Linguistic competency of bonobos (*Pan paniscus*) raised in a language-enriched environment

by

Andrea Rabinowitz

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

Major: Anthropology

Program of Study Committee: Jill Pruetz, Major Professor Maximilian Viatori Douglass Gentile

Iowa State University

Ames, Iowa

2016

Copyright © Andrea Rabinowitz, 2016. All rights reserved.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	iii
ABSTRACT	v
CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW	1
CHAPTER 2: METHODS	15
CHAPTER 3: RESULTS	25
CHAPTER 4: DISCUSSION	32
CHAPTER 5: CONCLUSION	46
APPENDIX A: COMPLETE WORD LIST	48
APPENDIX B: EXAMPLE OF PICTURES USED IN PICTURE TASKS	49
APPENDIX C: WORDS REMOVED IN TRAINING 5	50
APPENDIX D: KANZI'S AVERAGE WORD ACCURACIES	51
REFERENCES	54

ACKNOWLEDGEMENTS

There are many people without whom I could not have successfully completed my thesis, and I am eternally grateful for all of their contributions. Firstly, I must thank my advisor, Dr. Jill Pruetz, for her endless advice and support. Her patience and understanding throughout the many stages of my project were invaluable, and I continue to be inspired by her experience and passion for primatology. My committee members, Dr. Max Viatori and Dr. Doug Gentile provided innovative insight and critiques in developing and refining my thesis, which I truly appreciate. I also thank the Department of Anthropology at Iowa State for their financial support and honoring me with the Nancy R. Coinman Award for anthropological research, allowing me to contribute to this incredible project.

The directors of the Ape Cognition and Conservation Initiative, Drs. Jared Taglialatela and William Hopkins, provided priceless guidance from their many impressive years of research experience. Their commitment to producing reliable scientific research, as well as their dedication to the five incredible apes at ACCI, continually enriched this study. I am indebted to Dr. Ken Schweller for his endless ideas, help, and patience in solving all of ACCI's programming and computer needs, especially through developing specialized training and testing protocols for the bonobos. There would not even be a completed project without the staff members of ACCI who were present during my study. I thank you for your daily help working with the bonobos, shifting them between rooms, and keeping track of Kanzi's grape calories for many months of data collection. I know the apes all appreciate your care even more than I do. I also thank Eric Mittman, of the Iowa State Statistics department for his assistance and patience in analyzing my data. I am additionally thankful to those who pioneered the original study years ago, Dr. Duane Rumbaugh

and Dr. Sue Savage-Rumbaugh, as this project will allow us to to learn from Kanzi and his family of bonobos for many years to come.

The words do not exist to adequately express the undying love and support I have received from my family, Fred Rabinowitz, Gilda Glaubach-Rabinowitz, and Patti Rabinowitz. My parents have always encouraged me to pursue my true interests and passions through education, and I truly would not have accomplished this without them. I am incredibly lucky to have Patti as a sister, friend, confidant, cheerleader, and sounding board. Thank you Mom, Dad, and Patti for your comforting hugs, listening ears, proofreading nights, loving reassurance, and belief in my capabilities and aspirations.

Last but certainly not least, I thank the bonobos, Kanzi, Nyota, Elikya, Maisha, and Teco, who taught me more about patience, compassion, and communication than I thought possible. Despite many frustrations of research and method development, they were a constant reminder of why I study apes. I do not take for granted the amazing opportunity to peak into the minds and souls of these animals who repeatedly surprised me with their individual personalities and intelligence. I am grateful to be reminded of our relationship with other animals and our responsibility to protect them as we learn from their species.

ABSTRACT

The present study expanded upon the ongoing research of bonobos (Pan paniscus) raised in a language-enriched environment at the Ape Cognition and Conservation Initiative. The study subjects, Kanzi, Nyota, Elikya, Maisha, and Teco, display varying degrees of research participation and experience with spoken English and written lexigram symbols. While Kanzi's linguistic and cognitive capabilities have been well documented in his early life, this project evaluated a subset of his current vocabulary. A series of three computerized match-to-sample tasks tested his ability to match a picture to spoken English, lexigram to spoken English, and picture to lexigram symbol for 120 words commonly encountered in his daily life. Kanzi displayed a greater comprehension of spoken English words than their associated lexigrams, although his overall average score was higher than expected for the majority of tested words. Results also revealed that his understanding of individual words was dependent on input modality. An assessment of multiple communication methods used by Kanzi provides data on the receptive capacities of an ape who plays an important role in the study of language development and ape language research. As the remaining four bonobos had limited previous experience in language and experimental research. I developed several training protocols to include them in future studies. By examining potential effects of rearing, environment, and motivation on their testing performance, this project will serve as a foundation for further research on the linguistic abilities of nonhuman primates.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Background and Significance

Human language is unique in its ability to convey meaning with increasingly complex composition and organization, and there has long existed a pursuit to uncover its evolution (Deacon, 1990; Chomsky, 1988; Wade, 1980). Humans exist in extremely intricate societies that require the ability to communicate ideas and thoughts effectively, and therefore, the adaptation of language systems would have been beneficial in ancient hominids, likely increasing the fitness of communicative individuals. Because spoken language does not leave evident traces in the archaeological record, understanding the linguistic capacities of nonhuman primates provides one opportunity to help expose its ancestral history. We often turn to our closest living evolutionary relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), to understand their abilities in language comprehension and production (Kojima, 2003; Greenfield et al, 1990; Gardner and Gardner, 1978; Yerkes, 1925). If language and cognition are intrinsically linked, it follows that studying the linguistic processes of great apes will further our knowledge of the evolution of human language and thought, based on the argument of homology that closely related species are more likely to exhibit similar evolutionary adaptations to selective pressures, or cladistically, that traits shared among closely related species are most parsimoniously considered primitive to that clade.

Although the vocal mechanisms of humans and other mammals are quite similar, subtle anatomical differences prevent nonhuman primates from producing human speech. They both include lungs to generate sound power, a larynx and vocal tract for phonation and articulation, and ears to perceive sounds, but humans have a unique modified anatomy that allows for sophisticated manipulation of the vocal tract and complex speech (Matsuzawa et al, 2006; Kojima 2003). Physical modifications to any portion of the vocal tract can alter a sound's pitch, frequency, duration, or pronunciation. Humans' anatomy allows for rapid modifications of the vocal tract while producing multiple phonemes in a single exhalation, an ability not present in other species (Matsuzawa et al, 2006). Because chimpanzees and bonobos cannot physically acquire spoken language, ape language research often investigates developmental and cognitive traits with the expectation that shared linguistic capacities evolved prior to our last common ancestor. There have been many attempts to teach nonhuman primates human language (Terrace, 1979; Hayes, 1971; Gardner and Gardner, 1969; Kellog, 1933), but previous studies have not examined the acquisition of a novel symbolic language system over an extended period of time. To add to the multidisciplinary field of ape language research, I examined the linguistic competency of bonobos raised in a language-enriched environment at the Ape Cognition and Conservation Initiative (ACCI) in Des Moines, Iowa. Research subjects at ACCI vary in their degree of language enculturation. Two bonobos, Kanzi and Nyota, were actively taught and encouraged to communicate with lexigrams, a novel symbol-based language system (shown in Figure 1.1), while Maisha and Elikya were not. The fifth and youngest bonobo, Teco, has been socially exposed to lexigrams and spoken English, but he had not previously participated in a formal assessment of his ability.

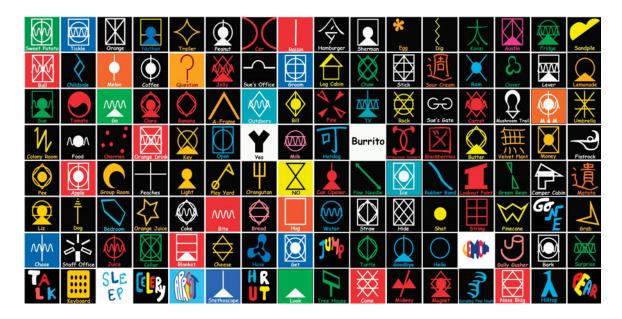


Figure 1.1 Example of one of three panels of lexigram boards. The full keyboard includes three panels with a total of 309 lexigram symbols.

Objectives

While Kanzi's comprehension has been well documented in his early life (Savage-Rumbaugh et al. 2001; Lyn and Savage-Rumbaugh 2000; Savage-Rumbaugh et al, 1993; Savage-Rumbaugh et al, 1984), the published research of his language comprehension has not been maintained with recent experimental methods. In addition, we lack a comparative analysis of his competency, which requires a standardized evaluation of his abilities in comparison with his bonobo peers. Specifically, this long-term bonobo project is lacking a vital comparison of all of the apes' comprehension of lexigrams and spoken English words. Creating a database of their current linguistic competencies will allow for future research to investigate the more detailed processes of language acquisition and comprehension. In order to accomplish this task, Nyota, Elikya, Maisha, and Teco must complete training protocols to become familiarized with various testing methods.

This study provides a current foundational assessment of Kanzi's spoken English and lexigram comprehension, which is necessary for continuing future research of this project and Kanzi's more complex linguistic capabilities. I have also taken the primary steps to create an inclusive body of data on the linguistic competencies of the four remaining bonobos raised in this unique environment. Despite the decades of research conducted with Kanzi, no researcher has yet to directly compare his linguistic competency with that of his peers. Such research will allow for increased understanding of individual, age, experience, and sex variation in language acquisition, as well as produce a baseline reference for future studies.

Recognizing the history and linguistic experience of the subject apes, I predicted that Kanzi would demonstrate the highest performance in the prescribed testing methods. Due to extensive publications of Kanzi's linguistic ability and experience with similar studies (Savage-Rumbaugh et al. 2001; Lyn and Savage-Rumbaugh 2000), I hypothesized that he maintained an extraordinary comprehension of both lexigram symbols and spoken English, despite recent inactivity regarding lexigram use. Furthermore, I expect that Kanzi would yield a higher comprehension of words and objects that he encounters frequently throughout his environment. Although a standardized assessment of the other apes was not completed in the scope of this study, I would also expect that they possess a greater understanding of spoken English than lexigrams. With the exception of Nyota's limited research experience, they were not actively taught any lexigram symbols, but regularly interact with human caretakers and other bonobos who communicate with lexigrams and spoken English, and are therefore predicted to have acquired some linguistic ability.

By assessing multiple methods of communication utilized by Kanzi, I will analyze his relative comprehension of both spoken English and abstract lexigram symbols, determining if lexigram comprehension translates to increased understanding of English for a set of words, as

4

well as if there exists an inherent bias for learning auditory or visual communication systems. The completion of my project allows for further investigation of the linguistic development of extraordinary apes and ultimately, the role of language features vital to our evolutionary lineage.

Bonobo Ecology and Behavior

Studies of captive primates allow researchers to address many complex behaviors that cannot be fully explored in the field. Captive research, however, requires an understanding of the natural species specific behavior and ecology displayed by their wild populations. I will therefore describe such characteristics of *Pan paniscus* relevant to the present study in addition to a review of ape language research. Bonobos (Pan paniscus) are found only in The Democratic Republic of the Congo (DRC), in the Congo River Basin and minimal dry forest and savanna at the edges of their known range in central Africa, and they are only isolated from chimpanzees (Pan troglodytes) by the Congo River (Kano, 1992). Bonobos are often compared to chimpanzees with regard to all aspects of their morphology and behavioral ecology, as the two species of *Pan* share many physical traits and ecological constraints (Kano, 1992). Not described until 1929, bonobos were considered to be a subspecies of pygmy chimpanzees (Coolidge, 1933), and due to a history of political instability in the DRC, there have been relatively short periods of time when researchers have been able to collect data on wild bonobo populations, resulting in limited long-term study groups and research sites. Current studies document only four habituated bonobo communities beginning in 1974, compared to 18 chimpanzee groups under constant observation since 1960 (see Wilson et al. 2014, Extended Data, for summary of number of observer years studying *Pan* species at various sites). Along with their recent species recognition, this may be a catalyst for the prevalence of comparative studies published with regard to the genus Pan.

In addition to the slight morphological differences between bonobos and chimpanzees, there are a number of behaviors that characterize the bonobo as a unique ape species. Indicated by their previous identification as a pygmy chimpanzee, bonobos are more gracile in stature, and are distinguished by pink lips, a dark face, parted dark hair on the head, and the persistence of a white tail tuft into adulthood (Kano 1992; Smith and Jungers, 1997). Both bonobos and chimpanzees live in large multi-male, multi-female social groupings, and while both communities also fission into smaller parties, these parties or sub-groups are larger in bonobos than those of most chimpanzees (Furuichi 1989; Hohmann and Fruth, 2002; Stanford, 1998; but see Pruetz & Bertolani 2009). The greater size and cohesion of bonobos' and travel subgroups is suggested to be related to temporal food availability and decreased competition in their isolated habitat (Mulavwa et al, 2008; Furuichi et al, 2008; Kuroda, 1979). Like chimpanzees, bonobos are highly frugivorous, but Stanford (1998) suggests that bonobos are not limited by the same competition for resources as chimpanzees, allowing them to adopt a diet high in widely available pithy foods in order to mitigate the complications of unreliable fruit patchiness. Additionally, individual subgroup composition differs between the two species, with bonobo parties often including more unrelated females and all-female subgroups (Furuichi et al, 2008; Hohmann and Fruth, 2002). Furthermore, the social behavior and within group relationships of bonobos best distinguishes them from chimpanzees.

Similar to chimpanzees, male bonobos remain within their natal group, while females disperse around the time of sexual maturity, at approximately 7-8 years old (Hohman and Fruth, 2002; Kano, 1992). Although males may create strong affiliative bonds with one another due to their relatedness with the other group males, females are not dominated by males as in chimpanzee groups. In fact, female bonobos are considered to be codominant or dominant to males (Furuichi,

1989; Kano, 1992). Competition within groups is more relaxed in bonobos than in chimpanzee groups, with fewer displays of aggression and agonistic behaviors between males (Wilson et al 2014; Wrangham 1999; Stanford 1998). Despite the popularized belief that bonobos are a peaceful species, both hostile and affiliative interactions have been observed between different communities of bonobos in the wild, more than half of which involve some amount of agonism (Wilson et al, 2014; Hohmann and Fruth 2002; Stanford, 1998). In bonobo communities, bouts of high aggression or tension in bonobos are often mitigated by social-sexual behaviors, especially between female individuals, in contrast to more aggressively territorial chimpanzees (de Waal 1995; Kano, 1992).

Bonobos are susceptible to many threats due to their unique behavior and geographic species range, making their conservation a priority for researchers. According to the International Union for Conservation of Nature (IUCN), bonobos have been endangered since 1996 and classified as vulnerable since 1986. Similar problems face bonobos' conservation efforts as seen in other great ape populations (i.e. bush meat, pet trade, and deforestation), however due to the long standing political instability in the DRC, studies of bonobos are rare and increasingly important to their survival. Many local cultures recognize bonobos' similarity to humans and hold a customary taboo against hunting and eating the primate, although dynamic shifts of populations result in greater instances of ape poaching. Additionally, the presence of militant groups throughout the country provides easier access to forested habitats, as well as guns and ammunition (Fruth et al, 2014, Reinartz & Bilia-Isia, 2000). The DRC strives to maintain a commitment to conservation with federally protected land, animal sanctuaries, and wild reintroductions (Andre et al, 2008), and researchers are hopeful that the unique behavioral ecology of this species will permit a more successful reintroduction process. It is imperative to continue to monitor this species,

furthering our understanding of their behavior to ensure the survival of released individuals, as well as improve the status of wild populations.

Communication in Pan

Catalogues of complex bonobo and chimpanzee vocal and gestural communication have been established in wild and captive populations (Pollick et al, 2008; Wrangham et al, 1994; Goodall, 1986). Although bonobos' communication strategies are comparable with those of chimpanzees, bonobos' vocalizations are characterized by a higher pitch (Pollick and de Waal 1998; Kano 1992), as well as slight variations that reflect differences in social behavior, including more frequent invitations for copulations and fewer agonistic encounters in bonobos (de Waal, 1988). The primary bonobo language studies have been completed in captivity (de Waal, 1988), but Bermejo and Omedes (1999) have determined that the wild bonobos at the Lilungu site consistently use 15 identifiable vocal units and 19 combination sequences in predictable contexts, most often during feeding and social behaviors.

It is hypothesized that vocalizations are more emotive and inflexible than gestures (Goodall, 1986; Wrangham et al, 1994), but there is evidence for learned dialects in apes (Goodall, 1986; Mitani, 1992; Crockford 2004) and symbolic vocalizations in several other primate species (Slocombe and Zuberbuhler, 2005; Zuberbuhler, 2000; Seyfarth and Chaney, 1992). Current research also indicates the ability of chimpanzees and bonobos to learn and modify vocalizations in various social situations (Clay et al 2015; Hicks et al 2013; Hopkins et al, 2007), which implies a cognitive plasticity previously thought to be a uniquely human trait. There has been further analysis of context-specific vocalizations in bonobos, revealing that the acoustic structure of female copulation calls is not dependent on reproductive receptivity or identity of sexual partner

(Clay and Zuberbuhler, 2011; Taglialatela et al, 2003). Food calls, however, provide evidence of referential vocalizations, as sequences differ with food type, as do the listeners' response (Clay and Zuberbuhler, 2009). Specifically, food peeps display functional flexibility in a variety of contexts similar to that of prelinguistic humans, furthering evidence for complex linguistic capacities in nonhuman primates (Clay et al 2015). Long-term vocal recognition is also reported in bonobos, suggesting the importance of cognitive skills in highly social species (Keenan et al, 2016).

Non-vocal signaling also differs between the two species of *Pan*, as interactions between bonobos include a greater instance of eye gaze and tactile gestures than those of chimpanzees (Frolich et al 2016; Rossano 2013). Studies documenting bonobos' non-vocal communication have identified dozens of discrete manual gestures, many of which are observed in a variety of social contexts (Pollick and de Waal, 2007; Pollick et al, 2008; de Waal, 1988). Multimodal communication is often observed as apes combine types of communicative symbols, including vocalization, facial expression, posture, and gesture, allowing for increased contextual flexibility (Musgraves, 2012; Pollick et al, 2008). Although field studies of wild populations are vital to the understanding of nonhuman primate species, it is challenging to clearly examine the acquisition of such communicative abilities without the experimental control provided by captive settings.

Captive Considerations

There exists an issue in primate research concerning the differences between captive and wild populations of the same species of primate. Consistently, studies do their best to illustrate differences between the activities and behaviors of captive and wild populations as a method of creating healthier habitats for the captive subset. Researchers cannot deny that captivity and

9

environment may affect animals' behaviors, but over the past 40 years there has been a movement to create captive habitats to more closely resemble the wild conditions of the captive animal (Stevens et al, 2008). Originally, captive animals were kept in primitive cages with little enrichment simulating anything near their native homes, and recent attention and increase in funding have been focused on this cause of naturalizing habitats (Coe, 1989). Ideally, this would allow for the animals to behave in a way most similar to their "natural" pattern of activities, i.e., species-specific behavior. Using this information, captive institutions may better design habitats to best stimulate the primates who are housed there.

Furthermore, cognitive ability can be affected by the environment and the enrichment given to the apes. It is especially important to consider this phenomenon when understanding captive bonobos and other primates with complex cognitive function. With regard to enrichment, the more stimulation and puzzle devices available to the apes, the more their natural behaviors, as well as their cognitive capabilities, will develop. Many enrichment devices employ food in order to coax tool use and problem solving acts from the apes, and successful design creates beneficial social development and successful reproductive behaviors. This greatly increases the need for successful and complex captive environments (Stoinski et al, 2001). Dependent on research goals, projects may also be designed to incorporate rewarding enrichment for the subjects, as it promotes more natural behaviors and serves as increased motivation for study participation. While conservation of wild species is a goal of many researchers, well-maintained captive settings can serve as an important instrument in learning about primate behavior and ecology, as well as providing a connection between the layperson and nonhuman primates.

10

Great Ape Language Studies

Human and nonhuman primates are highly social individuals, and communication plays a vital role in the structure of many species. Bonobos and chimpanzees, our closest primate relatives, do not possess our level of linguistic complexity, but understanding their potential communicative abilities can provide insight to the relatively short evolutionary history of language. There exist numerous studies of the communications of wild primate species, though these are few relative to studies of ecology and other types of behavior, especially in terms of ape research (Arcadi, 1996; Bard, 1992; Crockford and Boesch, 2003). Although it is necessary to study and understand apes' species-specific communication strategies, controlled language studies allow researchers to precisely quantify linguistic abilities within the complex skillset required for language and language learning. Although withstanding considerable critique, ape language studies offer the opportunity to dissect numerous aspects of language production and comprehension that can inform our understanding of human communication strategies.

Throughout the history of this multidisciplinary field, we can document several research concentrations. Initially, there was considerable focus on teaching great apes human language. Several efforts to raise chimpanzees to speak English (Kellog, 1933; Hayes, 1951) were largely unsuccessful due to anatomical constraints of the nonhuman vocal tract (Kojima, 2003). In both studies, young chimpanzees, Gua and Vicki, respectively, were cross-fostered with human families testing the hypothesis that through instruction and social stimuli, the chimpanzees would learn to speak as human children do. Because their ultimate language production was minimal and inarticulate, research then shifted to gestural communication, employing chimpanzees' natural use of symbolic gestures to acquire American Sign Language (Gardner and Gardner, 1969; Terrace, 1979).

Initiated by the Gardners in 1967, Project Washoe involved Washoe, a female chimpanzee, cross-fostered with a human family and exposed to American Sign Language (ASL) as a Deaf child would in a signing environment. Roger Fouts continued the project, eventually teaching several other chimpanzees ASL. Each individual varied in their language learning, but Washoe acquired approximately 200 signs, which she used to communicate with other apes and human caretakers (Gardner and Gardner, 1985). Washoe has since passed, but several of the project's remaining chimpanzees continue to use ASL, including Washoe's adoptive son. Terrace (1979) also attempted to teach a chimpanzee, Nim Chimpsky, sign language. Focusing on more objective methods, he utilized instructional sessions in a home setting, ultimately concluding that Nim could not fully learn the language and was merely reproducing gestures he saw. Reviews of such ASL studies note the consistent understanding and use of signs, but critique the lack of grammatical syntax and novel ideas, as well as the abundance of anecdotal evidence (Terrace, 1985). Additionally, the differing anatomy of apes' hands, most notably a much longer palm than humans', may inhibit accurate understanding of their signs, leading to greater interpretation from their caretakers. Such critiques inspired a new method of researching apes' language abilities, implementing objective symbolic representation for words.

The origins of ACCI began with the LANA (Language Analogue) project, pioneered by Duane Rumbaugh and Eric von Glaserfeld in 1971 at the Language Research Center in Atlanta, Georgia. Lana, a young female chimpanzee, learned to communicate with researchers on a computerized keyboard using created symbols, or lexigrams following simple grammatical rules (Rumbaugh, 1977). Upon joining the project, Sue Savage-Rumbaugh taught the lexigram system to two chimpanzees, Sherman and Austin, focusing on vocabulary and categorization (Savage-Rumbaugh, 1986). Bonobos were included in the research in 1980 with the addition of Matata, a wild-born female, who did not successfully acquire the skills to comprehend the lexigrams after exhaustive instruction (Savage-Rumbaugh and Lewin 1994). Her adopted son, Kanzi, however, spontaneously began to use lexigrams to communicate with researchers without formal training at a young age.

With English comprehension comparable to a two-and-a half-year-old human child, eightyear-old Kanzi then became the focus of the Language Research Center (Savage-Rumbaugh et al, 1993; Savage-Rumbaugh and Lewin, 1994). Kanzi's daily life was enriched with communication and lexigrams, allowing him to acquire language through enculturation, as seen with human children. Kanzi has established a substantial vocabulary, and continues to utilize lexigrams in regular communication with human researchers and caregivers (Savage-Rumbaugh and Lewin, 1994; Segerdahl et al, 2005). Matata's daughter, Panbanisha (deceased 2012) also participated and excelled in linguistic research (Savage-Rumbaugh, 1984). As language is acquired through generations, researchers included Panbanisha's offspring, Nyota and late Nathan (deceased 2009), in the lexigram project. Maisha and Elikya, also born to Matata, have served as control subjects without participating in any structured linguistic studies. Although there is great potential for enlightening research with this unique group of bonobos, there is not currently any published data on their inclusive linguistic competencies.

There has recently been a substantial shift in the bonobos' lives at ACCI. In 2014, new directors and care staff reformed the institution, the Great Ape Trust, prioritizing the apes' welfare and research participation. Research production has since increased, and the present study is the first in many years to formally assess the bonobos' language competencies with current data (Pedersen 2012; Savage-Rumbaugh 1986). Other studies have focused on tool use (Roffman et al 2012), and vocal and multimodal communication (Klag 2009; Musgraves 2012), and the majority

of previous research included Kanzi as the only participant. Although ape language studies have historically been criticized, most recently by Cohen (2010), we cannot discount their potential to contribute to our understanding of the linguistic and cognitive abilities of our last common ancestor. With the ability to research discrete aspects of language and language learning in controlled analyses, we may further analyze underlying mechanisms for language processing in nonhuman primates, and therefore precursors of human communication.

CHAPTER 2

RESEARCH METHODS

Within this chapter, I will address the primary sections of this study and its methodology. I will first describe the study site and the five bonobos who participated in this project. Kanzi (35 years old; male) became my main subject, followed by Nyota (17, male), Elikya (17, female), Maisha (16, male), and Teco (5, male). I then detail the data collection methods, outlining the distinct procedures developed for individual apes. Lastly, I will summarize the methods used to analyze the data.

Study Site

The Ape Cognition and Conservation Initiative (ACCI), formerly the Great Ape Trust, is located at 4200 Evergreen Avenue, Des Moines, Iowa. ACCI houses five bonobos on 230 acres of Iowa hardwood forest, including 20 acres of ape-accessible outdoor space. The bonobos interact daily with human caretakers, utilizing spoken English and lexigrams, as well as nonverbal behavioral communication. They are socially housed, with regularly alternated grouping to emulate the fission-fusion grouping of wild bonobos (Furuichi et al, 1998; Idani, 1990). The research station accessible to the apes consists of a touch screen monitor mounted on a platform in an indoor enclosure, with the experimenter in an adjacent room separated by glass, as seen in Figures 2.1 and 2.2.

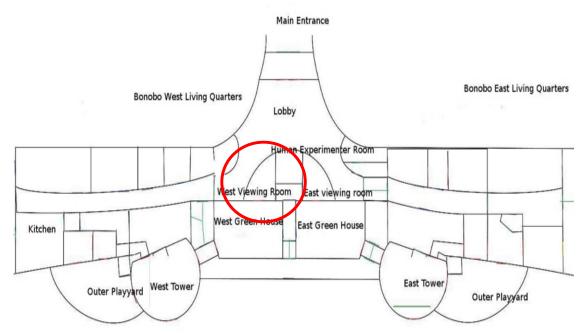


Figure 2.1 Schematic of ACCI building: The bonobos were tested in the west viewing room with the researcher in the human experimenter room.



Figure 2.2 Setup of testing station: Elikya sits on the platform in the experimental viewing room, while a researcher controls the test from the human experimenter room.

Subjects

Kanzi (m) was born in 1980 at Yerkes National Primate Research Center, Atlanta Georgia. Raised by adoptive mother Matata, he was present during her linguistic and lexigram training at the Language Research Center (LRC). Without previous formal instruction, Kanzi displayed understanding of spoken English and lexigrams at two and a half years old. His spontaneous acquisition of language systems has since been a primary focus of ape language research, as scientists continue to actively teach him lexigram symbols and test his competency.

Nyota (m) was born in 1998 at the LRC to Panbanisha. Co-raised by Panbanisha and humans, he was exposed to lexigrams and spoken English during development and enjoys social interaction. While there is anecdotal evidence of his understanding of English and lexigrams, he has limited experience with formal experiments testing his level of linguistic competency.

Elikya (f) was born to Matata at the LRC in 1997. As a member of the control group, Elikya was not taught to use lexigrams or spoken English. She is more involved with other bonobos and species-typical bonobo communication and has shown limited interest in the lexigrams. Her vocabulary and language skills have never been formally tested. Elikya is the mother of Teco, who is also present at the Ape Cognition and Communication Institute.

Maisha (m) was born to Matata in 2000 at the LRC. Like Elika, Maisha was a control subject and therefore not actively exposed to lexigrams or spoken English during development. He was raised with more bonobo interaction than with human caretakers and scientists, and his linguistic competency has not been clearly quantified.

Teco (m) was born in June 2010 at ACCI and was co-reared by human caretakers and his mother, Elikya. There has not been any formal instruction or assessment of Teco's linguistic

capabilities, but he seems to have some understanding of both spoken English and limited lexigrams.



Figure 2.3 Research subjects from top left: Kanzi, Elikya, Nyota, Maisha, and Teco

Experimental Methods

Research was conducted during the months of May 2015 through January 2016, between 11:00 and 16:00 hours, dependent on the daily schedule of the care staff and bonobos. All tests were performed based on voluntary participation of the apes and in accordance with ACCI's IACUC protocol. The touchscreen (88.8 x 50 cm) was connected to a Macintosh computer controlled by the researcher, and the software was written by Ben Thompson and Kenneth Schweller of Buena Vista University. Rewards of grapes, peanuts, and raisins were provided through a dispenser, following individual dietary restrictions, and subjects were alone in the testing enclosure during all reported trials. All subjects participated in delayed match-to-sample programs

of the same basic construction, displayed in Figure 2.4, with individualized variations as detailed in Tables 2.1, 2.2, and 2.3. Both correct and incorrect responses resulted in distinct playback sounds, and the apes were rewarded for correct answers. There are over 300 lexigram symbols on the provided boards, but 120 words were selected for the scope of this study. With the exception of Training 5, all tasks tested an identical list of 120 nouns, and their corresponding pictures and lexigrams, that are commonly encountered in the apes' daily lives, listed in Appendix A. This word set was purposefully selected with all five bonobos in mind. Because Kanzi's earlier life experiences were much more diverse and human-oriented, it is likely that he has encountered infinitely more words and ideas than the other apes. Additionally, the lexigram keyboard has been expanded over decades of research with Kanzi, with many symbols that only Kanzi has seen. I therefore selected a set of words that all of the bonobos were likely to have heard or seen during their lives, regardless of research experience.

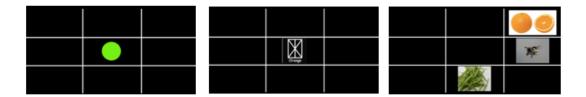


Figure 2.4 An example of Kanzi's Lexigram to Picture test. Trials began with a green circle, initiating the task when touched. The subject is then presented with a sample stimulus, followed by the target and distractor choices, from which an answer was chosen. Each task progressed only once the ape touched the screen to continue the trials

Kanzi

Kanzi's vocabulary was assessed using three computerized match-to-sample tests. He participated in a series of three tests to test his ability to match a (1) picture to spoken English, (2) lexigram to spoken English, and (3) picture to lexigram symbol. The components of each task are

outlined in Table 2.1. The three tasks were randomized throughout the testing period, and a minimum of 50 exposures were included for each word. In the English to Picture and Lexigram to Picture tests, at least three easily identifiable images were included for each word (Appendix B), as to avoid having Kanzi associate the word to particular pictures, rather than the general concept itself. Although he has participated in similar testing prior to this project, preexisting images were discarded and substituted with a newly selected set.

Test Lexigram to **English to Picture English to Lexigram** Picture English Lexigram Stimulus English Picture Lexigram Picture Response **Trials per Session** 75 75 75 Word Set 120 120 120 2 2 Distractors 2 1 1 1 **Intertrial Interval (sec) Reward Rate** 2 correct 2 correct 2 correct

 Table 2.1 Summary of three protocols assessing Kanzi's comprehension of English and lexigrams

Nyota, Elikya, Maisha, and Teco Training

I proposed that the remaining four bonobos use identical testing protocols as Kanzi, with the following minor adjustments. Nyota, Elikya, Maisha, and Teco were to be rewarded after each correct response, whereas Kanzi received a food reward after every two correct responses, and they were also tested with only one distractor instead of two. The other bonobos did not have previous experience participating in consistent research projects, and therefore required training to complete the task. Multiple training protocols were implemented, but the bonobos did not reach the competency required to progress to testing at the time of this study. Table 2.2 outlines the series of training tasks and their components, with alterations made under the guidance of Drs. Bill Hopkins, Jared Taglialatela, and Kenneth Schweller. Training Teco for the task also presented a unique set of problems, which caused researchers to attempt multiple different protocols, described in Table 2.3.

	Training 1	Training 2	Training 3	Training 4	Training 5	Training 6
Dates	6/12-6/17	6/24-7/23	7/25-7/28	8/2-9/22	10/1-1/7	11/7-1/7
Subjects	Ma, El, Ny, Tc	Ma, El, Ny, Tc	Ma, El, Ny	Ma, El, Ny	Ma, El, Ny	Ny
Stimulus	Eng + Lex	Eng + Lex	Eng + Lex	Picture	Picture	Picture
Response	Lexigram	Lexigram	Lexigram	Picture	Picture	Picture
Word Set	120	120	120	120	108	120
Distractors	1	1	1	1	1	1
Trials per Session	25	25	75	75	75	75
ITI (sec)	5 if wrong	1	1	1	1	3
Gap	0	2 (hor)	2 (vert)	2 (vert)	2 (vert)	2 (vert)
Correction	No	Yes	Yes	Yes	Yes	No
Reward Rate	Every correct	Every correct	Every correct	Every correct	Every correct	Every correct
Misc. Notes	Stimulus stays			No start button; set criterion	Remove words	

Table 2.2 Summary of training protocols performed on Maisha (Ma), Elikya (El), Nyota (Ny), and Teco (Tc). Includes differences between tasks, and unique properties are italicized.

Training 1 was the training protocol in place at ACCI prior to the current study. Researchers had previously begun to work with several of the apes in match-to-sample testing; however, the sessions were not consistently implemented or recorded in the terms of this project. It became apparent that the bonobos did not fully comprehend the task during Training 1, so alterations were made. When the stimulus remained on screen during the answering phase, the apes continued to choose it as a response, and it was therefore removed. Training 2 also added a gap between the target and distractor horizontally to ensure definitive answer choice, as pictured in Figure 2.5a.

The five-second delay after incorrect answers was also removed, as the apes lost focus or motivation during the long intervals. Lastly, Training 2 introduced a self-correction feature in which the target and distractor remained on the screen until the correct target was chosen. There was no feedback sound for incorrect choices, and the apes were rewarded for every correct response. Throughout Training 2, the bonobos were observed to display a side bias when selecting answers, and the Training 3 protocol altered the orientation of the choices, as pictured in Figure 2.5b. We also increased the number of trials per task session, as their attention and motivation increased.

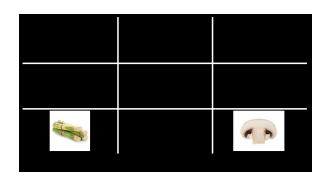
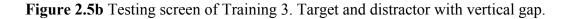


Figure 2.5a Testing screen of Training 2. Target and distractor with horizontal gap.

	1



Without substantial progress in performance, researchers chose to simplify the training protocol to a picture-matching task. In Training 4, the bonobos were asked to match the target to identical stimulus pictures for the 120 words, with only one distinct image included for each word.

The initial green start cue was no longer necessary without an auditory stimulus, and therefore removed to limit confusion in training. Once an individual reached a score of 50 correct responses out of 75 for five consecutive sessions of Training 4, they could progress to further testing. Nyota improved most consistently on Training 4 but was taking much longer than predicted to reach the set criterion. It was noted that he and Maisha perseverated on several words during training, in that they would continue to choose the incorrect picture without making the correction, therefore a collection of these words were removed from the set for Training 5, listed in Appendix C. Nyota was then the only individual to pass the criterion for the previous training protocols, so he progressed to Training 6. This task removed the self-correction feature and increased the intertrial interval to three seconds. His motivation and performance continued to improve, but he did not exhibit consistent understanding of the task at hand.

While highly motivated to participate in testing, Teco presented a number of difficulties during training sessions. Lacking focus, he touched whichever image he saw first without looking at the entire screen immediately after the stimulus display. He also regularly used both hands to press both the target and distractor simultaneously, preventing the formation of a choice-reward association. After minimal improvement in Trainings 1-3, several individualized protocols were attempted with Teco, described in Table 2.3. The Teco P protocol was developed to discourage his touching more than one image by playing a loud sound when the screen was touched in multiple places. This method was quickly discarded, however, due to Teco's apparent confusion and stress during testing. We then shifted focus to training him to only use one hand to select an answer by removing all distractors for various trial lengths, with one distractor trial interspersed. For Teco 20, 10, and 15, he was rewarded every two trials without a distractor and every correct response with distractors. Again, he did not seem to make considerable progress, and researchers ultimately

ceased Teco's training for this task. The bonobos continue to be trained on computerized testing as part of ongoing research at ACCI.

	Teco P	Teco 0	Teco 20	Teco 10	Teco 15
Dates	7/9-7/12	7/14-7/26	7/17-7/21	7/21	7/23
Stimulus	Eng + Lex	Eng + Lex	Eng + Lex	Eng + Lex	Eng + Lex
Response	Lexigram	Lexigram	Lexigram	Lexigram	Lexigram
Set	120	120	120	120	120
Trials per Session	75	75	75	75	75
ITI (sec)	1	1	1	1	1
Distractors	0	0	1	1	1
Trials Hidden Distractor	0	75	20	10	15

Table 2.3. Summary of training protocols for Teco

Data Analysis

In reporting the collected data, sessions with fewer than 10 trials were not included, as were sessions with potentially increased distractions. Distractions were defined as the presence of other bonobos or care staff in or around the testing enclosure, a public tour, or engaging enrichment items. I calculated the mean session score for all testing and training protocols, noting the total number of trials completed by each individual. Because Kanzi was presented with three answer choices in each trial, he was expected to perform at 33% by chance, and similarly, the score at chance level was 50% for the other bonobos presented with two choices. Mean scores found to be significantly greater indicate some level of linguistic comprehension. To compare Kanzi's performance on each competency test, an Analysis of Variance (ANOVA) analysis was applied to the average session scores of each task, with the null hypothesis of equal scores on all tests.

CHAPTER 3

RESULTS

The following chapter reports the findings of this study. I first discuss Kanzi's performance on in the English to Picture, English to Lexigram, and Lexigram to Picture tasks, reporting his average score for each treatment. I then explore his overall accuracy of the tested words across all tasks, highlighting the differences in average scores dependent on treatment type. The final section summarizes the results of each training protocol used by Nyota, Elikya, Maisha, and Teco.

Kanzi

Kanzi has extensive previous experience with testing methods similar to the ones used in this study (Pedersen 2012; Lyn 2007; Savage-Rumbaugh at al 1986) and did not require an additional training period before the assessment. He was highly motivated and would work for long uninterrupted periods of time; therefore, his data output was primarily limited by the amount of food rewards allowed by his daily calorie intake restrictions. With over 6,000 trials completed in all tasks, he was presented with each word stimulus between 50-60 times in each treatment. A summary of Kanzi's testing results is presented in Table 3.1. As predicted, he had the highest average session score on the English to Picture test (76.2%), though his performance in the English to Lexigram task (73.4%) was not significantly different. While Kanzi scored similarly in both tasks with a spoken English stimulus, he showed a significantly lower average score in the Lexigram to Picture task (65.4%) when compared with the other two tests (p<0.01), although still performing above chance levels.

Table 3.1 Summary of Kanzi's performance on English to Picture, English to Lexigram, and Lexigram to Picture tests. Average percent correct for test sessions are reported, excluding all sessions with fewer than 10 trials completed.

	Trials Correct	Total Trials	Average %	St. Error
Eng to Pic	5202	6663	76.2	0.009
Eng to Lex	4954	6749	73.4	0.007
Lex to Pic	4463	6779	65.4	0.005

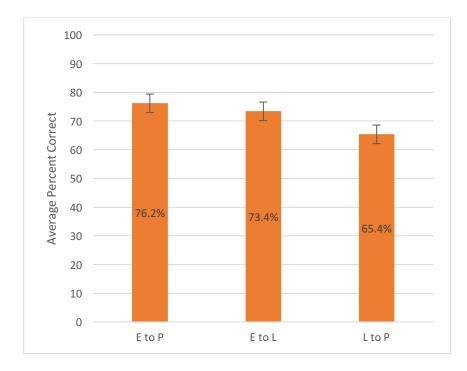
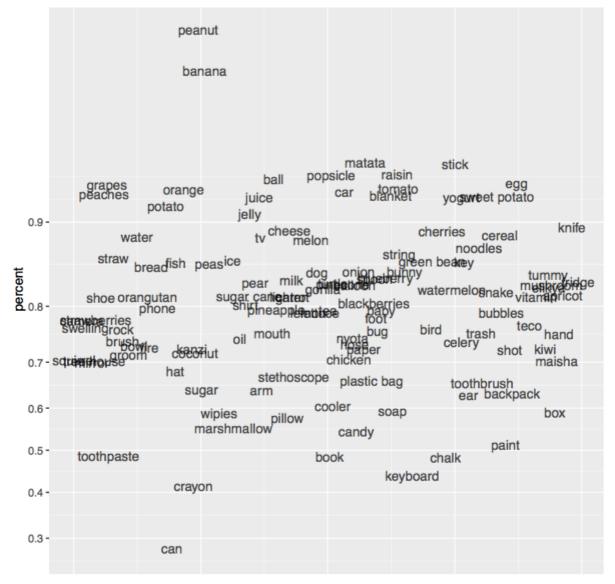
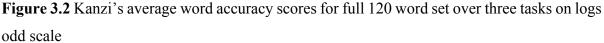


Figure 3.1 Average scores of English to Picture, English to Lexigram, and Lexigram to Picture sessions.

Although Kanzi scored higher on the English to Picture task overall, his performance was influenced by his individual comprehension of the tested words. Figure 3.2 displays the average accuracy of all 120 words over the three tests, the ten highest and lowest of which are shown in Table 3.2, and all average scores are listed in Appendix D. The top three words with the highest percent correct are "peanut," "banana," and "Matata," with 97.3%, 96.3%, and 92.0%,

respectively, and the lowest ranked words are "keyboard," "crayon," and "can," with 37.0%, 35.0%, and 22.7%. Despite his lower overall score on the Lexigram to Picture task, Kanzi scored higher than expected by chance for the vast majority of tested words, as seen in Figure 3.2.





Word	Rank	Average %	Word	Rank	Average %
peanut	1	97.3	pillow	111	49.0
banana	2	96.3	marshmallow	112	47.7
Matata	3	92.0	candy	113	46.7
stick	4	91.7	paint	114	45.0
popsicle	5	91.3	toothpaste	115	41.0
raisin	6	91.3	book	116	40.3
ball	7	90.7	chalk	117	40.3
egg	8	90.0	keyboard	118	37.0
grapes	9	90.0	crayon	119	35.0
tomato	10	90.0	can	120	22.7

Table 3.2 Kanzi's average accuracy of ten highest and lowest scoring words over three tasks.

Kanzi also exhibited varied word scores dependent on task type, meaning that he has a higher accuracy of certain words in spoken English or lexigrams. While his English stimulus scores were higher for the majority of words, Kanzi performed better in the Lexigram to Picture tests for some. Figure 3.3 displays the top 20 words ranked by his English to Picture scores, with their English to Lexigram and Lexigram to Picture scores as well. Interestingly, there is not a consistent difference in performance between the tasks, as it is highly variable by word and stimulus type.

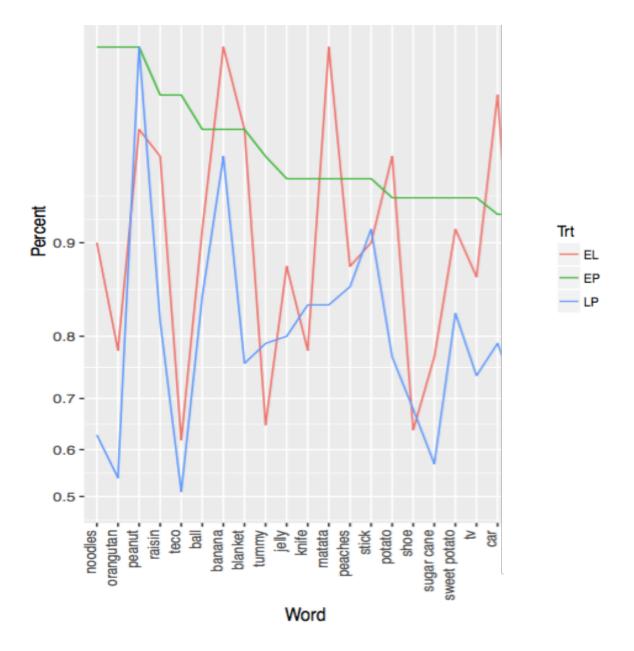


Figure 3.3 Percent correct of highest 20 words in English to Picture test, compared to scores in English to Lexigram and Lexigram to Picture on log odds scale

Nyota, Elikya, Maisha, and Teco Trainings

Nyota, Elikya, Maisha, and Teco had varying levels of motivation and success in each training protocol, and their performances are summarized in Tables 3.3 and 3.4. Among the three adult bonobos, Nyota showed the greatest interest and motivation in testing, as well as noticeable

improvement throughout, so his training was prioritized over that of the other apes. Elikya and Maisha were not consistently motivated to participate, rarely completing full sessions of 25 or 75 trials. Maisha participated in the fewest number of training sessions, as he only completed 14 trials in one session of Training 1 and zero of Training 3. While initially interested in the increased human interaction, they did not pay attention to the tests and ultimately lost interest without constant rewards. Nyota performed above 50% chance for Trainings 3-6, and although Elikya's and Maisha's performances improved with the modified tasks, they did not pass the criterion to progress training.

Table 3.3 Summary of training of Nyota, Elikya, and Maishsa. Total trial numbers and average percent correct for training sessions are reported, excluding all sessions with fewer than 10 trials completed.

Training Protocol		Nyota			Elikya			Maisha	
11000001	N Trials	Avg. %	St. Dev.	N Trials	Avg. %	St. Dev.	N Trials	Avg. %	St. Dev.
1	111	29.0	0.17	103	53.8	0.27	14	42.0	-
2	1013	50.9	0.12	173	43.8	0.19	191	40.7	0.24
3	683	56.7	0.07	56	23.5	0.06	0	-	-
4	6241	61.0	0.06	2230	49.9	0.09	2035	48.4	0.07
5	1161	66.0	0.06	617	49.0	0.08	697	49.5	0.07
6	1978	65.7	0.07	0	-	-	0	-	-

In the short time he participated, Teco completed a considerable number of sessions over six training procedures. He was always very interested in working but primarily motivated by food rewards and interaction with researchers, while paying minimal attention to the task at hand. Teco's average session score was not above 50% for the first three trainings, but clearly increased in training protocols with limited distractors. Despite the potential for his improvement, Teco's training was stopped due to the time constraints of this study and uncertainty of the causes of his challenges.

Table 3.4 Summary of Teco's training. Total trial numbers and average percent correct for training sessions are reported, excluding all sessions with fewer than 10 trials completed.

	N Trials	Avg. %	St. Dev.
Training 1	490	49.8	0.16
Training 2	989	38.3	0.14
Teco P	385	35.0	0.28
Teco 0	458	100	0
Teco 20	741	97.8	0.02
Teco 10	314	94.9	0.03
Teco 15	299	99.3	0.01

CHAPTER 4

DISCUSSION

Language Learning

There are many theories explaining the progression of human language acquisition, some of which may be applied to the apes of this study. Although I do not claim that the bonobos at ACCI possess fluency in a human or human-like language at its current state, this and future ape language studies can offer understanding of the linguistic properties of our shared evolutionary ancestors. The present study in particular also examines the process of learning an interactive and cognitive task, which possesses some similarities to the act of language learning.

Kanzi's greater understanding of spoken English compared to visual symbols prompts considerations of the cognitive and developmental aspects of learning visual and auditory word referents. In human development, prelinguistic infants acquire the skills to receive and understand language prior to producing it, primarily in the mode of auditory input (Lightbown & Spada 2013; Hoff 2009). Given that bonobos' species specific communication heavily relies of complex vocalizations, they may be more biologically adept at discerning spoken words than graphical symbols that they would not naturally encounter, especially during development. The widely accepted critical period hypothesis (Lenneberg, 1967) asserts that animals are innately programed to acquire skills, including language, at certain points in development, and that later attempts at learning are unsuccessful in the absence of necessary input past a particular age. This argument is challenging and unethical to reproduce and prove in nonhuman primates, but it is likely another source of varied results among the five bonobos, most notably the lesser knowledge of lexigrams and English observed in Maisha and Elikya, the control subjects of the original lexigram studies. Not only is it necessary for children to acquire their first language at a young age, but studies show that second languages are also affected by age of acquisition (Lightbown & Spada 2013; Patkowski 1980). Under the assumption that the bonobos' primary communication system would be their species-specific communication, we may say that Kanzi began to learn both lexigrams and English as secondary languages. As an infant during Matata's instruction, he was exposed to new methods of communication in an environment similar to that of a human child raised with multiple languages. Studies have also revealed evidence of interactions between Kanzi's various communication strategies, as is common in bilingual children (Lightbown & Spada 2013), As Hopkins et al (1991) found that Kanzi's vocalizations differed from species-typical bonobo calls and shared linguistic features with spoken English. Combined with his early language exposure and seemingly high motivation, Kanzi's increased positive interaction associated with language use is likely another contributing factor to his greater vocabulary and comprehension than the other bonobos.

While Nyota did not receive research-driven human interaction to the same extent as Kanzi, his upbringing involved significantly more human enculturation than Elikya's and Maisha's. That he also consistently displayed higher motivation and understanding of the computerized tasks than the other apes further indicates that supportive interaction early in life has lasting effects in later years. The interactionist perspective of human language acquisition emphasizes the importance of learner interaction during the development of both first and second languages (Lightbown & Spada 2013), and Vygotsky (1978) argues that conversational input is necessary for first language acquisition, as language is developed through social interaction. Furthermore, positive interactions with conversation partners, both with adults and peers, provide structure upon which language skills build throughout acquisition. Interaction is equally vital in second language learning, as

fluent speakers provide meaningful input and corrective feedback (Long 1996). Early research and with Kanzi included such aspects of interaction and conversation that the other bonobos lacked, influencing their lack of English and lexigram comprehension.

Kanzi

As predicted, Kanzi performed well above chance on all three comprehension tasks. That his average session scores for English stimulus tests were significantly higher than the lexigram stimulus test supports my hypothesis that Kanzi has a greater understanding of English words than their lexigrams. These results are unsurprising, as Kanzi and the other bonobos are constantly surrounded by spoken English every day, both in direct human-bonobo interactions and hearing the volunteers and care staff communicate with each other at ACCI. Another potential factor is that the recorded English stimuli were easier to hear while testing. Precautions were taken to minimize distractions, but it is possible that an auditory mode of input was easier to associate with the provided responses in the structure of this study.

Although people regularly use lexigrams to communicate with Kanzi, it is nearly always paired with spoken English. While talking to Kanzi, we often point to corresponding symbols on lexigram boards, and he reciprocates with the keyboards mounted in his enclosures. We do not, however, rely solely on the limited number of lexigrams to formulate complete and complex sentences that we can easily communicate through speech. Though lexigrams are not the most efficient strategy for people to relay information, they are quite effective for Kanzi, who cannot speak, to inform his caretakers of simple requests and needs. A core goal of any system of communication is to transmit information and meaning from a producer to a receiver, and the data revealed a relationship between the type of input Kanzi received and his average task score. Both spoken words and visual symbols are abstract representations of the tested words, but the present study primarily evaluated Kanzi's receptive comprehension, rather than his language production of such referents. Although English is the primary mode used by humans to communicate with the bonobos, Kanzi often utilizes the lexigrams to communicate his thoughts to others. This may explain his higher performance in the tasks with spoken input, regardless of the mode of his responses. It is also likely that there has been a decrease in lexigram use from previous years while Kanzi was participating more frequently in research projects (Savage-Rumbaugh and Lewin, 1994; Segerdahl et al, 2005), leading to a greater dependence on spoken English in communication for many common words.

The results of this study allows us to assess Kanzi's vocabulary of the 120 tested words to an extent that has not been previously explored with great detail. As seen in Table 3.2, the average word score of the three tasks ranges from 22.7% correct ("can") to 97.3% ("peanut"), and the next highest scored words are "banana" and "Matata." We can infer that he is more likely to genuinely understand words that are important in his daily life, which is consistent with the highest scoring words being for two strongly preferred food items and for his mother, Matata. Kanzi frequently uses the lexigram board to request food, as he was often rewarded and encouraged with dietary treats throughout his life. In fact, seven of his highest ten words are foods or drink, compared with only two of the ten lowest scoring words. Kanzi's word comprehension could also reflect behaviors typical to bonobos. Wild bonobos spend up to 50% of their daily activity feeding or foraging, so the ability to identify food items would be beneficial and prioritized as well (Kano, 1992). In the female-dominant social system of bonobos, the bond between a mother and son is strong and longlasting, especially if the mother holds a dominant position in their group. Matata was the matriarch of the bonobo family at ACCI, and Kanzi lived with her for most of his life, so it is unsurprising that he possesses a high comprehension of her and her name. Bonobos are also commonly cited for their socio-sexual behaviors (de Waal, 1995), which is occasionally observed between individuals at ACCI. Under previous care, Kanzi would self-stimulate with toy plastic balls (J. Tagliatelia, pers.comm) which may contribute to the high score for the word "ball," with the seventh average word score at 90.7% correct.

Low-scoring words may also provide clues to Kanzi's language exposure and comprehension throughout his life. Although there has been a lack of consistency throughout Kanzi's life, including human relationships, research participation, diet, and daily routine, this data is a potential indicator of his experiences and their effects on his vocabulary and memory. For example, the word "toothpaste" had an average score of 41.0%. Current care staff at ACCI acknowledge that previous efforts did not prioritize Kanzi's health, including his dental hygiene. This low score may indicate recent acquisition of the word or a lack of frequency in his learned vocabulary. It is surprising, however, that Kanzi did not perform well on the word "keyboard," though the Lexigram to Picture score was markedly lower than that of the English to Picture and English to Lexigram tests, following a pattern similar to the majority of tested words. Lastly, "can" was Kanzi's lowest scoring word for all three tasks. Although this could indicate that he simply does not know the word to a significant level, it is important to note that there exists more than one meaning for "can." Kanzi was tested on the noun form, as the tasks included pictures of canned foods and soft drinks, but he likely hears the word more often as an auxiliary verb from caretakers and researchers. Future studies could provide insight to his understanding or confusion of homophones, though it is challenging to clearly depict the more common form of "can" and similar words. As evidenced by the preceding examples, examining the level of Kanzi's word comprehension is an important step in identifying his overall linguistic capabilities, as well as his perception of his environment.

An unexpected finding of this study is that individual word accuracy scores varied depending on task type, pictured in Figure 3.3. We would assume that Kanzi produces consistent scores for words based on his overall comprehension of that word or concept. Although the majority of word scores are similar across treatments, there are several with surprising discrepancies. For example, the word "Teco" shows the fifth highest English to Picture score with 96.8%, but the English to Lexigram and Lexigram to Picture scores are much lower at 62.0% and 50.8%, respectively. I predict that this is due to the decreased use of lexigrams in recent years, coinciding with Teco's young life. Furthermore, Maisha was not assigned a lexigram until several years ago and was rarely grouped with Kanzi at ACCI, likely causing the low Lexigram to Picture score (44.0%), but also the lowest average score of all of the bonobos' names. A similar argument explains why Kanzi's score of the word "toothpaste" was higher in the English to Picture test than the English to Lexigram and Lexigram to Picture, scoring 56.0%, 32.0%, and 35.0%, respectively. It is only in recent years that Kanzi and the other bonobos regularly brush their teeth to maintain healthy habits, and it is therefore probable that items encountered more often in Kanzi's past display a higher performance in lexigrams than English, as seen with the words "car" and "Matata." That individual word scores vary with each tasks' mode of communication leads us to conclude that Kanzi's comprehension is affected by the type of abstract representations he receives.

This study demonstrates a clear method of assessing Kanzi's word comprehension in various linguistic formats, but it is a preliminary stage of assessing overall language competency. Although we cannot guarantee that Kanzi will regularly use high-scoring words in spontaneous conversation, it is improbable to expect correct use of those with lower average scores. Prior ape language studies have reported an individual's vocabulary by analyzing their mean utterance

length and the number of times they accurately use the sign or lexigram in context (Gardner and Gardner, 1984; Savage-Rumbaugh and Lewin, 1994; Segerdahl et al, 2005) in addition to performance on receptive tasks comparable to the present study. Once researchers are confident in his knowledge of a word and its meaning, we can further analyze Kanzi's ability to understand that word in the context of larger linguistic units. Previous research has reported his aptitude in recognizing English syntax, both in producing and receiving novel sentences (Savage-Rumbaugh and Lewin, 1994), but these results should be reevaluated with more current experimental methods. Data collected in the current study and continuing research can provide further assessments of Kanzi's cognitive and linguistic capabilities. By analyzing the errors he made in thousands of trials, we can determine common patterns in Kanzi's responses and compare with a similar previous study conducted by Lyn (2007). Anecdotal evidence suggests potential phonological errors, for example, choosing a picture of a bee in response to hearing the word "keys"), similar to findings by Gardner and Gardner (1984) in the chimpanzee Project Washoe, and detailed analysis can reveal similar informative patterns. Kanzi's test responses also provide data on his ability to categorize objects and words, as previous research looks to linguistic competency to understand conceptual categorization in the study subjects (Pedersen, 2012).

In addition to dissecting and accurately testing the complexities of language systems, there are several limitations to this study that are inherent to the field of ape language research. It is challenging to produce conventional scientific research on this matter because much of our understanding of the apes' abilities is through personal interaction. Language is a complicated and highly social concept that is produced organically, which is difficult to reconstruct in a purely experimental setting. Despite the significance of the present study, it cannot fully capture the extent of Kanzi's language use and comprehension with other human and nonhuman primates. Previous

studies have reported Kanzi's conversational behavior (Benson & Greaves, 2005) and communicative interactions between wild bonobo pairs (Frolich et al, 2016), but this important aspect of language research is difficult to methodically replicate and report. Lastly, there exists a very small sample size due to the requirements of extensive long-term rearing and further understanding of the ethical concerns of high degrees of human interaction. Because the establishment of comparable studies is unlikely to occur at present, it is increasingly important to explore the linguistic competence of the remaining nonhuman subjects in a controlled environment. Additionally, his ability to understand spoken English makes Kanzi an ideal subject in experiments not pertaining to language but requiring more complicated instruction and methodology. It is unlikely that his impressive aptitudes are representative of the larger bonobo population, but they can provide insight to the upper bounds of nonhuman primate cognition. Kanzi is therefore a valuable resource in appreciating the linguistic and cognitive capabilities shared between our species, and the testing protocol established in this study provides a foundation for many future research opportunities.

Nyota, Elikya, Maisha, and Teco Trainings

I originally proposed that Nyota, Elikya, Maisha, and Teco would complete the same match-to-sample tests as Kanzi to determine their current understanding of English and lexigrams of the provided words. Their language competencies have never before been formally assessed, and this information would allow researchers to analyze the effects of age, sex, and rearing experience on elementary word comprehension. As reported, they did not perform as expected in training tasks, and therefore did not progress to testing. There are several factors that potentially impacted their results, which I will further explore in this chapter.

Environmental Factors

Independent of the bonobos' individual motivation, there were a variety of external factors that affected research and data collection at ACCI, the most evident of which is the recent adjustment in management and care staff. While the bonobos are presently in much healthier conditions, changes in routine and environment may have affected the subjects. Previously, there was minimal structure in their daily lives, so current employees made a profound effort to ensure consistency in diet, enrichment, and husbandry in the bonobos' captive welfare. As a result, both the apes and staff were learning improved operating procedures and routines during data collection. While ultimately beneficial, the initial implementation of such procedures proved challenging to conducting systematic research. This was most evident when moving the apes between enclosures, especially when separating them individually in the testing room. Teco, Elikya, and Maisha were often uncooperative, either with seemingly playful intentions or in an attempt to assert control in their environment. As a juvenile, Teco frequently ran between enclosures, stopping in the doorway as staff members attempted to move the apes to another room. Elikya frequently came to his aid, further delaying the testing schedule. Additionally, Teco seemed extremely interested in working with the computer and researchers, and he would not leave the experimental room once given access, interfering with any other ape at the computer. It was therefore necessary to preemptively separate him before opening the testing room, which often required more time and effort than available in the newly re-established institution.

There were additional disruptions brought upon by the architectural makeup of the facility and testing room. Although there are two testing rooms at ACCI, only one was in use during data collection, which is located in the center of the building, with clear views of the lobby and front entrance. As a result, the apes were often exposed to potential distractions both inside "ape space" and by visitors and volunteers in the lobby. The temperature of the experimental room was also too hot for the bonobos to work comfortably with the door closed, but keeping it open would have allowed for increased distractions and for the apes to go in and out of the rooms while training. Furthermore, the platform that the bonobos rested on while using the touchscreen was curved against the wall (see Figure 2.1), potentially affecting their position and therefore their test performance. This was most evident with Elikya, as she would often sit at the side farthest from the experimenter with her sexual swelling off the platform's edge. In the initial training protocols, she, Nyota, and Maisha to a lesser extent, displayed a bias in answer choice for whichever option was closest. This led to the vertical response orientation found in Trainings 3-6 and pictured in Figure 2.5b.

For these reasons, we created a mobile cart (Figure 4.1) to allow for touchscreen research to be completed in various enclosures throughout ACCI. Modifications were made to an existing cart, including mounting a touchscreen monitor, enclosing all wires, speakers, and electronics, and building a storage shelf and tubing to provide food rewards through the wire mesh barriers. For several weeks, researchers experimented with utilizing the mobile cart to test the apes but encountered multiple obstacles. First, there were only two possible areas the cart could be used due to the fencing and the large dimensions of the cart. It was quite unwieldy and heavy to correctly position against the enclosure, and because it required researchers to stand very close to the apes' enclosures, it was unsafe to reposition within reach of the bonobos. It was also difficult to conduct the computerized tests without seeing the trials. We attempted various methods with second screens to monitor the testing screen and status, but again, the size of the cart and surrounding space prevented such modifications. Lastly, Kanzi was the only individual to successfully use the mobile testing station. Elikya and Maisha both exhibited behaviors associated with fear and stress while in the enclosure, and they would not move close enough to the cart to work. Although Kanzi would willingly work with the cart, I could not knowingly ignore any potential differences in performance caused by the altered environment during data collection, and therefore did not include any mobile cart trials in my data analysis. While a mobile testing station would likely be a useful research tool at ACCI, it ultimately was not feasible to advance at the time of this study. As evidenced by the evolution of the present study's methodology, it is imperative to work within the environmental restrictions of any research project, understanding its potential impact on the study subjects.



Figure 4.1 Mobile testing cart constructed at ACCI

Individual Factors

In addition to external elements affecting this project, the individual personalities and experiences of the apes also influenced data collection. When beginning initial training, the apes were all surprisingly interested in working with researchers. We were optimistic with their motivation to merely enter the experimental room, especially with Maisha and Elikya, who had been reared as a control group in the language project and received substantially less human interaction than the other bonobos. Even Nyota's involvement in previous research did not compare to the constant attention and praise attributed to Kanzi. Despite initial motivation, Maisha and Elikya seemed to quickly lose interest in working and rarely completed full training sessions consecutively. They did not pay attention to their answer choices, only answering quickly for the reward. Elikya would seemingly grow frustrated and bored with the self-correction feature when she repeatedly selected incorrect answers without receiving a reward. Maisha was more responsive in correcting his responses, but lost interest and left the testing room after only a few trials, often engaging in self-stimulating behaviors commonly observed in adolescent male bonobos (de Waal, 1995).

Although I expected Kanzi to perform at much higher levels that the other bonobos, it was surprising that Nyota, Elikya, Maisha, and Teco did not improve quickly throughout the various training treatments. Despite the many trials Nyota, Elikya, and Maisha completed, Elikya and Maisha did not perform above chance, and it took Nyota much longer to meet the criterion of Training 4 than expected. I noted that when presented with certain words as distractors, the bonobos took more trials to correct the answer choice. Interestingly, those images were all items they might be particularly aware of, such as preferred food items and other apes (words listed in Appendix C). Two incidents occurred at the beginning of Nyota's training that may provide additional insight to sensitivity to the images. Nyota displayed a strong reaction when presented with the picture and spoken word "Matata" during Training Protocol 1, causing him to scream, kick the screen, and flee the testing room. He also had an adverse reaction when Matata, Nyota's grandmother, passed away in 2014, displaying fewer species-typical social and feeding behaviors (J. Taglialatela, pers. comm), so it is unsurprising that this would affect his performance. Similarly,

Boysen et al (1997) found that chimpanzees trained with symbolic numerical representations were similarly impeded by a seemingly innate response to food. When presented with two selections of candy, the ape subjects were rewarded with the amount of the unchosen array. Although they consistently selected the smaller amount when represented by symbolic numerals (so as to gain the larger share of candy), they were unable to do so when choosing from the real food items. A possible explanation is that like the chimpanzees, the bonobos were unable to resist the impulse to select a desired item or individual, despite not receiving a reward. That Nyota's score improved in Training 5, after removing the words he perseverated on, suggests that his understanding of those pictures did influence his ability to perform on this task. Despite the observation of this behavior in Elikya and Maisha, they did not exhibit the same improvement in training.

I also hypothesize that rearing experience had a significant effect on the motivation and ability of the bonobos to succeed in this study. It is widely accepted that there is a critical period for language acquisition in human children (Lenneberg, 1967), and previous research has also identified that chimpanzees have difficulty acquiring new complicated behavior, such as tool use past an optimal age (Biro et al, 2003). As previously discussed, Nyota, Elikya, Maisha and Teco all experienced different levels of human interaction and research participation, so it is plausible that they did not obtain the required stimuli during a critical period of development to adequately perform on this type of task. It is, however, difficult to discern if this critical period applies to learning English and lexigrams or to learning how to participate in the activity itself. Hopper et al. (2007) also found differences in research participation between chimpanzees with varied amounts of human interaction, which may explain some of the variation at ACCI.

Although not reflected in the results of this study, it is evident through personal experience with the bonobos that they all understand some spoken English. Nyota and Teco have both spontaneously and correctly pointed to the lexigram boards to communicate with people, although their symbol use is repetitive and limited to preferred food items. Additionally, all five bonobos began regular body part inspections with care staff in 2014, providing evidence that they have some comprehension of the provided terms. Studies suggest that standardized measures of aptitude do not successfully apply to to all students (Lightbown and Spada, 2013), which likely applies to nonhuman primates as well. Researchers must develop experiments to adequately measure each individual ape's skillset and tasks in which they will participate. Current staff members at ACCI currently engage the bonobos in new research projects, but Elikya and Maisha are consistently the least motivated to participate. Further studies would need to be conducted to determine the likely roots of their lack of motivation as well as methods to increase their voluntary involvement in research.

CHAPTER 5

CONCLUSION

This project successfully completed fundamental steps in continuing linguistic research with the well-studied bonobo Kanzi. Despite the many years since the most recent assessment of his vocabulary, Kanzi consistently displayed great understanding of over 100 words in multiple modes of communication. Because he is surrounded by spoken English daily, he scored higher overall on the tasks with English stimuli, although he still performed above chance when presented with lexigrams. Dissecting Kanzi's word comprehension can also offer insight to his unique rearing environment, as well as bonobo species-specific behaviors. Unexpectedly, the type of stimulus treatment proved to be an important factor in his vocabulary accuracy, providing further evaluation of his perception and experiences. His performance may also indicate potential benefits of various communication strategies throughout hominoid evolution, leading to future research asking if symbolic language is more difficult to learn or if his performance merely a product of his environment. Kanzi's distinctly advanced capabilities for language and research could continue to answer questions about the underlying cognitive process underlying the development of complex communication.

Although Nyota, Elikya, Maisha, and Teco were not able to complete the proposed study, experimenting with multiple training protocols ultimately proved to be quite constructive in assessing experimental methodology. The projected methods would have resulted in a comprehensive dataset indicating the apes' individual language acquisition and comprehension, providing information on the influences of age, sex, and language experience on vocabulary. The actual results, however, exposed the potential effects of those factors on motivation and individual variation in research participation. Attempting various training procedures highlighted the many

factors that can impact testing, and the importance of ensuring the subjects' full understanding of the task at hand. Unlike Kanzi, these four bonobos did not regularly participate in controlled studies throughout their lives, but they are now better acclimated to research procedures and frequent positive human interaction. The knowledge gained in the present study will allow future research to include the other extraordinary bonobos at ACCI. Despite poor testing performance, we cannot deny that Nyota, Elikya, Maisha, and Teco possess some level of English comprehension, as human caretakers, researchers, and volunteers successfully communicate with them daily. Continuing to work with the apes, we can realize the most efficient methods to accurately assess their language comprehension. Additionally, increased frequent interactions will improve the quality of life and relationships among the bonobos in their captive environment.

The importance of understanding and appreciating ape cognition cannot be underestimated, as it is vital in unraveling the origins of human communication at its present state. Due to the close evolutionary relatedness between bonobos and humans, researching a range of individual linguistic capabilities in apes can inform our understanding of the precursors of human language. This study enhances the ongoing research initiated with the LANA project in the 1970s by determining the linguistic competencies and testing methods of language-enculturated bonobos, providing foundation for future ape language studies.

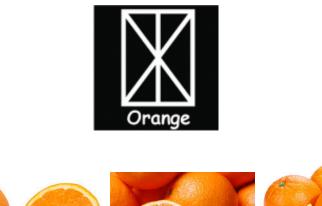
APPENDIX A

COMPLETE WORD LIST (N=120)

Apple	Foot	Phone
Apricot	Fridge	Pillow
Arm	Gorilla	Pineapple
Baby	Grapes	Pinecone
Backpack	Green Bean	Plastic Bag
Ball	Groom	Popsicle
Balloon	Hand	Potato
Banana	Hat	Raisin
Bird	Hose	Rock
Blackberries	Ice	Shirt
Blanket	Jelly	Shoe
Blueberry	Juice	Shot
Book	Kanzi	Snake
Bowl	Key	Soap
Box	Keyboard	Spoon
Bread	Kiwi	Squirrel
Brush	Knife	Stethoscope
Bubbles	Lemon	Stick
Bug	Lettuce	Straw
Bunny	Lighter	Strawberries
Camera	Maisha	String
Can	Marshmallow	Sugar
Candy	Matata	Sugar Cane
Car	Melon	Sweet Potato
Carrot	Milk	Swelling
Celery	Mirror	Теа
Cereal	Mouth	Teco
Chalk	Mushroom	Tree House
Cheese	Noodles	Tomato
Cherries	Nyota	Toothbrush
Chicken	Oil	Toothpaste
Coconut	Onion	Trash
Cooler	Orange	Tummy
Crayon	Orangutan	Turtle
Dog	Paint	Tv
Ear	Paper	Vitamin
Egg	Peaches	Water
Elikya	Peanut	Watermelon
Fire	Pear	Wipies
Fish	Peas	Yogurt
		~

APPENDIX B

EXAMPLE OF VARIED PICTURES USED IN KANZI ENGLISH TO PICTURE AND LEXIGRAM TO PICTURE TESTS

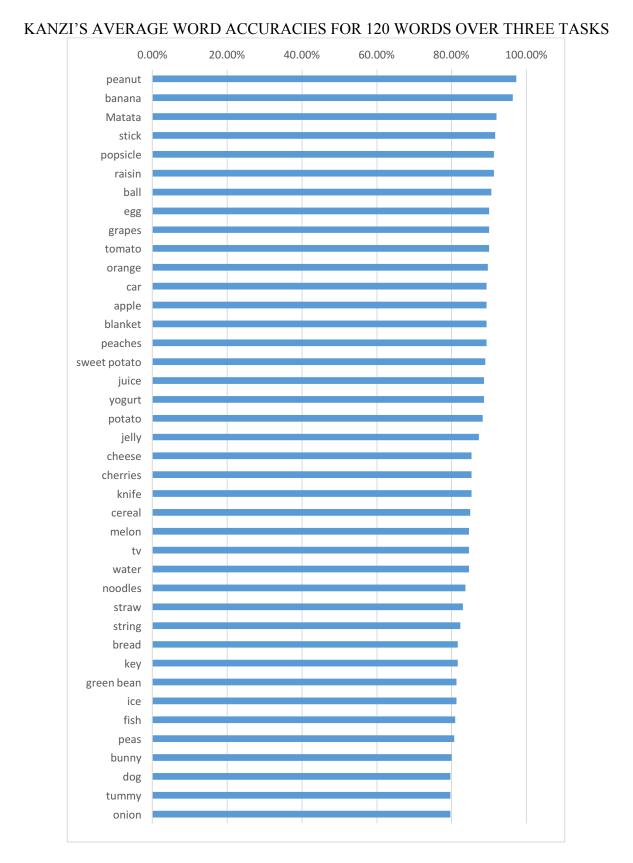




APPENDIX C

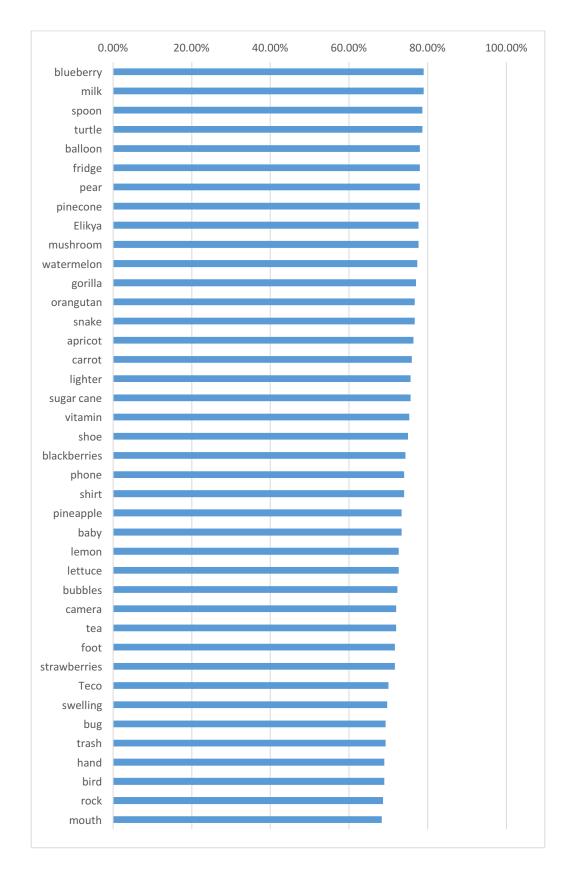
WORDS REMOVED IN TRAINING 5 (N=12)

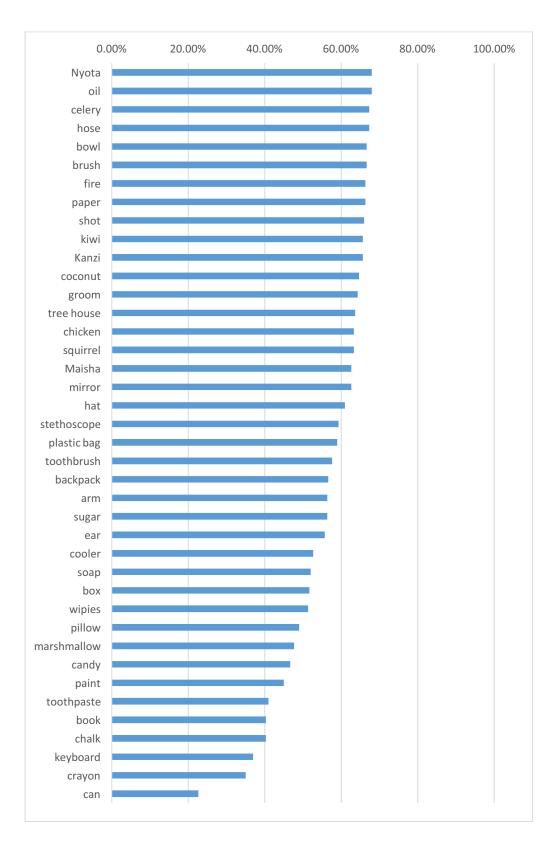
Celery Elikya Gorilla Grapes Kanzi Maisha Matata Nyota Orangutan Peanut Raisin Teco



APPENDIX D

51





REFERENCES

- André C, Kamate C, Mbonzo P, Morel D, Hare B. 2008. The conservation value of Lola ya Bonobo Sanctuary. In *The Bonobos*. p. 303-322. New York: Springer.
- Arbib M, Liebal K, Pika S. 2008. Primate Vocalization, Gesture, and the Evolution of Human Language. *Current Anthropology*. 49:1053-1076
- Arcadi, AC. 1996. Phrase Structure of Wild Chimpanzee Pant Hoots: Patterns of production and interpopulation variability. *American Journal of Primatology*. 39:159-178
- Bard KA. 1992. Intentional Behavior and Intentional Communication in Young Free-ranging Orangutans. Child Development. 63:1186-1197.
- Benson J & Greaves W (eds). 20015. Functional Dimensions of Ape-Human Discourse. London, UK: Equinox Publishing Ltd.
- Bermejo, M. and Omedes, A. 1999. Preliminary vocal repertoire and vocal communication of wild bonobos (*Pan paniscus*) at Lilungu (DRC). *Folia Primatol*. 70:328-357
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*. 6:213-223.
- Boysen S. 1997. Representation of Quantities by Apes. *Advances in the Study of Behavior*. 26:435-462.
- Chompsky N. 1988. Language and Problems of Knowledge. Cambridge, MA: MIT Press.
- Clay Z, Archbold J, Zuberbuhler K. 2015. Functional flexibility in wild bonobo vocal behaviour. PeerJ 3:e1124: DOI 10.7717/peerj.1124
- Clay Z, Zuberbuhler K. 2009. Food-associated calling sequences in bonobos. *Animal Behaviour*. 77:1387-1396
- Clay Z, Zuberbuhler K. 2001. Bonobos extract meaning from call sequences. *PLoS ONE* 6.4:e18786
- Clay Z, Zuberbuhler, K. 2011. The structure of bonobo copulation calls during reproductive and non-reproductive sex. *Ethology*. 117:1158-1169
- Coe J.C. 1989. "Naturalizing habitats for captive primates." Zoo Biology 8.S1:117-125.
- Cohen, J. 2010. Almost Chimpanzee: Searching for What Makes us Human, in Rainforests, Labs, Sanctuaries, and Zoos. New York, NY: Times Books.

- Coolidge HJJR (1933) "*Pan paniscus*, pigmy chimpanzee from south of the Congo River". American Journal of Physical Anthropology 18:1-59
- Crockford C. Boesch C. 2003. Context-specific calls in Wild Chimpanzees, *Pan troglodytes:* Analysis of Barks. Animal Behaviour. 66:115-125.
- Crockford C, Herbinger I, Vigilant L, Boesch C. 2004 Wild Chimpanzees Produce Group-Specific Calls: a Case for Vocal Learning? *Ethology*. 110:221-243
- Deacon T.W. 1990. Brain-Language Coevolution. The Evolution of Human Languages, eds. JA Hawkins and Murray Gell-Mann. Reading, MA: Addison-Wesley
- de Waal, F. 1995. Sex as an alternative to aggression in the bonobo. in Sexual Nature/Sexual Culture. Abramson P, Pinkerton S, University of Chicago Press.
- de Waal F, Lanting F. 1997. Bonobos the Forgotten Ape. London: University of California Press.
- de Waal, F. 1988. The Communicative Repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour*. 106:183-251.
- Frohlich M, Kuchenbuch P, Muller G, Fruth B, Furuichi T, Wittig R, Pika, S. 2016. Unpeeling the layers of language: Bonobos and chimpanzees engage in cooperative turn-taking sequences. *Scientific Reports*. 6
- Fruth B, Benishay J.M, Bila-Isia I, Coxe S, Dupain J, Furuichi T, Hart J, Hart T, Hashimoto C, Hohmann G, Hurley M, Ilambu O, Mulavwa M, Ndunda M, Omasombo V, Reinartz G, Scherlis J, Steel L, Thompson J. 2008. *Pan paniscus*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org>.
- Furuichi T, Mulavwa M, Yangozene K, Yamba-Yamba M, Motema-Salo B, Idani G, Ihobe H, Hashimoto C, Tashiro Y, & Mwanza N. 2008. Relationships among fruit abundance, ranging rate, and party size and composition of bonobos at Wamba. In Furuichi T and Thompson J (eds)The Bonobos: Behavior, Ecology, and Conservation. Springer, New York, pp 135-149.
- Furuichi T, Idani G, Ihobe H, Kroda S, Jitamura K, Mori A, Enomoto T, Okayasu N, Hashimoto C, Kano T. G. 1998. Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*. 19:1029-1043
- Gardner R, Gardner B. 1984. A vocabulary test for chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology. 98(4):381-404.
- Gardner R, Gardner B. 1978. Comparative Psychology and Language Acquisition. *Annals of the New York Academy of Sciences*. 309:37-76.

- Gardner R, Gardner B.1969. Teaching Sign Language to a Chimpanzee. *American Association* for the Advancement of Science. 165:664-672
- Goodall J. 1986 The Chimpanzees of Gombe: Patterns of Behavior. Cambridge, MA: Harvard University Press.
- Greenfield P, Savage-Rumbaugh S. 1990. Grammatical Combinations in *Pan paniscus*: Processes of Learning and Invention in the Evolution and Development of Language. Language and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives, eds. Sue T. Parker and Kathleen Gibson. Cambridge: Cambridge University Press.
- Hayes C. 1951. The Ape in Our House. New York: Harper.
- Hicks T, Roessing P, Menken S. 2013 Impact of Humans on Long-distance Communication Behaviour of Eastern Chimpanzees (*Pan troglodytes schweinfurthii*) in the Northern Democratic Republic of the Congo. *Folia Primatologica*. 84:135-156
- Hoff, E. 2009. Language Development. Wadsworth, Cengage Learning. Belmont, CA.
- Hohman G, Fruth B. 2002. Dynamics of social organization of bonobos (*Pan paniscus*) In: Boesch, C; Hohmann, G; Marquardt, L (eds) Behavioral diversity of chimpanzees and bonobos. Cambridge Univ Press, New York, pp 138-150.
- Hopkins W, Taglialatela J, Leavens D. 2007 Chimpanzees Differentially Produce Novel Vocalizations to Capture the Attention of a Human. *Animal Behavior*. 73:281-286.
- Hopkins, W; Savage-Rumbaugh, S. 1991. Vocal communication as a function of differential rearing experiences in *Pan paniscus*: a preliminary report. *International Journal of Primatology*. 12(6): 559-583.
- Hopper L, Spiteri A, Lambeth S, Schapiro S, Horner V, Whiten A. 2007. Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*. 73:1021-1031.
- Idani, G. 1990. Relations between unit-groups of bonobos as Wamba, Zaire: encounters and temporary fusions. *African Study Monographs*. 11:153-156
- Kano, T. 1992. The last ape: Pygmy chimpanzee behavior and ecology. Stanford University Press. Stanford, California.
- Keenan S, Methavon N, Stevens J, Guery J, Zuberbuler K, Levero F. Enduring voice recognition in bonobos. *Scientific Reports*. 6: 22046.
- Kellogg WN. 1933. The Ape and the Child. New York: Whittlesey House, McGraw-Hill Book Company.

- Klag, K. 2009. *Referential aspects in the vocal repertoire of bonobos (Pan paniscus)* (Masters Thesis). Iowa State University: Ames, IA.
- Kojima, S. 2003. A Search for the Origins of Human Speech: Auditory and vocal functions of the chimpanzee. Melbourne: Kyoto University Press
- Kuroda S. 1979. Grouping of the pygmy chimpanzees. Primates. 20: 161-183.
- Lenneberg, E.H., 1967. Biological Foundations of Language. New York: John Wiley and Sons
- Lighbown P and Spada N. 2013. How Languages are Learned. Oxford: Oxford University Press.
- Long, M. 1996. The role of the linguistic environment in second language acquisition. In W. Ritchie and T. Bhatia (eds): *Handbook of Second Language Acquisition*. New York: Academic Press. pp. 413-468.
- Lyn, H. 2007. Mental representation of symbols as revealed by vocabulary errors in two bonobos. *Animal Cognition*. 10:461-475
- Lyn H, Savage-Rumbaugh ES. 2000. Observational word learning in two bonobos (Pan paniscus): ostensive and non-ostensive contexts. *Language & Communication* 20(3):255-273
- Marquardt.1994 Chimpanzee Cultures. Cambridge: Harvard University Press.
- Matsuzawa, T., M. Tomonaga, and M. Tanaka. 2006 Cognitive Development in Chimpanzees. Tokyo: Springer.
- Mitani J, Hasegawa T, Gros-Louis J, Marler P, Byrne R. 1992 Dialects in Wild Chimpanzees? *American Journal of Primatology*. 27:233-243
- Mulavwa M, Furuichi T, Yangozene K, Yamba-Yamba M, Motema-Sale B, Idani G, Ihobe H, Hashimoto C, Tashiro Y, & Mwanza N. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In: Furuichi T and Thompson J (eds)The Bonobos: Behavior, Ecology, and Conservation. New York: Springer, p 135-149.
- Musgraves, D. 2012. A multimodal analysis of the communicative utterances of a language competent bonobo (Pan paniscus) (Masters Thesis). Iowa State University, Ames, IA.
- Patkowski, M. 1980. The sensitive period for the acquisition of syntax in a second language. *Language Leanring*. 30(2): 449-472.
- Pederson, J. 2012. *The symbolic mind: Apes, symbols, and the evolution of language* (Doctoral dissertation). Iowa State University, Ames, IA.

Pollick A, de Waal F. (2007). Ape gestures and language evolution. PNAS. 104.19:8184-8189

- Pollick A, Jenson A, de Waal F. 2008. Gestures and Multimodal Signaling in Bonobos. The Bonobos: Behavior, Ecology, and Conservation, eds Takeshi Furuichi, Jo Thompson. Chicago: Springer Science
- Pruetz J, Bertolani P. 2009. Chimpanzee (*Pan troglodytes verus*) behavioral responses to stresses associated with living in a savanna-mosaic environment: Implications for hominin adaptations to open habitats. *Paleoanthropology*: 252-262.
- Reinartz G, Bila-Isia, I. (2000). Bonobo survival and a wartime conservation mandate. In *Conference Proceedings, The Apes: challenges for the 21st Century, Brookfield Zoo* (pp. 52-56).
- Roffman I, Savage-Rumbaugh S, Rubert-Pugh E, Ronen A, & Nevo E. 2012. Stone tool production and utilization by bonobo-chimpanzees (*Pan paniscus*). *PNAS*. 109(36):14500-14503
- Rossano, F. 2013. Sequence organization and timing of bonobo mother-infant interactions. *Interaction Studies*. 14(2): 160-189.
- Rumbaugh DM. 1977. Language learning by a chimpanzee: the Lana project (ed) Duane M. Rumbaugh. New York: Academic Press.
- Savage-Rumbaugh ES. 1984. *Pan paniscus* and *Pan troglodytes*: Contrast in preverbal communicative competence. In: Susman RL, editor. The pygmy chimpanzee: Evolutionary biology and behaviour. New York: Plenum Press.
- Savage-Rumbaugh S, McDonald K, Sevcik Rose, Hopkinds W, Rubert E. 1986. Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology*. 115(3): 211-235.
- Savage-Rumbaugh ES, Fields WM, Taglialatela JP. 2001. Language, speech, tools and writing: A cultural imperative. *Journal of Consciousness Studies* 8(5-7):273-292
- Savage-Rumbaugh ES, Lewin R. 1994. Kanzi: The Ape at the Brink of the Human Mind. New York: Willey.
- Savage-Rumbaugh ES. 1986. Ape Language: From Conditioned Response to Symbol. Oxford: Oxford University Press.
- Savage-Rumbaugh ES, Murphy J, Sevcik RA, Brakke KE, Williams SL, Rumbaugh DM. 1993. Language comprehension in ape and child. *Monographs of the Society for Research in Child Development* 58(3/4):1-221

- Segerdahl P, Fields WM, Savage-Rumbaugh ES. 2005. Kanzi's primal language: The cultural initiation of primates into language. New york: Palgrave Macmillian. 237
- Seyfarth RM, Cheney DL. 1992. Meaning and mind in monkeys. *Scientific American* 267(6):122
- Slocombe, K, Zuberbuhler Z. 2005 Functionally referential communication in a chimpanzee. *Current Biology*. 15:1779-784
- Smith R, Jungers W. 1997. Body mass in comparative primatology. *Journal of Human Evolution*. 34:173-201
- Stanford, C. B. 1998. The Social Behavior of Chimpanzees and Bonobos: Empirical Evidence and Shifting Assumptions *Current Anthropology* 39.4 pp. 399-420.
- Stevens J, Vervaecke H, Van Elsacker L. 2008. The bonobo's adaptive potential: social relations under captive conditions. In: Furuichi T and Thompson J (eds)The Bonobos: Behavior, Ecology, and Conservation. Springer, New York, pp 19-38.
- Strier, K. B. 2011. Primate Behavioral Ecology 4th ed. Prentice Hall: Indianapolis.
- Stoinski, T. S., Hoff M, Maple T. 2001 "Habitat Use and Structural Preferences of Captive Western Lowland Gorillas (Gorilla gorilla gorilla): Effects of Environmental and Social Variables." *International Journal of Primatology* 22.3: 431-447.
- Stumpf, R. M. 2011. Chimpanzees and Bonobos, Inter- and Intraspecies Diversity. *Primates in Perspective*. 2nd ed. Oxford University Press: New York.
- Taglialatela J, Russell J, Pope S, Morton T, Bogart S, Reamer S, Schapiro S, Hopkins W. 2015. Multimodal communication in chimpanzees. *American Journal of Primatology*. 77:1143-1148.
- Taglialatela J, Russell J, Schaffer J, Hopkins W. 2011. Chimpanzee Vocal Signaling Points to a Multimodal Origin of Human Language. *Public Library of Science*. 6:4
- Taglialatela J, Savage-Rumbaugh S, Baker L. 2003. Vocal production by a language-competent *Pan paniscus. International Journal of Primatology*. 24 (1):1-17.

Terrace HS. 1979. Nim. New York: Knopf.

- Terrace HS. 1985. Animal Cognition: Thinking without Language. *Philosophical Transactions* of the Royal Society of London Series B, Biological Sciences 308(1135):113-128.
- Thompson J. 1995. A study of bonobo feeding ecology in a forest/savanna habitat. *Gorilla Gazette* (Colombus Zoo) 9:10-11.

Vygotsky, L. 1978. Mind in Society. Cambridge, MA: Harvard Univ. Press.

Wade, Nicholas. 1980. Does Man Alone Have Language? Science. 208:1349-1351.

- Wrangham, RW. 1999. Evolution of coalitionary killing. *American Journal of Physical Anthropology*. 29:1-30.
- Wrangham R, McGrew WC, de Waal F, Helte P. (eds) with Linda A. Marquardt. 1994. Chimpanzee Cultures. Cambridge: Harvard University Press.
- Wilson., et al., 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature*. 513:414-417.

Yerkes, R. 1925. Almost Human. New York: Century Company

Zuberbuhler K. 2000. Referential labeling in Diana monkeys. Animal Behaviour 59(5):917-927.