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The Gestural Communication of Bonobos (*Pan paniscus)*: Implications for the Evolution of Language

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Graduate School
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by

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Abstract

Primate studies allow us to examine origins of language because the methods of communication exhibited by living great apes may be similar to interactions of our last common ancestor. The study of homologous traits permits inferences about early human behavior that would otherwise be unsubstantiated speculation. The chimpanzee-bonobo clade shares approximately 98.8% of DNA with humans, making the genus *Pan* an excellent comparative group to study the origins of language.

The three categories of gestures include auditory, tactile, and visual contact with the recipient. Arbib, Liebal and Pika (2008) suggest the *modified gestural origins theory* in which they state that imitation and pantomime dominated the early evolutionary stages of gesturing. The theory proposes that practical manual skills promoted complex imitation, followed by pantomime, which in turn allowed for rich gestural communication.

An observational study conducted by Pika et al. (2005) generated a gestural repertoire of two bonobo groups, thereby providing a framework for understanding flexibility and variability of gesture use. Flexibility refers to the performance of the same action within different social contexts, while variability describes the range of multiple gestures within a repertoire. The present study aims to expand the current knowledge of gestural communication among bonobos. Additionally, this research will test the possibility there are other gestures outside of the previous study's inventory. Evidence of both similar and novel gestures from an independent group of bonobos would support claims that gesture usage is variable across groups, and may be indicative of learning mechanisms practiced by our last common ancestor.

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CHAPTER 1

INTRODUCTION

Non-verbal communication is a topic studied extensively in a wide range of fields, including neurobiology, psychology, and computer science (Flecha-Garcia, 2010; Matsumoto, 2010; Sheerman-Chase, Ong, & Bowden, 2009; Shimoe, Hamamoto, Nosu, & Ogawa, 2010). Within anthropology, study of primate non-verbal communication provides insight into the origins of human language by demonstrating that the complex methods of interaction found in living great apes may reflect behaviors of our last common ancestor (Arbib et al., 2008; Pollick & de Waal, 2007). The subject of gestural communication has provided research evidence suggesting that what we convey with our actions is just as informative as what we say with our words. In fact, before human children master verbal language, they use gestures to indicate wants and needs (Sauer, Levine, & Goldin-Meadow, 2010). Additionally, manual and orofacial gesturing often accompany verbal speech, while signed based languages have no vocal component. Taken together, the prevalence of meaning conveyed through movement suggests that "language" may not be grounded solely in speech.

Linguistic scholar and experimental researcher B.F. Skinner (1957) broadly defined language in such a way that did not constrain it to only verbal behavior, but also included gesture. In terms of language evolution, Skinner's concept allows us to place articulate language in a pre-vocal stage, and examine how language has "evolved" into its current structure and use. Specifically, the *gestural origins theory* argues that language first arose as visible gesture and draws upon support from anatomical fossil evidence, neurobiological research, and primate

studies (Armstrong, 2008). Moreover, Arbib et al., (2008) propose the *modified gestural origins theory*, and argue that gesture, rather than vocalization specifically, provided an evolutionary pathway toward open semantics, which characterizes the present versatility of language. Manual movement is a form of communication clearly evident in some living non-human primates, thus a comparison of gestures between humans and closely related primate lineages, such as bonobos and chimpanzees, may elucidate the method of communication practiced by our last common ancestor. Importantly, the identification of gestural repertoire across ancestrally related species might therefore provide insight into the origins of human language. Because humans (genus *Homo*) and the chimpanzee-bonobo clade (genus *Pan*) share approximately 99% of their DNA (Ebersberger, Metzler, Schwarz, & Paabo, 2002), bonobo apes are a logical comparative group for the study of language origins. Around six million years ago, the last common ancestor of bonobos and humans split, giving rise to separate *Pan* and *Homo* lineages (Patterson, Richter, Gnerre, Lander, & Reich, 2006). By studying similar forms of communicative gestures in species that are phylogenetically close, we can make inferences about shared ancestral traits, called "homologies" (Pollick & de Waal, 2007). Accordingly, the study of homologous traits in *Pan* and *Homo* will allow us to identify both primitive and derived traits associated with human language, and gain insight into the evolution of language from its early origin.

This study aims to expand on the primate gestural research of Pika, Liebal, and Tomasello (2005). Their observation of two bonobo groups has generated a gestural repertoire for the species and has provided a basis for understanding issues of flexibility and variability within their gestural capacity. The major goals of the present study are to better understand the full range of gestural communication among bonobos and to test the possibility that there are other gestures outside of the previous inventory. The presence of previously unidentified

communicative gestures in independent groups of bonobos may indicate that gestural communication varies across bonobo groups. Additionally, the current research examines variability within groups by comparing type and frequency of gestures according to age class, gender, and contexts.

The information generated in this study will be useful in future research involving comparisons of gestural registers in an evolutionary context by using the interactions of bonobos as a model of communication in our ancestors.

CHAPTER 2

LITERATURE REVIEW

Past Studies/Discussions

It has been noted as early as the 1890s that gestural communication appeared to play a fundamental role in ape communication. Garner (1896) first described gestures, as opposed to vocalizations, as the primary form of interaction among chimpanzees. Forty years later, Kellogg and Kellogg (1933) suggested an experimental approach to communicative studies through teaching apes sign language in order to understand the cognitive capacity for communication in chimpanzees and other apes. More recently, research has focused on linguistic models, including lexigrams (symbols on a visuographic keyboard), plastic symbols, and formalized hand signals in chimpanzees, (Fouts & Mills, 1997; Gardner & Gardner, 1989; Premack, 1976; Rumbaugh, 1977), gorillas (Patterson, 1981), and orangutans (Miles, 1990). Among the most compelling research is Savage-Rumbaugh's (1986) work with captive bonobos. By teaching apes symbolic language, her findings changed the way researchers think about general language acquisition and use. Specifically, her experiments have shed light on the cognitive and intellectual capacities of all primates, including humans, and have highlighted the importance of an adequate learning environment for the acquisition of human communicative skills (Savage-Rumbaugh & Fields, 2000). Acknowledging the capacity of a non-human primate to learn a new set of skills that is not adaptive in its native environment subsequently incited the most recent version of the important nature-versus-nurture debate (Shanker & Taylor, 2004).

Ape language research also serves to answer the question of whether language is uniquely human or shared broadly among primates. Researchers have previously proposed that structural elements of verbal language, including semantics and grammar, distinguish human

language from the communication of non-human apes (Chomsky, 1997; Pinker, 1994; Seyfarth & Cheney, 2008). Yet, bonobos and chimpanzees appear to comprehend adjectival and clausal modifiers, pronouns that indicate a previous reference, and the possessive structure (Savage-Rumbaugh & Fields, 2000). Through their research with lexigrams, Savage-Rumbaugh and Fields (2000) demonstrated that bonobos are able to not only efficiently use lexigrams in communication with researchers, as well as other apes, but do so through construction of entirely novel sentences structured according to the semantic and syntactic functions of language:

> When Kanzi […] was asked to 'Go get the ball that is in the bedroom', a ball (along with many other objects) was in front of him, as well as in the bedroom. Had Kanzi understood only the words 'ball' and 'bedroom', he might have given the experimenter any ball and then proceeded to go outdoors. Instead he brought the experimenter the one ball that was syntactically marked as residing in a specific location […] When the syntactical marking was clear, Kanzi's responses were equally clear (pp. 133-134).

Kanzi, the male bonobo referred to above, was reared at the Language Research Center in Atlanta, Georgia in a communication-rich environment alongside his mother and sister where he quickly acquired lexigram skills under the direct research of Sue Savage-Rumbaugh. Kanzi's mother specifically was the subject of intense ape-communication training. Before the age of two years, he had already demonstrated a broad capacity to understand human gestures, and lexigram symbols (Shanker & King, 2002). By the age of eight, Kanzi understood human speech at the level of a two-year-old child (Greenfield & Lyn, 2006). Today his lexicon includes more than 200 symbols (Savage-Rumbaugh, Shankar, & Taylor, 1998).

Similar to the ease with which Kanzi acquired a repertoire and knowledge of gesturing at a young age, human children use gestures for communication before they speak their first words. This relative ease with which non-verbal signals are utilized may suggest an innate predisposition for learning key aspects of gesturing. In fact, as adults, humans supplement articulate speech with expressive manual gestures (McNeill, 1992; McNeill, 2005), sometimes referred to as "co-speech gestures" (Arbib et al., 2008), while some humans who are unable to communicate verbally use a language consisting solely of gestures. In order to understand the actor's non-verbal communication, the recipient must have the "reading skills" required for parsing out the signaler's intent. Because these reading skills appear to be innate, it is presumed that prior to the evolution of articulate speech, human ancestors relied on gestural communication (Hewes, 1973).

It has also been theorized that human handedness is a direct result of these manual gestures, which allowed for a functional neural specialization linked to the evolution of language (Corballis, 1991; 2002). To address the emergence of human language, Arbib et al. (2008) argue that spoken word has its origin in gesture and pantomime—a form of communication clearly evident in some living non-human primates. The theory is rooted in evidence from Grafton, Arbib, Fadiga, and Rizzolatti (1996) that pinpoints a brain region activated for both the observation of grasping and the action itself of grasping. More importantly, this neural co-activation, called a *mirror system* region, for grasping is located within or around Broca's Area, which is a small portion of the inferior frontal region of the brain dedicated to speech production in humans. Arbib and Rizzolatti (1997) have expanded on such mirror system findings and generated the *mirror system hypothesis*. The hypothesis states that the evolutionary basis for language parity is provided by the evolution of brain mechanisms that support language atop the

mirror system for grasping. The *modified gestural origins theory* (Arbib et al., 2008) incorporates the mirror system hypothesis to explain how manual gestures provided the cognitive scaffolding for speech. In short, the fact that a brain region activated for both the observation of a manual gesture and the gesture itself, the mirror system, is located within the speech center indicates the relatedness of gesturing in the communication of modern humans.

Facial Expressions

Human and non-human primates engage in a class of gesturing that is not commonly studied, among them facial expressions. Such gestures are produced by orofacial movements and appear to be well utilized by all of the great apes (Chevalier-Skolnikoff, 1973). They are considered to occur independent of manual and total body gestures (Liebal, Pika & Tomasello, 2006). Because orofacial movements are generated during chewing and thus not always communicative in intent, they are regarded as gestures when their production is to the result of specific combinations of oral movements. For example, chattering of the teeth and smacking of the lips against each other are used in a functionally gestural way as submissive signals (Maestripieri, 1997). Additionally, the horizontal face pout in chimpanzees is linked visually to whimpering while a full open grin is visually linked to a scream (Goodall, 1986). In this way, facial expressions are related to the production of specific vocalizations and may indicate a lower-grade form of communication (Arbib et al., 2008). It is thought that facial expressions are a form of metacommunicative signals that serve to ensure an intended action. For example, "play" is generally not confused with a resemblant gesture context, such as "aggression". Chimpanzees, bonobos and orangutans use "play face" upon approaching another individual to make certain that a wrestling or a hitting gesture is understood as a "play" approach, not

"aggression" (Arbib et al., 2008). In another instance, a gorilla was observed attempting to cover up a play face with her hand (Tanner & Byrne, 1993). This finding is interesting because it demonstrates that the gorilla was aware of the implication of her facial expression and attempted to conceal it. The movement to hide her spontaneous reaction may indicate a less voluntary nature of facial expressions as opposed to a deliberate gesture, especially compared to intentional and controlled manual gesturing. It is unclear whether facial gesturing is an acquired behavior or an innate one. It is frequently debated whether facial expressions are simply side effects of emotional states, if they are used flexibly in regards to audience, and whether or not they are used in a referential manner. There are also questions as to whether the meaning of a facial expression is intrinsic or whether the social context conveys the intended connotation (Arbib et al., 2008). However, these questions are not raised solely by facial expressions; gestural communication of all kinds is subject to queries of intent and purpose.

Gestural Communication

Communicative gestures have been observed among many nonhuman primate species (Call & Tomasello, 2007; Chevalier-Skolnikoff, 1973). Studies of gesturing in apes show that there is both flexibility and variability in gestural communication across species (Goodall, 1986; Kummer, 1968). For example, wild orangutans typically use ten manual gestures, ranging from pushing and pulling to touching the recipient's face with an open mouth (Liebal et al., 2006), while captive siamangs employ a more varied twenty tactile and visual gestures. Captive gorillas appear to utilize over thirty gestures of tactile, visual, and auditory origin (Liebal, Pika, Call, & Tomasello, 2004). The gestural repertoire of bonobos in the wild includes around 24 signals that range from affiliative gentle touches with the feet to aggressive manual slaps, similar to that of

chimpanzees (de Waal, 1988); however, little else is known about the gesturing of wild bonobos. Bonobo studies largely focus either on gesturing associated with certain sexual interactions that are unique to the species (Arbib et al., 2008), or gestures of subadults, who are typically the most active members of the group. An increase in frequency of gesturing from infancy into adulthood is observed in most ape species (Tomasello & Call, 1997), indicating that juveniles are the most frequent gesturers and accordingly are the most common subjects of observational research into primate gesturing. Although gestural variability occurs within and between species, flexibility depends on context and recipient response. Therefore, gestural flexibility is influenced at least in part by experiential context because the use is not uniform between groups. The predominant social context in which gestures are used by captive apes is playful interaction with the exception of the more solitary orangutan, which tends to use gestures primarily in the context of feeding interactions to communicate the desire of another individual's food (Liebal et al., 2006).

Gestural Type

In general, gestures are classified into three categories: (1) auditory signals, that are generated independent of vocalization such as slapping the ground or shaking a branch to make a noise, (2) tactile signals that include physical contact with the recipient, and (3) visual signals, where a mainly visual effect is generated without auditory or tactile stimulus (Pika et al., 2005). All three categories may be further assessed according to two types of intent. When a gesture is used to solicit assistance in attaining a goal or action, it is deemed an *imperative gesture*. A gesture made to simply draw the recipient's attention to an object is called a *declarative gesture*.

Gestural Variation Between and Within Species

In terms of variability, different gestures are found among different groups of orangutans when manually offering food pieces (Liebal et al., 2006), and gorillas when "arm shaking" (Pika,

Liebal & Tomasello, 2003). Gesture variability is also found in bonobos when "punching", and chimpanzees when "leaf clipping" (Nishida, 1980) or operating the "grooming hand clasp" (McGrew & Tutin, 1978). A high degree of gesture uniformity has been found among animals in small and stable groups, such as siamangs and gorillas. Alternately, groups with a more flexible social organization, like solitary orangutans and fission-fusion-based bonobos/chimpanzees, are found to exhibit less uniformity in gesturing. It is hypothesized that gesture variability increases in species with more negotiated, and thus more complex, societies and decreases in species that are socially autocratic or simply live in small groups (Maestripieri, 1999).

Gestures can be additionally categorized as dyadic versus triadic. Dyadic gestures are performed as specifically directed to another individual and serve to attract the recipient's attention toward the actor. Triadic gestures incorporate an external object or event into the interaction of two individuals and are used to attract the attention of the recipient to the outside entity. Occasionally, triadic gestures are referred to as "referential gestures", and are commonly indicative of the ability to infer and adjust behavior in regards to another individual's state of mind (Camaioni, 1993; Tomasello, 1995). For example, a bonobo begging for food will outstretch an arm, palm open and faced upwards, toward an individual who has acquired a desired food piece. In this scenario, the recipient must possess the cognitive capacity to infer the signaler's meaning in order to complete the triadic gesture.

Acquisition of Gestures

There exist two predominant views on the acquisition of gestural intent. One view focuses on gestural knowledge as acquired via social learning, while the other view emphasizes that non-human animal behavior is instinctual, due to genetic determination. For example, isolation studies using rhesus macaques (Mason, 1963) and gorillas (Redshaw & Locke, 1976) have demonstrated the importance of genetic predisposition in some species-specific gestures. By highlighting the significant behavioral similarities between independently raised individuals, the finding that isolated apes still perform the same gestures supports the notion that gesturing is genetically hard-wired. There is also evidence that social and individual learning processes are the means through which non-human primates acquire a gestural repertoire. Idiosyncratic gestures (gestures used only by single individuals within a group) have been reported for all great ape species in captivity (Liebal et al., 2006). Importantly in the latter case, only one member of a group was observed to use a specific gesture, supporting the notion that the origin of the gesture could not be socially learned or genetically determined, and thereby leaving innovation as the explanation of production.

Tomasello and Call (1997) propose a process of ontogenetic ritualization in which an individual learns a new gesture through repeated shaping over time with another individual in the group. For example, chimpanzees and bonobos use a stylized arm raise to show that they are about to hit another individual in a playful manner (play hitting is an essential element in the rough-and-tumble play of subadults). It is widely considered that the raised-arm gesture originally indicates an agonistic intent, but after repeated use in the rough play context, comes to denote a playful intent over time (Tomasello & Call, 1997). This flexibility of context further highlights that gestures are not always defined in mutually exclusive categories.

In different social environments, the communicative signals of primates may be a learned invitation to play, or an innate display of aggression. Regardless of whether gestures are acquired genetically or through social learning, it is important to note that both perspectives on the use of gestural communication by individuals results from an inherent capacity of all great apes to convey meaning and intent.

Comparing Apes and Humans

"Cospeech gestures" and facial expressions are commonly used throughout human speech, and prelinguistic children appear to comprehend the dynamics of gestural communication from the very early age of 12 months (Marcos, 1991). Human and non-human primates employ similar types of dyadic gestural exchange between two or more individuals. For example, both high-chair-bound human infants and hungry subadult chimpanzees and bonobos frequently employ the act of "food begging", though this behavior emerges at an earlier age in human children (Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004). This type of gesture that is carried out when the sender aims a gesture at the recipient without the association to an independent entity or object, called a dyadic gesture, is the most common form of gestural communication among bonobos (Pika et al., 2005). Ground slapping and throwing gestures that are used to instigate play also fall into this category among bonobos, while any attention-seeking behavior in children can be labeled as dyadic. Although triadic gestures are rare among non-human primates (Pika et al., 2005), they do exist. Food begging is occasionally performed along with a "food offer", which is clearly triadic in nature: the desired food acts as the external object incorporated into the gesture meant to attract the attention of the receiver. Gestures that include presentation of objects and pointing to objects also meet the triadic criterion; however, pointing

behavior occurs primarily during interactions among humans, not with other primates (Pika et al., 2005).

There is also a similarity in the development of gesturing between human and non-human ape species. Perlocutionary acts are instances in which the communication can transpire only because the recipient is practiced in gesture communication, as with a prelinguistic infant and an adult. In this type of interaction, the sender has no intent to direct the behavior specifically at the recipient. For instance, human toddlers who wish to gain entry through a closed door but are unable to open it may whimper, thereby soliciting assistance or action from another. The ability to perform perlocutionary acts always precedes the ability to perform illocutionary acts, in which the signaler exhibits intentional and unambiguous gesturing. For instance, if the same child who is having difficulty with the door turns to his mother and whimpers directly at her, the act is illocutionary by nature of the social-communicative context (Tomasello, 1984). Both bonobos and humans develop the ability to communicate via perlocutionary acts prior to illocutionary acts, but this marked onset of imperative gestural use develops at a later stage in bonobos (9 to 12 months old) than humans (around 10 months old) (Plooj, 1987; Pika, 2008).

Implications for the Evolution of Language

The previously discussed *gestural origins theory* of human language has been further supported by anthropological research over recent decades (Corballis, 1991; 2002; Hewes, 1973), with additional evidence from paleoanthropology (Lieberman, Crelin, & Kaltt, 1972), infant studies (Petitto & Marentette, 1991), and neuropsychology (Annett, 1985; Hopkins & Leavens, 1998). Gesturing has even been observed at the same rates between blind and sighted subjects when interacting with a blind audience, which leads researchers to believe that gesturing

is largely involuntary (Iverson & Goldin-Meadow, 1998). Accordingly, it would be reasonable to infer that gestures are not just a pervasive component of communication in modern humans, but also a fundamental element of the prototypical languages used among our human ancestors.

The *modified gestural origins theory* (Arbib et al., 2008) suggests that the early evolutionary stages of hominoid gesturing involved both imitation and pantomime. In this case, imitation is defined as, "the attempt to repeat observed actions to achieve some goal with respect to an object" (p. 1053). Pantomime, which builds on imitation, involves "the repetition of some of the movements of a praxic action, but without acting on an object, as a way of communicating something about the action, object, or event concerned" (p. 1053).

Many of the great apes are able to generate novel gestures via a blending of ontogenetic ritualization and "simple" imitation (Berdecio & Nash, 1981; Mason, 1963; Redshaw & Locke, 1976), where an imitation necessitates an ability to comprehend novel actions as intended to facilitate movement towards a goal. According to Arbib et al. (2008), imitations are "simple" if single actions can be learned in about 15 trials and compound skills can be learned after a few months of exposure to the behavior. Alternately, a "complex" imitation necessitates an ability to acquire knowledge of a single action in one trial, which is a skill unique to humans (Arbib, 2002).

The *modified gestural origins theory* argues that vocalization alone did not have the capacity to allow simple imitation to evolve into goal-directed communication. Advocates of this hypothesis instead reason that, once practical manual skills (e.g., grasping) promoted complex imitation, gestures (or more specifically, pantomime) allowed for a cultivated repertoire of gestural communication. Furthermore, the theory proposes that this complex imitation served as the foundation for evolution of more sophisticated neural systems that are unique to humans.

Such systems are suggested to be structurally organized in order to develop communication from pantomime of manual praxic actions to protosign, and eventually, protospeech and protolanguage (Arbib, 2005).

It has been noted that apes exhibit an amplified use of hands as opposed to the highly practiced use of posturing and facial expressions in monkeys (Pollick & de Waal, 2007). This shift may be indicative of an evolutionary change from less-voluntary orofacial movements to more manual gesturing, which appears to be under more voluntary control. Waters and Fouts (2002) observed chimpanzees using sympathetic mouth movements during fine motor manipulations, a relationship they argue indicates that gestural communication (including orofacial expressions) provided scaffolding for the development of intentional vocal communication (see also Arbib et al., 2008).

In the case of bonobos, gestures are an important communicative channel and are characterized by flexibility of use in regards to adjustments made depending on the attentional state of the recipient. More specifically, visual gestures are performed more often when the attentional state of the recipient is focused on the signaler (Pika et al., 2005). Additionally, the majority of the gestures elicited a response by the recipient looking at the signaler, sending a response gesture, or interacting directly with the signaler (Pika et al., 2005). While this behavior is not found in orangutans or gorillas, the findings are similar to those focused on chimpanzee attentional states (Liebal et al., 2004), as well as human communication and cognitive functioning (Goldin-Meadow, Nusbaum, Kelly, & Wagner, 2001; McNeill, 1992; Morrel-Samuels & Krauss, 1992). Bonobo gesturing, however, is understudied compared to other primate groups. Yet because of our close phylogenetic relationship, bonobo-gesture studies can give us insight into the evolutionary origins of non-verbal communication.

The Present Study

Pika et al. (2005) undertook the construction of an inventory of known bonobo gestures in order to "focus on the underlying processes of social cognition, including learning mechanisms and flexibility of gesture use" (p. 39). Replicating the inventory construction in different groups of bonobos will contribute to determining whether or not the findings of Pika et al. are fully inclusive of all bonobo gestures. The current research aims to provide evidence in support of the inventory established by Pika et al., and intends to explore the possibility of previously unobserved gestures.

As with previous studies (Pika et al., 2005), I predict that, in my supplementary study of bonobo communication, there will not be a substantial difference in the gestural repertoire of male and female bonobos and that gestures will be performed most frequently in the affiliative context. I also predict that the observed gestural repertoire of subadults will be larger than that of the adults, given past research on gestural frequency among age classes (Tomasello & Call, 1997). The gestures observed most often in prior research were *grab, slap, touch* (100% occurrence), and *peer* (86%), while the least observed gestures were *present, grab-pull-push, pull, stomp*, and *shake* (29%; Pika et al., 2005). I expect similar results in the present study, however I anticipate that the addition of adults to the current sample will alter the observed frequency of these gestures slightly. In particular, I predict that *slap*, which was previously performed in the play context 50% of the time, will decrease in overall occurrence as a result of less general *play* behavior. In addition, I expect that the incidences of *present* and *pull* will increase with the number of adults in the sample, given the gestures' previously noted moderate sexual context (20% and 25%, respectively).

By comparing the gestural repertoires of bonobos according to sex, age, and context, this study will enhance our understanding of the role of gesture in multiple communicative environments from an evolutionary standpoint. What is learned about the communication of our closest phylogenetic relatives helps us to better understand the essential elements of human communication.

CHAPTER 3

METHODS

Subjects

Because humans are more closely related to bonobos and chimpanzees than to any other living primate, a study of chimpanzee and bonobo communicative systems may illustrate possible goal-oriented interactions of our last common ancestor. Additionally, bonobos were chosen as the focus of the study because less is known of the communicative behavior of bonobos than of chimpanzees. There is therefore a greater likelihood of identifying additional communicative behaviors in bonobos and supplementing the current knowledge of the species. In order to maximize the sample size, I studied two bonobo groups: one at the Cincinnati Zoo and Botanical Garden in Cincinnati, Ohio, and another at the Columbus Zoo and Aquarium in Columbus, Ohio. Both were close in proximity, allowing me to increase observation opportunities and keep travel time low.

Age class, sex, genealogy, and reproductive history of all 25 bonobos were obtained from the corresponding animal keepers, through interviews and information packets. Information on sex, age, and parent/offspring relationship (if known) is listed in Table 1.

Table 1

Sample Biographical, Age Class, and Location Information

Name	Sex	Age Class	Date of Birth	Mother	Father	Location
Jimmy	Male	Adult	1979 (est.)			Columbus
Toby	Male	Adult	1979 (est.)			Columbus
Maiko	Male	Adult	7/3/84			Columbus
Donnie	Male	Adult	12/28/93	Susie	Jimmy	Columbus
Ricky	Male	Adult	3/19/95	Lady	Jimmy	Columbus
Bila isla	Male	Adult	8/14/01	Ana Neema		Columbus
Gander	Male	Subadult	12/29/03	Unga		Columbus
Jerry	Male	Subadult	8/27/08	Unga	Donnie	Columbus
Susie	Female	Adult	1982 (est.)			Columbus
Lady	Female	Adult	1982 (est.)			Columbus
Ana Neema	Female	Adult	2/15/92			Columbus
Unga	Female	Adult	2/2/93			Columbus
Jo-T	Female	Adult	12/18/02	Lady		Columbus
Lola	Female	Subadult	1/15/04	Susie	Toby	Columbus
Gilda	Female	Subadult	2/6/06	Ana Neema		Columbus
Vergil	Male	Adult	1/24/94	Lisa		Cincinnati
Vim	Male	Adult	9/5/95	Louise		Cincinnati
Vic	Male	Adult	6/27/01	Lisa		Cincinnati
Vijay	Male	Subadult	12/28/03	Louise	Vijay	Cincinnati
Louise	Female	Adult	10/28/72			Cincinnati
Lisa	Female	Adult	6/14/81			Cincinnati
Zanga	Female	Adult	1/9/99			Cincinnati
Kimia	Female	Adult	6/13/99			Cincinnati
Maddie	Female	Subadult	3/24/09	Lisa		Cincinnati
Clara	Female	Subadult	3/29/10	Kimia	Vergil	Cincinnati

At both institutions, the bonobos were housed in indoor and outdoor enclosures. However, data were collected only from individuals when housed indoors due to observation restrictions. For instance, no animals were housed outdoors during winter months. Also, when the animals were permitted in the outdoor enclosures at both zoos, they preferred to spend their time hidden behind trees and rocky substrates, making observations difficult and biased toward the individuals that occasionally ventured into sight. In both settings, food was provisioned

exclusively on the ground and consisted of fruits and vegetables. Water was available throughout the day.

Cincinnati Zoo and Botanical Garden, Cincinnati, OH

Three adult males, one subadult male, four adult females, and two subadult (infant) females were observed (see Table 1). The observation setting consisted of a single enclosure of 1,500 sq. ft. equipped with a small rocky substrate (about 5 ft. tall × 10 ft. wide) and approximately three artificial trees (about 25 ft. tall) commonly used for play, resting, and grooming (see Figure 1). Cardboard scraps and plastic toys were used as enrichment on a daily basis. Of the total 160 study hours, 115 hours (72% of total observation) were conducted at the Cincinnati Zoo.

Figure 1. A photograph of the center portion of the indoor bonobo enclosure at the Cincinnati Zoo, housing two unidentified individuals. ZooChat. (October 5, 2009). *Jungle Trails - Bonobo bedroom*. [photograph]. Retrieved from http://www.zoochat.com/556/jungle-trails-bonobo-bedroom-109304/

Columbus Zoo and Aquarium, Columbus, OH

Six adult males, two subadult males, five adult females, and two subadult females were observed over 45 hours (28% of total study hours). The Columbus Zoo consisted of two adjacent indoor enclosures, both measuring 590 sq. ft., enclosed by glass on two sides and the ceiling, an adjoining wall between them, and a back wall used for transportation to and from various enclosures. The enclosure on the left of the viewing area consisted of a moderately sized rock substrate (approximately 15 ft. tall × 13 ft. wide) equipped with a climbable waterfall (no greater than six ft. in height), ropes, and wooden platforms. The enclosure on the right housed a children's play set, complete with a slide, ladder, and monkey (*or in this case, ape*) bars (see Figure 2).

Figure 2. Photographs of the indoor enclosure at the Columbus Zoo, featuring monkey bars (left) and a slide (right). Unidentified subjects. ZooChat. (January 18, 2009). *Bonobo Cage Six*. [photograph]. Retrieved from http://www.zoochat.com/558/bonobo-cage-six-60846/; AmyMarie Riley. (November 14, 2010). *Untitled*. [photograph]. Retrieved from http://lifeasriley.blogspot.com/2010/11/day-at-columbus-zoo.html

Variables

For the purposes of this study, a "gesture" is defined as a movement of the head and any limb, body postures, and locomotion patterns, including movements performed during solo play

(see Table 2 for a list of gestures and contexts; see Table 3 for coding definitions). A gestural interaction was defined as any posture or movement clearly directed at another individual by touch, posturing, and/or sight (gesture intended to be seen for a purpose). A non-tactile action was defined as "clearly directed" if the actor was in the line of sight of the recipient. Any repeated or exaggerated gesture leading to play-hitting or kicking, tickling, or play-wresting was placed in the *play* context.

Observational Procedure

Data were initially collected from June 2009 – September 2009 using Noldus Observer® on a personal laptop computer. Following the first phase of data collection, a software error resulted in a loss of 70 hours of observational data. Subsequently, data were collected in a second period, and was this time manually recorded on datasheets from November 2009 – May 2010, then transcribed into Excel© spreadsheets.

Over the course of approximately five consecutive hours during each day of observation, behavioral data were collected in the public viewing areas of enclosures, resulting in about 160 total hours of observation. Observation sessions were scheduled at fixed times associated with bonobo peak activity hours in order to maximize the number of gestural observations. Sessions typically began at 8:30 or 9:00 a.m., when the animals were released into the enclosure to feed. At both zoos, the number of gestural observations decreased around 10:00 a.m., when most of the food had been eaten and the animals began to rest. At the Columbus Zoo, "keeper talks" were sometimes scheduled around 11:00 a.m., which resulted in increased activity focused on the keeper, with little communication between the animals. Activity at both zoos was intermittent without any suggestion of a pattern after their first sleeping session.

Because of solo-play by subadults, and long sleeping and solo-eating bouts in both samples, observational samples were conducted on an *ad libitum* basis (Altmann, 1974). In order to avoid a visibility bias (due to activity that was not concealed by trees or rocky substrates), all observations were conducted at the indoor enclosures at both zoos. Observations were recorded whenever activity occurred, using a sequence sampling method. Using this methodology, the focus of the observation was an interaction sequence and the commencement of an interaction defined the start of a sample period. For example, an individual running in no particular direction while pirouetting would mark "solo play" and when the individual began to run at a conspecific, the gesture "gallop" would be marked as observed.

The gestural inventory established by Pika et al. (2005) was used as a template for possible gestures that may be observed in order to facilitate future comparisons in studies between and within species. For the same reason, gesture descriptions are listed in their original form by type (visual versus tactile), and the contexts in which the gesture was previously observed at least 25% of the time (see Table 2). The individual performing the gesture was defined as the actor, while the object of the action was recorded as the recipient.

Table 2

Total Observed Gestural Inventory and Descriptions of Each Gesture (as per Pika et al., 2005)

Gesture	Description	Context(s)	Type
Half embrace	arm of sender is stretched and raised till about head level with the palm facing downward or placed lightly on the recipient's body	affiliative	tactile
Grab	animal grasps another animal with the whole hand, fingers are bent	play, agonistic	tactile
Grab-Push-Pull	movement series which includes the animal grabbing another animal and directly pushing or pulling it	agonistic	tactile
Kick	animal uses legs to forcibly move another animal away	play, agonistic	tactile
Pat	one hand is placed on the partner's body, usually the head or back, and a series of gentle patting or stroking movements is made	affiliative	tactile
Pull	animal grasps another animal and forcefully moves it closer	play, sex	tactile
Punch	animal performs a brief forward or downward thrust on or against another animal with fist/knuckles or finger	play, agonistic	tactile
Push	animal uses arms or legs to forcefully move another animal away	play	tactile
Slap	animal hits another animal forcefully with the palm of the hand	play	tactile
GG	two females rubbing genetalia ventrally	sex	tactile
Sex	two animals of the opposite gender copulating in any position	sex	tactile
Mouth kiss	the open mouth is placed over the partner’s mouth	affiliative; directed toward subadults	tactile
Touch	gentle and short (<5 seconds) contact with flat hands, body part, or feet	play	tactile
Gallop	animal runs very fast toward or close to another animal	play, agonistic	visual
Pirouette	animal pirouettes with hands on the ground or in the air	play	visual
Jump	animal springs from or over an object close to another animal or on another animal	play	visual
Look	gaze at partner in a direct manner	affiliative, sex*	visual
Peer	animal sits or stands very close and puts lips/face very close to lips/face or hand of a feeding partner	play, agonistic*	visual
Present	animal presents genital region ventrally, rump or belly or penis	affiliative	visual
Reach	animal stretches out limp towards another animal; palm facing sideways or downward	play	visual
Move	animal moves an object in front of another animal, for instance a piece of cardboard or a ball	affiliative, play	visual
Stomp	animal brings the sole or heel of foot forcibly against the ground	play	visual
Shake	animal hangs upside down from a branch or rope and moves legs/arms from side to side in front of another animal	play, agonistic	visual
Somersault	animal makes a flip on the ground	play	visual
Swagger quadrupedal	animal sways back and forth quadrupedally (idiosyncratic)	affiliative	visual
Bow	animal raises and lowers its torso by stretching and flexing the limbs alternating includes also movements such as nod head, shake head, tip head or turn head	play	visual

Note. Contexts with an asterisk (*) indicate gestures that were performed relatively uniformally across contexts, resulting in the highest observed contextual percentages representing less than 25%.

Also following Pika et al. (2005), each signal was coded with the additional variables detailed in Table 3, referring to the context in which the gesture occurred, recipient's attentional state, and the response of the recipient.

Table 3
Coding Details for Gestural Context and Recipient Behavior

	Context
a)	affiliative: grooming, body contact, or protection
b)	agonistic: aggression and submission (i.e., avoiding, crouching, chasing, biting, hitting, threatening)
c)	play: play-wrestle, play chase, rough-and-tumble play, and teasing
d)	sex: mounting, genital inspection (not associated with grooming), and genital-genital rubbing (GG-rubbing)
	Recipient: Attentional State
a)	direct eye contact or head directed toward the actor
b)	head positioned 90˚ from actor
c)	head positioned more than 90˚ from actor
	Recipient: Response to Action
a)	no reaction
b)	attentional state of recipient changes (not looking vs. looking)
c)	recipient uses a gesture
d)	continued interaction follows

Data Analysis

Due to the complementary nature of the present study, the analysis of my data closely adheres to that of Pika et al. (2005). I chose the same methods of analysis in order to ensure the highest degree of reliability between the two studies. Pika and colleagues chose to observe only subadult bonobos to aid in comparisons to chimpanzee and gorilla subadults. Their study included seven bonobos observed over a total of 235 hours of observation equally distributed among the seven individuals. Consequently, the present study produced a smaller number of observation hours per individual.

In order to assess gestural flexibility, I analyzed signal type and frequency by context. Following the procedure of Pika et al. (2005), I took into account the gestures which were used within multiple contexts and which gestures were exclusive to one context. Analyses between age classes were performed to confirm the prediction that the greatest amount of gesturing is found in subadult bonobos, and to amend for any bias that may occur due to the high frequency found in the subadult age class. I compared gestural repertoires between sexes to test the notion that neither male nor female bonobos engage in gesturing at a higher rate than the other sex.

High uniformity of gestural repertoires within the combined bonobo groups would indicate either a social learning process or a genetic predisposition as the means by which gestural knowledge is acquired. Alternately, low uniformity would signify an individual learning process. As per Pika et al. (2005), a Cohen's Kappa statistic was intended to calculate the degree of uniformity within each group, and within the two combined groups. However, a small sample size and a lower number of observed gestures than expected did not allow for statistical testing. As an alternative, all data were assessed visually for trends in each subject's repertoire to make possible within-group comparisons of context, sex, and age.

CHAPTER 4

RESULTS AND DISCUSSION

Results

The most varied observed number of actions within a gestural repertoire performed by a single individual was 21 gestures (Vijay), while the two infants (Maddie and Clara) did not produce any observed gestures (see Figure 3).

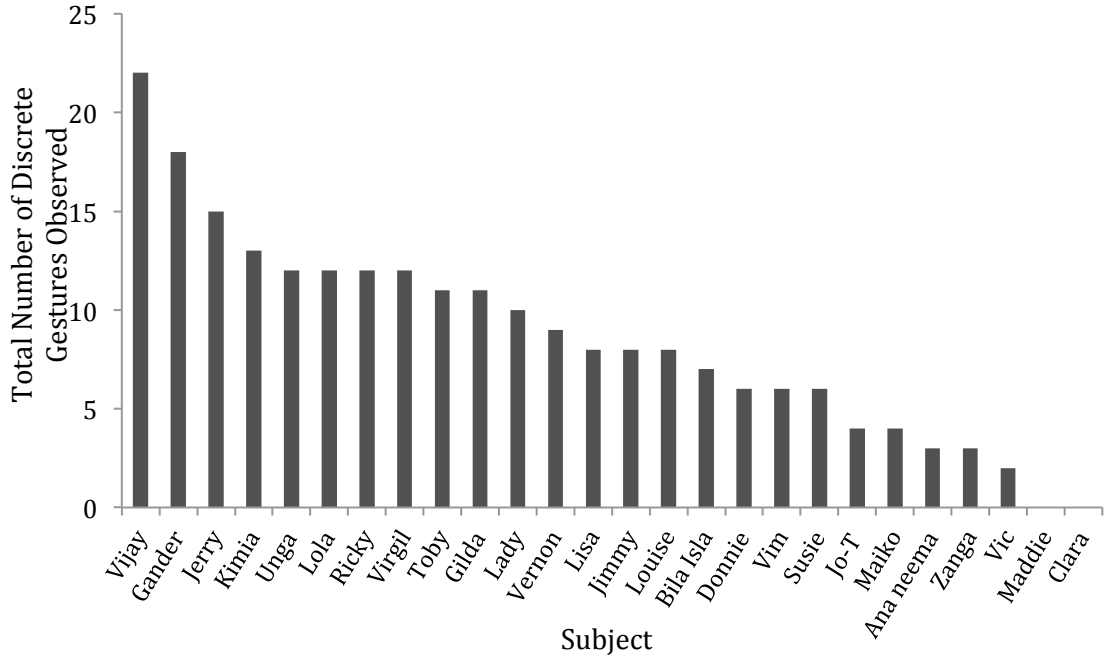

Figure 3. The number of total gestures within each subject's observed repertoire.

However, it should be noted that each individual was not observed for the same cumulative amount of time (*M* = 36:20 hrs., *SD* = 13:18 hrs.). For example, Vijay's total observed time (65:00 hrs.) ranks the highest of all subjects; however Zanga and Vic were only observed for a total of ten hours each. In addition, the infants were not seen gesturing due to obscuring of the individual by its mother or alloparent. The lack of observed gesturing by infants was also because the majority of the infants' time was spent clinging to their caregivers as opposed to

interacting with other individuals. A lack of observed gestures might also stem from a lack of knowledge or need to communicate with conspecifics. Vic and Zanga also demonstrated a low number of gestures, but this was most likely a result of low sampling opportunities. Each of these individuals was on display twice during the duration of the study and devoted most of the observation time to sleeping and eating alone. Therefore, in addition to examining the total number of unique gestures observed, or the gestural repertoire, it is also important to assess the number of unique gestures per total amount of time spent observing an individual (see Figure 4).

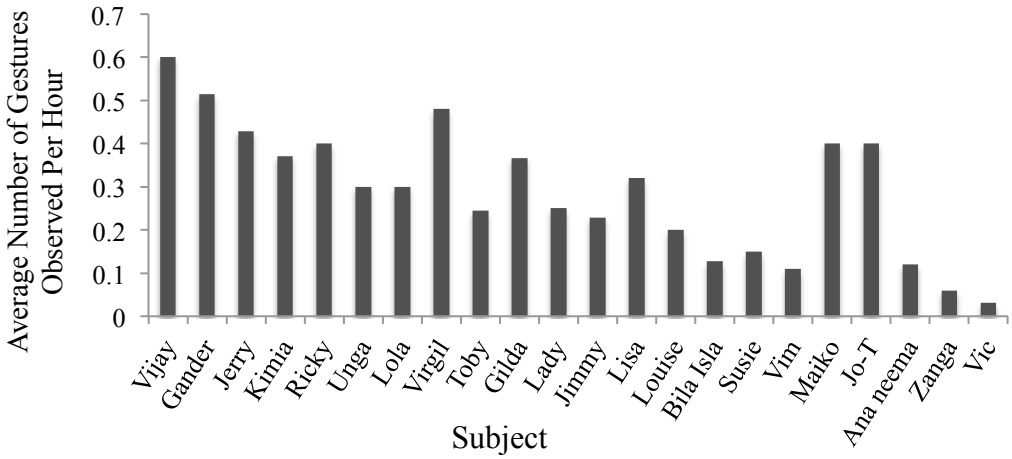

Figure 4. Observed gestural repertoire accounting for differences in observation time versus total hours of observation (*adjusted* rate).

In order to determine the incidence of independent gestures observed for the cumulative samples, an adjusted rate was calculated for each subject. The resultant value, referred to as the *adjusted* gestural rate, provides a temporally contextual reference for the raw range of observed gestures within an individual. Gestural repertoire between subjects was highly variable for both adjusted (M = 0.29 gestures per hour, SD = 0.15) and raw (M = 9.36, SD = 4.95) totals. As demonstrated by comparing Figure 3 and Figure 4, the magnitude of Virgil's gestural repertoire is more evident when the moderate proportion of observation time (25:00 total hrs.) is compared with the number of independent gestures he was observed executing (N = 12), resulting in a

comparatively high adjusted value of 0.48 average gestures per hour. Although Vijay demonstrated the widest range of gestural use, it could be argued that he also experienced highest amount of observation time. His adjusted rate of 0.60 gestures per hour, however, provides supporting evidence that he performed the widest variety of gestures among all subjects, regardless of observation time. Additionally, though Maiko and Jo-T received a relatively low amount of observation time (10:00 total hrs.), they each exhibited visibly noticeable increases in terms of their adjusted gestural rate as compared to most others. Both individuals changed from a low total of four gestures to a relatively high adjusted rate of 0.40 gestures per hour. Toby, on the other hand, had a relatively high amount of observation time (55:00 total hrs.), but only a moderate total gesture count ($N = 11$), thus the proportional weight of his gestural repertoire is lower than initially noted, as evidenced by his adjusted rate (0.24 gestures per hour). The same is true for Vic and Zanga, who were observed for a greater total amount of time (65:00 hrs. and 50:00 hrs. respectively), however the graph in Figure 4 indicates that a smaller, more proportional, adjusted gestural rate was observed for each (0.03 and 0.06 gestures per hour, respectively).

Overall, a total of 206 communicative signals was observed, which can be divided into 26 gestures (See Table 4). *Push, slap, touch, reach, jump*, and *present* were recorded in additional categories at a rate higher than previously observed (≥ 25%; Pika et al., 2005). Five new gestures or gesture types were established for bonobos: *half embrace*, *solo play, chase, look-chase*, and *head-shake* (see Table 5). Because sound was dampened by the enclosure wall, no attempt was made to study auditory gestures. There were no observations of any iconic gestures such as directional signaling reported in gorillas (Byrne & Tanner, 2006; Tanner, 1996).

Table 4

Observed Gestural Repertoire Per Subject

Cincinnati										Columbus															
Vijay	Virgil	Vim	Vic	Maddie	Zanga	Louise	Kimia	Lisa	Clara	Gilda	Jo-T	Lola	Unga	Susie	Lady	Ana Neema	Jimmy	Gander	Bila Isla	Maiko	Toby	Ricky	Jerry	*Total*	
x	x	x	x		x	x	x	x		x		x	x	x	x		x	x	x		x	x	x	*19*	Grab
x	x				x	x	x	x		x		x		x	x	x	x	x	x	x	x	x	x	*18*	Touch
x	x	x				x	x	x			x	x	x		x	x	x	x		x	x	x	x	*17*	Move
x	x	x					x	x		x	x			x	x		x	x	x	x		x		*14*	Look-at
x	x	x				x	x	x			x			x	x		x	x	x		x		x	*14*	Peer
x	x		x				x			x		x	x		x			x			x	x	x	*12*	Slap
x	x						x			x		x	x		x			x			x		x	*10*	Reach arm
x	x											x		x	x		x	x		x		x		*9*	Gallop
x		x				x	x	x			x		x	x					x					*9*	Pat
x							x			x		x	x					x			x		x	*8*	Jump
x	x	x								x			x				x	x				x		*8*	Chase
x	x						x					x	x					x			x		x	*8*	Look-chase
x						x						x	x					x				x	x	*7*	Pull
					x	x	x	x				x	x		x									*7*	GG
x						x		x				x						x				x		*6*	Push
x										x			x					x	x				x	*6*	Kick
	x						x									x	x				x	x		*6*	Sex
x										x		x	x					x					x	*6*	Solo play
	x						x								x							x		*4*	Present
x																		x					x	*3*	Somersault
x																					x		x	*3*	Stomp
x																		x					x	*3*	Grab-pull-
x										x													x	*3*	Pirouette
x																		x				x		*3*	Shake
										x											x			*2*	Punch
																			x					*1*	Half embrace
21	*12*	*6*	*2*	*0*	*3*	*8*	*13*	*8*	*0*	*11*	*4*	*12*	*12*	*6*	*10*	*3*	*8*	*18*	*7*	*4*	*11*	*12*	*15*	*206*	*Total*

Note. The actions are ordered by how frequently they occurred in the overall gestural repertoire (all subjects).

Table 5

New Gestures and Contexts

Gesture	Description	Context	Type
	Newly Observed Gestures or Gesture Types		
Half embrace	animal gently places one arm around the shoulders of another animal	affiliative	tactile
Head shake	animal looks at a conspecific and shakes head in a vigorous side-to-side rotating manner	play	visual
Chase	animal quickly pursues a conspecific for >5 seconds	agonistic, play	visual
Look-Chase	while being chased, an animal repeatedly looks behind them, at least 2 looks within a 5 second period	play	visual
	Newly Observed Contexts for Gestures		
Push	animal uses arms or legs to forcefully move another animal away	play, *agonistic*	tactile
Slap	animal hits another animal forcefully with the palm of the hand	play, *agonistic*	tactile
Touch	gentle and short (<5 seconds) contact with flat hands, body part, or feet	play, *affiliative, sex*	tactile
Reach	animal stretches out limp towards another animal; palm facing sideways or downward	play, *affiliative*	visual
Present	animal presents genital region ventrally, rump or belly or penis	affiliative, *sex*	visual

Note. Gestural contexts in which an action was newly observed at least 25% of the time are indicated in italics, with the exception of *touch*, which was observed in all four contexts. Therefore "majority" is constituted as observed 20% of the time. *Half embrace* was not observed previously in bonobos, but has been noted in chimpanzee studies.

It should be noted that, based on an analysis of the environment, the *agonistic* gestures also fit into the *play* context during rough-and-tumble play exercised by subadults. This grouping of gestures closely resembles the progression of gestural intent from one social environment to another found in the behavioral study of Tomasello & Call (1997), highlighting the flexible nature of communicative signals through categories that are not mutually exclusive. In the case of this study, all gestures that are usually categorized as *agonistic* were used in the context of *play* for the younger age group. Because many *play* gestures performed by subadults are an embellishment of *agonistic* gestures, it is possible that accounting for this age-specific behavior may change the way data is interpreted. When the *agonistic* gestures are corrected for the context of *play* in subadult bonobos, *play* changes from the lowest to the second highest context in which

gestures are used (see Figure 5). More specifically, all *agonistic* behavior is grouped together in the left subplot of this figure, regardless of whether or not it is in the rough-and-tumble play environment that is common in young chimpanzees and bonobos.

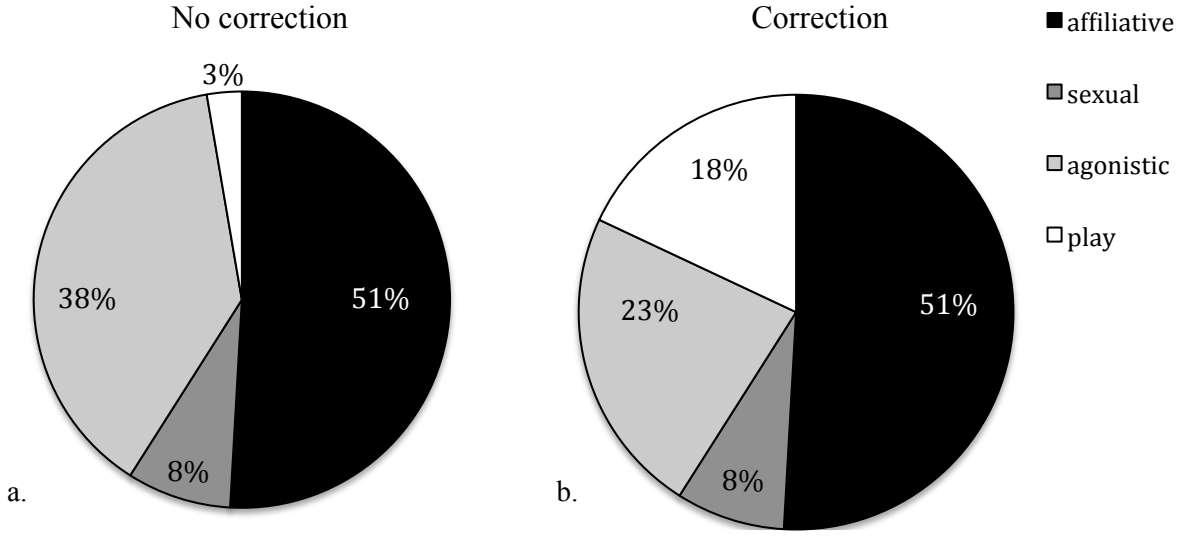

Figure 5. An illustration of the proportion of gestures in each context with a) no correction and b) correction for rough and-tumble play. The comparison highlights the difference between the inclusion and exclusion of *agonistic* gestures in the context of *play* as representative of a proportion of overall observed gestures.

In order to correct for observations during this type of play, gestures normally grouped in the *agonistic* context like *grab, slap, push, kick, stomp, punch, pull, chase, and look-chase*, are instead grouped with the *play* category for subadult recordings (see Figure 2b.). Now, it becomes evident that even though *affiliative* gestures are still used most often (51%), *play* and *agonistic* gestures are now found at almost equal proportions in the gestural repertoire, at 18% and 23%, respectively.

In terms of number of subjects that were observed performing a specific gesture, the rate of inter-subject incidence ranged from one individual to 19 ($M = 7$, $SD = 6$; see Figure 6). The previously observed gestures *swagger quadrupedal, kiss,* and *bow* (Pika et al., 2005) were not observed in the present study.

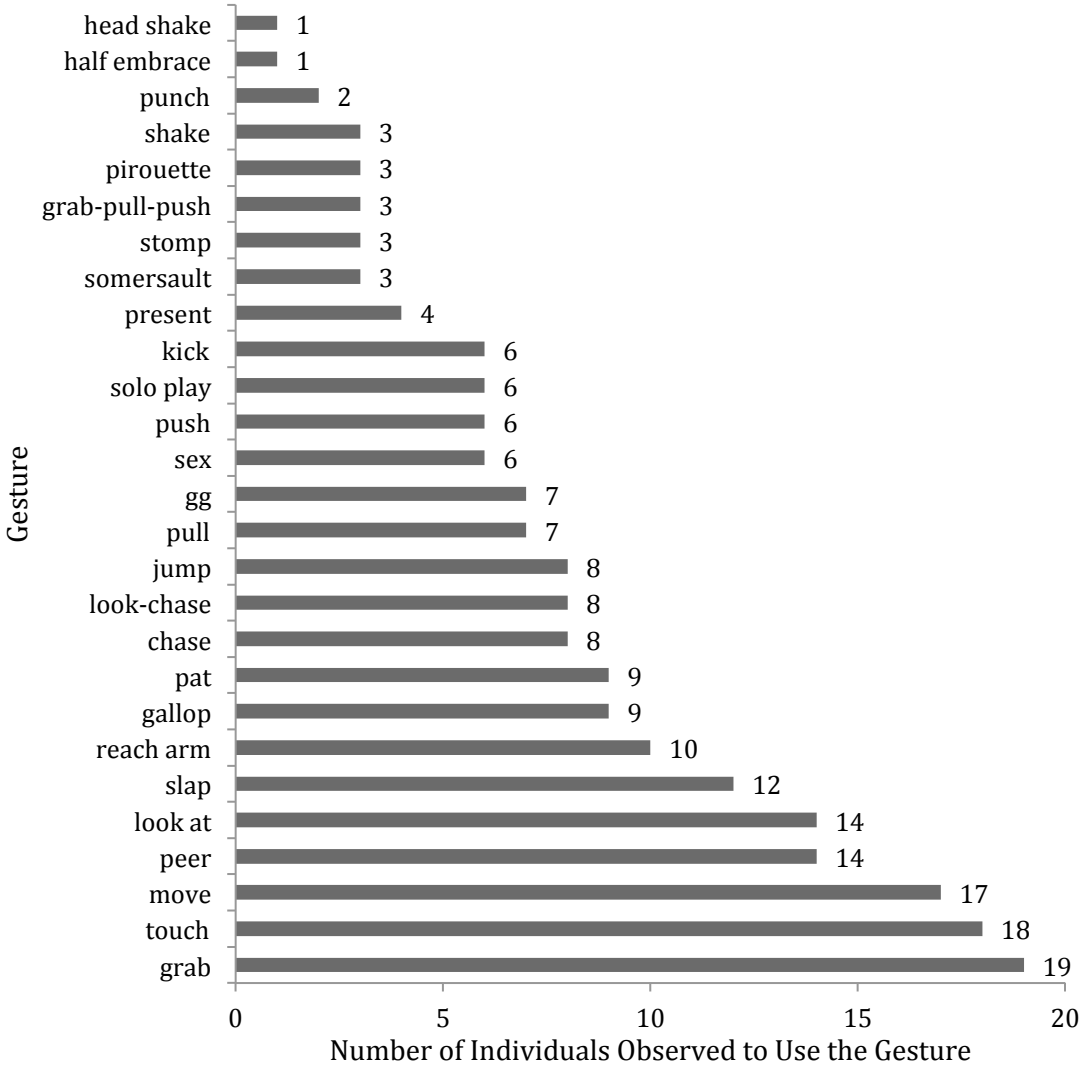

Figure 6. Comparison of total gesture use across all subjects. Note that this is a graphical representation of the marginal row totals from Table 4.

Of the 200 plus hours of observation, the gesture performed by the greatest number of individuals (19 individuals; 73% of the sample), was the agonistic/play *grab*, followed closely by *touch* (18 subjects; 69% of the sample). *Grab* is generally categorized as an *agonistic* gesture, while *touch* typically falls into the *affiliative* category. Both *touch* and *grab* were observed as a means of directing attention toward the actor, but given the differing nature of *grab* for adults and subadults, the purpose of gaining attention on behalf of the actor may have differed between age groups. For subadults, 100% of whom performed the gesture, the observed behavior was

consistently followed with an additional *play* action such as *somersault* or *pirouette*. For adults, however, only 75% of the individuals were observed performing the *grab* gesture, and moreover, it was never followed with a *play* gesture. Pika et al. (2005) found that the *play* context dominated 41.5% of the instances in which *grab* was used, but it is important to note that the population was only subadults, who were reported as performing gestures in the *play* context more often than adults. *Half embrace* and *head-shake* were each observed by only one individual, and *punch* was observed by only two individuals in the context of *play*.

As predicted, the total number of unique gestures observed was higher on average for subadults ($M = 15.4$, $SD = 4.16$) than adults ($M = 7.59$, $SD = 3.62$), as was the adjusted gestural repertoire (subadults: $M = 0.44$ gestures per hour, $SD = 0.12$; adults: $M = 0.25$ gestures per hour, $SD = 0.13$). Yet, when examining which age group performs individual gestures at a higher rate, it appears as though discrete gestures in the current study are performed more frequently on average by adult bonobos ($M = 4.45$, $SD = 4.40$) than subadult bonobos ($M = 2.65$, $SD = 1.82$), although subadults are generally found to gesture more often. However, considering that adults outnumber subadults in the study sample, an adjustment must be made for proportion. This correction was generated by comparing the percentage of individuals within the age group that performed the gesture as opposed to evaluating the number of instances in which the gesture was performed (see Figure 7).

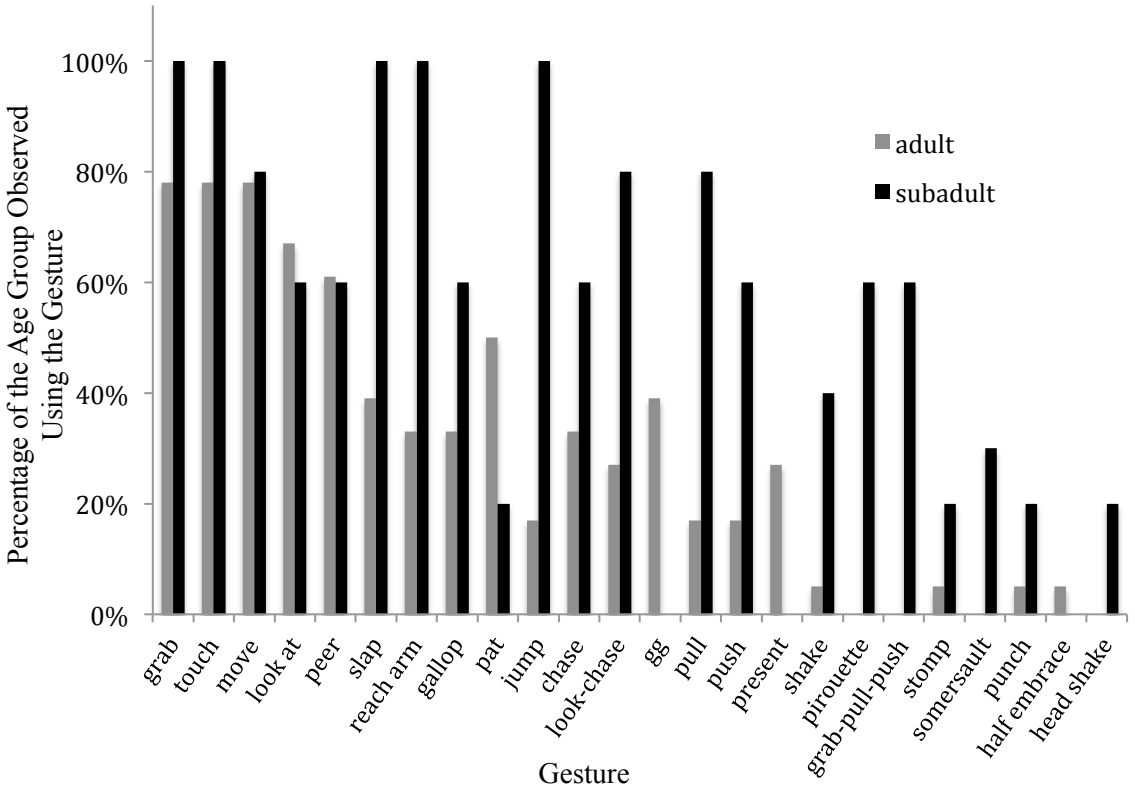

Figure 7. A comparison of gesturing percentages between adult and subadult age groups.

Now, it is evident that a greater percentage of subadults on average (M = 53%, SD = 37%) were observed performing individual gestures than adults (M = 26%, SD = 26%).

When comparing the number of gestures demonstrated between genders, males on average performed 56% of the gesturing (SD = 5.9%), and females on average performed about 44% (SD = 4.6%). In general, the number of times a gesture was used did not vary between genders (see Figure 8). Using *grab* as an example, the gesture was observed a total of 19 times, and 53% of the time *grab,* the most frequent gesture, was observed, a male was carrying out the gesture. Similarly, *touch*, the second-most observed gesture, was observed 18 times, with females and males each contributing to exactly 50% of the observations each.

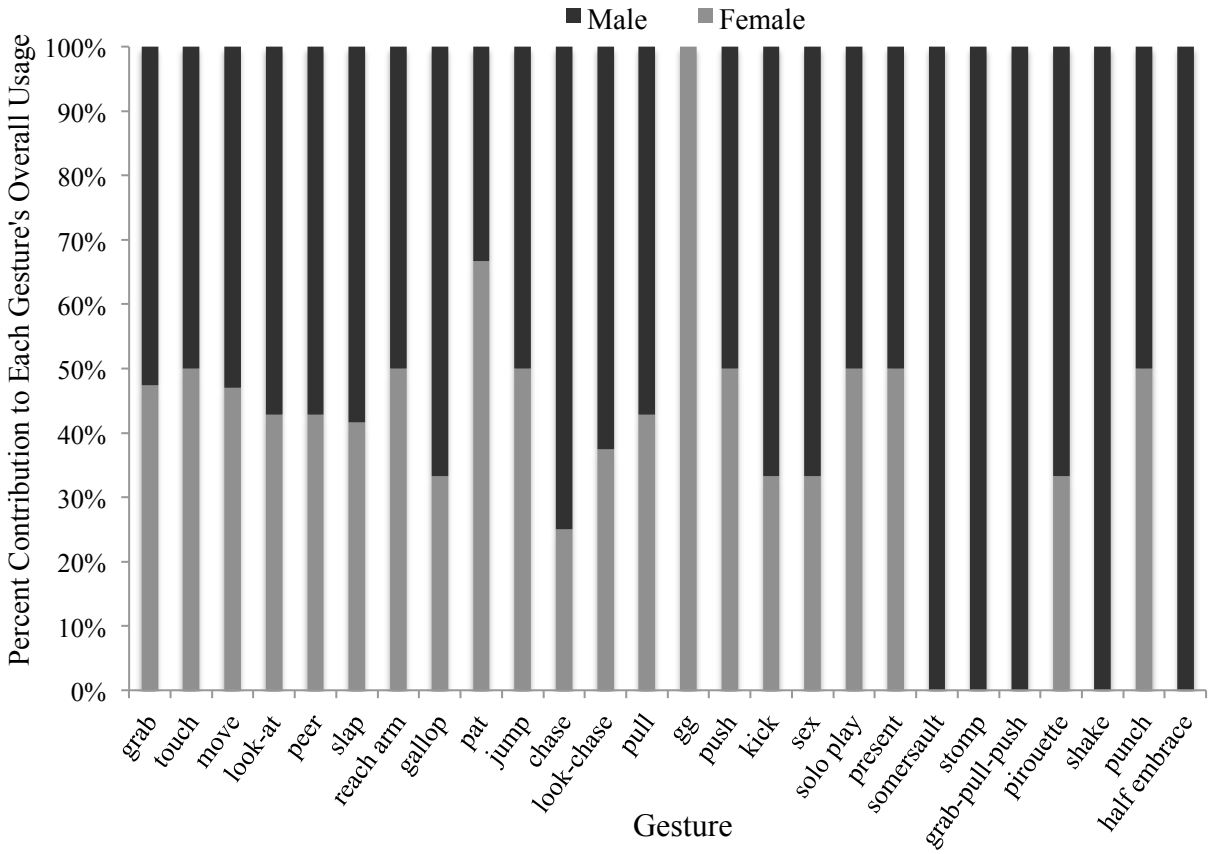

Figure 8. A comparison of the total gesture use percentages between males and females.

Some observations are represented as exclusively male or female, but it should be noted that observations of 100% do not mean the gestures are exclusive to males or females (with the exception of *GG rubbing,* which is by definition a gesture exclusive to females). Instead, they are an artifact of low observed occurrence where there are repeated observations. For example, the males represent 100% of the head-shake gesture because Vijay was the only subject observed performing this signal. In general, males exhibited a greater gestural repertoire and represent 100% of some gesture usage, but this is most likely due to the fact that the majority of subadult bonobos observed were males. On average, each individual performed about 35% of the given repertoire (*SD* = 19%).

Discussion

The goals of this study were to provide a gestural inventory for captive bonobos based on both past studies and the present study, as well as to examine the flexibility and variability of bonobo gesturing. In order to elucidate how captive bonobos utilize gestures as a form of communication, the data were analyzed comparatively based on age, sex, and gestural context.

The bonobos in this study were observed using 26 different gestures of a tactile or visual nature. Among the tactile gestures reported in previous studies, *grab, touch, kick, pull, reach arm, pat, grab-pull-push, sex, GG rubbing, push, slap,* and *punch* were similarly described by Pika et al. (2005), along with the visual gestures *gallop, jump, look-at, move, peer, present, stomp, reach, chase, pirouette, solo-play, shake,* and *somersault*. The gestures *swagger quadrupedal, kiss,* and *bow* were not observed in the present study, but have been observed in prior research (Pika et al., 2005). In the present study, the *beg* gesture was combined with *reach arm* because the action and context were always identical.

As previously noted, a wide range of gesturing was observed both within and between individuals, however the very high and very low counts mirror previous research (Pika et al., 2005), and may be explained by age class variability. The subject observed using the greatest repertoire of gestures (21 total; 0.60 adjusted rate) was Vijay, who was the only non-infant subadult in his group and was frequently propositioning for playmates and partaking in solo-play. Gander (18 total gestures; 0.51 adjusted rate) and Jerry (15 total gestures; 0.43 adjusted rate) were observed using a wide range of gestures for similar reasons. While such a subadult age class indicates the peak age for gesture usage, the infants, Clara and Maddie, were always grasping a mother or alloparent, and were never observed with the manual freedom to gesture. In terms of the varied occurrence between the gestures themselves, the gestures observed most

often in prior research were *grab, slap, touch* (100% occurrence), and *peer* (86%), while the least observed gestures were *present, grab-pull-push, pull, stomp*, and *shake* (29%; Pika et al., 2005). Similarly, *grab* and *touch* were the gestures performed by the highest number of individuals in the current study. This is not surprising, given that both actions fit into at least six of the eight contexts defined by Pika et al. (2005), and at least half of the present communicative contexts. This flexibility may allow for their appropriate use more often. As predicted, *slap* was no longer observed at the same high rate, presumably because the *play* context within which it was formerly performed (50% of the time) did no longer dominate the present social environment of both adults and subadults. Relatedly, the prediction that a more adult sample would increase the incidences of *present* and *pull* in the *sexual* context was also upheld. In terms of the other gestures that were previously observed less frequently, *grab-pull-push, stomp*, and *shake* were all observed in less than 15% of the current population. It may also not be surprising that *half embrace* was observed so infrequently (one individual), considering that the action has been observed primarily in chimpanzees (de Waal, 1988; Nishida, Kano, Goodall, McGrew, & Nakamura, 1999), and not in the research that I aimed to complement (Pika et al., 2005).

As an additional objective of the study, is it important to note that four previously undefined gestures were observed, and one (*half embrace*) had only been observed in chimpanzee populations. One group-specific gesture that has not been described in previous literature is *head-shake*, which was performed twice by only one individual (Vijay, a subadult male at the Cincinnati Zoo). There were no observations of *head-shake* among the subjects at the Columbus Zoo, indicating there may be an individual learning process present. The context of the newly identified gesture was exclusively *play,* which supports the findings of Pika et al.

(2005) that indicate *play* as a noteworthy context of communication for subadult bonobos. In their study, 95% of the observed gesture occurred in the context of *play.*

Solo play, chase and *look-chase* were not noted in the previous inventory reported by Pika et al. but were demonstrated by subjects in both zoos. Observations of the two chase signals are not surprising, given the widespread knowledge that other primate species utilize chasing as a means of rough and tumble play among subadults. However, *look-chase* has not been defined as a separate gesture from *chase* in any previous literature. Both gestures have aggressive and play affiliations, and they are generally seen within the same observation time. *Solo play* has been described anecdotally in prior research (e.g., Fagen, 1993; Pereira & Leigh, 2003), but has not yet been used as a variable in generating a gestural repertoire. This distinction is important, given that it may functionally precede affiliative or playful behavior initiated by another individual.

Due to the fact that the Columbus group and the Cincinnati group have shared Kimia as a member, the origin of some gestures is unspecified. In other words, it is unknown whether a gesture was originated by a subject within one of the captive groups and transferred, or whether the behavior was learned elsewhere. For example, Lady, Susie and Maiko were born in the wild and may have become familiar with a behavior outside of captivity. Therefore, they may have inadvertently taught the behavior to members of the zoo group through social learning. It can be speculated, however, that the *head-shake* gesture is an expansion of *shake*. It is also possible that the individual observed humans making this gesture in an attempt to elicit a response and simply performed an imitation.

During the instances in which *head-shake* occurred, Vijay was just out of reach of a playmate (Maddie, aged 13 months at the time) and performed the action after the recipient attempted a *grab, kick,* or *punch* gesture. It can be inferred that Vijay uses the *head-shake*

gesture when the aim is to tease the recipient. A similar situation was found for *look-chase* in which the actor was being chased and repeatedly looked over his or her shoulder to make sure he or she was still being chased. Once the chase involving *look-chase* ended, the actor focused his or her energy on getting back in the line of sight of the recipient in many cases. *Look-chase* was often a precursor or response to rough-and-tumble play.

Overall, the gestural repertoire generated in this study is very similar to those created in prior studies. Additionally, the production of individual gestures in multiple contexts implies that signalers can differentiate between gestures of differing intent. Four new gestures were identified, one of which may be indicative of an individual learning process. The frequent and flexible use of gesturing when interacting with conspecifics indicates that gestural signaling is an important function of communication for captive bonobos. The interactive gesturing of captive bonobos supports the *gestural origins theory* by providing evidence of a capacity for communicative intent and understanding among our closest phylogenetic relatives.

CHAPTER 5

CONCLUSION

This study supports the previous research of Pika et al. (2005) by demonstrating that the gestural repertoire of captive bonobos is flexible and variable. The flexibility of use is indicated by the overlap of *play* and *agonistic* gestures, while the wide range of repertoires within the two groups implies variability within the repertoire. In the previous study, bonobos performed eight different gestures on average, which is equal to this study's average of eight different gestures.

A major goal of the present study was to expand the current knowledge of gestural communication among bonobos and test the possibility there are other gestures outside of the previous repertoire set forth by Pika et al. (2005). The observation of *head-shake* and *look-chase* in the present study, both of which are hypothesized to be *play* gestures, expand upon gestures already noted in the gestural repertoire of bonobos. *Half embrace,* though also newly observed, has been noted in the chimpanzee repertoire (de Waal, 1988; Nishida et al., 1999). In addition, the *solo play* gesture may continue to be identified in the future, or may provide an additional gestural context for detailing the gestural range of non-human primates.

An additional goal was to compare the number of different gestures observed between gender, age class, and context. The information gleaned from this study indicates that the majority of gestures are used in the *affiliative* context, followed by *agonistic* and *play*. Few gestures in the *sex* context were observed, but this was most likely due to the fact that only three gestures fell into this category. Males were observed performing a wider range of gestures, but this was due in part to the greater number of males represented in the study. Additionally, the

results of this study are consistent with those of previous gestural communication studies (Pika et al., 2005) in that frequency decreases in adult bonobos and subadults perform the majority of gesturing.

The presence of variability and flexibility of use indicates a process of learning instead of a more instinctual means of acquiring gestural knowledge. Furthermore, the presence of gesturing across contexts suggests explicit knowledge of intent on the behalf of the actor and the recipient. In order to perform a gesture for an explicit reason, the acting individual must be aware of how the gesture is received and the recipient must be knowledgeable of the gesture's intent in order to respond effectively. As such, the present study supports the *gestural origins theory* of language, but future research would need to be conducted in order to incorporate the variability and flexibility of auditory communication in bonobos.

The research of Pika et al. (2005) produced a comprehensive catalog of bonobo behavior that indicated a high degree of flexibility and variability of signaling. My supplementary study supports their findings on the use of gesturing, as well as adds to the observed gestural repertoire of captive bonobos. The success of these endeavors thereby fulfills the aim of contributing an enhanced understanding of primate communication.

In the introduction of this study, I noted that a comparison of gestural communication with our closest phylogenetic relative allows for conjectures concerning early human interactions. By effectively generating an observed inventory of bonobo gestures, I can infer that the flexibility and variability of communicative signals found in their repertoire most likely illustrates methods of interactions found in our last common ancestor, and possibly, the origins of gestural language.

In conclusion, the results of this study support previous research on the gestural repertoire of bonobos and endorse the *gestural origins theory* of language. Further study may include data on the auditory signals of bonobos as either separate communications or as collaborative signals with tactile and visual gesturing. Additional comprehensive studies of wild bonobo interactions will also serve as support for comparative studies based on environment. In sum, the communicative signals observed in the present study may have contributed to a characterization of the interactions of our last common ancestor with the *Pan* lineage, and thus our evolutionary human ancestors.

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