Differences in the Communicative Behavior and Neurobiology of Chimpanzees (Pan troglodytes) and Bonobos (Pan paniscus)

Brittany Moore
Kennesaw State University, bmoore47@students.kennesaw.edu

Follow this and additional works at: http://digitalcommons.kennesaw.edu/integrbiol_etd
Part of the Integrative Biology Commons

Recommended Citation
Moore, Brittany, "Differences in the Communicative Behavior and Neurobiology of Chimpanzees (Pan troglodytes) and Bonobos (Pan paniscus)" (2014). Master of Science in Integrative Biology Theses. Paper 3.
Differences in the communicative behavior and neurobiology of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)

Brittany Moore

Kennesaw State University

Department of Biology and Physics

Major Advisor: Jared Taglialatela, Ph. D.

Committee Members: Marcus Davis, Ph. D.

Antonio Golubski, Ph. D.
Table of Contents

Abstract..................................................................................................................page 1

Chapter 1 – Background.......................................................................................page 2

Chapter 2 – Communicative Behavior and Ecology.............page 5
  2.1 Introduction .....................................................................................................page 5
  2.2 Methods .........................................................................................................page 12
  2.3 Results ...........................................................................................................page 14
  2.4 Discussion .....................................................................................................page 15

Chapter 3 – Neurobiology....................................................................................page 18
  3.1 Introduction .....................................................................................................page 18
  3.2 Methods .........................................................................................................page 22
  3.3 Results ...........................................................................................................page 24
  3.4 Discussion .....................................................................................................page 25

Summary..............................................................................................................page 27

Integration of Thesis Research.................................................................page 29

Acknowledgements...........................................................................................page 30

Tables and Figures............................................................................................page 31

References..........................................................................................................page 41
Abstract

Chimpanzees and bonobos have distinctly different vocalizations, but it is unclear why these differences have evolved. We hypothesized that differences in habitat and feeding ecology have selected for bonobos to have an increased reliance on vocal communication compared to chimpanzees. To evaluate this hypothesis 1571 chimpanzee vocal events and 612 bonobo vocal events were analyzed. After analyzing and coding video of communicative interactions it was determined that chimpanzees are more likely than bonobos to utilize multimodal communication and to direct vocalizations to an individual conspecific. Bonobos were more likely than chimpanzees to produce a vocalization that was not bound to a specific social context. We further hypothesized that these behavioral differences should be reflected in neuroanatomical differences between bonobos and chimpanzees. In humans, there is a left neuroanatomical asymmetry in Broca's area – an inferior frontal region of the brain known to be involved in language production and processing. Therefore, we hypothesized that this would also be seen in bonobos as they putatively rely on vocal communication more than chimpanzees. However, quantification of the inferior frontal gyrus (IFG) on magnetic resonance images showed that bonobos had a larger right than left IFG, while chimpanzees had a larger left than right IFG. There was also no difference in lateralization of neuropil fraction (a measure of the space between neurons and glial cells in the gray matter) of Brodmann's areas 44 or 45. These data are discussed in relation to the hypothesis that observed differences in the communicative strategies and neuroanatomy of the two Pan species were driven by differences in foraging strategies since they diverged from a common ancestor approximately one million years ago.
Chapter 1 - Background

There are distinct differences in the vocalizations of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), but there has been very little research to determine the origins of these differences or how they affect the communicative strategies of the two species (de Waal 1998 and Pollick and de Waal 2007).

These differences are interesting due to the fact that chimpanzees and bonobos are so closely related to each other and to humans, allowing phylogenetic hypotheses to be made in regards to each species’ evolution. The *Homo* and *Pan* lineages split approximately 6 million years ago (mya), and chimpanzees and bonobos diverged approximately 1 mya (Becquet et al 2007 and Hey 2010). This close phylogenetic relationship means that the differences in bonobo and chimpanzee communication could give some indication into the evolution of human language. If there are traits that two or more of the species share it is likely that the last common ancestor of these species also shared that trait. Extant chimpanzees and bonobos both could exhibit communicative strategies that were present in early hominids. However, the stark differences between the acoustic properties of chimpanzee and bonobo vocalizations indicate that there was considerable selection on this characteristic since their divergence approximately one mya. In this way, the similarities and differences of the communicative strategies of both the extant *Pan* species can provide us with a better understanding of the communicative capabilities of early hominids.

A unique aspect of human communication is autonomous speech. Autonomous speech is the ability to deliver the entirety of a signal meaning in vocalizations without any sort of manual gesture. As the hominid lineage was evolving there was a shift from simple
foraging to a hunter-gatherer society and there was an increased need to code discrete information in vocalizations in order to coordinate more complex group movements and social contexts, while also freeing up the hands to hunt (Tooby and De Vore 1987, Pinker 2003 and Corballis 2004). The connection between feeding and foraging strategies and changes in communicative strategies in early humans suggests that niche occupation and feeding ecology may similarly have played a significant role in the evolutionary origin and selection of communicative strategies in chimpanzees and bonobos. In order to understand why the differences in vocalizations of chimpanzees and bonobos exist it is important to understand the communicative strategy for both species.

Physically, bonobos and chimpanzees are extremely similar and were only recognized as separate species in the early 1930's (de Waal 1988). The biggest differences are body size and coloring of the face. Bonobos are typically more gracile than chimpanzees, and chimpanzees have a wider array of coloring in their faces. Chimpanzees range from completely black to completely brown face while bonobo faces are typically black with brown lips. It is striking that such physically similar species would have such vast difference in behaviors. In the wild, chimpanzees are known to be male-dominated, with a strict social hierarchy, and males that are aggressive and territorial. It is not uncommon for altercations to occur at territory borders (Goodall et al 1986). In contrast, bonobos are a female-dominated, not highly territorial, and are characterized by their unique use of sexual behavior, or genital-genito rubbing, to relieve social tensions (White 1998). These differences in the wild are supported with experimental studies done in captivity, as bonobos are more likely to cooperate on a task and share food with a conspecific than chimpanzees (Hare et al 2007, 2010).
Another striking difference between chimpanzees and bonobos that has been found in the wild is the difference in cooperative hunting. Chimpanzees have been known to hunt in the wild since the early 1980's (Goodall 1986; Boesch and Boesch 1989). Goodall (1986) describes events where chimpanzees chase bush pigs and small monkeys into the path of waiting conspecifics. Hunting behaviors have not been observed directly in wild bonobos, although recently indirect evidence (from fecal samples) suggests that bonobos do consume meat (Surbeck et al 2009). However, it is unknown whether the meat found in the samples was obtained through scavenging or hunting.
Chapter 2 Communicative Behavior and Ecology

Introduction

Chimpanzee vocalizations are typically characterized as low frequency and noisy, whereas bonobo vocalizations are high frequency and tonal (de Waal 1988). Although it is unclear as to what may have led to the differences in the vocal repertoire of these two species, it has been found that oscine birds will alter their vocalizations based on the habitat that they are in. When in the forest habitat, not the marsh or grassland, the birds adjusted their calls to include more repetitive elements and side bands, increasing the complexity of their vocalizations (Wiley 1991). Wiley (1991) believed that the temporal changes evolved in order to reduce the effects of reverberation in the forest habitats. It is possible that the vocalizations of chimpanzees and bonobos have similarly evolved to match the habitat that they live in.

Chimpanzees live in a variety of different habitats and sub-habitats that can range from rain forest to savannah grassland. At the Gombe Stream National Park, Tanzania, the chimpanzees studied visited five different habitat types daily: subalpine moorland, woodland, semideciduous forest, evergreen forest and grassland (Goodall 1986). Chimpanzees rely on fruit for the majority of their nutrition, but will use figs, terrestrial herbaceous vegetation (THV) and meat as fallback food sources (Conklin-Brittain et al 1998 and Furuichi et al 2001). The variety of habitats frequented by chimpanzees correspond with differences in behavior (Boesch 1994). For example, forest chimpanzees are more likely to exhibit meat-sharing and cooperative hunting than savanna-woodland chimpanzees (Boesch and Boesch 1989).

We reasoned that if there are noticeable differences in hunting behavior among
habitats for chimpanzees, then it is possible that communicative differences have evolved as well. Savanna-woodland habitats are more open and visual signals would be able to travel farther than in a forest. Forest habitats are more dense such that visual signals would only be available to conspecifics in immediate proximity. The daily variance between forest and grassland habitat, and visual proximity, would select for chimpanzees to rely on both gestures and vocalizations to communicate.

Bonobos live in three different types of forest: swamp, primary and secondary (Hashimoto et al 1998). Despite the fact that there are wet and dry forest habitats available in their range, bonobos spend a majority of their time in the dry microhabitat, but will visit every type of forest throughout the day (Hashimoto et al 1998). Along with a reliance on forest habitat, bonobos gain most of their nutrition through THV even during times of ripe fruit availability (White 1998). Another factor that may allow bonobos to utilize THV where chimpanzees do not is the absence of gorillas in bonobo habitats that typically eat the same THV materials (Malenky and Wrangham 1994). As THV is a readily available food source that is spread out relatively evenly throughout the habitat, compared to fruit trees, bonobos do not have to stay in groups to protect the resource. A reduction in conspecific aggression would further select for bonobos to use THV as a main food source, the reduction of aggression and injuries would increase the fitness of the individuals who avoided the heavily visited and easily guarded fruit trees. Fruiting trees bring higher numbers of conspecifics to one finite resource, which would evoke a territorial response, especially from highly ranked individuals. This could correspond to the increased aggressive behaviors that are typically seen in chimpanzees as compared to bonobos (Hare et al 2007). Given that individuals are spread out across the territorial range, it is
important that vocalizations are able to travel rather long distances and are flexible across contexts to coordinate group movements and social interactions.

The high frequency calls of bonobos are easier to localize than the low-frequency calls of chimpanzees (Brown et al 1978). I hypothesize that the high frequency, tonal vocalizations of bonobos have the potential to have more temporal and spectral modulation to create a wider range of signal meanings than the noisy, grunt-like vocalizations of chimpanzees. This is because it is easier to detect slight changes in higher frequency vocalizations as compared to lower frequency vocalizations. For example, slight changes in the high frequency “whistle” vocalizations of dolphins are used to create novel vocalizations that become their individual indentifiers (Quick and Janik 2012). Selection for the ability to localize the caller as well as the potential to carry complex information may have led to an increased reliance on vocalizations in bonobos, which live in low visibility areas, as compared to chimpanzees. If bonobo vocalizations do in fact have the potential to carry more specific information as compared to chimpanzees, they should be used in multiple contexts because it is not the emotional state or context that contains the meaning but the temporal or spectral parameters of the vocalizations. For example, a grunt that only occurs during or in the presence of food would not be a flexible vocalization, but if that same grunt were given during different social contexts, e.g. grooming, resting or locomoting, it would then be considered flexible. If bonobos have been selected for reliance on vocal signaling, slight changes in the structure and length of vocal utterances could change the information that is being conveyed without changing the broad vocal type.

In addition to their vocalizations, both chimpanzees and bonobos use manual
gestures, facial displays and body postures to communicate with conspecifics as well. Sometimes the different communicative modalities are combined into one signal. Despite numerous communicative studies of primates, there is a notable lack of multimodal data (Slocombe et al 2011). Human language is multimodal, involving not only the auditory domain, but manual gestures, facial expressions, etc. For example, if there is a communication barrier between two people, both will often use gestures to assist the recipient in understanding the message and if the message does not seem to be understood different modes of communication will be tried until it appears that the message is understood. Rieser and Lemon (2010) found that when given the choice for clarification, people were more likely to choose clarification in a multimodal way as opposed to just vocalizations. Another example of multimodal preference is that it is commonly understood that gestures are used as a stepping-stone for autonomous speech in human infants, where infants and children will often use pointing gestures to gain attention and reactions from adult caretakers in a more efficient manner than vocalizations alone (Kishimoto et al 2007).

If the tonal vocalizations of bonobos do contain more information than the chimpanzee grunt vocalizations then bonobos should not need to combine communicative modalities as often as chimpanzees would need to. By using multiple modalities, the caller is utilizing several different types of signals in order to either convey the same message or utilize the combination of signals to convey different messages. For example, Pollick and de Waal (2007) found that both chimpanzee and bonobo gestures are not as tied to specific social contexts and emotional states as vocal and facial signals, so it is possible that vocalizations are strict in chimpanzees but the flexibility of the gestures causes the signal to
change. Along with not needing to combine vocalizations with another communicative modality, the bonobo vocalizations should be less likely to be tied to a specific emotional state or context, than chimpanzee vocalizations. If bonobos have been selected for reliance on vocalizations slight changes in the vocalization structure and length, as seen in oscine birds, should change the information that is being conveyed without changing the vocal type.

It is essential to compare the use of other modalities during vocal events between chimpanzees and bonobos to understand the basal characteristics of the last common ancestors of these three species. If more than just one species is utilizing a communicative strategy it is likely, based on parsimony, that the last common ancestor also used that strategy. Understanding which of these basal characteristics have persisted or changed can give us a better understanding of the evolution of human language. The persistence of a specific trait in humans would suggest that early hominids were in a similar habitat and the behavior convergently evolved. For example, as both humans and chimpanzees utilize multimodal signaling it is likely that the last common ancestor of humans and the *Pan* species utilized multimodal signaling and some other phenotype was selected for in bonobos (Leavens et al 2010).

*Hypothesis 1: Chimpanzees will utilize multimodal and directed communication more than bonobos because bonobo vocalizations have a more complex acoustic structure and are therefore more likely to carry sufficient information encoded in the vocal domain that does not require multimodal signaling.*

There are clear differences in the vocalizations of chimpanzees and bonobos; with
chimpanzees utilizing low frequency, noisy barks and grunts, whereas bonobos typically use high frequency, tonal peeps and yelps (de Waal 1988). It has even been found that a bonobo would interact and respond vocally to human caretakers in a pattern similar to a human conversation (Taglialatela et al 2003). Vocal communication is not the only form of communication utilized by human and non-human primates. Gestures, facial expressions and body postures can all be used to convey a message. In fact, humans, chimpanzees and bonobos all combine different communicative modalities to ensure a conspecific understands the signal’s meaning (Leavens 2010 and Pollick and de Waal 2007).

While it has not been determined what has caused the differences in vocalizations in chimpanzees and bonobos, it may be due to differences in the habitat and feeding ecologies of the two species. Wiley (1991) has shown that birds alter the length and other temporal elements of their vocalizations based on the habitat they are in. The habitat differences seen in chimpanzees and bonobos, create differing levels of visual proximity, a forest would prevent the ability to see a conspecific except at very close ranges, while a savanna-grassland would allow visual proximity to be much greater. I hypothesize that bonobos, which live strictly in forests, utilize a vocal method, while chimpanzees will rely on a combination of vocal and non-vocal signals.

The habitat and feeding ecology can also be connected to whether or not a vocalization will be directed to a specific individual. In order to consider a vocalization directed, there must be a directed gaze or glance to a conspecific as chimpanzees and bonobos do not have signature vocalizations that represent individuals like dolphins (Quick and Janik 2012). A forest habitat would prevent, or at least hinder, the ability to view a conspecific. Since bonobos live in forests exclusively, I predict that directed
communication is not as likely to occur compared to chimpanzees that live in a variety of habitats. This is further enforced by the feeding habits of the two species. The patchy distribution of THV explains that bonobos travel greater distances from each other with large groups to gather food, while chimpanzees mostly gather at large fruit trees with smaller group sizes, where they are within visual proximity of each other (Furuichi 2009).

I hypothesize that the forest habitat and reliance on THV as a food source of bonobos creates an environment where it is adaptive to rely on an exclusively vocal form of communication. Therefore, I predict that chimpanzees will use multimodal signaling and directed vocalizations more often than bonobos, while bonobos will rely strictly on vocalizations without having to direct vocalizations to a specific individual due to these ecological differences.

_Hypothesis 2: Bonobo vocal types will not be as tied to a specific social context as compared to chimpanzees because of the need to coordinate group movements in an environment that does not support visual signals._

Bonobo reliance on vocalizations suggests that there is a potential for a variety of information to be coded in the signal, similar to autonomous speech, meaning that the vocalizations will not be tied to a specific context. The habitat and feeding ecology differences discussed above may have selected for bonobos to rely on vocal communication and chimpanzees to rely on multimodal communication. Chimpanzees often travel through more than one habitat types every day with different levels of visibility (Goodall 1986). While chimpanzees do spend time in different types of forest, they also rely on fruit for their main protein sources, which causes them to gather in large groups at the trees. This
allows chimpanzees to utilize nonverbal communication despite the lack of visibility of forests. There is no strong pressure towards vocal communication alone in chimpanzees, so vocalizations can be effective for several different contexts and situations when combined with gestures and body postures. I predict that the vocal types of bonobos will be less tied to social context as compared to chimpanzee vocal types.

**Methods**

**Subjects**

In order to test the two behavioral hypotheses above a total of 26 hours (1571 vocal events) of video and audio were analyzed and coded for chimpanzee vocal events. The chimpanzee video all came from Yerkes National Primate Research Center in Lawrenceville, GA. In the group there were 17 individuals, 13 female and 4 males, ranging in ages from 18-37 years old. All video was taken from an above view of the outdoor section of the compound. The compound had only grass on the ground, but had a 3 tiered structure for climbing with firehoses and ladders connecting the upper two levels to the ground. Large tractor tires and cement culverts were placed throughout the compound. When the subjects were let out for the day the doors to the indoor area of the compound were closed. Subjects were let out and in to switch the groups access to the outside portion of the compound, approximately 2 hours worth of video contained the whole group.

A total of 20 hours (612 vocal events) of video and audio was analyzed and coded for vocal communication from San Diego and Jacksonville Zoos, resulting in a total sample number of 18, 11 females and 7 males. San Diego Zoo housed a group of eight bonobos, 5 female and 3 male, with 2 juveniles and 6 adults. Jacksonville Zoo had a group of 10
bonobos with 6 females and 4 males that ranged in age from 3 to 44 years old, with 2 infants and 1 juvenile. However, three individuals from the San Diego Zoo were left out of statistical analysis due to a lack of data (<10 vocal events). A total of 20 hours of video was analyzed and coded. The San Diego Zoo had two levels to their outdoor enclosure; the lower level had a structure for climbing with fire hoses that connected the upper and lower levels on the structure as well as the compound. A river of constantly flowing water with a waterfall flowed between the lower and upper levels of the compound. Jacksonville Zoo had a two level structure compound that had ropes. A moat of still water was on the outside edge of the compound; on the opposite side of the compound there was a waterfall with a pool to collect it on the bottom that was turned on for only one day of video recording. Both San Diego and Jacksonville Zoo would switch out which individuals were given access to the outside compound.

**Video Analysis**

Digital audio/video recordings from San Diego and Jacksonville Zoos and Yerkes National Primate Research Center were viewed and analyzed for vocal events. A vocal event was defined as any vocalization that did not occur in a series. In order to code the vocal event the observer had to have a clear view of the vocalizer and the conspecific the vocalization was directed to. A series of vocalizations was counted as one vocal event, but if there was a pause of three seconds or more between vocalization they were counted as a separate vocal event. The type of vocalization (Table 1 and 2) was identified and then determined if the communication is directed, whether it occurs with a concomitant signal (Table 3) and the social context (Table 4) of the caller. The vocalization will be considered directed if the subject’s gaze is focused on another conspecific. The vocalization was not
coded if it was directed at a human or the “inside” part of the enclosure. A concomitant signal (CCS) will be any vocalization, manual gesture, facial display or body posture that occurs at or within two seconds of the initial vocalization.

**Statistical Analysis**

For every subject, the number of vocal events that occurred with and without a concomitant signal was recorded, as well as the number of vocal events that were and were not directed. Next, each vocal type was split into the different social contexts to determine which context the vocal type occurred in most. For analysis, the number of vocalizations that occurred in the most common context and not in the most common context were calculated. This also allowed the context tie index (CTI) to be calculated (# of vocalizations in most common context/total vocalizations in vocal type). Three separate univariate analysis of variance (ANOVAs) were run, using SPSS (IBM, version 20). The dependent variable was the percentage of vocalizations that occurred with a CCS, the percentage of vocalizations that were directed, and the percentage of vocalizations that occurred in the most common context, respectively, with species (bonobo or chimpanzee) serving as the fixed factor in all 3 analyses. All p-values were adjusted using Bonferroni’s correction.

**Results**

I found that chimpanzees were more likely than bonobos to pair their vocalizations with a CCS ($F(1,31) = 32.07, p<0.001$). Bonobos only paired their vocalizations with a CCS approximately 20% of the time, while chimpanzees paired the vocalizations with CCS 50% of the time (Figure 4). A similar pattern was seen with the directed vocalizations, with chimpanzees directing more vocalizations to conspecifics than bonobos ($F(1,31) = 27.21,$
Bonobos only directed their vocalization 20% of the time, but chimpanzees directed their vocalizations to conspecifics 60% of the time (Figure 5). However, chimpanzees were more likely to produce vocalizations in their most common context as compared to bonobos ($F(1, 31) = 12.409, p<0.001$). Chimpanzees produced vocalizations in their most common social context 60% of the time while bonobos only produced vocalizations in the most common social context 48% of the time (Figure 6).

**Discussion**

Chimpanzees were much more likely to pair their vocalizations with CCS than bonobos (Figure 4). In fact, chimpanzees utilize a CCS 50% of the time while bonobos only utilize a CCS 20%. This supports the hypothesis that chimpanzee communicative strategies do not involve reliance solely on vocal communication. One reason this could be is the reliance of chimpanzees on fruit trees would place them in close proximity to conspecifics (Conklin-Brittain et al 1998). This close proximity would place emphasis on visual communication because conspecifics are more often than not in visual proximity, which allows gestural, facial and body postures to be used effectively as signals. The directedness data also supports this hypothesis of feeding strategies influencing communicative strategies. Chimpanzees direct 60% of their vocal events at conspecifics, while bonobos only direct 30% of their vocalizations at conspecifics (Figure 5). A reliance on gestural communication would lead chimpanzees to be looking at the conspecific that the signal is intended for. Chimpanzees have been known to adjust their communicative strategies based on the observers attention to the signal, where gestural communication was only added in when the observer was actually looking at the chimpanzee (Leavens et al 2010).
On the other hand, bonobos get a majority of their protein from THV which is spread throughout the forest. This permits bonobos to spread out farther from each other to prevent aggressive conflicts if needed. Since conspecifics will not be necessarily in visual proximity a shift towards reliance on vocal communication would be beneficial. This would explain the decreased use of CCS and directed vocalizations.

Bonobo vocalizations appear to be less tied to social contexts than chimpanzee vocalizations. Whereas chimpanzees use vocalizations in their most common social context 60% of the time, bonobos only use vocalizations in their most common context 45% of the time (Figure 5). This further supports the hypothesis that bonobos are able to rely more on vocalizations to convey information alone. The flexibility of the vocalizations allow them to be efficiently used in a variety of situations and contexts, and the lack of combination of vocal and nonvocal signals suggests that the information is sufficiently transmitted with vocalizations alone. When chimpanzees use gestures to convey meaning, the vocalizations can be connected to specific social contexts while flexible gestures are used to create differences in the signals. In fact, it has been found that chimpanzee gestures are less tied to social contexts than bonobo gestures (Pollick and de Waal 2007).

The difference in the number of vocal events of each species could be due to one day of video data from the chimpanzees. On that day one of the female chimpanzee subjects was very antagonistic and caused several fights. In response to the fighting there was a lot of alarm calling and screaming from all individuals, this accounted for a lot of vocal events. For the next two days the chimpanzees were very anxious and more vocal, possibly from tension due to the fighting. Another potential reason for the difference in the number of vocal events is the fact that I counted a series of vocalizations as one vocal event unless
there was a pause of 3 seconds or more between vocalizations. Several bonobos would vocalize in series for several minutes, but there would never be a pause long enough to count as multiple vocal events. While this was not an issue for analysis purposes it is interesting to note because it is possible that this is evidence of bonobos altering temporal elements of the vocalizations to include a greater array of information as some birds have been seen to do (Wiley 1991).

Overall, the data suggests that chimpanzees do not rely on vocalizations alone as much as bonobos do to communicate with conspecifics. The results of this study suggest that the communicative strategies follow the foraging strategies (lack of visual proximity leading to reliance on vocal communication). There are many behavioral differences between chimpanzees and bonobos that could be explained with feeding strategies and also contributed to these observed differences in communicative strategies. For example, chimpanzees are a male-dominated society while bonobos are female-dominated (Wobber et al 2010). Furthermore, chimpanzees are known to be aggressive and extremely territorial, but bonobos are more tolerant and typically have overlapping territories (Hare et al 2007 and Hare and Kwetuenda 2010). The clumped fruit patches frequented by chimpanzees would increase territoriality and aggression for the best resources, but the scattered distribution of THV should decrease the aggression seen in bonobos as there is plenty of resource available. Further experiment based communicative studies need to be done to determine the role food quality plays in communicative strategies.
Chapter 3 - Neurobiology

Introduction

The hypothesized differences in the communicative behaviors, discussed in Chapter 2, of chimpanzees and bonobos should also be evident in the neurobiology of the two species. There are several ways that the brain is typically studied to determine possible mechanisms for the observed behavioral changes. Some of the most common are through anatomical or cytoarchitectural methods (Semendeferi et al 1998; Taglialatela et al 2008; and Spocter et al 2012). In this study, I use magnetic resonance images (MRI) to trace a region of interest in order to determine if there are anatomical differences and neuropil fraction to investigate the cytoarchitecture of two areas of the brain.

The region of interest for the anatomical study was the inferior frontal gyrus (IFG). This area was chosen because it is known to include Broca’s area, a region in the human brain that is critical for the planning and execution of language in humans (Catani et al 2005). Homologues of Broca’s areas have been identified in chimpanzees at the gross anatomical and cellular levels (Gannon et al 1998, Cantalupo and Hopkins 2001, Schenker et al 2009, and Spocter et al 2010; Cantalupo, C. and Hopkins, W. D. 2001). The chimpanzee homologue of Broca’s area is located in the inferior frontal gyrus (IFG) (as it is in humans) and is active during the production and perception of communicative signals (Taglialatela et al 2008, 2009, 2011). However, all previous work has anatomically defined the IFG, in the axial plane, as the area between the frontal opercular sulcus (FO) and precentral inferior sulcus (PCI), with the top of the FO being the ceiling for tracing (Cantolupo and Hopkins 2001). When Broca’s area was cytoarchitectonically identified in chimpanzees by Schenker et al (2009) it was discovered that Broca’s area often included more cortex,
specifically below the inferior frontal sulcus (IFS) than was being included in MRI tracings. Furthermore, Taglialatela et al (2008) discovered that the cortex posterior to the PCI (not included in previous definition) was activated when chimpanzees were communicating suggesting that the IFG extended more posterior than was previously defined. We redefined the IFG to include these previously excluded cortexes in order to determine if there is any difference in the anatomical structure of the IFG of chimpanzees and bonobos.

The cytoarchitecture technique that was used was the neuropil fraction of Brodmann’s areas (BA) 44 and 45. A neuropil, or the space between neurons and glial bodies, is composed of dendrites, axons, synapses and glial cell processes (Spocter et al 2012). The fraction of the gray matter in a defined area can serve as a representative of connectiveness of the area, both local and far-reaching connections (Wree et al 1982). The more potential for connections, the larger the neuropil fraction. BA 44 and 45 are known to be included in Broca’s area that functions in communication (Amunts 1999). Particularly, BA 44 is involved in language processing in humans, while BA 45 is utilized in language execution in humans (Ojemann 1991, Burton 2001). As the IFG is being traced anatomically in this study it seemed appropriate to also look at the cytoarchitecture of that area as well.

An interesting feature of brain evolution is lateralization or asymmetry. Asymmetry is when the volume of one hemisphere is significantly larger than the other hemisphere. Asymmetry allows different sections of the brain to become specialized and handle greater amounts of information at once. Lateralization is not uncommon in the evolution of vertebrates. Many avians, reptiles and amphibians have shown lateralization due to senses or motor abilities (Rogers and Andrew 2002). In fact, even invertebrates such as
nematodes, fruit flies and octopuses have shown lateralization (Hobert et al 2002, Byrne et al 2004 and Pascual et al 2004). For example, octopuses, which prefer monocular vision, show preference for one eye over the other, but there does not appear a population level preference (Byrne et al 2004). Chimpanzees have been previously known to show lateralization in their neuroanatomical structures that relate to handedness (Hopkins et al 2003 and Hopkins and Cantalupo 2004).

Hypothesis: Bonobos will possess a larger volume and a greater degree of lateralization in the left hemisphere of the inferior frontal gyrus (IFG) than chimpanzees due to an increased reliance on vocalizations.

While Broca's area homologues have been indentified in bonobos there has been little analysis of the volumetric differences in those areas and then comparing it to chimpanzees. Rilling et al (2012) found several different gray matter differences doing a voxel-based morphometry analysis (VBM), which compares MR images at the smallest level (voxel or 3-dimensional space of the scan), in the neurological areas involved with empathy and tension release. In addition to that there have been studies showing differences in volume and lateralization between chimpanzees and bonobos in other brain structures (Hopkins et al 2009).

I completed a comparative study of chimpanzee and bonobo MRI scans with a new definition of the IFG to determine if there was any difference in the volume and asymmetry of the IFG in chimpanzees and bonobos. Since it is hypothesized that bonobos have greater reliance on vocalizations, similar to autonomous speech in humans, there should be a greater volume in areas involved in communication, particularly the IFG, than
chimpanzees. Also, it has been found that a leftward asymmetry was related to dominance in language in humans and chimpanzees, so it is hypothesized that there should be a more prominent leftward asymmetry in bonobos, similar to what is seen in humans, because of the hypothesized differences in vocal usage (Foundas et al 1998 and Taglialatela et al 2008).

Hypothesis: Bonobos and chimpanzees should display similar neuropil fractions, the amount of space between neurons available for connections in the gray matter, in Brodmann’s areas (BA) 44 and 45, based on the previous research comparing humans and chimpanzees.

It is hypothesized that the amount of space, area between cells, available for connections throughout the brain increases with the complexity of the systems, particularly in areas responsible for human language and cognition (de Sousa et al 2010, Semendeferi et al 1998, 2001, 2011). There are two structural options that could have evolved, one is that the gray matter could be filled with neurons or the number of neurons could decrease and the number of connections increases. This second option would allow for quicker signal transmission over greater lengths, as the time it would take to create action potentials in the multiple neurons would be a more timely process than keeping a signal travelling through one neuron. The way I chose to analyze this is to look at the neuropil fraction, or the amount of space in the gray matter that is taken up by cells as compared to area that is open to connections. Spocter et al (2012) looked at several different areas in the brain and discovered that there was no statistically significant difference between the neuropil fraction in humans and chimpanzees, including BA 45. Given this information, there should be no difference between the percentage of neuron
coverage between chimpanzees and bonobos. While so far there has been no significant
differences found between chimpanzees and humans, it is important to look at bonobos as
well, particularly since there have been no studies done looking at the neuropil fraction of
communicative areas of the brain in bonobos. It is important to be certain that there are no
true differences in the neuropil fraction because it could potentially explain why there are
differences between chimpanzee and bonobo vocalizations.

**Methods**

**MRI-Analysis**

**Subjects**

Thirteen bonobo and chimpanzee MRI scans (4 *in vivo* and 9 cadaver each species) that were matched for age, sex and scan type were utilized in this study. For the asymmetry quotient, all 26 subjects were used, however, when comparing the volumetric differences 3 pairs had to be dropped due to resolution differences between the scan types.

**IFG Tracing**

Tracing of the scans was done using the program Analyze. The scans were resliced and realigned from the raw scans so that the sagittal view could be used for tracing. Tracing started when PCI came into view, tracing all the cortex from the PCI until the skull. Once the FO came into view it was used as the rostral boundary, with tracing occurring from the FO to the posterior gray matter of the PCI. The IFS is used as the dorsal boundary, tracing went from straight up the FO to the IFS then posterior to the most posterior gray matter of the PCI. The Sylvian fissure becomes the ventral boundary when it was in view. Insular cortex was not included in the tracings of the IFG unless directly below the PCI.
Tracing continued until the insula is no longer in view (Figure 1). These boundaries were used for both the left and right hemispheres.

*Statistical Analysis*

To calculate the asymmetry quotient (AQ) the equation \((R-L)/(R+L)/2\) where \(R\) = right hemisphere IFG volume, \(L\) = left hemisphere IFG volume. This equation would result in a positive value indicating right lateralization and negative values indicating left lateralization. The AQ’s of chimpanzees and bonobos were then compared utilizing a paired samples t-test (each bonobo scan was compared to their age/sex matched chimpanzee scan) using the SPSS software package. To analyze the volume differences a repeated measures ANOVA using SPPS (IBM, inc.) was used.

*Neuropil Fraction*

*Subjects*

There were six chimpanzee subjects (5 males and 1 female) ranging from 17 to 41 years old. These were compared to 5 bonobo subjects (4 males and 1 female) ranging from 8 to 38 years old. All of these samples were previously Nissl stained following the procedure of Schenker et al 2010.

*Tracing BA44/45*

Three consecutive 10 mm apart that contained either BA 44, 45 or both were chosen for each hemisphere per subject. Broca’s area 44 and 45 were identified via the cytoarchitecture as described in Schenker et al 2010. Using layers II-VI, the entire area was traced and then viewed under 20X magnification. The region of interest was then broken into 40 sample images using Systematic Random Sampling (SRS) in StereoInvestigator
software that optimized the area of the picture. Each sample image was captured as a digital photo at a standard light intensity on the mounted digital camera (Figure 2). The images containing only gray matter in layers II-VI were then converted to binary where a histogram then calculated the amount of white and black space for all of the images using ImageJ64 software (Figure 3). The three sets of images for each hemisphere and area were then averaged which calculated the neuropil fraction, or the percentage of space between neurons and other cells in the gray matter.

Statistics

The same AQ equation was used as seen above in the MRI tracing and SPSS was used to run a two sample t-test on the AQ’s. A repeated measures ANOVA was used to determine if there was an interaction between the neuropil fraction of either BA 44 or 45 in each hemisphere between the two species.

Results

MRI Tracing

When looking at volume differences of the IFG there was a statistically significant interaction between hemisphere and species (F (1,9) = 4.35; p = 0.051), the bonobos appeared to have a greater right IFG and chimpanzees had a greater left IFG (Figure 7). This was confirmed by the AQ’s that were statistically significant when a paired t-test was run (T = 2.59; p=0.02). Bonobos did have a more rightward IFG asymmetry, while chimpanzees were leftward (Figure 8).

Neuropil Fraction
There was no significant difference between either BA44 or 45 in either the right or left hemisphere (p>0.05). Bonobos did have a higher BA45 in the left hemisphere, but the standard deviation was much larger than that seen in chimpanzees (Figure 9). In fact, the standard deviation for all areas and hemispheres studied in bonobos was much larger than standard deviations seen in chimpanzees. Bonobos were left-lateralized for both BA44 and 45, but chimpanzees were rightward for BA45 and leftward for BA44. (Figure 10)
However, the standard deviations were very large for both chimpanzees and bonobos.

Discussion

MRI Tracing

While there was a significant difference between the species and the hemispheres volume of the IFG it was not the difference that I was expecting (Figure 7). There was a significant difference between chimpanzees and bonobos asymmetry quotient (Figure 8). Bonobos were right-lateralized in the IFG while chimpanzees were left. This is the opposite of what was expected based on the literature regarding human communicative centers lateralization. Based on Foundas et al 1998, where humans were identified as being left lateralized in communicative areas, it was expected that the reliance on vocal communication seen in bonobos would result in similar lateralization in the IFG. However, the fact that chimpanzees utilize gesture more frequently in communication could explain this difference that is seen. Communication is not the only behavior that correlates to lateralization in the brain. For example, handedness is often associated with asymmetries in several parts of the brain including communicative centers (Hopkins and Cantolupo 2004 and Hopkins et al 2003). The physical action of using arms, hands, legs and feet when
communicating with a gesture could possibly create the leftward asymmetry seen in chimpanzees. Chimpanzees, but not bonobos, are also known to use tools for feeding (termite-fishing) in the wild, this type of problem solving would also occur in the frontal lobe of the brain, furthering the leftward asymmetry (Goodall 1986, Suzuki et al 1995 and Sanz 2009). It is also possible that the hemisphere that is lateraled does not affect the communicative abilities of the two species. Octopuses have different individual and population level asymmetries of eye preference, but there does not appear to be a correlation between eye preference and survival (Byrne et al 2004). The direction of the asymmetry may not be important when it comes to chimpanzee and bonobo communicative abilities, just the fact that one hemisphere is larger than another.

Even though bonobos are right-lateralized in the IFG does not mean that the left hemisphere is not utilized more in communication. One possible way to achieve this is with the amount of gray matter in each hemisphere. The right IFG may have a larger volume, but if the left IFG contains more gray matter that means that there is a greater number of neurons in that area. This would be a more effective communicative center than one filled with white matter. A second possibility of determining the actual use of the IFG in communication would be to look at the connections between the IFG and other areas of the brain that deal with communication, such as the planum temporale which is were Wernicke’s area is located (Catani et al 2005 and Rilling et al 2008).

**Neuropil Fraction**

As expected, due to the lack of significant difference in the neuropil fraction of chimpanzees and humans found in BA 45, there was no difference between BA 44 and 45 in chimpanzees and bonobos (Spocter et al 2012 and Figure 9). Even in the asymmetry
quotient there was no significant difference between the species, but both BA 44 and 45 were left lateralized in bonobos (Figure 10). Chimpanzees had a rightward lateralization of the BA45 neuropil fraction. It is suggestive that there is a greater potential for connections in the chimpanzee in the right BA45 then the left BA45. When combined with the MRI data it is possible that while the volume of the IFG is left lateralized in chimpanzees the connections utilized for communication actually occur in the right hemisphere. This also could explain the bonobo data, the IFG volume was right lateralized, but the neuropil fraction for both BA44 and 45 was left lateralized.

This study contained a very small sample size; it is possible with more subjects a pattern in the lateralization or neuropil fraction of BA44 and 45 may become more pronounced. It appears that the greatest difference between chimpanzees and bonobos was found in the left BA45. Bonobos appear to have a higher neuropil fraction than chimpanzees, which suggests that there is a greater potential for connections in the left bonobo BA45 than the chimpanzee left BA45. However, there is a large standard deviation in the all of the bonobo neuropil fractions. One of the reasons that the large standard deviation could have come about is the rearing history of the subjects. One bonobo subject that had a much higher neuropil fraction than chimpanzees and most of the bonobo specimens was raised in a language-learning environment. This subject was also the youngest at 8 years old and it is possible that the connection in his brain were not fully developed. Both of these could have altered the cytoarchitectonics of the subjects' communicative areas of the brain.

Summary

Chimpanzees and bonobos have clear differences in their vocalizations and their
communicative strategies. The data suggest that these communicative strategies appear to be adapted for their specific habitat and feeding ecologies. Bonobos live in strictly forested environments and tend to spread out for their main food resource, THV, which restricts their visual proximity to other conspecifics. In order to communicate effectively with out-of-sight conspecifics bonobos were selected for a heavy reliance on vocal communication. My data shows that bonobos do not often combine their vocalizations with CCS’s or direct the vocalizations at individuals. Since bonobos do not utilize other modalities with their vocal signals as frequently as chimpanzees do, vocal types must be less strictly tied to social contexts. Instead of using CCS’s to elaborate the message, bonobos may alter the temporal elements of their vocalizations to create more information in the signal. This is similar to what is seen in birds and autonomous speech of humans. Chimpanzees, however, live in a variety of habitats that includes forests and grasslands. Even when in the forests the heavy reliance on fruit causes individuals to be within visual proximity of each other, which would allow vocal types to be tied to specific social contexts and CCS’s to be used to pass along more information. My data supports this hypothesis, as chimpanzees were more likely to vocalize with a CCS then without. The chimpanzees also directed more vocalizations at conspecifics than the bonobos did and their vocal types were more closely tied to specific social contexts than bonobos. While these data supports the hypothesis that feeding ecology has influenced the communicative strategies of these two species it is important to run experimental tests in captivity or the wild that compares the communicative strategies of both species when high and low quality food is either clumped or scattered.

The behavioral differences were also reflected by the anatomical differences in the
anatomy and cytoarchitecture of the IFG. Chimpanzees were left lateral in the IFG, while bonobos were right lateral. It is unclear if the hemisphere that is more asymmetric is significant to the communicative abilities or strategies of these two species, but it does suggest that there may have been a change in genetic expression in development. This change in expression could be accompanied with other genetic changes that have caused this difference in communicative strategies. Bonobos appear to have a greater neuropil fraction in the left hemisphere BA 45 than chimpanzees. The left and right hemispheres of BA 44 and right BA 45 appear to be extremely similar in chimpanzees and bonobos. Chimpanzees also appear to be right lateralized for BA 45, but left lateralized for BA 44. However, bonobos are left lateralized for both BA 44 and 45. While these trends are interesting the sample size that I used was far too small to determine if any of these patterns are true, as seen by the standard deviations (Figures 9 and 10). Further investigation of the connections between the lateralization of the IFG and BA 44 and 45 is needed to determine the importance of the patterns found in my study.

**Integration of the Thesis Research**

This research currently involves several aspects of biology that ranges from the ecological scale to the genetic scale. Known ecological literature was used to form the hypothesis and predictions regarding the behavioral data. Then, neurobiological data was utilized as a way to determine where the genetic change causing these different communicative strategies might have occurred. However, not only was anatomical data used by cytoarchitectonic data was used to choose the regions of interest and to further look for evidence of genetic changes, in the form of a neuropil fraction. My research could be further integrated by actually looking at gene and protein expression data in the known
communicative gene FOXP2. Most importantly, this data can and is used to answer questions regarding the evolution of human language by utilizing the two closest extant relatives of humans.

Acknowledgements

I would like to thank the Yerkes National Primate Research Center, San Diego Zoo and Jacksonville Zoo and Gardens for allowing me to collect data at their facilities. I would also like to thank Chet Sherwood, Cheryl Stimpson and Serena Bianchi (George Washington University, Department of Anthropology) for allowing me to utilize their lab and their assistance in the neuropil study, and Bill Hopkins of the Neuroscience Institute at Georgia State University for all of his assistance with the MRI scans. I would like to thank Jamie Russell, Division of Developmental and Cognitive Neuroscience, Yerkes National Primate Research Center for collecting part of the video data. Also, I would like to thank Ryan Bohnenkamp, Kennesaw State University, for her assistance in defining the new IFG boundaries. Finally, I would like to thank my advisor, Jared Taglialatela, for all of his support and assistance throughout this project.
### Tables and Figures

**Table 1. Chimpanzee vocalizations.**

<table>
<thead>
<tr>
<th>Vocalization Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pant Hoots (PH)</td>
<td>Voiced on both inhalation and exhalation and incorporate a series of “hoo” sounds which may or may not escalate to a climactic scream or piercing “ahh” vocalization.</td>
</tr>
<tr>
<td>Alarms (AL)</td>
<td>Loud, sharp vocalizations that may sound like “wraa,” or “waa”. Alarms are given in the context of a real or perceived danger (snake, truck, etc.). Some chimpanzees may also make a quieter “hoo” sound in this context. Alarms are often made by bystanders during a fight.</td>
</tr>
<tr>
<td>Barks/Grunts (BG)</td>
<td>Vocalizations that are produced by short exhalations sounding like ‘aaa.’ They are often produced in a series and can range in pitch from low to high. Grunts are relatively low frequency and noisy, whereas barks tend to be more tonal and higher in frequency than grunts. These calls are typically associated with the anticipation of eating or receiving food or other positive experiences.</td>
</tr>
</tbody>
</table>
| Pants and Pant Grunts (PG)| Fast, repetitive low frequency vocalizations made on both inhalation and exhalation. Pants are very quiet and breathy and are sometimes accompanied by placing an open mouth on another individual while panting. Grunts (PG) Pants can be
difficult to hear from a distance and are most easily recognized by the quick, rhythmic movements of the body. Pant grunts are quiet vocalizations but louder than pants and sound like a series of “ohoh” or “uhuh” sounds made in quick succession.

<table>
<thead>
<tr>
<th>Screams and Whimpers (SC)</th>
<th>Screams are loud, high-pitched, voiced shrieks and at its most intense can be raspy or even hoarse sounding. Screams are associated with fear, submission, distress or agitation. Whimpering sounds a bit like modulated, high-pitched ‘hoo’ sounds or crying and often progresses into screams. Whimpering occurs in chimpanzees of all ages during distress or fear and by infants when being weaned.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Others (OT)</td>
<td>Any vocalization that does not fall into one of the above categories was classified as “other.” This would include idiosyncratic grooming sounds.</td>
</tr>
</tbody>
</table>

Table 2. Bonobo vocalizations

<table>
<thead>
<tr>
<th>Vocalization Types</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hoots (HO)</td>
<td>Relatively loud vocalizations that are produced in a series and are voiced on both inhalation and exhalation. Hoots are often produced by a number of individuals simultaneously.</td>
</tr>
<tr>
<td>Alarms (AL)</td>
<td>Loud, sharp vocalizations that may sound like “wraa” or</td>
</tr>
<tr>
<td>Category</td>
<td>Description</td>
</tr>
<tr>
<td>-------------------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td><strong>Peeps/peep yelps</strong> (PE)</td>
<td>Generally short, tonal, high pitched vocalizations that are produced in a variety of contexts. They may occur in a series or as a single call. The may be modulated or not (i.e. no change in frequency)</td>
</tr>
<tr>
<td><strong>Pants/Grunts (PG)</strong></td>
<td>Relatively low frequency, noisy vocalizations that are usually produced in a series. Pants are fast, repetitive, low frequency vocalizations made on both inhalation and exhalation (e.g. panting laugh). Grunts are also relatively quiet (but louder than pants) and sound like a series of “ohoh” or “uhuh” sounds made in quick succession.</td>
</tr>
<tr>
<td><strong>Screams (SC)</strong></td>
<td>Very loud, high pitched, relatively long vocalizations that have both tonal and noisy components.</td>
</tr>
<tr>
<td><strong>Other (OT)</strong></td>
<td>A vocalization that does not meet any of the above requirements for a category should be classified as other. These vocalizations could include copulation screams (much like that of a regular scream but higher pitched and produced by females during copulation) or any combination or unidentified vocalization heard.</td>
</tr>
</tbody>
</table>
Table 3. Categories of chimpanzee and bonobo concomitant signals (CCS)

<table>
<thead>
<tr>
<th>CCS Category</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manual gestures</td>
<td>This includes any manual gesture made with the hand or arm,</td>
</tr>
<tr>
<td>(MG)</td>
<td></td>
</tr>
<tr>
<td>Facial displays</td>
<td>This includes fear grimace, facial inspection, kiss, pout face</td>
</tr>
<tr>
<td>(FD)</td>
<td></td>
</tr>
<tr>
<td>Body postures</td>
<td>This includes bouncing, chasing, crouching, displaying, head bobbing,</td>
</tr>
<tr>
<td>(BP)</td>
<td>mounting, presenting, rocking, swaggering</td>
</tr>
</tbody>
</table>

Table 4. Chimpanzee and bonobo social/behavioral contexts.

<table>
<thead>
<tr>
<th>Context</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copulation/GG Rub</td>
<td>Caller is actively engaged in sex or genital-genital contact with a conspecific</td>
</tr>
<tr>
<td>Displaying</td>
<td>Caller is swaying, charging, drumming, slapping the ground/walls/barrels, or throwing objects; accompanied by pilo-erection</td>
</tr>
<tr>
<td>Feeding/Foraging</td>
<td>Caller is consuming food or actively searching for food</td>
</tr>
<tr>
<td>Fighting</td>
<td>Caller is is slapping, biting, hitting, or chasing a conspecific, while pilo-erect or is being slapped, bitten, hit, or chased by a pilo-erect conspecific</td>
</tr>
<tr>
<td>Greeting</td>
<td>Caller is approaching or being approached by a conspecific that they previously had not been in contact with</td>
</tr>
<tr>
<td>Grooming</td>
<td>Caller picks through the hair or skin of a conspecific, searching for and removing debris from body using hands or</td>
</tr>
<tr>
<td>Category</td>
<td>Description</td>
</tr>
<tr>
<td>--------------------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Locomoting</td>
<td>Caller is walking, running, brachiating, or climbing</td>
</tr>
<tr>
<td>Playing</td>
<td>Non-aggressive interactions between two or more individuals that can include a combination of tickling, wrestling, biting, sparring, chasing, kicking, play-face, and laughing</td>
</tr>
<tr>
<td>Resting</td>
<td>Caller is sitting, laying, sleeping or standing stationary</td>
</tr>
</tbody>
</table>
| External Influences| **Human/Food** – Approach of humans to the area to give out food or enrichment  
**Outside Events** – Events that cause tension or excitement, but are not happening to the caller, e.g. fights, loud noises, other animals entering enclosure |

Figure 1. Example of right IFG as traced in one slice of an *in vivo* bonobo MRI scan.
Figure 2. Nissl stained SRS section of BA 45 from the left hemisphere of a chimpanzee before conversion to binary. Section is 1 mm thick with an area of 350\(\text{m} \times 350 \text{m}\).

Figure 3. Nissl stained SRS section of BA 45 from the left hemisphere of a chimpanzee after conversion to binary. Section is 1 mm thick with an area of 350\(\text{m} \times 350 \text{m}\).
Figure 4. Percentage of vocalizations that occurred with and without a concomitant signal, error bars are standard error (n=1571 chimpanzee vocalizations, 612 bonobo vocalizations).

Figure 5. Percentage of vocalizations that were and were not directed, error bars are standard error (n=1571 chimpanzee vocalizations, 612 bonobo vocalizations).
Figure 6. Percentage of vocalizations that occurred in the most common context (MCC) and non-most common context (NMCC), error bars are standard error (n=1571 chimpanzee vocalizations, 612 bonobo vocalizations).

Figure 7. Volumes of the left and right hemispheres of the IFG of 10 bonobos and 10 chimpanzees, 3 subjects dropped due to technical issues with the scans, error bars are standard error.
Figure 8. Asymmetry quotient of the volumes of the IFG for all 26 subjects, error bars are standard error.

Figure 9. Neuropil fraction averages for chimpanzees and bonobos for Broca's areas 44 and 45 for both the left and right hemispheres, error bars are standard deviation.
Figure 10. Asymmetry quotient of the neuropil fraction for Broca’s area 44 and 45, error bars are standard deviation.
References


Corballis, M. C. 2004. The origins of modernity: Was autonomous speech the critical
factor. Psychological Review 111, 543-552.


Hare, B. and Kwetuenda, S. 2010. Bonobos voluntarily share their own food with others.
Current Biology 20, R230 – R231.


vocal perception in the chimpanzee brain. Cerebral Cortex 19, 1151-1157.


