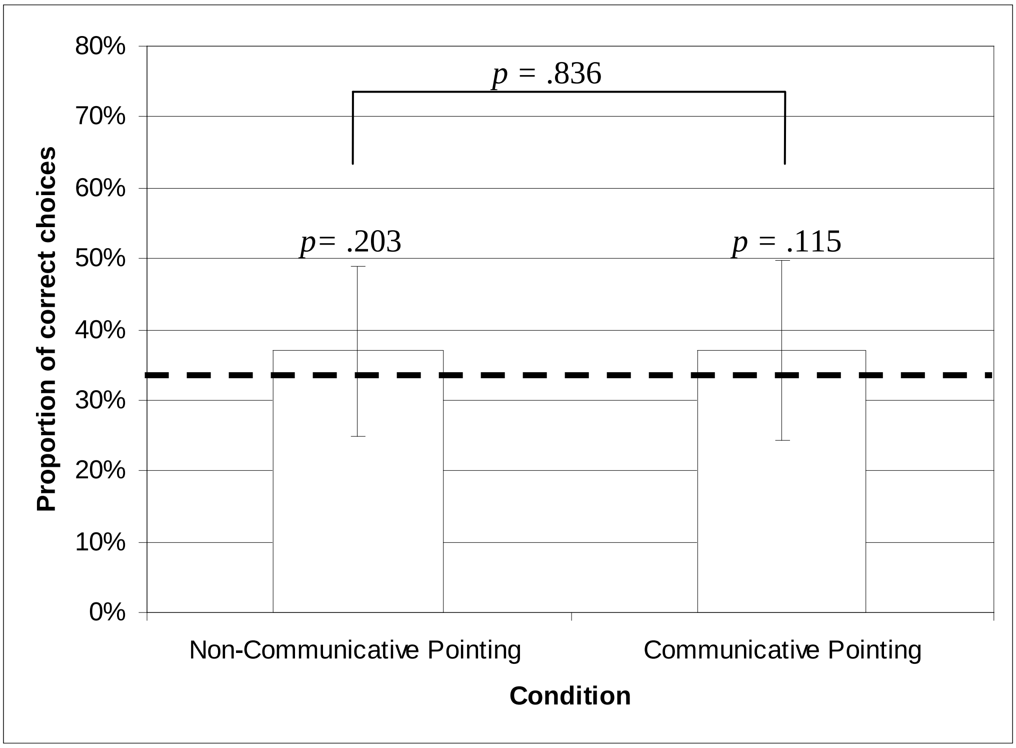

Figure 2: Performance of apes in both conditions (SD); chance level (33.33%) in dashed line

The position of the target in the first trial performance had no influence on the apes' choice (for communicative pointing condition: Fisher's exact test, *p* = .351; for non-communicative pointing condition: Fisher's exact test, *p* = 1.00). When comparing the first and second half of the trials of each condition against chance, no significant deviation from chance is found (communicative pointing condition, trial 1-9: correct choices MEAN 40.74% (SD ± 15.95), Wilcoxon test, z = -1.697, *p* = .117; trial 10-18: correct choices MEAN 35.18% (SD ± 14.86), Wilcoxon test, z = -0.784, *p* = .532; non-communicative pointing condition, trial 1-9: correct choices MEAN 40.74% (SD ± 15.23), Wilcoxon test, z = -1.630, *p* = .137; trial 10-18: correct choices MEAN 33.33% (SD ± 15.71), Wilcoxon test, z = -0.144, *p* = .922). No learning effect was found when comparing the first half of trials with the second half (communicative pointing condition, Wilcoxon test: z = -0.930, p = .402; non-communicative pointing condition, Wilcoxon test: z = -1.672, p = .098).

Discussion

The apes tested in the current study were not able to use the conspecific's imperative pointing gesture successfully to infer the location of the food. Although the apes permanently witnessed that the conspecific's gesture indicated the correct location, they did not improve their performance. Furthermore, we could not detect any species differences.

In contrast to previous studies investigating apes' comprehension of pointing gestures, apes' production of pointing had mainly been investigated in imperative contexts. In the present study the pointing gesture observed by the subject was imperative and occurred in a context familiar to the subject. Due to the third party context no joint attentional and intentional communicative framework had to be established, and no understanding of cooperative motives was necessary. Therefore, the context-based argument fails to explain the general discrepancy between pointing production and comprehension skills. The apes in the present study were not able to infer information from an observed pointing engagement, which accurately matched their own in terms of appearance, underlying motives and intentions.

Interestingly, as mentioned above, under certain circumstances some apes seem to be good at using (declarative) pointing gestures. One such exception are apes raised with extensive human contact, so-called enculturated individuals (Lyn et al., 2010; Okamotho-Barth, Tanaka, Tomonaga, & Matsuzawa, 2008; Itakura et al., 1999; Call & Tomasello, 1994). One reason for being so sophisticated at using human pointing could be that apes with such a background learned that such gestures are relevant when produced by humans, as they have experienced humans being cooperative, especially in the food context (see Tomasello & Call, 2004 and Kaminski, 2011 for a discussion of this topic). However, a recent study by Mulcahy and Call (2009) suggests that apes raised in a more natural group structure are also able to comprehend a declarative pointing gesture if it is presented in a more distal setting. In their study the authors compared a distal setting with a more proximal setting, which had been repeatedly used in other studies. In the distal setting the two referents (the cups containing the food) were presented in two different rooms and the experimenter stood between them and pointed to one or the other. The apes were successful in this version of the task but failed in the proximal version in which the two referents were presented in close proximity to each other on a table between the experimenter and the subject. The authors argue that it may be the additional cost of moving between the rooms, which motivates subjects to attend to the gesture more closely. Losing the food would be more costly in the distal setting than in the proximal setting. However, an alternative explanation of these results is that the pointing gesture is indeed not a triadic gesture anymore and instead a spatial directive conveying the information in which direction the ape should move (a situation that apes in a zoo-like setting are very familiar with). While the apes receive the gesture, the referents are never in view simultaneously, which is why the apes do not have to attend to the referential nature of the gesture at all. Once the subject has moved in the indicated direction, the respective cup to be found in that room is the only possible referent (Kaminski, 2011). Furthermore, this kind of use of the pointing gesture is encouraged daily by the human caretakers in order to lead the apes from one cage to the other. As Itakura (1996) showed in a study with non-enculturated subjects, apes do indeed follow a human pointing gesture visually; they are just not able to use it for their own benefit. Under these circumstances a training effect easily arises which allow apes to use this device somehow (this is true in general for declarative pointing gestures in the context of food).

However, as mentioned above, to date apes have, by and large, been found to point imperatively and in food requesting contexts. The present results suggest that they do not comprehend an imperative gesture, uttered in a parallel setup (in the requesting context). Therefore, production and comprehension skills regarding the pointing gesture are found isolated; up to date apes were found to produce pointing gestures imperatively, but to comprehend them only (and in exceptional cases, see above) when used declaratively. This might indicate that they do not use this gesture bi-directionally. However, apes' failure to use pointing in this context is not due to a general inability to understand other individuals as intentional beings. Apes have shown in several independent studies that they assign intentional motives to the actions of other individuals. For example, they discriminate accidental from intentional actions (Call & Tomasello, 1998; Call et al., 2004) and rationally integrate their knowledge about another individual's intentional state in their own behaviour (Tomasello & Carpenter, 2005; Buttelmann, Carpenter, Call, & Tomasello, 2007; Warneken & Tomasello, 2006; Warneken, Hare, Melis, Hanus, & Tomasello, 2007).

Nevertheless, in the present study subjects did not extract indexical information from their counterparts pointing behaviour[1]. This might be due to a general inability to do so or to their excitement which might be caused by the competitive context.

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[1] One might suggest that the apes in the present study were inattentive and did not notice their counterparts' behaviour. That is unlikely since only those trials were counted in which the subjects were attentive towards their conspecific counterparts' behaviour. Subjects' first trial-performance in the non-communicative pointing condition, confirms this, since apes showed to act dependent on the *demonstrators* behaviour: they avoided the target container (presumably the assumed the respective container to be emptied by the other ape).

However, those reasons are improbable, as apes have not only shown to extract indexical information from other individuals' behaviour, but also to do so in competitive contexts (Hare & Tomasello, 2004; Hermann & Tomasello, 2006).

Many studies other than this one have tried to investigate whether apes comprehend pointing gesture. Nevertheless, only subjects exposed to intense human contact (Lyn et al., 2010) or those with significant experience of the concrete testing situation (Mulcahy & Call, 2009) were able to use those gestures. However, assuming apes' ability to interpret other individuals' actions in terms of motives/intentions, the fact that apes are in the position to extract indexical information from other individuals' behaviour and their ability to follow a pointing gesture visually, one might assume that apes do not view a pointing gesture as an intentional act indexing a specific location. Referential pointing in terms of mental agency is a conventional gesture, thus bidirectional. Apes failure to comprehend the gesture in our study might suggest that when they produce it, they do not necessarily discretely reference a specific location and do in consequence not extract indexical information when they perceive it. In terms of production they might just have learned to insert their fingers through the caging at the location, which is enhanced through a previous action on it or the pure existence of food; it may thus be conducted with no intention to inform the human about a location. This would imply that the apes learned how to use the gesture appropriately to manipulate the humans' behaviour in the desired fashion, with no deeper knowledge of how their gesture works on their communicative partner's mind. We might, therefore, conclude that the apes in the present study did not subscribe to the motive/intention of their counterpart's pointing behaviour to index a specific location, but instead interpreted it as a dyadic attention-getter, saying: " give food to me" and not "give me the food from this cup”. Important in this context, a recent study by Tempelmann, Kaminski and Liebal (2011) shows that apes, when begging for food from a human, act according to the human’s attentional state; but only when the human and the food are linked in a way that dyadic communication towards the human is sufficient to get the food. These results suggest that apes’ have a problem referring to third entities in general.

In contrast to apes, human infants’ production and comprehension skills occur around the same age (see Carpenter, Akhtar, & Tomasello, 1998, for further evidence), with only some exceptions which could be explained by different perception efforts (Franco & Butterworth, 1996). This indicates a general understanding of the pointing gesture as an act of indexical reference. Some authors assume this difference between apes’ and humans’ communication is due to the fact that apes, as opposed to humans, do not have the motivation to share information and attitudes with others (e.g. Tomasello, 2008). Therefore, irrespective of other fundamental cognitive skills that are potentially involved, the motivational framework may function as some kind of catalyser for skills necessary to communicate referentially.

Apes only point in captivity (but see Vea and Sabater-Pi, 1998) and for the majority it is directed imperatively towards a human. The cumulating reports of pointing production in apes living in captivity and the isolated cases of pointing comprehension reported from enculturated apes provides at least an ‘artificial’ motivation for communicative interaction with outside entities. It is reasonable, that unlike living in a natural environment, captivity and the related dependency on human food-givers somehow creates a conducive environment for the development of a means to manipulate third entities through influencing other individuals (communicatively).

This development seems to constitute a motivational step in the direction of triadic communication, and might shed light on the evolution of human communication. From the present study one cannot make statements about apes’ general skills regarding triadic, referential communication, particularly since sample sizes were rather small. However these findings suggest that living in captivity and the related close contact with humans does not cause an understanding of pointing as an intentional act of indexical reference per se.

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References

Baldwin, D. A. (1995). Understanding the link between joint attention and language. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 131 – 158). Hillsdale, NJ: Erlbaum.

Bates, E., Benigni, L., Bretherton, I., Camaioni, L., & Volterra, V. (1979). *The emergence of symbols: Cognition and communication in infancy*. New York: Academic Press.

Bräuer, J., Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2006). Making Inferences About the Location of Hidden Food: Social Dog, Causal Ape. *Journal of Comparative Psychology, 120*, 38-47.

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated apes imitate rationally. *Developmental Science, 10*, 31-38.

Butterworth, G. (2003). Pointing is the royal road to language for babies. In S. Kita (ed.). *Pointing: Where language, culture, and cognition meet* (pp. 9-33). Mahwah, NJ: Lawrence Erlbaum Associates Publishers.

Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). Unwilling or unable? Chimpanzees' understanding of intentional action. *Developmental Science, 7,* 488-498.

Call, J., & Tomasello, M. (1994). The production and comprehension of referential pointing by orangutans. *Journal of Comparative Psychology, 108*, 307-317.

Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*) and human children (Homo sapiens). *Journal of Comparative Psychology, 112,* 192-206.

Carpenter, M., Akhtar, N., & Tomasello, M. (1998). Fourteen- through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behavior & Development, 21*, 315-330.

Csibra, G., & Gergely, G. (2006). Social learning and social cognition: The case for pedagogy. In Y. Munakata & M. H. Johnson (eds.), *Processes of Change in Brain and Cognitive Development. Attention and Performance XXI* (pp. 249-274). Oxford: Oxford University Press.

De Waal, F. 2001. Pointing primates: Sharing knowledge without language. *The Chronicle of Higher Education*, B7–B9.

Franco, F., and G. Butterworth. 1996. Pointing and social awareness: Declaring and requesting in the second year. *Journal of Child Language 23*, 307–336.

Greenfield, P. M., & Savage-Rumbaugh, E. S.(1991). Imitation, grammatical development, and the invention of protogrammar by an ape. In N. A. Krasnegor, D. M. Rumbaugh, R. L. Schiefelbusch, & M. Studdert-Kennedy (eds), *Biological and Behavioral Determinants of Language Development* (pp. 235–258). Hillsdale, NJ: Lawrence Erlbaum Associates.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science, 298*, 1634-1636.

Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in co-operative cognitive tasks. *Animal Behaviour, 68*, 571 – 581. *Cognitive Sciences, 9*, 439-444.

Hermann, E., & Tomasello, M. (2006). Apes' and children's understanding of kooperative and competitive motives in a communicative situation. Developmental Science 9, 518- 529.

Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. *Japanese Psychological Research, 38,* 174–180.

Itakura, S., B. Agnetta, B. Hare, and M. Tomasello. (1999). Chimpanzees use human and conspecific social cues to locate hidden food. *Developmental Science, 2,* 448–456.

Kaminski, J. (2011). Communicative cues among and between human and non-human primates: Attending to the specificity in triadic gestural interactions. In M.Boos, M. Kolbe, T. Ellwart & P. Kappeler (eds), *Group Coordination*. Heidelberg: Springer,

Krause, M. A., & Fouts, R. S. (1997). Chimpanzee (Pan troglodytes) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology, 111,* 330 – 336.

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology, 34*, 813 – 822.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology, 110,* 346 – 353.

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: epigenesis and ecological validity. *Current Directions in Psychological Science, 14*, 185-189.

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential communication by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology, 118,* 48 – 57.

Leavens, D. A., Russell, J. L. & Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (Pan troglodytes). *Child Development, 76*, 291-306.

Lyn, H., Russel, J.L., & Hopkins, W.D. (2010). The Impact of Environment on the Comprehension of Declarative Communication in Apes. *Psychological Science* 21 (3), 360-365.

Menzel, C. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee after extended delays. *Journal of Comparative Psychology, 113*, 426-434.

Mulcahy, N., & Call, J. (2009).The Performance of Bonobos (*Pan paniscus*), Chimpanzees (*Pan troglodytes*), and Orangutans (*Pongo pygmaeus*) in Two Versions of an Object-Choice Task. *Journal of Comparative Psychology, 123*, 304–309.

Okamoto-Barth, S., Tanaka, M., Tomonaga, M., & Matsuzawa, T. (2008). Development of using experimenter-given cues in infant chimpanzees: Longitudinal changes in behaviour and cognitive development. *Developmental Science,* 11, 98–108.

Povinelli, D.J., Reaux, J.E., Bierschwale, D.T., Allain, A.D., & Simon, B.B. (1997). Exploitation of pointing as a referential gesture in children, but not adolescent chimpanzees. *Cognitive Development, 12*, 423–461.

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition, 14*(3), 433-439.

Tomasello, M. (2006). Why Don’t Apes Point? In N. J. Enfield & S. C. Levinson (eds.), *Roots of Human Sociality: Culture, Cognition and Interaction*. Oxford & New York: Berg, pp. 506-524.

Tomasello, M. (2008). *Origins of human communication*. Boston: MIT Press.

Tomasello, M., & Call, J. (2004). The role of humans in the cognitive development of apes revisited. *Animal Cognition, 7(4)*, 213-215.

Tomasello, M., Call, J., & Gluckman, A. (1997). The comprehension of novel communicative signs by apes and human children. *Child Development, 68*, 1067-1081.

Tomasello, M., & Carpenter, M. (2005). The emergence of social cognition in three young chimpanzees. *Monographs of the Society for Research in Child Development. 70*, (1, Serial No. 279).

Vea, J., & Sabater-Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatologica, 69*, 289 – 290.

Warneken, F., Hare, B., Melis, A., Hanus, D., & Tomasello, M. (2007). Roots of human altruism in chimpanzees. *PLOS Biology, 5 (7)*, e184.

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science, 31*, 1301-1303.