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Self-directed behaviors, handedness & lateralization in the bonobo (Pan paniscus)

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Self-Directed Behaviors, Handedness & Lateralization in the Bonobo (*Pan paniscus*)

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

in

Biology

by

Elysa Anne Everson

Committee in charge:

Professor David Woodruff, Chair
Professor David Holway
Professor James Nieh

2011
The Thesis of Elysa Anne Everson is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California, San Diego

2011
This thesis is dedicated to Edna Everson, the best grandma in the world. Who gladly assisted in building a thousand birthday cakes out of sand, who makes the best Mac-N-Cheese on the planet, and who taught me never to give up...
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As an advisor, David saw me through several years (what probably should have been months!) of project changes and edits- with lots of interesting surprises along the way. What I am most thankful for, other than for allowing me to operate a clandestine kitten nursery in his lab, is that David never lost faith in this project. Without David’s support, guidance, and friendship this project would have been as sad and lonely as all those sweet little kittens he refused to adopt. I couldn’t have made it here without him.

I would also like to thank Dr. Christine Johnson for her valuable insight with regards to the mysterious eccentricities of bonobo behavior and for helping me set up and guide this project. I’d like to thank David Holway and James Nieh, for being on my committee, and acknowledge all my friends from all over the world who never failed to respond to my frantic e-mails regarding stats and graphics: Daren Eiri, Rebecca Dai, Meg Eckles, Matt Tucker, and Katie LeVan.
ABSTRACT OF THE THESIS

Self-Directed Behaviors, Handedness & Lateralization in the Bonobo (*Pan paniscus*)

by

Elysa Anne Everson

Master of Science in Biology
University of California, San Diego, 2011
Professor David Woodruff, Chair

The bonobo, *Pan paniscus*, originated from central African chimpanzees (*Pan troglodytes*) 1–2 million years ago and has been used as a model for the ancestral human condition. This study focuses on the handedness and directional lateralization of a set of behaviors known as self-directed behaviors, which are often used as an index of emotional arousal with regards to the stress response. They arise from unconscious defense mechanisms that are thought to serve as arousal-inhibiting systems within the central nervous system during the stress response.

This study was based on the nonintrusive videotaping of a group of 10 captive bonobos living at the San Diego Zoo during two periods about ten years apart. 1,174 self-directed behavior events were identified and micro-analyzed, in nearly 20 hours of recorded observation. The directional laterality and population-level handedness...
for each self-directed behaviors were calculated, along with individual handedness scores for each bonobo, which were compared to the handedness scores reported previously by others for these same individuals. It was predicted that, on an individual level, there would be a shift away from symmetrical control in the brain of self-directed behaviors. This prediction was confirmed by the observation of several significant individual-level preference determinations in the execution of self-directed behaviors, presumably reflecting a corresponding asymmetrical functional lateralization in the cerebral management of stress. Significant population-level handedness was neither expected nor observed, confirming a lack of population-level bias in this species and supporting the idea that the alignment of lateralization may not be under selective pressure.
Introduction

In this thesis I explore the question of what we can learn from the study of the behavior of our sister taxon, the bonobo, that might enable us to better conserve these now endangered primates. The bonobo or pygmy chimpanzee, Pan paniscus, originated from central African chimpanzees (Pan troglodytes) 1–2 million years ago (Caswell et al., 2008) and has been used as a model for the ancestral human condition based on genomic, anatomical and behavioral evidence (Zihlman et al., 1978; de Waal and Lanting 1997). A few of the remaining 50,000 bonobo have been studied in their native Congo forests (Kano, 1992) but the species is better known from observations of the few hundred apes kept in zoos (Sandin, 2007; Woods, 2010). The well-being of these captive apes is of paramount concern and the focus of a Species Survival Plan organized by the Association of Zoo’s and Aquariums (Reinartz, 1994). Although the public’s imagination was captivated by the bonobos designation as the “make love, not war” species (de Waal, 1995), the welfare and sustainability of the captive populations hinges more on their adaptation to the stresses of confinement than their reproductive behavior. For that reason I have focused this thesis on the quantification of selected aspects of stress-related behavior in one population. I examine the use of self-directed behaviors (SDBs), which are also known as “displacement” or “referential behaviors”, and are associated with stress. In addition to offering my own interpretation of these behaviors I have, in a series of short essays in Appendix A and B, discussed the possibly analogous behaviors in humans.

By comparing behavioral synapomorphies between sister-taxa, we gain insight
into the evolution and character of derived ancestral psychological features. From this insight we can suggest mechanisms regarding the evolution of homologous behavioral patterns. Chimpanzees and bonobos are the best candidates to exhibit precursors of human features (Chapelain & Hogervorst, 2009), however, bonobos have not been investigated to the extent of their chimpanzee counterparts. The deficit of research on bonobos would be appropriately addressed by a more inter-disciplinary approach, and by integrating information from both in-situ and ex-situ sources. Both genotypic and phenotypic inquiries with regards to the bonobo are applicable in the fields of anthropology, biology, medicine, psychology, cognitive science, neuroscience, and primatology.

My study specifically investigates the mechanisms that underlie cerebral lateralization with regards to stress. Other lateralized behaviors include handedness, language, and the emotional response, which may be derived traits that existed in a common ancestor of humans and apes several million years ago (Byrne & Byrne, 1991; McGrew & Marchant, 1997; Chamberlain & Hogervorst). Similarly, the human stress response may differ with regards to cerebral lateralization, only in degree rather than nature from other non-human homininds.

In Freudian psychology, displacement describes an unconscious defense mechanism whereby the mind redirects affects from an object felt to be dangerous or unacceptable to an object felt to be safe or acceptable (Akhtar, 2009; Schmid-Kitsikis, 2005). This subconscious mechanism is categorized as a “primary” psychological process, meaning that the transference of physical intensities occurs along an "associative path" so that ideas charged with emotional investment have their intensity
displaced onto other less strongly emotionally potent ones (Freud, 1966), often resulting in the display of SDBs. Julian Huxley (1968, 1970) described these behaviors as the result of two contradicting instincts in a particular situation, which often involve actions to bring comfort such as scratching, drinking or feeding.

In the field of ethology, Nikolaas Tinbergen (1951) and Adriaan Kortlandt (1955) described SDBs and displacement activities as behaviors which are out of context with the behavior which closely precedes or follows them, either in the sense that they do not seem functionally integrated with the preceding or following behavior or that they occur in situations in which causal factors usually responsible for them appear to be absent or at least weak compared with those determining the behavioural envelope (Delius, 1967). These causal factors may manifest as a conflict between motivational drives within an individual, and result in SDBs particularly when uncertainty plays a role, for example, the animal must resolve a desire to approach an object, while at the same time being fearful of that object (Maestripieri et al., 1992).

Uncertainty is often implicated during intraspecific social interactions, and was shown to increase rates of SDBs in macaques (Aureli et al, 1999). Higher levels of uncertainty about how to behave during a feeding situation induced SBDs when hierarchical social ranking and dominance relationships were undefined within a group (Hopkins et al., 2006). Dollard (1939) suggests that the occurrence of behaviors reflects a homeostatic process operating towards cancelling the arousal generated through motivational conflict, frustration, and the physical thwarting of performance. This attempt to maintain some sort of emotional balance or equilibrium may occur
through the activation of an arousal-inhibiting system within the central nervous system, which probably operates within a very specific range of conditions in order to facilitate efficient sensory communication. It is this system that probably underlies the manifestation of stereotypic and self-directed behaviors. Leavens et al. (2001) categorized stereotypic self-directed behaviors in humans as rubs, gentle scratches, and rough scratches, which are differentially displayed as a function of social interactions, anxiety related drugs, and a response to outcomes during learning tasks.

Because these behaviors are evident in a variety of stress related contexts, they’ve come to serve as an index of emotional arousal within behavioral research (Mason, 2011), and are directly proportional to the physiological indicators of stress response, such as plasma cortisol, plasma ACTH, catechoamines, heart rate, and blood pressure (Esler et al., 1989; Gotthardt et al., 1995; Hutt & Hutt, 1965; Sausen et al., 1991). Interspecies variability in these stereotypic behavior patterns could potentially be used in the future to pinpoint the fundamental origins of this behavior, and are widely used in welfare research, but not to date in evolutionary or ecological work despite the fact that they might provide ‘evo mecho’ insights into the evolution of different types of behavioral control mechanisms (Mason, 2011). Animal behaviorists paid little attention to SDBs until Maestripieri et al. (1992) pointed out that quantification of these behaviors might be a more appropriate measure of anxiety as compared to measuring the physiological indicators of stress (i.e. blood cortisol levels, heart rate, ACT, etc.), which may actually confound the measurement by actually inducing stress.
The quantification of SDBs is a passive way to observe animals without invasively interrupting the present context of social interactions within the group, and for this reason was chosen as an index by which to measure stress in two captive bonobo groups. Understanding what cerebral mechanisms regulate these behaviors could be useful in understanding the evolution of brain organization and hemispheric specialization. Assuming that the sensory neurons associated with the itch are projected contralaterally (Leavens, 2006), and that the stress response is indeed governed by the right hemisphere (Hopkins, 2006a), I would expect to see an asymmetry in SDB responses, possibly reflected in the choice to direct most SDBs to the left side of the body.

As far as I know, there have been no previous studies published on the lateralization of SDBs specifically in Pan paniscus. However, the lateralization of handedness in bonobos has been addressed in two other important studies. These are relevant because handedness is directly related to brain lateralization and presumably interacts with the same neurological pathways to control the frequency and nature of SDBs. Shafer (1997) and Zuniga (2006) both attempted to detect population level lateralization and handedness in bonobos, using the same captive individual bonobos at the San Diego Zoo. Although Shafer (1997), Zuniga (2006), and my own studies investigate different questions, there are many overlapping areas that permit comparison.

Shafer (1997) identified this group as having significant individual hand preferences with regards to a generalized variety of different behaviors, and detected a significant
population-level right hand bias. Zuniga (2006) studied handedness only in regards to termite fishing, a dextrally complex tool-use behavior, and also found individual preferences, despite a lack of significant population-level handedness. In chimpanzees there is evidence for lateralization in certain cognitive tasks, irrespective of population-level limb preference, which supports the idea that an organism can have both individual and population-level lateralization for different functions (Hopkins & Carriba, 2002).

My study focuses on the same group of captive bonobos at the San Diego Zoo, and addresses the handedness and lateralization of SDBs, which are related to the stress response. Based on the findings of Shafer (1997), Zuniga (2006), and Hopkins & Carriba (2002), I predict that the 9 bonobos observed in this study would also display an individual level preference of using one hand versus the other in the execution of self-directed behaviors. This presumably would reflect asymmetrical lateralization with regards to SBDs and the cerebral management of stress. On the other hand, significant population-level handedness was not necessarily expected. These predictions are in agreement with the findings of previous studies documenting individual handedness in both species of Pan despite a lack of population-level bias (Chapelain & Hogervorst, 2009; Hopkins, 2006; Zuniga, 2006), concordant with the idea that the alignment of lateralization may not be under selective pressure. The selective pressures and causal mechanisms involved in the shift away from symmetrical control of function in the brain and ambidexterity are still mysterious, and more research is called for. The most common theories proposed to explain the
evolution of handedness include social/ environmental learning, hormonal regulation, genetics, postnatal postural origin, and brief explanations of each of these theories is provided in Appendix B (B-5, B-6, B-7, B-8 and B-9 respectively).
Methods

Handedness and SDBs were studied in a colony of bonobos kept in a small, naturalistic enclosure at the San Diego Zoo. Using videotapes taken under the direction of Dr. Christine Johnson (Department of Cognitive Sciences, University of California San Diego), it was possible to compare behaviors of up to ten focal individuals in two time periods: 1996–1997 and 2007–2008. The individuals studied are described in Table 1, and include two juveniles. Nine individuals in total were observed in both time periods. The dates and times of observations are listed in Appendix C; over 1000 hours of videotape are archived and digitized. For the purpose of my study, a sample of about 30 hours was chosen for analysis, without any prior knowledge of a time frame’s behavioral content. However, the videotape from 1996-1997, which was composed of footage of Congo, LaVerne, and Lolita, was chosen based on the findings of a previous study, suggesting that these individuals, at that time, were socially “tense”. Dr. Christine Johnson (personal communication) stated that the colony appeared stressed based on a study examining bonobo gaze and communication, and therefore, it seemed appropriate to compare this footage to the observations from the 2007-2008 group.

All observed SDB events were recorded for each focal individual in an Excel file for analytical purposes. The individual SDB type (Table 2), the SDB agent, and the SDB target location (Table 3) were recorded. Other individuals near the focal animal at the time of each event were also recorded in order to provide a social context for the SDB. The agents and the target locations (Table 3) of the SDBs were used to measure the directionality of each SDB event, in an attempt to describe the SDBs as
being symmetrically or asymmetrically directed with regards to the median bodyline. Recording the agent of the SDB also enabled the qualification of individual handedness scores.

This study of self-directed behaviors was based on the nonintrusive videotaping of a group of 10 captive bonobos living at the San Diego Zoo during two periods about ten years apart. 1,174 self-directed behavior events were identified and analyzed in the nearly 20 hours of recorded observation. Each SDB was analyzed separately using a chi-square test to detect directional laterality (by using a ratio describing contralateral and isolateral events) and population-level handedness (Tables 4-10). The individual handedness scores for each bonobo were also calculated using a chi-square test (Table 11) and compared with handedness scores reported previously by Zuniga (2006) during termite fishing and Shafer (1997) in a variety of activities (Table 12). Finally, overall directional laterality was recorded in Table 13.

Subjects

Data were collected for two groups of bonobos living at the San Diego Zoo about ten years apart. Each subject’s age class was determined based on the definitions provided by Kano et al. (1992) and details of lineage and the status of rearing can be found in Table 1. In the 1996-1997 study, the group was significantly smaller (3), and generally all members were equally represented on the tape. The videotapers were instructed to get as many bonobos within the frame, so as a result, all three adolescents were observable most of the time. No other bonobos were in the enclosure at this time. There were significantly more members in the 2006–2007 study (8), all which were confined in the same enclosure. Because of the larger size of this group, most of the
tapes had dyadic focal-level observations, which concentrated on Kesi and Lana, the only mother-infant dyad in the group. Therefore, the members of the second group were differentially represented as their proximity to the dyad changed. The two individuals who were definitely under-represented in the second study were Makasi and Mchumba, who did not spend much time around the focal dyad. However, the dyad that was the focus of the videotaping in the 2007-2008 study was rarely separated from the rest of the group, and generally most of the other bonobos within the enclosure could be observed at any given time within the frame of the video.

Because the observational periods of each individual were not equal or comparable, it is impossible to define relative levels of activity with regards to SDBs. Unless the data had been transformed into events per unit of time, which was complicated by the movements of the animals in and out of the frame of observation, then the animals are not actually comparable in this study. Relative activity would address whether some individuals are more likely to exhibit this SDB than others, and could only be addressed by personal observation rather than empirical evidence. The disproportionate observational periods confound the results for relative activity, however handedness and laterality are unaffected by this, and therefore, several hypotheses could be tentatively addressed within the scope of these two studies.

One other factor that influenced the videotaping of both these groups was weather. If the weather was deemed too cold (lower than 60°F) or wet for the bonobos to be outside, they were not released into the public enclosure, and were therefore not taped for that day. Also, if one bonobo was sick, had a health exam that day, or had recently antagonized another member of the group (leading to a potentially dangerous
social climate), then that individual was sequestered from the rest of the group and was not present during the video-taping for that day. The list of who was present during the video-taping on any given day can be found in Appendix C. Also, Lolita was present in both studies, first as a nulliparous adolescent just reaching adulthood, and then 10 years later, as a post-parous adult. Therefore, the summation of subjects from both studies gives a total sample size of 10.

**Bonobo Group 1996-1997**

The first group included a male adolescent named Congo, and two female adolescents named Lolita and LaVerne. This group was monitored and video taped on weekdays from 9am-1pm, for approximately 10 months, between September 1996 and July of 1997. Although Congo’s lineage and date of birth are unknown, it is significant that LaVerne was the daughter of the dominant matriarch of another group (Lana) and was reared by her biological mother, presumably giving her a high rank. Lolita on the other hand was nursery-raised by zoo-keepers, and was considered to be “less dominant” than LaVerne.

**Bonobo Group 2007-2008**

The second group consists of 8 individuals of varying sex and age class between October 2005 and November 2008, on weekdays from 9am-1pm. Lana, the adult matriarch of this group, was born in 1979 and was nursery raised by zoo-keepers. Ikela and Lolita, born in 1991 and 1989 respectively, at this time were both adult subordinate (to Lana) females that were also nursery raised. The adult males in this group are called Yenge and Junior. Junior is the son of the matriarch, Lana, and had just entered adulthood just prior to this study. The oldest female juvenile is named
Mchumba, and was hand-reared by her mother, Lolita. It is important to note that
Mchumba was, at the time of this study, was reaching the stage of life where females
undergo an intense period of erratic behavior, which in nature, ultimately leads to the
eviction of that female from the group. This phenomenon is common in female
primates living within social organizations based on male-philopatry. Mchumba’s
behavior at the time of this study was indeed erratic, and she was often excluded from
the rest of the group, which accounts for her under-representation on the tape. The two
infant/juveniles in the group are Kesi, the daughter of Lana and Yenge, who was hand-
reared by Lana (presumably giving her a higher status), and a male nursery raised
orphan named Makasi who is the lowest ranking individual in this group, based on his
age and lack of kin. He also was frequently excluded from the core social group.

Table 1: List of subjects observed at the San Diego Zoo amongst 30 videotapes over a period of 15
years. These subjects were subdivided into two separate study groups.

<table>
<thead>
<tr>
<th>Bonobo</th>
<th>DOB</th>
<th>Lineage</th>
<th>Gender &amp; Age class</th>
<th>Rearing Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>Approx. 89</td>
<td>Unknown</td>
<td>Male adolescent</td>
<td>Conspecific</td>
</tr>
<tr>
<td>Lolita</td>
<td>20 April 89</td>
<td>Louise &amp; Vernon</td>
<td>Female adolescent/adult</td>
<td>Nursery</td>
</tr>
<tr>
<td>LaVerne</td>
<td>Approx. 89</td>
<td>Lana &amp; ?</td>
<td>Female adolescent</td>
<td>Conspecific</td>
</tr>
<tr>
<td>Lana</td>
<td>13 April 79</td>
<td>Linda &amp; Kakowet</td>
<td>Female adult</td>
<td>Nursery</td>
</tr>
<tr>
<td>Kesi</td>
<td>15 Aug 04</td>
<td>Lana &amp; Yenge</td>
<td>Female infant/juvenile</td>
<td>Conspecific</td>
</tr>
<tr>
<td>Mchumba</td>
<td>22 Dec 00</td>
<td>Lolita &amp; Congo</td>
<td>Female juvenile</td>
<td>Conspecific</td>
</tr>
<tr>
<td>Makasi</td>
<td>22 April 04</td>
<td>Retta &amp; Jumanji</td>
<td>Male infant/juvenile</td>
<td>Nursery</td>
</tr>
<tr>
<td>Yenge</td>
<td>25 Dec 82</td>
<td>Salonga &amp; Mato</td>
<td>Male, Adult</td>
<td>Conspecific</td>
</tr>
<tr>
<td>Junior</td>
<td>14 Jan 95</td>
<td>Lana &amp; Maiko</td>
<td>Male, Adult</td>
<td>Conspecific</td>
</tr>
<tr>
<td>Ikela</td>
<td>27 Nov 91</td>
<td>Louise &amp; Akili</td>
<td>Female, Adult</td>
<td>Nursery</td>
</tr>
</tbody>
</table>
Setting
The current San Diego Zoo bonobo enclosure opened April 1993, and has an area 6,000 square feet (557m²), which translates to about 0.13 acres or 0.0557 ha. The exhibit is enclosed by faux rock outcroppings and the substrate consists of grass and dirt. Several twisted palms grow throughout the enclosure. Log formations and rope swings that connect four main areas of the exhibit and attempt to mimic the structural complexity of an arboreal habitat. The different areas are categorized as 1, 2, 3, and 4 and are visible to the public through large glass windows. The enclosure is open-air, with a large waterfall that connects to two small streams. The enclosure also features a heated “cave”, which is also within public view, made of rock outcroppings and surrounded by grass and palms in area 1. On days where the weather is excessively rainy or cold, the bonobos are kept within their indoor enclosure, which is out of the public’s view. The secondary enclosure is situated outside and below the public enclosure, and is accessible to the bonobos via a small staircase located in area 1.
Figure 1: San Diego Zoo Bonobo Enclosure

Figure 2: San Diego Zoo Bonobo Enclosure Floor-Plan
Experimental Protocol

The definitions for the type of SDBs investigated within this study were based on the definitions provided by Leavens et al. (2001) in humans, and are listed in Table 2. Stereotypic self-directed behaviors in humans were described as rubs, gentle scratches, and rough scratches, which were differentially displayed as a function of social interactions, anxiety related drugs, and a response to outcomes during learning tasks (Leavens et al. 2001). Our categories were appropriately modified to incorporate species-specific behaviors for bonobos. Also, in order to anticipate any potential differences with regards to context, we categorized uni-directional vs. bi-directional rubs separately. The final categories, therefore, include rough-scratching, gentle-scratching, uni-lateral rubbing, bi-lateral rubbing, picking, wiping, and self-grooming. Self-grooming includes using fingers or mouth to sift through hair gently while concentrating visually on that area, which is in direct contrast to self picking, a more vigorous and aggressive approach towards self-grooming, often aimed at plucking hair or picking scabs, often without visualization or focused attention.

I chose to include self-grooming as a self-directed behavior, which can be induced by stress. Self-grooming can be thought of as an activity that re-directs an individual’s attention away from a source that causes anxiety or discomfort. By shifting attention to a more benign source, an affected individual can internalize environmental stress and displace focus on another activity, which can be directly controlled by the individual. This type of self-directed behavior is not limited to primates, and has been documented in several other vertebrate species. Maestripieri et al. (1992) found that preening was a common stress behavior found in gulls, and
reported that cats and rats also used self-grooming as a type of displacement behavior. Grooming and preening, defined by a specific set of movements, are largely controlled by neuro-physiological mechanisms, which are also responsible for de-arousal and sleep (Delius, 1967). Self-grooming may be conducive to de-arousal possibly through stimulus reduction (cut-off), via a change of attention to stimuli of little novelty or generation of repetitive stimulation. In light of this theory, self-grooming was included in this study as a SDB, although in practice it may stem from a very different motivational context as compared to the more self-damaging SDBs (such as rough scratching or picking), which are more commonly used as an index of emotional arousal.

Another behavior that was not observed in this study, but common amongst primates is coprophagy (C), which is the consumption of fecal matter. Because this behavior was not identified in either the 1996-1997 or 2007-2008 groups, it was omitted from the analysis of this study. Other behaviors frequently observed and archived were “Nose-Picking” and “Nail-Biting”, however these behaviors were often very difficult to differentiate from a distance and on tape, and often did not seem related to any sort of stressful context. These behaviors were archived to facilitate future potential studies, but were not ultimately analyzed as SDBs. Very little empirical evidence within the literature on primate stress behaviors implicate these two relatively common behaviors as normal displacement SDBs.

Idiosyncratic (stereotypic) behaviors unique to certain individuals were observed in both groups. The “Head roll” seems isolated to Lolita and is characterized by a fast circular turn of the head. The “Ear clutch”, or holding/clutching one side of
the head/ear was only observed in Lana. Ikela demonstrates a behavior which was omitted from the archive, due to its ambiguous function or source, which involved the rapid movement of the lower mandible of the jaw. This could be related to a physiological condition, and therefore may not be indicative of a stereotyped stress behavior.

The “agents” of the SDBs, were the body part directed at a target that actually performed the SDB, and were categorized as either: the right hand, left hand, or mouth. Based on our observations, no SDBs were performed by the feet, although morphologically I suppose it is possible. By scoring the agents of these behaviors, we can infer the handedness/ laterality for each subject in relation to SDBs. The “target” locations of SDBs (i.e. part of the body to which SDB is directed) are listed in 3, and help establish the directional laterality of the individual SDB events. The proximity of individual subjects, in relation to one another, was also scored based on the following protocol. A value of “0” denoted two individual directly in contact with one another (i.e. touching), such as during grooming, sex, cuddling, etc. A value of “1” described situations where both individuals are within arms reach of each other, although they are not directly touching (i.e. sitting beside each other…). A value of “3” indicates individuals are within approximately 5 body widths of one another- therefore, within a distance that might facilitate social contact. A value of “5” denotes that individuals are separated by a distance greater than 5m, which is a distance that does not facilitate social contact. Several context categories were also archived based on the social climate of the subjects in each group, including grooming, being groomed, before sex (within 3 minutes), after sex (3 minutes after copulation), feeding, while others feed,
while locomoting. If none of these categories apply to a given subject at the time of a SDB, it is assumed the focal individual is at rest. Interobserver reliability was calculated to be 100% between both observers based on the fact that each archived film was watched and scored by each participant and all discrepancies in scoring were discussed and ultimately unanimously agreed upon.

**Table 2:** Self-Directed Behavior types.

<table>
<thead>
<tr>
<th>Behavior Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rough Scratches (SS)</td>
<td>Self-touching involving the ends of digits/nails, including movement of the shoulder joint. Generally bi-directional. Curved finger joints.</td>
</tr>
<tr>
<td>Gentle Scratches (GS)</td>
<td>Self-touching involving the ends of digits/nails, but no discernable movement of the shoulder joint. Generally bi-directional. Curved finger joints.</td>
</tr>
<tr>
<td>Rubs (UR [unidirectional], BR [bidirectional])</td>
<td>Self touches <em>not</em> involving the ends of digits (finger tips or nails). Light movements performed by the palms, sides, or backs of the hand, including the palms of fingers and knuckle joints (back of fingers).</td>
</tr>
<tr>
<td>Wipes (W)</td>
<td>One single, independent, and unidirectional movement of the hand or forearm directed at the head or face.</td>
</tr>
<tr>
<td>Self Pick (P)</td>
<td>A vigorous, directed, and aggressive approach towards self-grooming, often aimed at plucking hair or picking scabs from the surface of the skin.</td>
</tr>
<tr>
<td>Self Groom (Self Groom)</td>
<td>Includes using fingers or mouth to sift through hair gently while concentrating visually on that area.</td>
</tr>
</tbody>
</table>
Table 3: Target Locations. Right and left sides were distinguished in an attempt to measure the ratio of contralateral to isolateral events.

<table>
<thead>
<tr>
<th>Location</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsal back (D)</td>
<td>Includes the neck, shoulders, upper and lower back, as well as the buttocks.</td>
</tr>
<tr>
<td>R or L side</td>
<td></td>
</tr>
<tr>
<td>Ventral body (V)</td>
<td>Includes the neck, shoulders, collarbone, torso, and pelvic area</td>
</tr>
<tr>
<td>R or L side</td>
<td></td>
</tr>
<tr>
<td>Left Leg (GL)</td>
<td>From the thigh down to the ankle, including the left foot</td>
</tr>
<tr>
<td>Right Leg (GR)</td>
<td>From the thigh down to the ankle, including the right foot</td>
</tr>
<tr>
<td>Left Arm (AL)</td>
<td>From below the shoulder socket down to the left hand</td>
</tr>
<tr>
<td>Right Arm (AR)</td>
<td>From below the shoulder socket down to the left hand</td>
</tr>
<tr>
<td>Head (H)</td>
<td>The top of the cranium to the sides of the head, including the ears and back of head</td>
</tr>
<tr>
<td>Face (F)</td>
<td>The entire surface of the face including the forehead</td>
</tr>
<tr>
<td>Nose (N)</td>
<td>The entire surface of the nose</td>
</tr>
</tbody>
</table>
Results

Rough Scratches

Rough scratches were the third commonest behavior type observed (after Gentle Scratches and Wipes) and were exhibited in each individual as described in Table 4. 226 instances were observed (106 right and 120 left) but the difference is not statistically significant, [the chi-square test result gave a p-value 0.352, d.f.=1]. In contrast, the lateralization of the behavior was statistically significant (69 contralateral and 39 isolateral, [P-value = 0.004, d.f.=1]. The head and torso (both the ventral and dorsal, right and left sides) were the most common targets of this behavior.

This behavior was not uniformly distributed across the sample of individuals (Table 4). 45% of the observations involved one male individual (Congo) and 44% involved just three other adults (Lolita, LaVerne, and Lana).

Table 4: A total of 227 Rough scratches were recorded, with significantly more contralateral than isolateral behaviors recorded. No population-level handedness was detected.

<table>
<thead>
<tr>
<th>SDB: Rough Scratch</th>
<th>Events</th>
<th>Targets</th>
<th>Contralateral</th>
<th>Isolateral</th>
<th>Right Handed</th>
<th>Left Handed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>103</td>
<td>H</td>
<td>17</td>
<td>9</td>
<td>49</td>
<td>54</td>
</tr>
<tr>
<td>Lolita</td>
<td>43</td>
<td>H,VR</td>
<td>20</td>
<td>9</td>
<td>17</td>
<td>26</td>
</tr>
<tr>
<td>LaVerne</td>
<td>21</td>
<td>H</td>
<td>4</td>
<td>5</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td>Lana</td>
<td>36</td>
<td>H</td>
<td>15</td>
<td>10</td>
<td>15</td>
<td>21</td>
</tr>
<tr>
<td>Junior</td>
<td>4</td>
<td>AR</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Kesi</td>
<td>8</td>
<td>VR</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Yenge</td>
<td>8</td>
<td>DL</td>
<td>6</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Ikela</td>
<td>2</td>
<td>H,VL</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Makasi</td>
<td>2</td>
<td>VR,VL</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
</tbody>
</table>
Gentle Scratches

Gentle scratches were the most common behavior type observed and were exhibited by each individual as described in Table 5. 449 instances were observed (234 right and 215 left) but the difference is not statistically significant [the chi-square test gave a p-value of 0.370, d.f.=1]. Similarly, the lateralization of the behavior was not statistically significant (77 contralateral and 88 isolateral), [P-value = 0.392, d.f.=1]. The head and face were the most common targets of this behavior.

This behavior was not uniformly distributed across the sample of individuals (Table 5). 27% of the observations involved one female individual (Lana) and 42% involved just two other adults (Congo and Lolita).

Table 5: A total of 449 gentle scratches were recorded, showing neither a significant lateralization nor population-level handedness.

<table>
<thead>
<tr>
<th>SDB: Gentle Scratch</th>
<th>Events</th>
<th>Targets</th>
<th>Contralateral</th>
<th>Isolateral</th>
<th>Right Handed</th>
<th>Left Handed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>102</td>
<td>H</td>
<td>17</td>
<td>9</td>
<td>53</td>
<td>49</td>
</tr>
<tr>
<td>Lolita</td>
<td>88</td>
<td>H,F</td>
<td>14</td>
<td>16</td>
<td>51</td>
<td>37</td>
</tr>
<tr>
<td>LaVerne</td>
<td>57</td>
<td>F,H</td>
<td>4</td>
<td>12</td>
<td>26</td>
<td>31</td>
</tr>
<tr>
<td>Lana</td>
<td>127</td>
<td>F,H</td>
<td>29</td>
<td>39</td>
<td>59</td>
<td>68</td>
</tr>
<tr>
<td>Junior</td>
<td>8</td>
<td>H</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Kesi</td>
<td>14</td>
<td>H,F,VL</td>
<td>4</td>
<td>4</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>Yenge</td>
<td>24</td>
<td>H</td>
<td>0</td>
<td>1</td>
<td>19</td>
<td>5</td>
</tr>
<tr>
<td>Ikela</td>
<td>26</td>
<td>H,F</td>
<td>8</td>
<td>6</td>
<td>8</td>
<td>18</td>
</tr>
<tr>
<td>Makasi</td>
<td>3</td>
<td>DL,H</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>
Unilateral Rubs

Unilateral rubs were a common SDB, exhibited by each individual (except for Makasi, probably due to the fact that he was rarely focally observed), as described in Table 6. 96 instances were observed (46 right and 50 left) but the difference is not statistically significant, [the chi-square test resulted in a p-value of 0.683, d.f.=1]. In contrast, the lateralization of the behavior was statistically significant (14 contralateral and 4 isolateral), [P-value = 0.018, d.f.=1]. The face and head were the most common targets of this behavior.

This behavior was not uniformly distributed across the sample of individuals (Table 6). 25% of the observations involved one female individual (Lana) and 59% involved just three other adults (Lolita, LaVerne, and Congo).

Table 6: A total of 96 unilateral rubs were recorded, with significantly more contralateral than isolateral behaviors recorded, and no population-level handedness for this SDB.

<table>
<thead>
<tr>
<th>SDB: Unilateral Rubs</th>
<th>Events</th>
<th>Targets</th>
<th>Contralateral</th>
<th>Isolateral</th>
<th>Right Handed</th>
<th>Left Handed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>17</td>
<td>F,H</td>
<td>1</td>
<td>1</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Lolita</td>
<td>22</td>
<td>F,H</td>
<td>4</td>
<td>1</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>LaVerne</td>
<td>18</td>
<td>F</td>
<td>4</td>
<td>1</td>
<td>4</td>
<td>14</td>
</tr>
<tr>
<td>Lana</td>
<td>24</td>
<td>F,H</td>
<td>4</td>
<td>0</td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td>Junior</td>
<td>2</td>
<td>F,H</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Kesi</td>
<td>6</td>
<td>F,H</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Yenge</td>
<td>3</td>
<td>F,H</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Ikela</td>
<td>4</td>
<td>N</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Makasi</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
**Bilateral Rubs**

Bilateral rubs were a relatively uncommon behavior type observed, and were not exhibited in at least 3 different individuals as described in Table 7. Only 67 instances were observed (33 right and 34 left) but the difference is not statistically significant, [the chi-square test yielded a p-value of 0.903, d.f.=1]. In contrast, the lateralization of the behavior was statistically significant (2 contralateral and 9 isolateral), [P-value = 0.035, d.f.=1]. The face was the most common target of this behavior. This behavior was not uniformly distributed across the sample of individuals (Table 7). 46% of the observations involved Lana and 43% involved just two other adults (Lolita and Congo).

**Table 7:** A total of 67 bilateral rubs were recorded, with significantly more contralateral than isolateral behaviors recorded, and no population-level handedness for this SDB.

<table>
<thead>
<tr>
<th>SDB: Bilateral Rubs</th>
<th>Events</th>
<th>Targets</th>
<th>Contralateral</th>
<th>Isolateral</th>
<th>Right Handed</th>
<th>Left Handed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>17</td>
<td>F</td>
<td>1</td>
<td>1</td>
<td>11</td>
<td>6</td>
</tr>
<tr>
<td>Lolita</td>
<td>12</td>
<td>F</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>LaVerne</td>
<td>4</td>
<td>F</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Lana</td>
<td>31</td>
<td>H,F</td>
<td>1</td>
<td>4</td>
<td>12</td>
<td>19</td>
</tr>
<tr>
<td>Junior</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Kesi</td>
<td>2</td>
<td>F,VR</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Yenge</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ikela</td>
<td>1</td>
<td>N</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Makasi</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Picks

Picking was an uncommon behavior type observed, and was differentially exhibited amongst the individuals in the group, as described by Table 8. 20 instances were observed (15 right and 5 left) and the difference is statistically significant, [the chi-square test resulting p-value was 0.025, d.f.=1]. Similarly, the lateralization of the behavior was statistically significant (7 contralateral and 1 isolateral), [P-value = 0.033, d.f.=1]. Each individual seemed to have different preferential target for this particular SDB, as shown in Table 8. Lana, Junior, and Makasi were never observed picking. However 75% of the observations were equally distributed among Lolita, Yenge, and Ikela.

Table 8: A total of 20 picks were recorded, with significantly more contralateral than isolateral behaviors recorded, and population level-handedness.

<table>
<thead>
<tr>
<th>SDB:Pick</th>
<th>Events</th>
<th>Targets</th>
<th>Contralateral</th>
<th>Isolateral</th>
<th>Right Handed</th>
<th>Left Handed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>1</td>
<td>F</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Lolita</td>
<td>5</td>
<td>F,N</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>LaVerne</td>
<td>3</td>
<td>N,F</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Lana</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Junior</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Kesi</td>
<td>1</td>
<td>F</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Yenge</td>
<td>5</td>
<td>DL,GL,VR</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Ikela</td>
<td>5</td>
<td>AR</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Makasi</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Wipes

Wipes were the second commonest behavior type observed, and were exhibited by each individual as described in Table 9. 234 instances were observed (137 right and 97 left) and the difference in hand preference is statistically significant, [the chi-square test resulting p-value was 0.009, d.f.=1]. In contrast, the lateralization of the behavior could not be calculated, based on the fact that wipes, by definition, were directed towards the nose and face, both targets residing on the midline of the body.

This behavior was not uniformly distributed across the sample of individuals (Table 9). 32% of the observations involved one male individual (Congo) and 56% involved just four other adults (Lolita, LaVerne, Lana, and Yenge). Another question these results address is whether this SDB proceeded locomotion to another part of the enclosure, or a directed action towards some sort of social interaction. As evident on Table 9, this did not seem to be the case.

Table 9: A total of 234 wipes were recorded. Because this SDB could not, by definition, be either contralateral or isolateral, these definitions were not applicable. However, there was a significant population-level handedness for this SDB. This behavior was not significantly displayed prior to locomotion.

<table>
<thead>
<tr>
<th>SDB:Wipe</th>
<th>Events</th>
<th>Targets</th>
<th>Right Handed</th>
<th>Left Handed</th>
<th>Prior to Locomotion</th>
<th>% Pre-Locomotion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>74</td>
<td>N,F</td>
<td>48</td>
<td>26</td>
<td>10</td>
<td>14%</td>
</tr>
<tr>
<td>Lolita</td>
<td>38</td>
<td>N</td>
<td>20</td>
<td>18</td>
<td>10</td>
<td>26%</td>
</tr>
<tr>
<td>LaVerne</td>
<td>29</td>
<td>N</td>
<td>17</td>
<td>12</td>
<td>7</td>
<td>27%</td>
</tr>
<tr>
<td>Lana</td>
<td>38</td>
<td>N</td>
<td>18</td>
<td>20</td>
<td>0</td>
<td>0%</td>
</tr>
<tr>
<td>Junior</td>
<td>2</td>
<td>H,N</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>50%</td>
</tr>
<tr>
<td>Kesi</td>
<td>17</td>
<td>N,F</td>
<td>10</td>
<td>7</td>
<td>0</td>
<td>0%</td>
</tr>
<tr>
<td>Yenge</td>
<td>27</td>
<td>N</td>
<td>14</td>
<td>13</td>
<td>0</td>
<td>0%</td>
</tr>
<tr>
<td>Ikela</td>
<td>7</td>
<td>N,F</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>29%</td>
</tr>
<tr>
<td>Makasi</td>
<td>2</td>
<td>N,F</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0%</td>
</tr>
</tbody>
</table>
**Self Grooming**

Self grooming was a common behavior type observed and was exhibited by most of the individuals (excluding Junior and Makasi), as described in Table 10. 96 episodes were observed (29 right and 29 left, some being performed by the mouth) but the difference is not statistically significant, [the p-value resulting from the chi-square test was 1, d.f.=1]. In contrast, the lateralization of the behavior was statistically significant (44 contralateral and 10 isolateral), [P-value= 0.000, d.f.=1]. Both the right and left arms were the most common targets of this SDB, however, sometimes the legs were also targeted.

This behavior was not uniformly distributed across the sample of individuals (Table 10). 23% of the observations involved Lana and 54% involved just three other adults (Lolita, LaVerne, and Congo).

<table>
<thead>
<tr>
<th>SDB: Self-Groom</th>
<th>Events</th>
<th>Targets</th>
<th>Contralateral</th>
<th>Isolateral</th>
<th>Right Handed</th>
<th>Left Handed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Congo</td>
<td>18</td>
<td>AR</td>
<td>12</td>
<td>3</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Lolita</td>
<td>17</td>
<td>AL</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>LaVerne</td>
<td>17</td>
<td>AR</td>
<td>9</td>
<td>2</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Lana</td>
<td>22</td>
<td>AL</td>
<td>13</td>
<td>1</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>Junior</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Kesi</td>
<td>1</td>
<td>GL</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Yenge</td>
<td>12</td>
<td>AL,AR,GR</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Ikela</td>
<td>9</td>
<td>AL,AR</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Makasi</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Handedness and Laterality

Individual handedness determinations were calculated for all 9 bonobos using chi-square analysis (Table 11), and then compared to previous handedness values reported in previous studies by Shafer (1997) and Zuniga (2006), (see Table 12). In the analysis for population-level handedness, all 9 bonobo handedness determinations were added together and analyzed as a whole. Population-level biases were not observed during scratching, rubbing, or self-grooming. However, there was a significant right hand bias observed during picking and wiping (which was generally directed at the nose). This may reflect different motivational biases associated with these kinds of self-directed behaviors. Interestingly, all of the different self-directed behaviors, with the exception of gentle scratching, showed significant contralateral to isolateral ratios, meaning that the right hand generally targeted the left side of the body and vice versa. However, the favoring of one side versus the other as far as being the primary target of SDBs was not detected, refer to Figure 13. These findings relate to the contralateral hemispheric control of SDBs. All of the different self-directed behaviors observed in both groups of bonobo, with the exception of gentle scratching, showed significant contralateral to isolateral ratios, meaning that the right hand generally targeted the left side of the body and vice versa. The fact that contralateral responses are more evident than isolateral ones reinforces previous models of the neurological management of the stress response, with contralateral control directed by the left and right hemisphere independent of one another.
Table 11: Individual Handedness Scores. Age is denoted in years. Left and Right refer to the number of SDBs events executed by either hand. Total refers to the summation of all SDBs observed, irrespective of which hand performed them. HI refers to the “Handedness Index”, found by subtracting the amount of left handed events from the amount of right handed ones, and dividing by the total number of SDBs observed for each individual (Hopkins, 2005). The C:I ratio refers to the ratio between contralaterally and isolaterally directed behaviors.

<table>
<thead>
<tr>
<th>Individual</th>
<th>Sex/ [Age]</th>
<th>Left</th>
<th>Right</th>
<th>Total</th>
<th>X²-score</th>
<th>HI</th>
<th>Handedness</th>
<th>C:I Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Junior</td>
<td>M/[12]</td>
<td>5</td>
<td>11</td>
<td>16</td>
<td>0.133</td>
<td>0.375</td>
<td>Insignificant R Bias</td>
<td>Insig.</td>
</tr>
<tr>
<td>Congo</td>
<td>M/[~7]</td>
<td>157</td>
<td>184</td>
<td>341</td>
<td>0.144</td>
<td>0.079</td>
<td>Ambidextrous</td>
<td>Sig.</td>
</tr>
<tr>
<td>Ikela</td>
<td>F/[16]</td>
<td>26</td>
<td>21</td>
<td>47</td>
<td>0.466</td>
<td>-0.106</td>
<td>Ambidextrous</td>
<td>Sig.</td>
</tr>
<tr>
<td>LaVerne</td>
<td>F/[~7]</td>
<td>84</td>
<td>53</td>
<td>137</td>
<td>0.008</td>
<td>-0.226</td>
<td>Left</td>
<td>Insig.</td>
</tr>
<tr>
<td>Yenge</td>
<td>M/[25]</td>
<td>18</td>
<td>44</td>
<td>62</td>
<td>0.001</td>
<td>0.419</td>
<td>Right</td>
<td>Sig.</td>
</tr>
<tr>
<td>Kesi</td>
<td>F/[3]</td>
<td>15</td>
<td>34</td>
<td>49</td>
<td>0.007</td>
<td>0.388</td>
<td>Right</td>
<td>Insig.</td>
</tr>
<tr>
<td>Lana</td>
<td>F/[28]</td>
<td>156</td>
<td>125</td>
<td>281</td>
<td>0.064</td>
<td>-0.110</td>
<td>Insignificant L Bias</td>
<td>Insig.</td>
</tr>
<tr>
<td>Makasi</td>
<td>M/[3]</td>
<td>4</td>
<td>3</td>
<td>7</td>
<td>0.705</td>
<td>-0.143</td>
<td>Ambidextrous</td>
<td>Insig.</td>
</tr>
<tr>
<td>Lolita</td>
<td>F/[7],[18]</td>
<td>107</td>
<td>127</td>
<td>234</td>
<td>0.191</td>
<td>0.085</td>
<td>Ambidextrous</td>
<td>Insig.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Lolita</td>
<td>A</td>
<td>L</td>
<td>R</td>
</tr>
<tr>
<td>LaVerne</td>
<td>L</td>
<td></td>
<td>R</td>
</tr>
<tr>
<td>Congo</td>
<td>A</td>
<td></td>
<td>R</td>
</tr>
<tr>
<td>Yenge</td>
<td>R</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Kesi</td>
<td>R</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ikela</td>
<td>A</td>
<td>L</td>
<td>R</td>
</tr>
<tr>
<td>Makasi</td>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Junior</td>
<td>R</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Lana</td>
<td>L</td>
<td>L</td>
<td></td>
</tr>
<tr>
<td>Mechumba</td>
<td>L</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 13: Directional Laterality Results. The amount of SDBs directed by the right hand to the left side of the body, by the left hand directed towards the right side of the body, the total amount of isolateral SDBs executed by both hands, and the total amount of lateralized SDBs.

<table>
<thead>
<tr>
<th>Individual</th>
<th>R--&gt;L</th>
<th>L--&gt;R</th>
<th>Isolateral</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Junior</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Congo</td>
<td>44</td>
<td>36</td>
<td>32</td>
<td>112</td>
</tr>
<tr>
<td>Ikela</td>
<td>8</td>
<td>9</td>
<td>12</td>
<td>29</td>
</tr>
<tr>
<td>LaVerne</td>
<td>8</td>
<td>13</td>
<td>20</td>
<td>41</td>
</tr>
<tr>
<td>Yenge</td>
<td>12</td>
<td>0</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Kesi</td>
<td>4</td>
<td>2</td>
<td>12</td>
<td>18</td>
</tr>
<tr>
<td>Lana</td>
<td>23</td>
<td>39</td>
<td>54</td>
<td>116</td>
</tr>
<tr>
<td>Makasi</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Lolita</td>
<td>16</td>
<td>26</td>
<td>27</td>
<td>69</td>
</tr>
<tr>
<td>Totals</td>
<td>116</td>
<td>129</td>
<td>163</td>
<td>408</td>
</tr>
</tbody>
</table>
Discussion

Hopkins (2006a) was the first to focus on the lateralization of the stress responses associated with self-directed behaviors (SDBs) in *Pan troglodytes*. As far as I know, there have been no previous studies published on the lateralization of SDBs specifically in *Pan paniscus*. This is unfortunate because SDB research in bonobos may have important implications for the evolution of the stress response in hominids. However, the lateralization of *handedness* in bonobos *has* been addressed in two other studies. These are relevant because handedness is directly related to brain lateralization and presumably interacts with the same neurological pathways to control the frequency and nature of SDBs. The selective pressures and causal mechanisms involved in the shift away from symmetrical control of function in the brain and ambidexterity are still mysterious, and more research is called for. The most common theories proposed to explain the evolution of handedness include social/environmental learning, hormonal regulation, genetics, postnatal postural origin, and brief explanations of each of these theories is provided in Appendix B (B-5, B-6, B-7, B-8 and B-9 respectively).

Shafer (1997) and Zuniga (2006) both attempted to detect population level lateralization and handedness in bonobos, using the same captive individual bonobos at the San Diego Zoo. Some notable similarities exist between Shafer (1997), Zuniga (2006), and the present study that make these studies comparable in some respects, for all three studies were designed to investigate different, yet sometimes overlapping questions. However, because of some major technical differences in the methods these
researchers used to qualify handedness, it is difficult to detect any consistent patterns of individual or population-level handedness among the three studies. All three were conducted at the San Diego Zoo, from the same exact visitor areas, which facilitated observing the animals at a relatively close range through the glass. Similarly, the bonobos were outside in relatively warm (over 60°F) and rain-less weather during all 3 studies, which is an artifact of zoo policy, requiring the bonobos be kept indoors during “poor” weather. Similarly, age class determinations among all three studies were based on Kano’s (1992) classifications, described as follows: infants: under 2 yrs; juveniles: 2-7 yrs; adolescents: 7-13 yrs; adults: older than 13 yrs. However, not all of the bonobos in the first study were present and represented in the later two.

The San Diego Zoo participates in an international breeding management effort, which requires that bonobos from this institution be moved to other zoos and institutions, both within the United States and internationally. This artificial migration imitates the natural flux of fission-fusion social organization, which naturally characterizes this species, and attempts to maintain a level of genetic heterozygosity in the small captive population worldwide. Because of artificial migration and the management of behavioral incompatibilities, it is not unusual to have different individuals present from one year to the next at the San Diego Zoo and Wild Animal Park. This accounts for why not all the individuals represented in Shafer (1997) are present in the later two studies (Everson, 2011; Zuniga, 2006). The only individuals present in all 3 studies are Lolita, Ikela, and Lana, and based on Table 16, there is very little consistency between the three studies in the handedness determinations of Ikela and Lolita. Lana, however, seems to show a consistent left-hand preference. The other
6 individuals, who are disproportionately represented amongst these three studies, also show inconsistent handedness values (with the exception of the two adult males).

It is possible that these discrepancies reflect the differential nature of the behaviors under investigation: Shafer (1997) focusing on all lateralized behaviors, Zuniga (2006) focusing only on manually-complex behaviors associated with termite-mound tool use, and myself focusing only on SDBs, which are simple and involuntary movements. There may be different motivational biases that influence hand preference based on the type of behavior executed. While Shafer (1997) definitely addresses generalized handedness much more comprehensively than either of the later studies, she admitted that the population-level handedness trends might not be representative of the lateralization of certain behaviors, like tool use or stereotypy. Shafer (1997) suggested that a video tape archive would be a more accurate way to examine the lateralization of specific behaviors, which is essentially what Zuniga (2006) and I did during our investigations of tool use and SDBs, respectively. Although the later studies lack the statistical significance to accurately compare their handedness findings with the findings published by Shafer (1997), they do elucidate specific behaviors that may be regulated by very different mechanisms within the brain with regards to the lateralization of handedness. Some behavioral overlap is apparent between the three studies, as Shafer (1997) did include SDBs in her study of handedness, and grouped them into a generalized category called “Self-Touches”, including any repetitive behavior, such as scratching or picking. Other stereotypic behaviors, not reported in Zuniga (2006) or the present study, were also mentioned—including catching urine, feces, and regurgitation using both hands. None of these
behaviors were observed in the later two studies, however, that could reflect smaller sample sizes or observational periods. Similarly, one might speculate that this may be related to a different social climate between the bonobos at the San Diego Zoo during the 1990’s compared to 10 years later.

Shafer (1997) unexpectedly found evidence of lateralized termite mound fishing, a form of tool use, which was a later focus of the Zuniga (2006) study. In both bonobo individuals that displayed this behavior, there was a distinct left-hand preference for tool use, despite the fact that both were otherwise categorized as right-handed. This finding suggests that for right handed individuals it is more convenient to use the left hand for coarse tool manipulation, leaving the right hand free for more dextrally complex work of picking off food from the tool, or it may reflect a cerebrally lateralized behavior pattern. The phenomenon of left-lateralized tool use has also been observed in chimpanzees (Sugiyama et al., 1993; McGrew & Marchant, 1992), supporting the hypothesis that lateralization patterns are differentially displayed as a function of motivation, which may be regulated by different areas of the brain. This may be relevant to other behaviors, including those associated with the stress response, such as SDBs. In my study, there was a significant right hand bias observed during picking and wiping. It would seem that either hand would suffice equally during wiping, however, picking requires more dexterity with regards to the fingers. Further investigation might elucidate the causal mechanisms controlling this phenomenon, by supporting or refuting a differential sensitivity in one hand versus the other in primates.
The other lateralized behavior categories in Shafer’s study included touching others, hitting, knocking, throwing, eating, the manipulation of large and small objects, digging, sifting, gesturing, and hanging — all of which were ignored in both Zuniga’s (2006) and my own studies. Shafer (1997) studied two groups of bonobos housed separately at the San Diego Zoo and the San Diego Wild Animal Park. Shafer (1997) investigated a much broader range of behaviors, in order to get a more holistic perspective with regards to generalized handedness patterns, in a sample size of 14. The bonobos were focally observed at different times of day, [versus just between 10am–5pm (Zuniga, 2006), or 9am–1pm (my study)], for all right, left, and bi-manual behaviors. A total of 36,288 behaviors were recorded. Zuniga (2006), on the other hand, studied six individuals, exclusively at the San Diego Zoo. Her focus was handedness, related to one very specific behavior (termite fishing), and therefore she recorded significantly fewer (approx. 700) behaviors. Likewise, I studied a total of 9 individuals, exclusively at the zoo location, for a narrow range of behaviors (SDBs), with a total of 1,174-recorded behavior events. Shafer (1997), Zuniga (2006), and I all collected observations opportunistically, however only Shafer (1997) collected enough data [in a total actual observation time of 164 hours] to equally represent each individual in the analysis.

The Shafer (1997) study categorized handedness based on z-scores at the 5% significance level, whereas Zuniga (2006) and myself based our determinations on chi-square analysis and p values at the 5% significance level. Shafer (1997) found that 11 individuals were significantly right-biased, two individuals were significantly left-
biased, and one was right biased, but not significantly. Therefore, overall, the bonobo populations in this study appeared to exhibit a strong right bias. Zuniga (2006) found that all five bonobos analyzed (one was excluded based on his lack of participation in the activity) showed a significant hand preference for the act of termite fishing (Table 12), and although an overall left-hand trend was observed, population-level handedness was not significant. In this study, I found fewer individual preferences as compared with the earlier studies. Four out of nine of the individuals observed were categorized as ambidextrous with regards to SDBs, while only three showed a significant hand-preference and two were insignificantly biased. Similarly, no population level handedness was detected. The differences between the studies could be attributed to the variation in behaviors observed or simply an artifact of small sample sizes.

Shafer (1997) found that infants and juveniles were not as strongly lateralized as adolescents and adults. However, Zuniga (2006) and I cannot accurately address this question based on their small sample sizes and the nature of the behaviors they focused on. Zuniga (2006) excluded the two youngest juveniles (under the age of 2 years) on the basis that they did not actively “fish” for termites, and the older juvenile actually displayed a left hand bias with regards to this behavior. I only observed enough SDBs in one juvenile to make a preference determination, and that individual ultimately showed a right-hand preference. Therefore, the development of lateralization cannot be accurately compared between the three studies. Similarly, sex differences in handedness could not be compared, because in all three studies, the strength of hand preference of the males was somewhat confounded by either age or
small number of subjects.

Measuring relative SDB activity would address whether some individuals are more likely to exhibit this SDB than others, but could not be rigorously quantified in this study (see “Broader Questions” that follow). Several individuals did routinely show more SDBs than others, which may be explained by dominance relationships, age, gender, and or rearing history. However, the disproportionate observational periods (based on opportunistic sampling) that characterized this project confound any significant qualification of relative activity. Using the data presented in this study, it is impossible to define relative levels of activity with regards to SDBs without transforming the data into events per unit of time. This was complicated by the movements of the animals in and out of the frame of observation within the videotapes. Thankfully, handedness is not affected by the discrepancies between observational periods, so the statistically significant findings of this study pertain to the laterality of handedness.

Based on personal observation, there seemed to be a significant increase in the frequency of stress behaviors among individuals that were raised by human attendants rather than by conspecifics, in these two groups. It could be argued that human interference in rearing young primates induces stress due to the lack of normal conspecific interactions and intra-social conflicts, and in the establishment of a dominant authoritative force outside of the perimeters of the normal primate social structure. Research on non-human primates has demonstrated that self-mutilation (analgesia) is a common reaction to extreme disruptions of parental caretaking in other mammalian species, for example isolated young rhesus monkeys engage in self-biting
and head slapping and banging (Mineka & Suomi, 1978). Future research is needed to address the causal mechanisms regulating human rearing interference and the development of associative idiosyncratic stress behaviors. This research would directly benefit the health of the animals by clarifying the ambiguity surrounding the best protocol for rearing orphaned primates ex-situ.

It could also be argued that the videotaping observers, zookeepers, and zoo-visiters surrounding the enclosure might also influence the frequency of SDBs (see Appendix A-3). However, I would argue that this has a negligible effect on the behavioral observations made in this study. Firstly, this group of bonobos has been routinely observed by hundreds of video-tapers over the last 15 years, through the efforts of Dr. Christine Johnson, so it is quite feasible that they have been habituated to the presence of academic observers. Secondly, I would argue based on personal observation, that although there was a notable effect on bonobo behavior when keepers were present around the enclosure, keepers were very rarely observed when the bonobos were on public display — so I think there is a negligible effect overall in this regard.

Very few opportunities for the quantification of behavioral changes related to passing zookeepers and authoritative zoo staff presented themselves, so there was minimal interference with respect to zoo staff and the social climate within the enclosure. Lastly, zoo-visitor density was low during the observational periods, and no contact between visitors and bonobos was possible through the glass. The majority of visitors come to the San Diego Zoo on the weekends, which is why the weekdays were chosen for observing the bonobos. The few visitors that were present during weekdays
were generally ignored by the bonobos, so I don’t think visitor presence had much of an impact on their behavior.

One of the most interesting results of this study addresses the lateralization of the stress response. Assuming that the sensory neurons associated with the itch are projected contralaterally, we expected to see an asymmetry in SDB responses, possibly reflected in the choice to direct most SDBs to one side of the body versus the other (Leavens, 2006). Hopkins (2006a) predicted that the right-hemisphere contralaterally stimulates the left side of the body during a stress response, which would explain his finding that common chimpanzees directed most SDBs towards the left side of their bodies. My findings in bonobos do not support this prediction, for the bonobos I studied seemed to direct a relatively equal amount of SDBs towards both sides of the body. This seems to imply that the right hemisphere does not exclusively regulate the stress response in bonobos. However, in accordance with Hopkins (2006a), bonobos did significantly direct most of their SDBs contralaterally, meaning, that the right hand generally targeted the left side of the body, and that the left hand generally targeted the right side of the body. This supports the idea that sensory neurons associated with “itchiness” (related to the stress response) do work contralaterally (Leavens, 2006). As evident in Table 13, isolateral SDB events (right hand to right side, left hand to left side) were much less frequently observed.

In chimpanzees there is evidence for lateralization in certain cognitive tasks, irrespective of population-level limb preference, which supports the idea that an organism can have both individual and population-level lateralization for different functions (Hopkins & Carriba, 2002). Based on this, it was predicted that the
individual members of the two bonobo groups at the San Diego Zoo would also display a preference of using one hand versus the other in the execution of self-directed behaviors, reflecting asymmetrical cerebral lateralization on an individual level. On the other hand, significant population-level handedness was not expected. Although population level handedness was not observed during the display of specific self-directed behaviors (scratching, rubbing, or self-grooming), it was present, with a significant right hand bias, in regards to the behaviors “picking” and “wiping”. This may reflect different motivational biases associated with these two kinds of self-directed behavior, which may relate to the regulation of the stress response within the brain. Picking is generally considered a more extreme form of self-directed behavior and may be indicative of a different neurological stimulus (such as a more intense degree of negative-arousal) during the stress response. These predictions are in agreement with the findings of previous studies documenting individual handedness in both species of Pan despite a lack of population-level bias, which is concordant with the idea that the alignment of lateralization may not be under selective pressure. This is the first time, as far as I am aware, that the hemispheric lateralization of SDBs has been addressed in bonobos, and these results may further assist other researchers in their investigations related to the evolution of the stress response.

The present study would have had more statistical significance with a much larger sample size (over 170 individuals), longer observational periods (proportionally distributed amongst all the individuals in the group), and a design that facilitated the measurement of relative SDB activity (data in events per unit of time). A surplus of
focal level observations equally representing each individual, rather than opportunistic sampling, would be the best way to accurately calculate relative SDB activity, however it would call for a much bigger project all together. Presumably, with more observers to collect and analyze these behaviors, one could create an impressive data archive that could be used to address other interesting aspects of the stress response as well. Ideally, the bonobos would be observed not only on public display, but within their off-display enclosures as well. Similarly, instead of focusing on a narrow window of time (9am-1pm), it would be more accurate to choose an equal proportion of different times of the day, to be able to differentiate between morning, afternoon, and nighttime patterns of behavior. This would only be feasible with more participation on the part of the zoo, for not only would researchers need access to off-exhibit areas, but it would require more communication between the observers and the zoo staff. One of the main limitations of only having access to on-exhibit behaviors, is that observers are not aware of important interactions that may have occurred between individuals while not on display- interactions that may explain changes in social climate or context.

Although videotaping can be a very beneficial tool in studying complex behavioral interactions that happen rather quickly in real-time, there are several drawbacks. One major issue is that focal individuals can easily fall out of frame, and it is hard to infer a realistic “story” in terms of time when individuals constantly fall in and out of frame. Using videotape to filter for certain specific behaviors makes it almost impossible to focally observe individuals without having gaps between important interactions. Because opportunistic sampling is much more feasible when
using video, it is important to choose which individuals to focus on based on their associations with other bonobos. This requires the observer to be familiar with the interpersonal relationships between animals, i.e. whom is related to whom, whom is in estrus, and whom is the dominant matriarch of the group. Despite some of the drawbacks in using video, it is still the easiest way to study small and complex movements. It is much easier to use video to perform microanalysis on dextrally sensitive behaviors, such as SBDs, because you can zoom in on animals that are relatively far away and literally see the precise movements of the fingers and hands. This is virtually impossible without the use of a video camera, and because the movements occur rapidly and in succession, they can easily be mislabeled initially.
Broader Questions

There are a number of interesting behavioral questions that can be addressed with the data available in the bonobo videotapes. Unfortunately, most of these cannot be answered with my more focused observations. Nevertheless, some interesting observations were made, and I shall discuss them briefly here. Hopefully, these observations may be of some value to future researchers.

Do behaviors change over 10 years? On an individual basis? On a group basis?

Observations of a captive colony on two occasions ten years apart should be relevant to a large number of interesting issues. The animals in the 1990’s and their counterparts in the 2000’s should be comparable. In fact, one individual was present on both occasions. The habitat was basically unchanged over this time. It would be most interesting to know if the levels of stress associated behavior declined with time and habituation. Unfortunately, my analyses does not permit me address this question in any significant way.

The SDB I observed did not change in any discernable manner between the 1990’s study and the 2000’s study. More importantly, the frequency of behaviors did not change significantly. These behaviors were pretty consistent in both groups, and even though the group structure, individuals, and dominance patterns shifted significantly- the display of SDBs did not. This could be due to the fact that at the time of day the animals were on display (between 9am-1pm), most individuals, save the youngest ones (Makasi and Kesi), were generally in a resting pattern. This frequent resting may reflect boredom, or it could be a normal trend that mirrors natural
behaviors in the wild. Either way, it would be expected that most SDBs would occur during a resting period, because during involved activities (foraging, grooming others, playing, etc.) the hands are usually occupied with that activity. Stationary resting, however, frees the hands to perform SDBs.

One way to illustrate the consistency of behaviors observed between these two groups is to focus on the most obvious types of idiosyncratic stereotypies. These are behaviors that frequently accompanied bouts of SDBs, and could indeed be classified as stress behaviors, however, because they are unique to one individual they have very little statistical significance. Some of the idiosyncratic behaviors, such as Lolita’s head-roll, were consistent between each data set. Unfortunately, Lolita was the only individual present in both studies- and in the second study there were very few data points collected on her because the focal animals were generally the mother-infant dyads, and by this time her daughter was nearly grown and their dyad was nearly disintegrated (another example is Lana’s stereotypic ear-clutch. None of the other individuals in the group do it, and she has reportedly maintained this unique behavior since infancy). Lolita’s head-roll was consistently frequent in both studies, it did not change characteristically within this time.

The protocol for scoring the traditional SDB behaviors (scratching, rubbing, picking, etc.) was fashioned to exclude exceptional instances and quantify only the most straightforward SDBs. Idiosyncratic behaviors, despite their intrigue, are not very straightforward, and therefore they were not included in the analysis of this study. Very little could be definitively implied regarding where they come from, if they stem from a different motivational bias, or if they are learned. Interestingly, Mchumba
(Lolita’s daughter) was caught rolling her head a couple times, which might suggest that this idiosyncratic stereotypy may have actually been learnt, although the immediate argument would be that Mchumba was simply imitating a curious behavior her mother frequently performed. Because there were only 2 cases of this actually happening, and both cases did not seem to be in the context of any stressful event, I would hesitate to support that this behavior was actually an honest and learnt SDB.

Furthermore, the sexual behaviors previously recorded by De Waal and associates in the early 1990’s, in captive bonobos at the San Diego Zoo, were not frequently observed in either group. This could be based on the fact that the social groups I studied consisted of different individuals, who were not predisposed to these behaviors, that the individuals had habituated to captivity and no longer struggled to de-arouse a heightened stress level (presumably causing the behaviors), or that the social dynamics within the group at the time of observation somehow modified these behaviors. Another factor could have been, again, the time frame of which we observed both groups. Maybe these behaviors were more noticeable in the late afternoon, or the evening, for example.

Based on these observations I am inclined to believe that SDBs are a reflection of the hyper-arousal of the central nervous system, rather than a flexible, learned, or conscience behavioral expression of stress. Research supports that environmental stressors actually cause a biochemical cascade that can activate cutaneous sensitivity, literally causing the sensation of “itchy-ness”, as part of the “flight or fight response”. The body responds to stress by increasing sensitivity to touch, sound, smell, etc., as to prepare the individual for intense action. Because of the positive impact this response
may have on an animal’s individual fitness in the wild, and based on the fact that this response is relatively conserved in most species of mammal, it is possible that there is not much selective pressure acting on this response to change. Therefore, I wouldn’t have predicted that the actual SDBs themselves would have changed between both groups of bonobos included in this study.

Are the 1990s really comparable with the 2000s?

The main differences between each group observed was the size and age distribution of the individuals composing them. Each subject’s age class was determined based on the definitions provided by Kano et al. (1992) and details of lineage and the status of rearing can be found in Table 2.1. The first group included a male adolescent named Congo, and two female adolescents named Lolita and LaVerne. This group was monitored and video taped between the hours of 9am-1pm during weekdays (fewer zoo visitors) for approximately 10 months between September 1996 and July of 1997. Although Congo’s lineage and date of birth are unknown, it is significant that LaVerne was the daughter of the dominant matriarch of another group (Lana) and was reared by her biological mother. Lolita on the other hand was nursery-raised by zoo-keepers, and considered to be “less dominant” than LaVerne. The fact that this group consisted of 3 adolescents, all short of social or sexual maturity, makes this group comparably different from the second group. This group was characterized by dynamic high-intensity social interactions (presumably associated with hormonal changes), during which time both females were impregnated.
The second group consisted of 8 individuals of varying sex and age class between October 2005 and November 2008, during the same daily time frame as the first group. Lana, the adult matriarch of this group, was born in 1979 and was nursery raised by zoo-keepers. Ikela and Lolita, born in 1991 and 1989 respectively, in this data set are both adult subordinate females that were also nursery raised and subordinate to Lana. The adult males in this group are called Yenge and Junior. Junior is the son of the matriarch, Lana, and was just entering adulthood. Mchumba was a 9 year old female who was just reaching sexual maturity. In the wild, females of this species are known to migrate out of their natal group around this time, after a period of erratic and antagonistic behavior. The two infant/juveniles in the group are Kesi, the daughter of Lana and Yenge, who was hand-reared by Lana (N), and a male nursery raised orphan named Makasi who is the lowest ranking individual in this group based on his status as an orphan and his age. The second group, therefore, is much more diverse with regards to age when compared with the first group, and also contained mature adults as well as infants- which were lacking in the first group.

Comparing the results from both of these studies may be confounded by the fact that both groups contained very different characters, social dynamics, and age-classes. Although the behavioral profiles of this species may change slightly based on age and experience, I do think that individual personalities (reflecting individualistic and plastic behavior) account for most of these subtle changes. Rather than comparing the two studies, I think it is more useful to consider them as a whole, with each individual representing one behavioral profile that might subtly change during transitions towards maturity.
Does morning behavior compare to late afternoon when they are tired?

The bonobos were fed at noon, and the bulk of stress behaviors actually observed were focused just before and slightly after feeding time, which was at 12 noon. Unfortunately many of the dramatic interactions that occurred between individuals actually happened within the bedrooms, out of the public domain, and out of sight of this study. The bonobos were only actually out and on display for a short window of the day, generally from about 9am–1pm. Any variation in weather or routine often prompted them to return to the bedrooms sooner, which were located outside and below the enclosure. Needless to say, the social interactions we observed were only a small fraction of the story, and as a result, it is difficult to conclusively say whether the time of day had any effect on their behavior. Because of the small window of time we had to actually observe them interact and because it was difficult to infer what interactions had taken place during the hours the animals were off display, we could only assume based on our observations that the majority of the time between 9am-1pm were spent resting in one part of the enclosure. Although there were slight variations to this pattern, no obvious trends were readily noticeable.

For juveniles did behaviors change over a period of a year?

There were only two juveniles in the second study, and only one is adequately represented in the data. Kesi, who was very young at the beginning of study, demonstrated what we coined “pseudo-SDBs”, which were very difficult to categorize using the protocol we designed. Furthermore, most of these strange behaviors we observed seemed to happen outside of the context of stress. Kesi would have strange
bouts of scratching/ rubbing/ nose-picking where the boundaries of our strictly defined protocol was challenged as one behavior fused into the next, all within a short matter of time. This phenomenon seemed confined to Kesi. However, as she grew older and more agile, her SDBs seemed more and more like the typical SDBs observed in the other adult bonobos, hence they became more consistent with the protocol definitions and seemed to be in the right context. How did we treat the earlier pseudo-SDBs in the data? We basically noted it in the comments area following each individual SDB, and marked these bouts as “Other” rather than categorizing them individually as real SDBs. Anything behavior that seemed out of place or questionable was included in this category, and archived to facilitate potential research in the future.

The other juvenile, Makasi, was an orphan and therefore not included in any dyad, so he was poorly represented in the video footage. In fact, the only footage we have on him is when he is in the same frame or interacting with a dyad.

*Are there gender differences?*

It is hard to say the frequency of SDBs varies consistently between genders in this species, partly because the dominance relationships are not as linear as they are in other species, (please refer to the Appendix A) on gender differences. Generally, stress is associated with dominance, and most species of primate (where rank is a function of gender) dominance is linear, hierarchical, and straightforward. This is not the case with bonobos. I am under the impression that rank disparity is less pronounced between the genders than they are from individual to individual, in bonobos. Each bonobo seems to adopt a very different behavioral social strategy, which seems
independent of gender. This is fascinating because in the closely related common chimp, gender differences are significantly more pronounced as far as social dominance is concerned. Based on my observations, I can conclusively say that “male dominance” did not characterize either of my study groups. The social climates defining both groups could be described as dynamically equalitarian. Often, the 2-way dominance interactions changed or were reversed from one day to the next, presumably based on the interactions that occurred overnight or behind the scenes. Sometimes these dominance interactions were a function of sexual receptivity, the monopolization of food resources, or in response to environmental circumstances.

As for how the different genders reacted to stress, that is a really neat question, especially in this sort of equalitarian social arrangement. Although my sample size was small, and therefore unsuited to this question, there is ample evidence in the literature (refer to the Appendix A) to argue that gender differences do exist on a physiological and behavioral level. It has been suggested that there is currently selection acting on some primate females to affiliate with other females during stressful events. Bonobo females, who often form female-coalitions during conflicts, seem to support this theory. It is important to keep in mind that these coalitions are composed on non-related females, being that bonobos are male-philopatric. Unfortunately, I am not able to pursue this issue further with the data at hand; but a future worker could re-examine the tapes and perhaps see if there are parallels in these bonobos.
Do infants show mother's patterns?

Both studies only contained two dyads, therefore, my conclusions fail to reach statistical significance, however, based on my observations I am under the assumption that infants do not actually “inherit” or “learn” stress behaviors. It has been suggested that SDBs are the product of overarousal of the central nervous system, and remain somewhat independent from social learning. In the 2000’s study, Kesi never adopted Lana’s “ear clutch” or predisposition to regularly perform SDBs. Likewise, Mchumba really only demonstrated Lolita’s “head roll” a couple of times, and both times may have been an artifact of some other expressionistic behavior, or merely an imitation. Based on this, I can’t argue in favor of heritability with regards to SDBs. Behavior can be very difficult to study, for it is characterized by flexibility and variability in this species. Infants generally interact with their environment and conspecifics much more than in other species of primate. This may translate to greater variation in “cognitive styling”, versus the traditional “infant-imitating-mother” systems that characterize other primate species. This may possibly account for why the two daughters I observed seemed to deal with stress in a completely different way than their mothers. I’d also like to add, that although Kesi is represented rather well in the data, Mchumba is not. At the time when she was being filmed she was almost an adult, and therefore the Mchumba-Lolita dyad was beginning to disintegrate, as is common in species with male-phipatry. I can’t speak too confidently about Mchumba’s stress behaviors, compared with Kesi’s.
Do low ranked individuals show more SDB? How does presence of high ranked animals effect these behaviors?

Based on the equalitarian nature of this species and the dynamic 2-way dominance interactions from day to day, actually ranking individuals in any sort of social hierarchy is a challenge. The two factors that seemed to contribute to dominance were age and maternal status. Based on this, seemingly “low-ranked” individuals in both groups failed to show any more SDB tendencies than seemingly “high-ranked” individuals. In the 1990’s the highest “ranking” individual would have been LaVerne, who was the naturally-raised daughter of the previous matriarch. At the beginning of the study, LaVerne showed very few SDBs compared to the other two bonobos in her group (Congo and Lolita). As the study progressed, LaVerne seemed to show more SDBs. This might be related to the fact that both LaVerne and Lolita became pregnant during the study. As the pregnancy progressed, LaVerne’s SDB frequency seemed to increase, whereas Lolita’s (which was relatively high initially) seemed to decrease. How pregnancy (and it’s associated hormones) may have influenced the stress profile of these two is an interesting question, which may or may not have anything to do with rank. In contrast to LaVerne’s initial low frequency of SDBs and corresponding high “rank”, is Lana’s high frequency of SBDs and confirmed high-status amongst the current group of bonobos at the Zoo. Lana accounted for a disproportionate amount of SDBs in the 2000’s study, despite the fact that she is the matriarch of the group. Although it is tempting to search for trends
associated with dominance and rank in primate species, I think the dynamic and
egalitarian nature of bonobo groups makes this very difficult.
Appendix A

Review of Self-directed Behaviors in Primates

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AI. Self-directed Behavior Research in Nonhuman Primates

Welfare scientists often make explicit inferences about animal feelings (e.g. pain, fear, frustration), states that cannot be measured directly but are inferred using a toolbox of indices, including the avoidance of potential threat (e.g. escape responses), associated acute stress responses (e.g. catecholamine and corticosterone release) and their functional consequences (e.g. increased heart and ventilation rates), and long-term responses such as adrenal enlargement, compromised growth, reproductive suppression and immunosuppression (Mason, 2011). Peripherally, the body's stress response is a reaction to increased physical or psychological demands, and is stimulated by the arousal of the hypothalamic–pituitary–adrenal (HPA) axis, which floods the body with adrenocorticotrophin (ACTH) and triggers the release of norepinephrine and epinephrine. These hormones help the body mobilize the energy necessary to deal with stressors, ranging from increased glucose release to enhanced immune function (Van der Kolk & Saporta, 1991). In a well functioning organism stress produces rapid and pronounced hormonal responses (Gertz, 1987; Westlund et al., 1985), although persistent stress eventually desensitizes the stress response, which may lead to significant changes in the central nervous and endocrine systems. In a structural magnetic resonance imaging study, Jovev et al. (2007) examined the relationship between pituitary gland volume and self-destructive behaviors in
teenagers diagnosed with bi-polar disorder. Hierarchical regression analysis revealed a significant relationship between these behaviors and PGV, implicating the over-arousal of the HPA axis (Jovey et al., 2008), and or more information on how this system operates in humans, please refer to Appendix A. Similarly, rhesus monkeys with a high frequency of self-directed biting have increased urinary cortisol and attenuated suppression of cortisol by dexamethasone (indicating HPA hyperactivity), compared to low frequency self-bitérs (Tiefenbacher et al., 2004). Such findings support an association between a high frequency of self-injury and HPA hyperactivity. SDBs may reflect some sort of vestigial behavior pattern, originating from the calming effect of grooming in most primate species, which attempts to de-activate this negative arousal. An increase in the intensity of stress may over-stimulate the intensity of the SDB, causing behavioral shift away from appropriately calming to inappropriately harmful. Support for this theory is reflected in primate studies that have revealed heart-rate elevation prior to self-directed biting, which reduces rapidly following the biting episode (Novak, 2003).

In both nonhuman primates and humans, self-directed behavior (SDB) appears in situations characterized by social tension and is likely to reflect increased autonomic arousal (Troisi, 2002). The study of such behavior is therefore useful in both the monitoring of stress levels in captive animals and the identification of the causes of such behavior, and ultimately in alleviating the causes of such stress. Simply identifying the causes of self-directed behavior is only the first step in improving the welfare of animals kept in captivity for conservation breeding purposes. For example, Major et al. (2009) found that self-injurious behaviors, an extreme type of SDB similar to those described in humans, were sensitive to the pharmacological manipulation of mood using anxiogenic (anxiety-causing) and anxiolytic (anxiety reducing) drugs in captive rhesus macaques. Although this may alleviate some tensions it doesn’t address the source of anxiety controlling these behaviors. Social interactions shape the psychological profile of individuals within a group, and play a very large role with regards to the stress environment in captive populations. Dyadic, triadic and more complex social interactions must all be considered when assessing the overall social
climate of an individual or a group. For example, Hopkins et al. (2006a) found that SDBs were commoner in chimpanzees exposed to videotape showing conspecifics fighting over watermelon versus videotape showing chimpanzees sharing watermelon peacefully.

Kutsukake (2003) suggests that social relationship quality depends on 3 factors: value, security, and compatibility, and that anxiety-inducing situations may differ between the sexes based on the interactions of these three things. There is a varying degree of dominance in relation to gender amongst different primate species, but the general trend is that males are dominant and females are more submissive and this may differentially affect the nature of the stress response of males and females. Similarly, dominance relationships exist between same-sex dyads, and therefore we could expect that stress might be unequally distributed based on rank as well as gender. In chimpanzees, dominance rank plays a much more obvious role than in humans or bonobos. In male chimpanzees, self-directed behaviors were inversely correlated with dominance rank, when males were amongst other males (Kutsukake, 2003). Rough self-scratching was more common in less dominant males, and less common in high-ranking males. These results did not vary with proximity or association level. Interestingly, females preformed self-directed behaviors more frequently when a non-affiliated group member was near, irrespective of dominance rank, suggesting that relationship security in females chimpanzees is a function of kinship (Kutsukake, 2003). These findings, however, cannot be generalized to the bonobo, *Pan paniscus*, which maintain different and atypical dominance patterns compared to most other species. Forty years of primate research has established that early disruption of the social attachment bond reduces the long-term capacity of an individual to cope with subsequent social disruptions and to modulate physiological arousal (Van der Kolk & Saporta, 1991). Trauma early in life has long term effects on the neurochemical response to stress including the magnitude of the catecholamine response, the duration and extent of the cortisol response, and the serotonin and endogenous opioid systems (Kramer et al., 1984; Reite & Field, 1987; Van der Kolk et al., 1991). Trauma may be related to the absence of conspecific social stimulation.
during early development, which carries significant implications for captive bred and nursery raised primates. Inversely, too much social stimulation might also lead to negative arousal in captive situations where social dynamics between individuals or the density of individuals are inappropriate. For example, Aureli and De Waal (1997) found elevated rates of behavioral indicators of anxiety, such as rough scratching and yawning, in a high-density captive population of chimpanzees kept at the Yerkes Regional Primate Research Center.

Cognitive challenge is also a source of stress related to the display of SDBs and can be linked with the element of uncertainty during the process of learning tasks. When chimpanzees were given easy tasks to perform and then switched to harder tasks, there was a significant increase in SDBs (Leavens et al., 2001); in contrast, chimpanzees that were given hard tasks throughout a trial did not show any increase in SDBs. Interestingly, the frequency of SDBs decreased after auditory feedback signals denoting the accomplishment or failure of a task, suggesting a link between such behavior and uncertainty. During auditory signals no SDBs were observed, irrespective of whether the signals were positive (chime) or negative (buzzer), disproving the notion that there is an increase in SDBs after aversive stimulus and supporting the notion that uncertainty about outcome itself causes significant anxiety. This is further supported by studies of macaques (Hopkins et al., 2003).
A.II: Rank and Dominance Patterns in Bonobos

Takayoshi Kano (1998) argued that although chimpanzees and bonobos have basically similar social systems, including fission-fusion multimale polygyny, male-philopatry, and female dispersal, there exists a behavioral dichotomy between the species. One of the most obvious differences is the male-female dominance pattern. Unlike chimpanzees that live in a strictly male dominated society, dominance relations between male and female bonobos have been described as being egalitarian (De Waal, 1995) or female dominated (Parish, 1996; Vervaeke et al., 2000). Females are always dominant in the feeding context, and because most intra-group conflicts occur during feeding, this is a significant indicator of which gender is dominant. Typically, when high-ranking females approach a male, the act generally provokes a submissive response in the male, which includes behaviors such as grinning, bending away, etc. (Kano, 1998).

Both in captivity and in the wild, female bonobos form coalitions which are not based on kinship and which serve to maintain social dominance. In a genetic study of a wild population, Hashimoto (2007) found high variation in a matrilean marker indicating that females transfer between groups (as expected from behavioral observations) and that, for females, there was no relationship between genetic closeness and social closeness, measured by frequencies of proximity or grooming. After immigration into a new group, females form social associations with senior females without regard to kin relationship, and sex plays a role in establishing these relationships. This phenomenon is in interesting contrast to most primate (and vertebrate) behavioral systems. While female chimpanzees tend to range alone except for during estrus period, female bonobos tend to stay within a mixed party and keep close association with one another (Furuichi, 1987; Kano, 1992).

Another behavior common to chimpanzees, yet absent in bonobos, is marked intergroup aggression. Intergroup encounters in wild bonobos generally invoke affiliative behaviors, and bonobos are very gregarious even at times of food shortage.
Mating between individuals from different groups has been observed during inter-group encounters in the wild (Idani, 1990), further supporting the argument that bonobo inter-group social behavior is significantly more cooperative and peaceful than chimpanzees.

Bonobos also differ from chimpanzees in their behavior towards infants. Infanticide, associated with male group take-overs in chimpanzees, is unknown in bonobos. In contrast, it is common, both in the wild and in captivity to observe male bonobos playing, carrying, and sharing food with infants, even if the infants are not known to be kin. An interesting example of this type of behavior was reported in wild bonobos where a 5-6 year old male was observed ranging alone without a mother. Adult males were frequently observed carrying, feeding, and grooming this juvenile (Hashimoto et al., 2007). These researchers were able to genetically identify the individual’s mother who had apparently abandoned her infant about two years earlier. Clearly, only the supportive behavior of the adult male bonobos had enabled this orphaned juvenile to survive.

Another example of this type of altruistic behavior in bonobos occurred during the observation period of the present study at the San Diego Zoo. During this time two infants were born and promptly abandoned by their mothers. An older male juvenile in the group, named Makasi, took great interest in the two infants and immediately took on the role of an alloparent for both. He was frequently observed carrying the infants throughout the enclosure and introducing them to the rest of the group. Makasi himself was also an orphan, who was introduced to the group at a young age. Without inheriting the status of his mother, and due to his young age, he is considered the lowest ranking individual within the San Diego Zoo bonobo group.

These gentle, affiliative behaviors in male bonobos led to the argument that male and female bonobo androgen secretion levels were comparable, and that they underpinned a form of demasculinisation of male bonobos not seen in chimpanzees (Sannen et al., 2003). However, this argument has been weakened by the T-metabolite data published by Dittami et al. (2007), showing that wild males have higher and more
variable testosterone levels than females, comparable to levels observed in chimpanzees. Similarly, a positive correlation between adrenal and gonadal steroids was found in urine samples of wild bonobos, which would be characteristic for early phases of agonistic encounters, but not for prolonged fights or subordination. In conflict situations, with no apparent winner, or within socially unstable societies, the two endocrine systems can be up-regulated in parallel and the fission-fusion nature of bonobo societies and the relatively peripheral social role of males support this positive correlation (Dittami, 2007). Sexual competition in bonobos is not associated with monopolization, and males can and do engage in agonistic interactions but regularly withdraw before the conflict escalates. Dittami (2007) suggests that bonobos may have a degree of resistance to stress-related gonadal down-regulation. This hypothesis is based on the finding that elevated adrenal activity, which is related to social and/or physical stress and suppresses testicular function, is not seen in bonobo males (Dittami, 2007). Unfortunately, female production of adrenal androgens like epitestosterone, androstenedione, or DHEA is still very poorly understood, so it is difficult to argue their role in the atypical dominance patterns observed in bonobos. Although these androgens have little inherent biological activity in females, they are important as precursors or prohormones of testosterone, DHT or estrogens, and may have roles in reproduction, immune function or mineral and fat balance (Dittami, 2007). Further research is needed to understand the function of these metabolites and their regulatory control of the reproductive and social systems observed in females.
Welfare science suggests that good reproductive rates (compared to benchmark populations), and no stereotypic behavior, are the two variables that indicate good captive welfare. It has been suggested that the species that thrive in captivity may have moderate behavioral flexibility, without being excessively intelligent or innovative (Club & Mason, 2007. Mettke, 1995). Research addressing intrinsic species differences using data from captive populations, therefore, can’t overlook the differential welfare response of each of the species under investigation. The species categorized as behaviorally inflexible generally do poorly in captivity and fail to habituate to human presence or refrain from unnecessary behaviors previously required for life in the wild. These species may not adjust to the new husbandry or social climate of a ex-situ environment, and will therefore fail to thrive in captivity. In theory, behaviorally-flexible animals would adapt much better to captivity, however, this is not always the case. In the wild, many of these species are under constant cognitive-stimulation, requiring them to explore and exploit their environment, ultimately to survive. In captivity, behaviorally-flexible animals may become frustrated by enclosures that fail to provide structural complexity, inter and intra-species interactions, and/or a lack of cognitive challenge in the form of environmental enrichment. Mettke (1995) showed that six species of parrots, prone to the self-destructive behavior of feather-plucking, performed far more protracted examination of novel objects placed in their aviaries than the three species not prone to feather-plucking. This suggests an association between environmental enrichment and animal welfare. Similarly, many of the more potentially dangerous SDBs seen in primates and other highly cognitive and social mammals may stem from the lack of pre-emptive provision of opportunities to explore and interact with their environment. It is known that the captive situation is likely to affect social relations, competition for resources and the expression and execution of dominance (Dittami, 2007). Suboptimal captive environments induce abnormal, repetitive stereotypic behavior by eliciting sustained attempts to perform specific normal activities, and in some cases by disrupting normal
brain development, leading to general tendencies to show behavioral inflexibility (Mason, 2006. Club & Mason, 2007. Van Zeeland, 2009). Captivity releases animals from the need to forage, facilitates more opportunities for social interaction through enforced proximity, and can also lead to boredom (Stanford, 1998). Accordingly, hormonal and behavioral profiles may change as a function of these conditions. There might be a significant difference between the stress behaviors observed in wild-caught captive bonobos and individuals reared ex-situ, and a drastic disparity between these and the behaviors observed in their wild counterparts.

Visitor presence also effects stress levels in captive animals, and may be a critical component in SDBs and aberrant behaviors in confined primates. Chamove and colleagues (1988) found that human proximity caused increases in activity in 12 different primate species. In a study conducted in India, visitor presence was found to influence the behavior of captive lion-tailed macaques in a negative way suggesting that visitor presence adversely affects primate welfare (Mallapur, 2005). Levels of aggression exhibited by captive macaques, generally towards zoo visitors, were ten times higher in comparison to free-ranging individuals, and the types of SDBs observed included repetitive circling, hair plucking, stereotypic pacing, self biting, bouncing, head-tossing, oral stereotypies, regurgitation and re-ingestion, repetitive rocking, and rubbing (Mallapur, 2005). Visitors were associated with 20% more abnormal SDB with higher levels of stereotypic behaviors (6%), begging, self-biting, and stereotypic pacing (16%). Aberrant behaviors and aggression in primates are not exclusively directed towards the source of stress, nor towards the self, but are often displaced in a social context. Mallapur et. al (2005) found that aggressive biting by captive macaques was only exhibited by males towards females during visitor presence and recorded higher levels of social/reproductive behaviors during visitor absence.

These observations are concordant with the findings of Anderson et al. (2002), that petting-zoo animals in enclosures with greater flight distances were significantly less stressed than animals housed in small enclosures with short flight distances. Similarly, a shift in space use patterns was documented in petting zoos in which some
animals were observed to use enclosure space strategically in order to avoid interactions with visitors (Anderson, 2002). It seems clear that visitor presence effects the fitness of captive individuals through the agency of stress which over-taxes an individual’s control systems (Kiley-Worthington, 1977).
A.IV: Sex as a mechanism to diffuse stress

Mason (2011) suggests that stereotypic and self-directed behaviors can also help to identify (based on their form and timing) specific natural responses that are predisposed to persist even without apparent proximate benefits, somehow reflecting underlying control mechanisms that do not require reinforcing feedback from the environment. Potential mechanisms for such effects might include the activity involved instead being intrinsically self-rewarding or having the property that its prevention causes stress (Mason, 2011). Fraser & Duncan (1998) suggest an “evo-mecho” hypothesis that some of these stereotypic behaviors are pleasure-driven, and on an evolutionary scale are both low-cost and adaptive. If non-reproductive sex, or sex-play, were to immediately reduce tension, in both wild and captive populations of bonobo, then presumably this behavior would be highly adaptive, and relatively low-cost to the bonobos themselves, particularly in captivity where predation is not an issue. Although sex-play is frequently observed wild bonobos, it is even more pronounced in certain captive populations, and this could be an artifact of captivity. The function of sex may be to reduce stress and enhance social cohesion (as I will discuss shortly), but why does this species exhibit such a variety of behaviors with regards to sex? Presently, bonobos are famous for their rich array of sociosexual behaviors, which have been observed in the wild, although with less frequency when compared to their captive counterparts. In 1987, De Waal’s observations of a captive population of bonobos at the San Diego Zoo perpetuated the idea that as a species, bonobos are hypersexual compared to most primates, including the closely related chimpanzees (De Waal, 1987, 1995a, 1995b, 1998). De Waal admitted that this phenomenon could be an artifact of captive confinement and not reflective of naturalistic mating patterns, but both in the wild and in captivity, conflict situations do provoke both sexes to regularly perform dyadic interactions that contain components of sexual behavior (Hohmann & Fruth, 2000). The study of sex-play behavior in bonobos may provide insight with regards to the adaptive value of this unusual phenomenon.
“Play” is characteristic of juvenile behavior, and is not commonly seen in adult mammals. It has been asserted that the play patterns reflect the social organization of a species, and that the presence of play between adult individuals may reflect a neotenous characteristic in the bonobo (Enomoto, 1990) and humans. The adult play interactions observed in both wild and captive bonobo populations may be reflective of other behavioral patterns, such as behavioral flexibility, pronounced personality differences, and a variable dominance hierarchy (De Waal, 1987). Sexual behavior is often found within the play context, and playful copulations and variously modified sexual behaviors were frequently associated to the resolution of tensions among bonobos. This suggests that because play is functionless in a direct way, it creates a subtle flexibility in adult behavior, and that the self-handicapping, characteristically observed in play, promotes reciprocal interactions based on an equality principle (Enomoto, 1990). Because interactions between individuals tend to be more symmetrical in bonobos they are less predictable than asymmetrical actions/responses based on dominance and kin perimeters. Subordinate animals must refer to other factors, such as past interactions with the participant and the situation at the time. Thus, when interacting in more symmetrical ways, improved learning capacity of the animals may be required — and this learning, when combined with the flexibility of play and self-handicapping, may promote variations in behavior during various social interactions, including sex (Enomoto, 1990).

The egalitarian nature of bonobo society with its heightened development of play affords us an opportunity to study the behavioral evolution of sociosexual stress management. If play and sexual behaviors coevolved in the bonobo, it might account for the frequency and variability of both types of behaviors observed during episodes of social stress, along with the higher degree of cooperation versus agonistic violence in bonobo societies. It is possible that once these play-like behavioral patterns evolved in this species, they have been maintained through various social interactions, and could acquire some new function in the future (Enomoto, 1990).

How special is bonobo behavior? Is it really different from that seen in its closest living relatives? The notion that bonobo sexual behavior is markedly different
from that of chimpanzees is still widely held, even though it is strongly debated by some primatologists. The following brief review of some of the biological and behavioral differences with regards to sex between the two species of *Pan* is provided to facilitate further discussion later in this thesis. Although the length of the menstrual cycle varies among different populations of the two species, chimpanzees and bonobos are similar in the fraction of the of the cycle during which female swelling occurs. Among primates, only bonobo and human females are sexually active outside the periovulatory period, and this non-conceptive sex has been considered an evolved mode of social communication (De Waal, 1987; Parish, 1994; Wrangham, 1993). A distinction must be made between sex-play and successful mating (involving male intromission), because the latter occurs infrequently during bonobo sexual interactions. Furuichi (1987) found that although bonobos engage in nonconceptive sex outside of the periovulatory period, nearly 95% of successful matings occurred during the period of maximum swelling, which is comparable to chimpanzee sexual trends. Although copulations are more frequent during the period just before ovulation, sexual behavior occurs throughout the menstrual cycle, a characteristic of both *Pan paniscus* and *Homo sapiens* (Dane, 1987; Furuichi, 1987; Savage-Rumbaugh & Wilkerson, 1978).

Males of both species are equally and perpetually attracted to non-ovulating swollen females, and this attraction plays an important role in the initiation of non-reproductive sex. Adult and adolescent male copulation rates in the wild are actually higher among chimpanzees, during the intervals in which a female is swollen and therefore sexually receptive. However, bonobos show slightly higher copulation rates overall, because the duration of the period of swelling occupies a slightly larger fraction of the menstrual cycle of bonobos than it does in chimpanzees (Kano, 1996). There are various types of solicitous behavior in the initiation copulation performed by both sexes, although female solicitation is more pronounced in the bonobo (Enomoto, 1990). Despite the controversy surrounding alleged bonobo hypersexuality compared to chimpanzees, there are indeed several differences between the two species with regards to sexual behavior.
Three additional differences between the species have to be noted here. First, nearly every mixed sex bonobo foraging party has at least one sexually swollen female (Kano, 1992); such females may be absent from chimpanzee groups. Therefore, access to reproductively active females is greater for bonobo than for chimpanzee males, a feature that may account for lower levels of inter-male aggression in bonobos (Stanford, 1998). Second, in contrast to chimpanzee social structure, bonobo females are often dominant over males (primarily with regards to feeding access); this may contribute to the increase in female gregariousness enabling coalition formation (Kano, 1992). Third, one manifestation of female-female bonding seen in bonobos is an affiliative behavior known as genital-genital rubbing which serves to reduce intercommunity tensions surrounding food partitioning (White, 1988). This behavior is probably the strongest argument for the idea that sex functions to reduce stress during times of social tension in bonobo society. Idani (1984) and Hashimoto et al. (1996) suggest that females do not selectively immigrate into a group that includes their elder sisters, nor choose matrilineal related females when choosing new group association partners. Newly immigrated females tend to seek partners among senior adult females of high social status, and concentrate their affinitive social interactions, such as following, grooming, and genital contact on these senior partners (Furuichi, 1989; Idani, 1991). Female bonobos frequently use sexual behavior to regulate inter-individual relationships (De Waal, 1995; Kano, 1992; Wrangham, 1993). Sex-play may significantly reduce tension during the stressful process of adjusting to a new group’s social climate, especially as female’s are the dispersing sex in this species.
A.V: Bonobo Tool Use and the Effect of Novel Enrichment on SDBs

According to McGrew & Marchant (1997) bonobos show 21 of the 27 different modes of tool use. Unfortunately, little quantitative data are available and, as anecdotal, idiosyncratic, habitual or customary behaviors are often confused, little can be inferred with regards to the origin of tool use in this species. Nevertheless, it is clear that tool use tasks generally require more skill than non-tool tasks. Furthermore, as several species of non-human hominids show spontaneous tool use in both in-situ and ex-situ settings, we can assume that human influence is not sufficient to explain differences in expressed technology (McGrew and Marchant, 1997). In captivity, the repertoires of tool use of chimpanzees, bonobos, and capuchins are similar- and induced tool use has been successful for all three species in captivity, but not in nature. It could be argued that in nature, the ethological needs of these primates are being met, so there is no functionality associated with frivolous or novel tool use. In captivity, however, these cognitively complex animals are relatively under-stimulated, and therefore novel activities are quickly incorporated into the behavioral repertoire. Although tool-use may not be an effective way to actually measure handedness in non-human hominids, it may be an effective behavior to encourage, as it might contribute to improved animal welfare. This brings me to the topic of ex-situ environmental enrichment and it’s significant potential with regards to stress reduction.

Novel behavioral challenges, namely “environmental enrichment”, reduce stereotypic behaviors associated with captivity in many different vertebrate species. In one group of bonobos, enrichment significantly decreased the frequency of problems such as stealing and rough handling of newborn infants (Csatiadi et al., 2008) and positively affected reproductive behaviors and general health of the animals. Enrichment programs often aim to add structural and behavioral complexity to the daily management of confined animals. Hopkins (2006) noticed that in captive populations of both species of Pan, boredom was often a problem as most of individuals spent the majority of their time at leisure on the floor. Likewise, in the present study situation, behavioral enrichment was rarely introduced, and despite the
large, structurally complex enclosure, most of the bonobos spent the majority of their time in stationary rest. This idle time seems to lead to social conflicts and the onset of SDBs. When enrichment was provided, the bonobos were significantly more active and often moved throughout the enclosure. Dangerous behavioral problems can often be eliminated by offering alternative ways for animals to engage in other activities, by keeping them busy with challenging environmental tasks (Csatiadi et al., 2008). At the San Diego Zoo, two enrichment interventions were particularly successful: gift boxes and hiding food treats. First, presented with several large boxes gift wrapped in brightly colored paper, streamers, and ribbon, the bonobos gladly disassembled the gifts and used the wrapping to decorate their enclosure. Second, hiding small food rewards in the vegetation of the enclosure, induced the bonobos to actively forage.

Unfortunately, enrichment programs cost time and money. Furthermore, each animal responds differently to different forms of enrichment, and rapid habituation requires that keepers offer a variety of alternate enrichment activities. For both chimpanzees and bonobos, tasks that involve cognitively challenging problems and some sort of reward or positive reinforcement are particularly successful. An example of the difficulty of designing effective primate enrichment is illustrated in Csatiadi et al. (2008), who tested several types of feeders for a group of eight captive bonobos. A swinging feeder did not have a significant effect on group activity because the group usually emptied it quickly and returned to inactivity. A “molecule ball” feeder was easily monopolized so only kept certain individuals busy. In contrast, fixed (hanging above the floor) enrichment types (tube and plate feeders) activated all the individual bonobos and motivated the whole group for an extended time period, even though there were only a few animals actively manipulating the object.

In many ways, institutionalized humans show many of the repetitive stereotypies observed in captive zoo animals, including harmful SDBs. In these cases, environmental enrichment has also been employed to help reduce maladaptive behaviors. Autistic children observed under four conditions of increased environmental complexity experienced a reduction of stereotyped behaviors when an adult intervened and attempted to engage each child in object manipulation (Hutt &
Hutt, 1964). When denied enrichment opportunities, children who would otherwise have a chance to attain higher levels of adaptive behavior, may fail to develop even the most rudimentary skills needed for adjustment to the community; the institutional environment contributes to the further development of the maladaptive behavior it was established to treat (Blatt, 1970). One way an increase in adaptive object-directed behavior can be promoted is to structure an environment that prompts and reinforces adaptive behavior (Homer, 1980). Introducing activities that are cognitively challenging and then rewarding the accomplishment of these tasks may help regulate problem-behavior. It is evident, based on vertebrate and human studies, that the use of an enriched environment and differential reinforcement of adaptive behavior often promotes group cohesion and reduces psychosocial stress and it’s associated SDBs.
A.VI: Self-directed Behavior Research in Humans

In the literature on nonverbal communication, self-directed behaviors are referred to by a variety of terms, such as displacement behaviors, self-stimulatory behaviors, referential behaviors, self-injurious behaviors, synkinetic (involuntary) muscle or limb movements, autistic movements, body-focused movements, self-manipulations, or self-adaptors. The quantification of these behaviors has been used to more accurately access psychological states, based on the principle that nonverbal behavior is more telling of a subject’s true emotional state as compared to verbal statements (Troisi, 2002). These honest indications of anxiety can be described as “emotional leakage”, and it has been argued that these self-adapting behavior patterns reflect the subject’s affective state more accurately than subjective self-reports on emotion, hence they involuntarily “leak” from the subject (Kinsbourne, 1991). These behaviors are most obvious in patients affected with psychological conditions marked by high levels of anxiety or depression. Troisi et al. (1998) found a positive and significant correlation between anxiety in humans (as diagnosed by clinical physicians) and the manifestation of these behaviors using an ethological coding system for interviews protocol for the identification by quantifying these behaviors during doctor-patient interviews. Although the function of these behaviors is largely unknown, it has been proposed that SDBs serve to deactivate negative emotional arousal, consistent with the findings that gentle body touching causes relaxation and a reduction in heart rate in milder cases of anxiety (Maestripieri, 1992). They may also serve as a coping mechanism during more severe episodes of self-injurious behaviors related to a variety of psychological disorders associated with the “Frustration-Aggression” hypothesis proposed by Dollard et al. (1939), which described SDBs in context of displaced aggression and frustration. Several neurological and psychological human studies have provided valuable insight into the function of these seemingly destructive behaviors.
The majority of research into this category of behaviors has focused on
the human stress response, particularly in repetitive movements of
children and people diagnosed with autism spectrum-disorder. Indi-
viduals with autism were presumed to have an atypical and unstable
arousal system, which causes a constant state of over arousal
(Dawson & Lewy, 1989; Hutt & Hutt, 1964; Kinsbourne, 1991). Indi-
viduals with autism spectrum disorder have particular difficulty in
negotiating social situations and this may correspond to this state of
over arousal, because social interactions are often unpredictable and
emotionally arousing. Liss & Saulner et al. (2006) suggested that “senso-
ry seeking” is a compensatory coping strategy used to diffuse the
intensity of arousal, moderating it when it rises to uncomfortable
heights, through a variety of repetitive behaviors that have been thought
to induce sensory self-stimulation (Liss et al., 2006). Over-focus and
perseveration would also be included in the repertoire of compen-
satory behaviors, serving to reduce sensory input into a narrow,
controllable scope. However, repetitive movements were prominent
also in under-reactive low-functioning participants with autism-spectrum
disorder and have also been observed in intellectually impaired indi-
nuals who do not have autism (Alvarez, 1999), in typical children
who are in residential care (Troster, 1994), in typical infants
confined in cribs, and in caged or isolated animals (Berkson & Mason,
1964). These stereotypic repetitive behaviors seem to stabilize the
subject’s level of arousal in monotonous, frustrating, or over-stimulat-
ing situations (Bauman, 1999).
SDBs might also be a function of specific environmental conditions, i.e.
in situations that offer few response opportunities to individuals who
become over-aroused within the context of a very specific circumstance.
When response capabilities are limited, these behaviors might be better
described as self-soothing rather than stimulation seeking (Liss et al.,
2006). In a study on maladaptive self-directed behaviors in autistic
children, SDBs were defined as slaps or picks at one or more body parts
with an object or another body part, banging one or more body parts
into object or another body part, rocking upper part of body 10 or more
back and forth movements,
placement of body parts or clothing against the mouth, the pulling hair from one’s own body, touching of saliva, feces, urine, etc. with fingers, rubbing one or more body parts against objects or another body part, and throwing of one’s self on the floor. Interestingly, many of these behaviors correspond with the repertoire of behaviors categorized as SDBs in many species of primates. Researchers found that the use of an "enriched" environment and differential reinforcement of adaptive behaviors resulted in reduced frequency of maladaptive SDBs and a corresponding increase in adaptive object-directed behavior beyond that observed in an "enriched" environment alone (Van der Kolk et al., 1991). This suggests that these behaviors can be adjusted through learning and encouragement and are not necessarily a reflection of a permanent behavioral impairment.

Trauma and psychological disorders

In 1939, John Dollard et al. introduced the “Frustration-Aggression Hypothesis” to the field of psychology, and identified the display of self-destructive behaviors as a form of displaced aggression stemming from frustration. Frustration was defined as “interference of the occurrence of an instigated goal-response at it’s proper time in the behavior sequence”, hence stemming from external occurrences (Dollard et al., 1939). Frustration manifests in situations characterized by social tension, motivational conflict, or in situations where goal-directed behavior is thwarted, such as the condition known as alexithymia (Troisi et al., 2000). Alexithymia is a personality trait distributed normally in the general population that involves a marked difficulty in identifying feelings and communicating them to other people (Bagby & Taylor, 1997). The alexithymia construct is relevant to stress research because a deficit in modulating distressing emotions through cognitive processing might result in exacerbated responses in the autonomic nervous system (Troisi et al., 2000). In addition, there is evidence that alexithymia is associated with a variety of psychiatric and medical disorders (Taylor, 2000). Troisi et al. (1996) studied the relationship between alexithymia and nonverbal behavior and found that the frequency of self-directed
behaviors during patient interviews was indeed a significant predictor of alexithymic traits. It can be argued that the inability to identify and communicate emotion in a social context can lead to frustration, which in turn triggers displaced self-aggression. Even mild hyper-arousal of the autonomic nervous system could be enough to induce a mild SDB response such as self-picking, scratching, or other stereotyped behaviors, which may serve to soothe the intensity of response.

SDBs have also been frequently reported in cases of schizophrenia, and many insightful discoveries have been made to explain these behaviors through the investigation of schizophrenic subjects. Schizophrenia has also been significantly associated with particular hand preference and brain lateralization phenotypes, which will be discussed later in this study. SDBs therefore may have important clinical implications that can be applied directly in relation to this common international disorder. One of the most interesting cases investigating SDBs involved a young girl diagnosed with schizophrenia as a toddler. The onset of self-destructive behaviors, primarily “head-banging” (forcefully against walls and furniture), “arm-banging” (against sharp corners), pinching and slapping herself, and setting her hair on fire by sticking her head into the electric wall heater, dated back to her third year of life (Lovaas et al., 1965). Her “appropriate” social behaviors (including speech) were minimal, and she engaged in considerable self-stimulatory behavior (fondling herself, and moving her arms and hands in repetitive, stereotyped manners). Likewise, her interaction with physical objects (play toys, etc.) was stereotyped and restricted. Through a series of experiments, Lovaas et al. (1965) recognized patterns of lawfulness and regularity during the display of SDBs and were able to suggest a functional relationship between very specific environmental operations and the display of SDBs, based on the finding that the reinforcement and extinction of certain other behaviors, in a given setting, controlled the frequency and magnitude of SDBs. The delivery of social reinforcement (i.e. attention), contingent upon the occurrence of self-destructive behavior, actually increased the frequency and magnitude of that SDB, and the data also showed a systematic reversal of self-destructive responses with appropriate social behaviors. Therefore, social interactions may have a huge
modulating effect with regards to the stress response, and the display of SDBs. Lovaas et al. (1965) argued that conceptually, SDBs in humans could be regarded as learned, operant, or instrumental behaviors. The occurrence of operant behavior is controlled by two kinds of stimuli: discriminative (which “cue” the SDB), and reinforcing (which reward the SDB) and since, in this study, both of these kinds of stimuli were social (i.e., provided by another person), SDBs were categorized as social behaviors. There was a sudden reduction of SDBs to a zero level when new stimuli were introduced into the environment (Lovaas et al., 1965). Although that study focused on schizophrenia, these destructive behaviors are associated with a variety of disorders.

Self-injurious behavior is at an extreme of the SDB spectrum, and has been studied in depth by both physicians and psychologists. Deliberate self-harm typically starts in adolescence and involves numerous episodes and a variety of methods, including cutting, anorexia or purging, burning, slashing, banging, picking, and bone breaking (Van der Kolk et al., 1991). Clinical reports suggest that many adults who engage in self-destructive behavior have childhood histories of trauma and disrupted parental care (Van der Kolk et al., 1991) and nearly 90% of these individuals are diagnosed with borderline-personality disorder (Jovey et al., 2008). In a study that explored the relationships between childhood trauma, disrupted social attachment, and self-destruction, using both historical and prospective data, seventy-four subjects with severe personality disorders were followed for an average of 4 years and monitored for self-destructive behaviors such as suicide attempts, self-injury, and eating disorders (Van der Kolk et al., 1991). It was found that histories of childhood sexual and physical abuse were highly significant predictors of self-destructive behaviors, and that the onset of childhood trauma generally initiated these severe SDBs, which were maintained by a lack of secure social attachments during adulthood (Van der Kolk et al., 1991). Van der Kolk et al. (1991) reported that patients who repetitively attempted suicide or engaged in chronic self-cutting were prone to react to current stresses as a return of childhood trauma, neglect, and abandonment and experiences related to interpersonal safety, anger, and emotional needs precipitated dissociative episodes and self-destructive behavior.
Liss & Saulner et al. (2006) introduced the “sensory seeking” hypothesis to explain the mechanisms behind this type of inappropriate regulation of negative arousal. According to this hypothesis, physical sensation (commonly pain) allows an individual to dissociate from an emotional situation, triggering a shift in focus away from an emotional stimuli (perceived as out of their control) and unto a physical one (perceived as controllable). This atypical pattern of regulating negative arousal presumably has a physiological basis. Jovey et al. (2007) examined the relationship between pituitary gland volume and SDBs in individuals also diagnosed bi-polar disorder and supported an association between self-injury and hypothalamus-pituitary-adrenal axis hyperactivity. Another bi-polar disorder case-study reported an increase in urinary cortisol in the days prior to self-harm (Sachsse et al., 2002), suggesting that self-harm might serve as a coping mechanism for increased levels of arousal or stress and that stress reduction might alleviate self-injurious behavior. Again, SDBs are implicated as compensatory coping strategies used to diffuse the intensity of arousal, moderating it when it rises to uncomfortable heights, through a variety of repetitive behaviors that have been thought to induce sensory self-stimulation (Liss et al., 2006). Understanding how these behaviors evolved, as well as the underlying mechanisms controlling them is invaluable to the treatment of many psychological and neurological disorders related to the stress response.
Appendix B: Review of the Hypothesized Evolutionary Origins of Cerebrally Lateralized Behavior

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B.I: Handedness, Brain Lateralization, and Behavioral Response

Handedness refers to a consistent asymmetry in skill or preferential use between the hands. It is related to lateralization of other functions such as language within the brain (Medland et al., 2009). According to Marchant & McGrew (1997), there are five possible levels of laterality that describe handedness: always left or right preferential, significantly left or right preferential, and ambidextrous (see Table 1.1). By understanding handedness and the corresponding functional lateralization within the brain of different primates, we may explain the evolution of cerebral asymmetries. Hand preference is a presumed reflection of the active hemisphere, and most likely the dominant hemisphere, of an individual. Right-handedness therefore reflects a left-hemispheric dominance, whereas left-handedness is thought to reflect a right hemispheric dominance. Left hemispheric specialization has been linked to motor
skills and language functions, and consequently right-handed individuals would presumably express the specialized characteristics of the left hemisphere, such as the tendency to approach novel environmental stimuli and direct object manipulation. In contrast, right hemispheric specialization has been linked to emotional response, across many vertebrate species, and consequently left-handed individuals presumably express the characteristics of the right hemisphere, such as a heightened fear and avoidance response, see Table 14 (Valortiaggara & Rogers, 2009). These complex associations are supported empirically in the literature, yet the mechanisms by which they work are still mysterious.

The association between hand preference and language dominance in humans, has led to a number of evolutionary and biological theories proposing that hemispheric specialization and higher cognitive functioning coevolved. There is a growing body of ethological evidence that these neurological asymmetries related to behavior and often reflected in limb preference, are ubiquitous in many species of animal. The study of lateralization may serve as a bridge between the seemingly separate disciplines of neuropsychology and developmental/evolutionary biology, as we gain insight into the possible homologies or homoplasies of cerebral lateralization among vertebrates. Are the observed trends in neurological processing of emotional stimuli indicative of convergent evolution or do variations between the species reflect differences in behavioral strategies?

To understand the mechanisms that control the evolution of the human brain’s organization, we need to understand what selective pressures were present during our own speciation, and why these adaptations may have increased individual fitness. There are several feasible advantages to cerebral lateralization, including a possible increase in brain capacity. In saving neural circuitry the brain can avoid the unnecessary duplication of functions in both hemispheres and actually increase it’s capacity to carry out simultaneous processing (Chaplain & Hogervorst, 2009. Corballis, 1989. Rogers, 2002. Valortiaggara, 2005). Independence between the hemispheres may help animals such as fish, reptiles, and birds scan their asymmetrical environment more effectively, processing data from two different fields of perception
via complex inter-hemispheric communication systems that serve to reduce
competition of response emission to stimuli in both fields. If the development of these
systems allows for a measure of plasticity, arguably through the interaction of innate
and epigenetic cues, cerebral lateralization may have evolved as an evolutionary stable
strategy very early in vertebrate history. It could also be argued that with the
development of complex social interactions, selective pressures influenced the
coordination of the alignment of asymmetric behaviors amongst individuals at a
population level.

This coordinated alignment may have developed as an evolutionarily stable
strategy, under conditions of frequency dependent selection. If the behavioral response
of group is unpredictable due to the asymmetry of responses (e.g. predator-prey
interactions), the species is much harder to exploit. Therefore, asymmetrical response
may develop because of the fluctuating interplay between the social pressure to
coordinate behavior and the corresponding predatory pressure to exploit it.
Fluctuations may be controlled by environmental stress, reduced heterozygosity, or
due to random deviations, but it is only after a pressure to align the direction of
asymmetries has been firmly established in one species (either in the prey or the
predator), can alignment of the asymmetries in the other species occur as a result of
mutual evolution (Vallortigiara, 2005). Social pressure may or may not have been
present during the speciation of any given species demonstrating behavioral and
neurological asymmetries, but it cannot be ruled out as an agent of selective pressure
in the case of brain lateralization.

Handedness and the development of the specialization of skill corresponding to
the anatomic pattern of left hemispheric dominance, may have developed before the
Pan-Homo split. The planum temporale (a language area of the human brain) is also
present in chimpanzees and was found to be significantly larger in 94% of chimpanzee
brains examined (Gannon, 1998). Correspondingly, great apes (orangutans, gorillas,
chimpanzees and bonobos) exhibit population level right-handedness, although many
more ambidextrous individuals exist in great ape than human populations. The ratio
of right to left-handed subjects is much lower in the apes (2:1) compared with humans
(8/9:1), but nonetheless the fact that the ratio is not 1:1 may indicate some sort of selective advantage involved in the lateralization of skill. Some presumably lateralized behaviors, such as handedness, aggression, language and music proficiency, etc., may also conform to frequency dependent selection- where a minority group has some sort of advantage, depending on the frequency of these individuals in a population. In this system, the selective advantage of certain behaviors may disappear as the minority group increases in relative abundance. Raymond et al. (1996) has provided evidence for frequency-dependent maintenance of left-handedness in humans, proposing that left-handers have a frequency-dependent advantage in fights and for that reason a fitness advantage. Consistent with this hypothesis, they found a higher proportion of left-handed individuals in interactive sports that reflect some elements of fighting, but not in non-interactive sports (Vallorgiara, 2005). McGrew and Marchant (1999) studied the efficiency of termite fishing in chimpanzees and found that individually lateralized chimpanzees, irrespective of the direction of their lateralization, gathered more prey for a given amount of effort than did ambidextrous chimpanzees. No evidence for a population-level bias was observed, which reinforces the idea that the direction of alignment may not be under selection, although lateralization itself is.

Similar to chimpanzees, the bonobo, *Pan paniscus*, is a prototype for the common ancestors of hominoids (Zühlmann 1984, 1996), and thus a good candidate for laterality studies (Shafer, 1997). Previous research has revealed significant or exclusive individual hand preference in this species (Zuniga, 2006), with a population level right-hand bias for behaviors such as gesturing and eating (Hopkins & De Waal, 1995) and for leading limb during locomotion (Shafer, 1997). Similarly, Chapelain & Hogervorst (2009) found that right-handed bonobos had stronger preferences overall than left-handed individuals, suggesting a stronger lateralization in right-handers. On the other hand, population level left-hand bias was reported for carrying (Shafer, 1997), as it is in the human population, with the strength of lateralization increasing with age (Shafer, 1997. Chapelain & Hogervorst, 2009). The phenomenon of a left-hand preference for carrying (infants) seems to be universal amongst hominoid species, and will be
discussed in more depth below. However, the fact that lateralization may actually increase with age in primates (first suggested by McGrew & Marchant in 1997) is also very interesting, and new research has become available in support of it. Immature chimpanzees exhibit weaker or less consistent hand preferences than adults (Hook & Rogers, 2000; Hopkins, 1994, 1995), as well as young bushbabies and ring-tailed lemurs (Milliken et al., 1991), baboons (Vauclair & Fagot, 1987), capuchins (Westergaard et al., 1997; Westergaard & Suomi, 1996), and rhesus macaques (Westergaard & Suomi, 1996). Chapelain & Hogervorst (2009) found in bonobos that the direction of preference did indeed vary between age classes and that the handedness-index values, which relate to the direction of preference, were significantly higher in adults compared to juveniles. Likewise, adults were found to have greater use of the right hand when compared to juveniles, however the number of data points per subject with regards to frequency varied between age categories, and fewer data points per subject were collected for juveniles than for adolescents and adults (Chapelain & Hogervorst, 2009). The fact that lateralization and handedness may develop differentially amongst the different age groups may justify excluding younger primates from laterality studies, however, not enough evidence supports this as of yet.
Table 14: Five Levels of Laterality (Marchant & McGrew, 1997): hypothesized distribution of 10 subjects. Level 1: The entire population is ambidextrous. Level 2: Each subject shows statistically significant (but not exclusive) preference, but the population remains balanced between the left and right. Level 3: Each subject shows an exclusive commitment to using one hand vs. another, but the population remains 1:1 right to left preferent. Level 4: When all members of a population show significant but incomplete bias to either the right or left hand, marking the emergence of handedness. Level 5: When all members of a population show an exclusive commitment to either the left or right hand, or “complete lateralization”. This is not actually ever observed in nature, and usually even in species where population-level lateralization is observed, it usually has a percentage variable from 10%-35% of individuals who do not conform to the pattern of the majority (Vallortigara 2005).

<table>
<thead>
<tr>
<th>Level</th>
<th>Always Left Preferential</th>
<th>Significantly Left Preferential</th>
<th>Ambidextrous</th>
<th>Significantly Right Preferential</th>
<th>Always Right Preferential</th>
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<tbody>
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<td>1</td>
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<td>2</td>
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<td>5</td>
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<td>3a</td>
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<td>5</td>
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<td>4a</td>
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<td>4b</td>
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<td>5b</td>
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<td>10</td>
</tr>
</tbody>
</table>
Table 15: Extant Data on Hemispheric Functioning (Valortiaggara & Rogers, 2005), current understanding of the differences between the specialization of the right and left hemispheres across several vertebrate species.

<table>
<thead>
<tr>
<th>Left Hemisphere</th>
<th>Right Hemisphere</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey discrimination (fish, toads)</td>
<td>Predator detection (fish, chicks)</td>
</tr>
<tr>
<td>Foraging and-or manipulation of food items (birds)</td>
<td>Predator escape (frog tadpoles, fish, toads, chicks, dunnarts)</td>
</tr>
<tr>
<td>Approach and manipulation of objects (birds, primates, apes)</td>
<td>Neurochemical changes with predator stress (rats, cats)</td>
</tr>
<tr>
<td>Inhibition of aggression (chicks, humans)</td>
<td>Avoidance-withdrawal &amp; fear (monkeys, apes, humans, chicks, rats)</td>
</tr>
<tr>
<td>Inhibition of intense &amp; negative emotions (humans)</td>
<td>Aggression (toads, lizards, chicks, monkeys)</td>
</tr>
<tr>
<td>Recognition of categories, attention to large changes (birds, rats)</td>
<td>Courtship and copulatory behavior (newts, birds)</td>
</tr>
<tr>
<td>Recognition of species-typical vocalizations (birds, mice, some monkeys, humans for speech)</td>
<td>Expression of intense emotions (monkeys, apes, humans)</td>
</tr>
<tr>
<td>Attention to landmarks (birds)</td>
<td>Contact-monitoring of conspecifics (fish, tadpoles)</td>
</tr>
<tr>
<td>Attention to local cues (birds, monkeys, humans)</td>
<td>Recognition-analysis of faces (sheep, monkeys, humans)</td>
</tr>
<tr>
<td></td>
<td>Recognition of individual conspecifics (chicks)</td>
</tr>
<tr>
<td>Considered responses: Able to inhibit responding while deciding between alternative responses Visio-spatial analysis centered on local features</td>
<td>Considered responses: Rapid, species-typical. Visual-spatial analysis centered on relational properties of the spatial layout</td>
</tr>
</tbody>
</table>
B.II: Cerebral Dominance and Functional Brain Asymmetries

It has been suggested that there is a differential localization of affective processing in the brain, and hand preference is a rough index of the pattern of brain organization. Left hemispheric specialization has been linked to motor skills, speech, time sequencing, and language functions, whereas right hemispheric specialization is associated with emotional response, musical talent, aggression, and a compromised immune response. The function of brain lateralization would be to improve brain efficiency by saving neural space, avoiding replication of functions, allowing for simultaneous processing of different types of stimuli, and avoiding hemispheric competition (Chapelain & Hogervorst, 2009; Corballis, 1989; Fagard, 2004; Rogers, 2002; Valortiaggara, 2005). Functional asymmetry occurs predominantly in superior temporal, temporo-parietal, mid-parietal, and frontal association cortical areas of the brain, and individual differences exist in the degree and direction of functional lateralization (Witelson, 1991). A study that supports this model of cortical asymmetries with regards to speech and language was published by Gannon et al. (1998), and examined the auditory evoked responses from the temporal region of both cerebral hemispheres of human infants, children, and adults in response to both speech and non-speech acoustic stimuli. It was found that, in general, the left hemisphere responses were larger in amplitude than right hemisphere responses for all groups. Non-speech stimuli produced larger amplitude responses in the right hemisphere. Interestingly, lateral differences to both types of stimuli were found to decrease with age. This might be related to the gradual decline in the total number of callosal axons after birth, for it is known that infantile connections are systematically lost as an individual matures and this loss of exuberant fibers is one manifestation of the naturally occurring regressive events during early brain development, resulting in a "pruning" of the connectivity patterns in the nervous system (Witelson, 1991). How lateralization develops and changes throughout an individual’s lifetime is beyond the scope of this review, but there is a definite association between the lateralization of certain cognitive behaviors and hand preference.
Cornish (1997) evaluated the two way interaction between speech and hand-preference, which presumably reflects right hemispheric language dominance, in a large sample of undergraduates and found that left-handers reported a three-fold increase in the incidence of speech problems compared to mixed left-handers, mixed right-handers and "pure" right-handers. According to Witelson (1991) this may be accounted for by the fact that left handers generally have a higher prevalence of atypical right-hemisphere representation of speech and language functions, and a greater degree of bihemispheric representation of verbal and spatial skills. In men this is represented by a larger callosal area, an area thought to be part of an anatomic substrate providing greater interhemispheric communication. Particularly, the isthmus, which provides the interhemispheric connections between the functionally asymmetric temporo-parietal regions, develops very differently between right and left-handers, indicating that callosal anatomy is a biological correlate of functional asymmetry, at least in men. This sexual dimorphism within the anatomy of the human brain will be further discussed below.

Emotion has also been understood as a biologically based state involving several components: perception, experience, physiological arousal, goal-directed activities and expression (Fernandez-Carriba, 2002a,b). It could be that the right hemisphere regulates the brains response to all emotions, or there could be a varying degree of hemispheric involvement that distinguishes between different emotions, like positive or negative ones. Davidson et al. (2004) introduced an “approach–withdrawal dimension” to emotional processing, hypothesizing that approach-related positive affects are preferentially represented in specific left-sided dorsolateral prefrontal territories, whereas withdrawal-related negative affects, particularly those forms of negative affects that involve heightened vigilance toward threat-related cues in the environment, are preferentially represented in specific right-sided lateral prefrontal territories. Segregating these functions in separate hemispheres might minimize the competitive interaction between these systems and facilitate adaptive responding to reward and punishment stimuli (Davidson et al., 2004; Fernandez-Carriba, 2002a,b). Right hemispheric dominance in association with emotional response has been
observed in studies involving muricide in rats (Garbanati et al., 1983), aggression in fish (Bisazza & de Santi, 2003), chickens (Bullock & Rogers, 1986), and reptiles (Deckel & Jevitts, 1997), and more recently using a 3D imaging method to interrogate the facial expressions of both humans (Davidson et al., 2004) and chimpanzees (Fernandez-Carriba, 2002a,b). Davidson et al. (2004) reported greater left-sided movement during the spontaneously produced expression of emotions, reflecting a contra-lateral right hemispheric dominance for affective processing. This finding has also been replicated in Pan troglodytes, which suggests that this functional asymmetry is homologous in many species of primate (Fernandez-Carriba, 2002a,b). In chimpanzees, no effect of expression type (positive versus negative) on facial asymmetry was found, although the approach-withdrawal hypothesis on the segregation of emotional processing into different areas of the brain cannot be discounted without further evidence. Ultimately, the mechanisms by which lateralization actually develops may be governed by subtle neurological stimuli, resulting in lasting changes in hand or limb preference without generally affecting fitness governed by other neuropsychological domains. But the underlying wiring and circuitry regulating these cerebral asymmetries in the brain may be shared with other functional developments, which may indirectly link handedness, behavior, and lateralization, sometimes resulting in deleterious associations. Left-handedness in humans is associated with reductions or reversals of normal brain asymmetries (particularly of cerebral cortical areas related to language perception and production: the medial temporal lobe, superior temporal gyrus, planum temporale and the overall brain anterior–posterior torque) which are implicated during the development of schizophrenia and other neuropsychiatric disorders including bipolar disorder, autism, language impairment (Francks, 2007) and with post-partum depression (Sieratzki & Woll, 2002). Schizophrenia affects roughly 1% of the adult human population, and in an attempt to identify a genetic basis for this disorder, Francks et al. (2007) performed a meta-analysis of 20 genome wide linkage scans and implicated the misregulation of the gene “LRRTM1” during early fetal neuro-development. It is known that subjects with a family history of left-handedness have a higher incidence
of right hemispheric language dominance (Knecht, 2000), which may have developed in response to pre and perinatal risk variables such as birth stress, anoxia, and ultrasound-exposure (Medland et al., 2009). Birth can have dramatic effects on the developing central nervous system, for it immediately induces drastic changes in the temperature, nutrient source, and hormone levels (including an rapid increase in cortisol), and it could be that some of these epigenetic factors actually influence the expression of LRRTM1 in some way, particularly if an individual is indeed genetically predisposed. Catalytic variables may not be limited to pre or perinatal experiences, rather they might extend into the adulthood, triggered by events such as the development of social learning or under specific environmental or social stressors, such as puberty, pregnancy, pathogenic insult, or substance abuse. These do not necessarily have to manifest early in life, for many of these disorders are actually triggered later in life, and left-handedness in the presence of certain covariates, such as strong cultural suppression, may be actually more clinically meaningful than left-handedness in general (Medland et al., 2009). Therefore, having reduced or reversed brain asymmetry, presumably reflected in the development of left-handedness, may not imply any existing neuropsychological disorder, but may indicate a predisposition to certain disorders regulated by the onset of very specific moderating stressors.

In humans, lower birth weight was also associated with higher rates of left-handedness, particularly in infants born earlier than 30 weeks of gestation, which suggests that extremely premature birth may interfere with the typical course of brain organization and laterality. Witelson & Nowakowski (1991) suggest that premature birth, which is characterized by conspicuous environmental changes compared to intrauterine life, including a drastic increase in the amount of patterned stimulation in visual, tactile and auditory modalities, interferes with the subsequent unfolding of events that are typical in-utero, affecting axon number and connectivity patterns. This is supported by research in rhesus monkeys delivered 3 weeks prematurely, where precocious visual stimulation resulted in atypical morphology and distribution of synapses in visual cortex (Bourgeois et al., 1989). This scenario regards the naturally occurring loss of axons of the corpus callosum (either symmetric or asymmetric, with
or without neuron death) as an underlying mechanism regulating the embryological development of hand preference and hemispheric anatomical and functional asymmetries in male, explaining the increased prevalence of left-handedness in children born prematurely at the gestational age prior to the likely onset of axon loss (Witelson & Nowakowski, 1991). This model accounts for the disparity in size and shape of the corpus callosum between people with mixed or left-hand preferences and consistent-right-handers.

There is also some debate surrounding the atypical development of the left cerebral hemisphere in left-handed people. Very little research has been done to address whether left-handed people express different behavioral trends related to reversed cerebral asymmetry as opposed to their right-handed counterparts, although there seems to be a trend relating musical talent to left-handedness, and consequently right hemispheric dominance. Some have speculated that the right-hemisphere ends up compensating for a weak left hemisphere, which is reflected in weakened immune function due to the associated between the left hemisphere and the development of the thymus gland. The thymus gland plays an important role in immunity and in the resistance of allergies so it is possible that if the left hemisphere is poorly developed, immune disorders may develop. One idea is that early exposure to excess testosterone may lead to a cascade of biochemical pathways that ultimately result in anomalous cerebral organization and left-handedness. The damaging effects of prenatal testosterone on immune function were recently proved in experimental studies with rodents, and a lateralized influence of the neocortex on immune function was also shown in mice: in left-lesioned but not in right-lesioned mice, spleen and thymus weights were reduced, and the number of T-cells were decreased to about 50% of that of controls (Hassler, 1993). This might suggest that people with right hemispheric dominance (reflected in a left hand dominance) might have enhanced function when it comes to emotional response and musical talent, but maybe at the expense of the typical development of immunity related structures such as the thymus and spleen. Therefore, a link between immunity, musical inclination, and left-handedness has been suggested. This is Supported by such examples as Mozart, Beethoven,
Rachmaninoff, Ravel, Bach, Schumann, Kurt Cobain, Jimi Hendrix, Leonardo daVinci, Escher, Michelangelo, and Raphael. All these musicians and artists were famously left-handed, challenged the status quo in their respective fields, and suffered either from a serious atopic or immune disorder or some degree of psychosis. Many scientists from seemingly disparate disciplines have come up with models to explain this phenomenon, and the most famous of these, is the Geschwind model.

The Geschwind model assumes elevated prenatal testosterone alters structures in the left and right cerebral hemisphere, causing variations in behavior and immunity (Geschwind & Behan, 1982). Hassler (1993) undertook an investigation to clarify these complex associations in a sample of 51 people, and related left-handedness to atypical dominance patterns and immune vulnerability, which was quantified by the presence of asthma/allergies, migraines, myopia, and physiological markers in blood serum. He found that left-handed males suffered more often than right-handed males from asthma/allergies, migraine, and/or myopia and that left-handed children of both sexes suffered more often than right-handers from asthma/allergies. His results also showed that left-handers surpassed right-handers on the test measuring musical talent. When Hassler tested the relationship between anomalous dominance for verbal processing and immune vulnerability, he found elevated IgE values in males and females with right hemisphere dominance, most notably in the most musically gifted females. Hassler’s findings fall in line with the Geschwind model, which implies that hemispheric dominance (reflected in handedness) plays a large role, not only on behavioral phenotypes but in physiological phenotypes as well.
B.III: Gender effects

Research has demonstrated that the brain is a sexually differentiated organ, that is, that fetal and perinatal sex hormones have organizational effects on brain structure and function and also have subsequent activational effects on the brain (Witelson, 1991). Manipulation of early levels of sex hormones affects naturally occurring cell death and may regulate callosal axon elimination and development of associated structures related to functional asymmetry. After compiling evidence from various neurological studies and conducting his own research on 50 human brain specimens, Witelson (1991) proposed that lower levels of testosterone lead to less axon elimination, a larger callosal isthmus and associated temporo-parietal structures, greater left-handedness, and greater bihemispheric representation of cognitive skills (correlated to less functional asymmetry) in men. The same hormonal mechanisms may not be operative in the development of these brain regions in women, because the morphology of the cortical surface of the regions related to functional asymmetry are very different in women. Some of the reliable sex differences in brain structure are actually measures of relative right-left asymmetry.

Witelson (1991) found that overall, men show greater brain asymmetry and brain size (both weight and volume) is about 15% larger in men than women, and this difference in size occurs well before boys and girls differ in height (around age eight years), so brain size is not determined solely by body size. Hassler (1993) also reported a tendency in males to be more left lateralized than females. The neurological variation between the sexes accounts for some reliable and significant cognitive differences that can be observed very early in life, although the disparity is not large. In general, females perform better on various tests of language fluency, phonetics, and fine motor skills and males perform better on various tests of spatial cognition and perceptual tasks (which is related to right-hand preference), and mathematical reasoning-, which suggests a dichotomy between the sexes in the neuroanatomical substrate of handedness and functional asymmetry (Witelson, 1991).
According to Witelson (1991), the temporo-parietal anatomical network (including isthmal area and the regions surrounding the sylvian fissure) appears to be a substrate of handedness in men; but what underlies right- or left-handedness in women is not yet evident. Only in men is callosal size (particularly isthmal area) or Sylvian fissure morphology related to hand preference, which is a measure of functional asymmetry. Right handed men have a smaller corpus callosum (including the midsagittal area), a lower percentage of grey matter, greater asymmetry in the sylvian fissure, and a smaller isthmus when compared to left-handed or mixed preference males, as well as most females (Witelson, 1991). Table 16 summarizes Witelson’s (1991) findings on sexual dimorphism of the human brain. From this we can infer that the functional organization of the brain is not equally distributed between the sexes, and there may be selective pressures differentially affecting lateralization in both men and women. Damage to certain of the areas of the brain affect men and women differently, and homologous structures in the brain may have different functional significance with regards to the complex cognitive processing. For more general verbal comprehension tasks, women appear to have more bihemispheric representation in posterior language regions than do men, and due to this diffuse representation of behavioral functions (such as speech and language) in the brain, women seem less affected behaviorally by trauma or pathogenic insult to certain areas of the brain compared to men. This evidence in humans therefore supports the idea that the anatomical representation of behavioral functions (inter- or intrahemispheric) is not identical in the sexes (Witelson, 1991).

In contrast to this evidence, there have been many recent studies that failed to find a significant correlation between the effects of gender on handedness. In a large sample of undergraduates, Cornish (1997) found no association between handedness and gender in a survey of 711 humans, and likewise, Knecht (2000), who examined the single and combined influences of gender, handedness, and cerebral language dominance, found no significant effect of gender. Similarly, in a study on human twins, there were no sex differences found during co-twin correlations of same sex pairs (within zygosity) nor between same and opposite sex dizygotic twin pairs.
(Medland et al., 2009). The theory is that hormonal transfer effects would presumably lead to differences in handedness between same and opposite sex twins, but when investigated, these effects were not present within a significantly large data set (Medland et al., 2009). In bonobos, Chapelain & Hogervorst (2009) found no difference between males and females in handedness-index values, nor any significant effect of sex on the direction or strength of laterality. In a study investigating asymmetries within the spontaneous asymmetrical facial expressions in chimpanzees, Fernandez-Carriba (2002a,b) also failed to detect any effect of gender on the processing of emotional stimuli. Similarly, infant gender was not significantly correlated with the lateralization of nipple preferences, carrying preference, or cradling in macaques (Tomaszycki et al., 1998). Therefore, though we know that there are definite anatomic and morphological differences in brain organization between the sexes, and that function may not be similarly distributed in males and females, however, we cannot infer which behavioral correlates are relevant with regards to lateralization. Based on this ambiguity, I think it is only acceptable to assume that the role of gender in bonobos is negligible with regards to the lateralization of behavior within the brain and with regards to hand-preference, until further evidence proves otherwise.

<table>
<thead>
<tr>
<th>Functional Area</th>
<th>Location</th>
<th>Description</th>
<th>Relative size/morphology</th>
</tr>
</thead>
<tbody>
<tr>
<td>SDN (sexually dimorphic nucleus)</td>
<td>Preoptic area of the human hypothalamus</td>
<td>Develops from 2-4 years old, based on the presence of perinatal testosterone</td>
<td>Larger in males</td>
</tr>
<tr>
<td>SCN (suprachiasmatic nucleus)</td>
<td>Hypothalamus</td>
<td>Involved in coordinating hormonal and behavioral circadian rhythms.</td>
<td>Larger in females, possibly suppressed by testosterone.</td>
</tr>
<tr>
<td>Massa Intermedia</td>
<td>A band of tissue which connects the right and left halves of the thalamus</td>
<td>Always present in nonhuman primates</td>
<td>Absent more frequently in males vs. females</td>
</tr>
<tr>
<td>Primary transverse gyri (Heschl's gyri)</td>
<td>Neocortex, in the primary auditory cortex</td>
<td>Processes incoming auditory information</td>
<td>Different morphology in men vs. women</td>
</tr>
<tr>
<td>Planum temporale</td>
<td>Neocortex, triangular area just posterior to the auditory complex</td>
<td>Forms the heart of Wernicke’s area, one of the most important areas for language, generally left lateralized.</td>
<td>Absent more frequently in women vs. men</td>
</tr>
<tr>
<td>Corpus callosum</td>
<td>Neocortex, wide flat bundle of neural fibers that connect the right and left cortical regions</td>
<td>Involved in interhemispheric communication, size is related to hand preference</td>
<td>Larger in men, different morphology between the sexes</td>
</tr>
<tr>
<td>Isthmus</td>
<td>Posterior part of the body of the callosum</td>
<td>Area through which interhemispheric axons pass between right and left posterior parietal and superior temporal regions.</td>
<td>Generally larger in women, but in men is associated with hand preference</td>
</tr>
<tr>
<td>Sylvian Fissure</td>
<td>Divides the frontal lobe and the parietal lobe above from the left hemisphere</td>
<td>Earliest developing sulci of the brain that runs through both hemispheres</td>
<td>More asymmetrical in men, particularly right handed men. Not associated with handedness in women</td>
</tr>
</tbody>
</table>
B.IV: Measuring Handedness and Hemispheric Specialization

Left-cerebral dominance for vocalization occurs in many tetrapods, including frogs, birds, and mammals (Corballis, 2003). Because language plays a central role in human interactions we’d expect to see the dominance of the left hemisphere reflected in a right-handed bias in the human population. Accordingly, approximately 90% of humans use solely their right hand for tasks involving dexterity (Annett, 1985; Chapelain & Hogervorst, 2009; Fagard, 2004; Francks, 2007; Hicks & Kinsbourne, 1978; Hopkins, 1995; Michels, 1981; Westergaard, 2000). Corballis (2003) argued that right-handedness could have arisen because of an association between manual gestures and vocalization in the evolution of language, by tracing changes in the function of Broca’s area in different species of primate. The Broca’s area homolog in monkeys, which has nothing to do with vocal control, contains “mirror neurons” necessary for the production of manual reaching movements and the perception of the same movements performed by others (Corballis, 2003). In this evolutionary scenario, language evolved from manual gestures, gradually incorporating vocal elements, leading to a population level left hemispheric dominance in humans. But what accounts for the minority of left-handed individuals in non-human primate populations? Left-handers compared to right-handers, have a higher prevalence of bihemispheric or right-sided speech representation and even those with left-sided speech dominance show a greater degree of bilateral representation on the basis of both clinical and experimental studies (Witelson & Nowakowski, 1991). Because bonobos exhibit linguistic abilities that could surpass those of other apes (Chapelain & Hogervorst, 2009), I would hypothesize that they would display left hemispheric specialization for language and manual functions as well as a group level right hand bias, however, there is no evidence to support this yet.

The fact that nearly 10% of the human population could be categorized as left-handed or ambidextrous, raises the question of whether there is frequency dependent selection acting on those individuals? How the relationships between handedness, brain lateralization, and behavior evolved may be much more complex than was
previously speculated. The neuroanatomical asymmetries associated with handedness may develop uniquely in the individual or there may be some sort of selection acting upon the brain organization of the entire population (Zuniga, 2006), but collecting data on the brain lateralization of different species can be costly and difficult. The most promising technological advance that has given researchers insight into this field is the functional transcranial doppler ultrasonography (fTCD), which is based on the same physiological principles as the functional MRI (fMRI). Using this perfusion sensitive technique, Knecht et al. (2000) was the first to clarify the association between handedness and language dominance in a representative and quantitative way in 326 human subjects. They reported that the incidence of right hemisphere language dominance increases linearly with the degree of left-handedness, although the relationship between both variables may be flexible. The more right-handed the subjects were, the lower was the relative incidence of right hemispheric language dominance and vice versa, and overall, strong left-handers demonstrated a nearly sevenfold higher incidence of right hemisphere language dominance than strong right-handers (Knecht, 2000). Although these observations support the traditional model of cortical asymmetries with regards to handedness and lateralization, they also allow for plasticity during human brain organization and development with regards to language function. It assumes that there exists a high degree of freedom with which the brain can instantiate language, and although language generally is lateralized to the left hemisphere, it can also manifest in the right hemisphere under certain circumstances, and this shift may not always be reflected in handedness. Nearly 4% of right-handed people studied actually had right hemispheric language dominance. This could be an artifact of societal pressures on left-handers to conform to right-handed cultural constructs, such as writing or using tools. Similarly, this phenomenon might occur in the event of trauma, in response to hormonal signals during early development, during early exposure to pathogens, or due to competition within the brain during the development of other neurological pathways. The recruitment of other intact areas of the brain normally independent from language function may be required in these circumstances, leading to irregular asymmetries in comparison with the majority of the
human population. Knecht (2000) suggested that handedness and language dominance are determined by multiple factors that may overlap to produce a threshold effect accounting for the 4% incidence of right hemisphere language dominance in the extreme right-handers, and a modifier effect accounting for the increase in incidence of right dominance along with the increase in left-handedness. This seems like a very plausible explanation.

Ideally, to understand the evolution of this phenomenon, the fTCD study would be replicated across several phyla of tetrapods demonstrating similar behavioral lateralities. Unfortunately, due to a moratorium on non-human ape research and the high cost of fTCD, this may not be feasible in closely related species. Nonetheless, research into the lateralization of brain function and limb preferences in more distantly related species has increased in the past few years. Collecting handedness and limb-preferences data by means of ethological observation may be a more acceptable and less invasive way to understand these complex associations.

The collection and analysis of limb preference data across different groups of animals can also be challenging due to their morphological and behavioral differences. There is evidence that some forms of lateralization in non-human animals are as strong as eye, hand, and foot preferences in humans (Vallortigara, 2005). Nonetheless, finding consistent methods by which to measure lateralization between unrelated species may prove difficult. Vast ranges of testing techniques have been used to assess handedness and limb preference, and some may be more effective in assessing handedness in certain groups than others. According to the “hypothesis of task complexity” (Fagot & Vauclair, 1991; McGrew and Marchant, 1997), strong preferences and group-level biases would be more likely to appear in complex tasks, such as tool use, however using this behavior as a standard by which to measure handedness is confounded by both interspecies variation and variation between captive and wild populations of the same species. Generally, the more complex the task is, the stronger the laterality is, and task complexity can be related to different aspects of the task (e.g. novelty, precision, manipulation, bimanual coordination, sequence of actions, subordinate hand used for postural support, complex balance control) that
make the task cognitively demanding (Chapelain & Hogervorst, 2009). In humans, handedness is generally self reported with regards to the preferred writing hand. This is complicated by the fact that cultural pressures have been hypothesized to decrease the prevalence of left-handedness in humans, whereas exposure to adverse environments and pathogenic insults have been hypothesized to increase left-handedness in humans (Medland et al., 2009). It might be difficult for a subject to self-report the influence of childhood cultural pressures or developmental pathogenic insult accurately. The literature over the last century has reported an increase in the frequency of left-handed individuals, which possibly reflects the cultural acceptance of left-handedness, rather than a true increase in the frequency of this phenotype.

The primary measure of handedness employed in primate studies has been simple reaching. This action may be complicated by the fact that situational factors, body posture, and grip morphology all significantly influence handedness for simple reaching in great apes and other primates, and may reflect a lack of complex motor skills (Hopkins, 2006). McGrew and Marchant (1997) suggested that the more complex the form of object manipulation, the more likely that manual division of labor (when hands specialize in different tasks) will be adaptive. Therefore, the least likely acts to be lateralized are those for which either hand will do, especially one-handed acts where the other hand is idle at the same time. And, if laterality changes based on the task at hand, then the expression of brain lateralization may be more sensitive to influential factors, like the position of the object relative to the hand (Hopkins, 2006; Warren, 1980), or the complexity of the task or posture of the subject (McNeilage et al. 1984).

Reaching in primates may not be an appropriate homolog to writing in humans. Similarly, tool use, despite its presence in most great ape populations, may also fail as a measure to consistently measure handedness. For example, both species of Pan differ widely in their use of tools in nature: the chimpanzee is well known to use a variety of tools in-situ, whereas the bonobo does not seem to mirror this tool-using culture in nature. This could be due to bonobo arboreality (which is inversely correlated with tool use) or could be an artifact due to a general lack of observations of
this species. Another consideration might be the possible lack of habituation at the very few observational sites that exist in their habitat in the DR Congo. Therefore, even between closely related species, in-situ tool use is a problematic measure of handedness. This is confounded by the fact that most great ape populations are threatened and are more likely to be studied in ex-situ research facilities, zoos, and sanctuaries. In these environments, more experimental variables can be controlled, but at the expense of authenticity with regards to natural behavior. Nonetheless, it has been suggested that various forms of enrichment tasks serve as a standard by which to measure laterality and handedness in great apes. Hopkins (2006) developed the “tube” task to test bimanual actions and defined hand dominance based on the active hand employed in the task of removing peanut butter from a cylindrical tube. This method is a significant improvement, for it induced individual hand preferences in more than 85% of the chimpanzees studied, and proved to be a highly replicable. When used in bonobos by Chamberlain & Hogervorst (2009) the method helped qualify individual preferences, however, no significant group level bias was detected.
B.V: The Social-Learning (or Environmental Learning) Hypothesis

The social-learning or environmental learning hypothesis suggests that hand preferences are essentially taught. If an infant imitates the behavior of conspecifics in their immediate environment, then their hand preferences will be reflected during the development of the infant’s own handedness, along with a corresponding lateralization of function within the brain. Generally, in primates and most other vertebrates, the infant is most exposed and most influenced by the behavior of its mother, so one would expect that infant hand preferences would correlate with maternal hand preferences, which might correlate with the hand bias of the group as a whole. The social-learning hypotheses assumes that natural selection may have favored populations in which the same limb was preferred to facilitate learning and teaching of manipulation tasks between individuals in a group (Zuniga, 2006). This hypothesis was supported by a study conducted with mice during the late eighties (Collins, 1988). Mice that were allowed to observe a trained female mouse opening a pendulum door to the right (or to the left) to enter a food compartment solved this problem faster than other mice that had been placed behind a visual barrier. This implied that observational learning was indeed possible, and may have stimulated some sort of lateralization of behavior. Interestingly, male mice that had observed a "left-handed" teacher performed sinistrally; whereas males that had observed a "right-handed" model performed dextrally. On the other hand, female mice did not exhibit their demonstrator's laterality. Such social learning could have lead to the emergence of local traditions and to the cultural diffusion of behavioral asymmetries (Collins, 1988). This hypothesis was also supported by a similar study on mice performed by Waters and Deneberg (1994), who further isolated three genetic loci that may have contributed to the strength of laterality observed in rodents.

Corballis (2003) suggested that population level right-handedness in humans may have arisen because of an association between manual gestures and vocalization during the evolution of language, in a scenario in which language evolved from manual gestures, gradually incorporating vocal elements. He based this hypothesis on
evidence that the Broca’s area homolog in monkeys, has nothing to do with vocal control but contains the same “mirror neurons” that have been implicated for the production of manual reaching movements and the perception of these same movements performed by others. This system is bilateral in monkeys, but predominantly left-hemispheric in humans, and in humans is involved with vocalization as well as manual actions (Corballis, 2003). It is important to keep in mind that all these individual hypotheses to explain the phenomenon of brain lateralization and limb preference may not be mutually exclusive, but rather reflect a continuum between several different regulatory mechanisms. Neither the sex differences in brain structure and function, nor the demonstrated influence of sex-related biological factors on neuroanatomy or behavior, indicate complete biological determinism. The role of biological factors in behavior does not preclude the influence of learning and cultural factors (Witelson, 1991). Social learning may regulate the expression of a certain gene, or the expression of a gene may govern an individual’s capacity for social learning. Posture, early developmental exposure to epigenetic stimuli, and other factors may also play a role.

In support of the social learning hypothesis, significant handedness was reported in studies of captive born apes, leading to the suggestion that the rearing environment has a significant impact on handedness in great apes (McGrew & Marchant, 1997). In captive populations of primate, particularly hand-reared individuals, this hypothesis would predict a right hand bias related to the population-level right hand bias observed in humans. The evidence collected however seems to refute more than support this hypothesis on the evolution of lateralization. Hopkins found no significant effect of rearing on hand preference in chimpanzees (1995, 1999), nor in gorillas or orangutans (Hopkins et al. 2003, 2005). Similarly in bonobos, Chamberlain and Hogervorst (2009) found no difference between mother-reared and human-reared infants with regards to handedness-index values. In an attempt to compare and analyze overall handedness in great apes while addressing rearing history (captive vs. wild), Hopkins (2006) again evaluated the distribution of handedness using a common index of hand use. If living or being reared in captivity has a significant effect on handedness in
great apes then captive born apes should have shown significantly more right handed behaviors than wild apes, which they did not. Moreover, there is still a dirth of evidence to support the idea that infants “learn” a hand preference from their parents. There are non-significant or weakly significant concordances in hand preference between offspring and their biological parents, suggesting that the offspring are not acquiring their hand preferences by modeling the hand preferences of their parents. Therefore, the social learning explanation doesn’t account for the lack of statistical difference in concordance rates between offspring and mothers reared together or apart (Hopkins, 2004). In bonobos, when the direction of hand preference was evaluated amongst related pairs, only 25% of mother-infant dyads showed matched preferences, and only 50% of siblings showed matched preferences (Chapelain & Hogervorst, 2009).

Similarly, if limb preference is controlled by the same mechanisms that control the hemispheric specialization for higher cognitive functions, such as learning, one would expect a correlation between handedness and behavioral plasticity in species with asymmetrical brain function, which is not always the case. Not all species with reported limb bias are flexible in regards to behavior, i.e. not all species “learn”. Social behavior varies widely between species and group size, and many of the tetrapod species studied have presumed innate behavioral responses that can be related to their unique hemispheric specialization independent of environmental learning. It could be argued that the neurological asymmetries controlling hand/limb preference developed convergently among different phylogenies, via very different neurological mechanisms. The social learning hypothesis may apply to primates, cetaceans, and other species with the “higher cognitive processing” required during complex social interactions, but it may not explain the development of limb preference in non-social species of amphibians and reptiles (Bisazza, 1998, 2000; Malashichev, 2006). These species do not all demonstrate a significant amount of behavioral plasticity or social learning, despite their implicit hemispheric specializations. Furthermore, arguing for completely “social” or “solitary” behavior is very difficult in tetrapods and the plausibility of extant “solitary” tetrapods deriving from social ancestors (i.e.
orangutans) cannot be discounted (Vallortigara, 2005). A similar argument can be raised with respect to ontogenetic development, for directional asymmetries in “solitary” adults might be retained from juvenile stages. Therefore, the perimeters by which we define “social” vs. “solitary” are not as clear-cut as necessary to explain this phenomenon. It is also very difficult to measure the influence of epigenetic factors on behavior and laterality empirically. Environmental or social learning may not have been the only mechanism by which lateralization and handedness evolved in all tetrapods.

Despite the obvious and numerous ambiguities surrounding the debate on the evolution of handedness, there could be other social factors that play a direct role in managing the frequency of these different phenotypes in a population. Vallortigara (2005) proposed a different way of explaining the strength of lateralization in context of sociality and learning. Based on the principles of game theory, he suggested that the percentage of the minority group is dependent on frequency dependent selection: it may therefore assume a range of values, depending on the advantage of the particular form of lateralization under consideration to the minority group relative to the majority one. Whenever the group advantage of lateralization is large, the relative percentage of the majority group (usually referred to as the “strength” of lateralization) should be larger. This would mean that species with more complex social structures would provide more conditions for individual behavioral lateralities to be forced and constrained into directional behavioral lateralities. If so, maybe the claim that humans tend to have a stronger lateralization over a greater number of functions is correct, because of the very sophisticated social life of humans (Vallortigara, 2005). Similarly, we’d expect that in lineages in which higher cognitive functions evolved to support these characteristics of sociality, there would be a clear selective advantage in maintaining different phenotypes.
B.VI: The Prenatal Environment: Hormonal Regulation of Laterality

There is evidence that behavioral laterality (linked to the lateralization of emotion) develops prenatally, and likewise, handedness is first demonstrated in humans between 9-10 weeks gestation as embryos begin to exhibit single arm movements (Medland et al., 2009). Francks et al. (2007), who investigated a genetic basis for lateralization and handedness, suggested that the LRRTM1 gene may actually become activated during this time and play an important role in the establishment, consolidation or elaboration of the left–right axis during human brain growth and development, sometime before 14 weeks of gestation, and by 16 weeks, a systematic anatomical asymmetry in Sylvian fissure morphology can be detected, just two weeks after its first appearance (Witelson, 1991). This is the time frame in which population-level morphological asymmetries of the cerebral cortex first become noticeable. Witelson (1991) presented the hypothesis that the development of the temporo-parietal region of the human brain is an anatomic network, dependent on the organizing effects of sex hormones, during embryonic and perinatal sexual differentiation, and that in each sex the pattern of functional asymmetries and cognitive attributes is differentially influenced by early sex hormone exposure. These asymmetries are then visible by ultrasound in normal fetuses at 20–22 weeks (Francks et al., 2007). The early development of these cerebral patterns begins before the exposure to or modification of social experience. In humans, a larger corpus callosum, specifically a larger isthmus, is due to less prenatal axon elimination and not to greater postnatal development of axons in response to experiential factors (Witelson, 1991). These processes gain momentum as early as 23 embryonic weeks, specifically when neuron death and axon elimination coincide with the onset of synaptogenesis, when the first synapses appear in the neocortex, which likely continue to develop until four months after birth (Witelson, 1991). Synaptic density may actually be regulated by a common genetic or hormonal signal (Bourgeois et al., 1989), but cerebral lateralization as a whole is probably not completely regulated by genes or hormones, because some asymmetries develop well before any regressive events have started and
before any sex hormone receptors are even present in the human cortex. Furthermore, hormone mechanisms similar to those present in humans exist in other mammals who have less or no anatomical or functional asymmetry. If these processes influenced lateralization one would expect to see more of it in other species. Witelson (1991) suggested therefore that testosterone acts to influence the regressive events in brain development by fine-tuning connectivity in an already asymmetric brain.

It could be argued that the lateralization of function within the brain could be linked to development of other morphological structures during this stage of embryonic development, which also may influence the manifestation of cerebral dominance. Previc (1991) hypothesized that the origins of cerebral lateralization in humans could be traced back to the asymmetric prenatal development of the ear and labyrinth. Previc emphasized the importance of aural lateralization, which he hypothesized resulted from an asymmetry in craniofacial development. This was in contrast to vestibular dominance, which was traced to the position of the fetus during the final trimester. Previc speculated that a right-ear sensitivity may have contributed to a left-hemispheric advantage in speech perception and language functions. Humans typically report a higher sensitivity to sound on the right side versus the left, and also have a contralateral left hemispheric dominance. The simultaneous development of certain structures may contribute to early organization of the brain, but may not have a lasting or permanent effect, for the prenatal brain is malleable and not fully developed even at birth. The brain can be re-wired and re-organized to some extent even after birth, although how this actually occurs is largely unknown and may be unique to each case. Recent genetic and environmental evidence in both humans and non-human primates calls for a fundamental revision of current theory and research orientation in the study of lateralization (Provins, 1997). There are many regulatory factors that contribute to this process and they may come to play at very different stages throughout an individual’s life.

The prenatal environment may initiate the first series of regulatory events controlling cerebral lateralization. A more recent hypothesis suggests a link between testosterone, which may be present and presumably transferred from the mother to
fetus, and the ontogenetic development of handedness and brain laterality. Evidence from various vertebrates indicates that the manipulation of early levels of sex hormones (through the modification of fetal gland function, brain cell receptors, or through maternal stress) results in changes in the structure and function of subcortical and cortical brain regions (probably due to the interruption of normal sequences of neuroendocrine events) along with changes in reproductive and non-reproductive cognitive behaviors (Witelson, 1991). Ward & Weisz (1984) noted that in rats, factors such as stress during pregnancy may lead first to higher than normal levels of prenatal testosterone, followed by permanently lower levels. Interestingly, the persistent effect of stress was observed only on testosterone (as opposed to progesterone) and only in males (Witelson, 1991). This steroid may also be employed by some species to intentionally diversify the phenotypes of offspring in response to a changing environment (Vallortigara, 2005). Maternal stress levels (measured by the hormone cortisol) of some vertebrates affect the development of individual lateralization causing variation among individuals in “cognitive styling”. In birds it has been demonstrated that the maternally deposited testosterone level in the eggs actually modulates the strength of individual lateralization reflected in behavioral differences possibly in response to social and ecological demands. The effect of steroid hormones on the development of asymmetry is of significance in birds because outside environmental factors, as well as some internal ones, influence the level of testosterone deposited by the mother into the egg. There is a linear relationship between the amount of testosterone deposited and the corresponding levels of aggressive behavior observed in the behavioral phenotypes of the offspring, and this is consistent within a variety of different bird species (Vallortigara, 2005). This kind of parental control might be very adaptive, especially if the mother can modulate offspring behavior based on ecological changes that she herself might experience, such as an increase in the presence of predators or an increase of intraspecific competition. This interpretation is consistent with experimental results showing that hormonal manipulation also affects structural aspects of lateralization in rats and asymmetrically represented motor skills in songbirds (Witelson, 1991).
The relationship between cortisol and testosterone has also been investigated in primates, with relation to handedness and laterality. Westergaard et al. (2001) tested the hypothesis that both cortisol and testosterone are correlated with handedness in male rhesus macaques, and found a significant positive relationships between both hormone levels sampled during adolescence, and the frequency of right- versus left-hand use sampled during adulthood. These observations indicate that stress and testosterone are indeed associated with hemispheric specialization, and suggests a relationship between stress reactivity and lateral asymmetries. The character and frequency of self directed behaviors therefore may reflect differences in cerebral lateralization phenotypes. Furthermore, this finding may support the assumption that neonatal stress and its physiological consequences influence the emergence of hemispheric specialization. Westergaard et al. (2001) found a significant negative correlation between cortisol and the strength of lateral bias (independent of direction), which implies that stress actually regulates the symmetry of response in primates. Interestingly, differences in the direction of macaque hand preference were primarily related to the behavior of subjects in the low cortisol group, and these animals were more biased towards the use of their left hand than were animals in the middle or high cortisol groups. A different pattern emerged during the analysis of the testosterone data, suggesting a more continuous relationship between hemispheric specialization and levels of the male sex hormone (Westergaard et al., 2001).

Geschwind & Galaburda (1985) championed the hypothesis that maturation rates between the cerebral hemispheres were mediated by circulating testosterone levels before and during puberty. They proposed that left-handedness emerged as a consequence of enhanced prenatal testosterone, which presumably delays maturation within certain areas of the left cerebral hemisphere, thereby promoting the enlargement of homologous regions in the right hemisphere. The reduced dominance of the left cerebral hemisphere for language functions and the subsequent and compensatory development of right hemisphere dominance would cause a disproportionate expression of traits controlled by that hemisphere (Geschwind & Galaburda, 1985; Hassler, 1993). This hypothesis was developed to account for earlier
empirical evidence supporting an association between left-handedness and autoimmune disorders (Geschwind and Behan, 1982), which was discussed previously in this review.

A less-dominant left-hemisphere in humans has often been associated with weak immune function, related to the damaging effects of prenatal testosterone (Geschwind & Galaburda, 1987), and these associations were supported in experimental studies with rodents, but have failed to find support within the human population. In mice with lesions on the left hemisphere, it was found that the development of the spleen and thymus was reduced, and the number of T-cells present in the blood was about half that of controls (Renoux, 1988). This association between immunity and handedness is not supported by studies of primates. When a large sample of undergraduate students were assessed with regards to the relationships between male gender, left-handedness, high visuo-spatial and mathematical skills, speech problems and increased vulnerability to immune disorders, the only significant finding was a two-way interaction between hand preference and incidence of speech problems. None of the other variables seemed to interact. Although, Witelson (1991) claims that increased levels of androgenic hormones appear associated with homosexuality and left-handedness in women based on her examination of the morphology of the human brain. A competing perspective is that low prenatal levels of testosterone contribute to the development of left-handedness and reduced functional asymmetry by reducing the probability of cell death and axon elimination in the temporo-parietal region (Witelson, 1991). The mechanisms by which laterality develops and the plausible cerebral trade-offs that may characterize them are still very ambiguous, although evidence supports that there is some degree of hormonal regulation controlling lateralization during development.

Lateralization is definitely not completely established at birth, and perinatal and early postnatal development of the cerebral cortex in both monkeys and humans continues after birth and is characterized by a dramatic increase in the number of synaptic contacts followed by a gradual decline around puberty. After birth, the brain must adapt and refine its function based on external environmental signals. The
infantile phase of cortical development may be particularly susceptible to these influences, and visual experience in particular may have an important role during the development of synaptic connections with regards to lateralization. Vision is arguably the most important sense available to most primate species, and therefore many biochemical mechanisms within the brain must exist to support it, and concurrently these mechanisms must be related to prenatal and postnatal neuroendocrine events. Similarly, if the development of lateralization is modified or refined by external input, one would expect the visual field to have the most influence over early primate brain organization. Bourgeois et al. (1989) have elucidated the influence of the visual field on neurological development. Synaptogenesis and the onset of segregation of the ocular dominance columns in the primate neocortex begin several weeks before birth and proceed in the absence of any light stimulation, and in normal animals displays a continuous increase that does not change at the time of birth (Bourgeois et al., 1989). In a study to determine whether the timing or rate of synaptogenesis in the rhesus monkey, which proceeds at a rapid pace during the first few weeks of postnatal life, could be accelerated or changed by exposure to visual stimulation, fetuses were delivered by caesarean section 3 weeks before term and exposed to normal light intensity and day/night cycles. Surprisingly, it was found that premature visual stimulation does not affect the rate of synaptic accretion and overproduction, and that synaptogenesis proceeds in relation to the time of conception rather than to the time of delivery (Bourgeois et al., 1989). However, the size, type, and laminar distribution of synapses were significantly different between preterm and control infants, correlated with the duration of visual stimulation, and these differences become less pronounced with age, and therefore, if the visual experience during infancy influences the maturation of the visual cortex, it must do so predominantly by strengthening, modifying, and/or eliminating synapses that have already been formed, rather than by regulating the rate of synapse production (Bourgeois et al., 1989). This fine-tuning results in statistically significant, mostly transient, differences in the size, basic morphological characteristics, and proportion of various classes of synaptic contacts in the rhesus monkey visual cortex (Bourgeois et al., 1989). This agrees with Witelson’s
interpretation (1991) of the mechanisms regulating lateralization the human brain: mainly that hormonal signals only fine-tune connectivity in an already asymmetric brain, they don’t actually trigger the development of asymmetries themselves. Similar to the concept of phylogenetic evolution, these neuroendocrine mechanisms can only regulate structures and systems that already exist in an individual.
B.VII: Postural Origin (Bipedalism) Hypothesis

Scheumann et al. (2011) hypothesized that body posture (postural origin/bipedalism hypothesis) had an important impact on the evolution of handedness in primates. Their idea is that bipedalism was the dominant method of locomotion in early hominids, and it directly contributed to the strengthening of an already existing tendency toward right-handedness, which first evolved ancestrally with the prosimians. The “postural origins” theory was first championed by MacNeilage in 1987 and was an initial attempt to provide a unified view of the evolution of cerebral hemispheric specialization and handedness. MacNeilage et al. (1987) hypothesized a left-hand specialization for visually guided movement and a complementary right-hand specialization for postural control (to cling on trees), arguing that both hand use and communication developed lateralized neural specializations to adapt to an asymmetrical arboreal habitat, and that both functions were dependent on whole-body postural organization. According to MacNeilage, posture is defined as the relative arrangement of the different parts of the body, and by nature, prosimians are forced into asymmetrical arrangements while vertical clinging and leaping through the trees. The reason that the origin of these specializations was assigned to early prosimians is that it was in these animals that the supposedly causal selective pressure for unimanual predation first arose, leading to the evolution of the prehensile hand. An unknown selective pressure may have favored a consistent choice of a particular asymmetry in the posture of these early primate ancestors, leading one hand to be the “stabilizing” hand and the other hand, bearing less weight, to be the one favored for reaching, grabbing, and predation. Consequently there would be complementary relation between the reaching hand and the contralateral side being used for postural support. Research into the hand-preferece of lemurs, lorises and bush babies helped support this hypothesis, although a recent study on gray mouse lemurs found no significant correlation between body-posture on hand preference, and would refute the postural origins concept all together (Scheumann et al., 2011). Theoretically, when chimpanzees and early hominids became terrestrial, the right hand no longer had to
support the body and became the primary hand for precision and manipulation handling. This might explain the population-level right hand bias in terrestrial species compared to more arboreal primate species that seem to lack any population level directional hand bias, although it fails to explain the development of cerebral asymmetries linked to limb preference in other tetrapods. Nonetheless, Westergaard et al. (1998) explored this hypothesis by comparing postural reaching data in eight different primate species with the bipedal reaching in humans and macaques and found that body posture alters both the direction and the strength of primate hand preference. Similar findings in gibbons supporting the postural origins hypothesis have been documented, suggesting the possibility that neurological asymmetries favored and preceded the cortical lateralization of other advanced cognitive functions, such as vocal communication (Morino, 2011).

Bonobos would be the non-human primates that most frequently use bipedal locomotion, and bipedalism has been proposed to be related to the emergence of right-handedness in humans (De Waal & Lanting, 1998; Susman, 1984; Susman et al. 1980; Chamberlain & Hogervorst, 2009). Bipedalism is extremely demanding as far as postures go, and could have constrained the performance of certain manual tasks, causing neurological asymmetries to develop in order to maintain equilibrium. The idea that bipedalism may have facilitated species-typical right-handedness in early humans was examined in an experiment with five bonobos. The effect of posture on hand preferences was studied by observing the postural decisions made by these individuals to maintain body equilibrium in seven different poses using positive reinforcement. All animals showed an increasing trend toward left-handedness while shifting to a bipedal posture from a seated posture by way of a quadrupedal posture (De Vleeschouwer et al., 1995). These findings contradict the theory that bipedalism accounts for a group-level right-bias, and the highest right-hand use among great apes. At least, in bonobos, group level biases and a high degree of right-handedness is not overwhelmingly obvious (Chapelain & Hogervorst, 2009), but that could be a function of too little research on this species.

Lateralization may have been influenced somehow by postural necessity, but the
postural origins hypothesis fails to address the span of time over which this process might have occurred. It is inherently assumed in both the postural origins and bipedalism hypothesis that the pressure of natural selection and transition towards lateralization developed over many generations during evolutionary time. It could be argued, however, that the effect of postural orientation on handedness occurs on an individual level, during the unique ontogenetic development of a single organism.

Arguing that the development of hand preference would be contingent upon the hand that is free from the function of clinging, i.e. the postural origins hypothesis, may not explain handedness entirely, because it is just as likely that the hand used to cling may receive greater motor and neurological stimulation than the free hand does (Hopkins, 2004). In a variant of the postural origins hypothesis, Hopkins (2004) addressed the effect of the asymmetrical postural environment during the development of handedness during early mother-infant interactions in a single individual. The mechanisms by which laterality developed within the individual in this case is rather independent from the population level biases that may be a function of historical shifts during the evolution of these traits.
B.VIII: Genetic control over Handedness

With the advent of non-invasive DNA sampling, PCR-based microsatellite genotyping, DNA fingerprinting, and automated DNA sequencing, characterization of the selective forces acting on many different species has been greatly facilitated. Using molecular markers, we can infer phylogenetic relationships between species, genetic variation within a population, estimated gene flow, and relatedness values between individuals or groups. The use of molecular techniques in ecology to study complex social behavior has proven to be a very effective method to explain observations in humans (Plomin et al., 1994), non-human primates (Di Fiore, 2003), and a variety of other tetrapods (Hughes, 1998; Wilson, 1982). However, the “nature vs. nurture” dichotomy that previously characterized behavioral research is outdated. The epigenetic and innate mechanisms that influence complex behavioral systems are not always mutually exclusive, and while genes may regulate the intensity of a response, environmental stimuli may also influence the development of the behavioral trait. The idea is that if a mutation were to arise in an individual that somehow influenced that individual’s behavioral phenotype in a beneficial way, presumably, the individual would enjoy a high reproductive success. Fundamentally, the allele regulating this behavior would then radiate throughout the population, moderated only by the dynamic selective forces that regulate evolution. This behavior, therefore, would be considered an innate behavior, and have a distinct genetic basis. Whether lateralized behaviors [i.e. language or handedness] have such a genetic basis is still largely unknown. Here I will briefly discuss the most current genetic models that aim to elucidate the mechanisms controlling the lateralization of handedness in primate populations, and how these mechanisms presumably interact with the environment to influence this behavior.

Some genetic models propose one or two loci coding for handedness or related lateralized brain functions [i.e. language] and assume that one or possibly two alleles, when present in an individual, will favor the expression of right-handedness. Michel & Harkins (1985) postulated that the relative frequency of these alleles in the population
accounts for the dextral bias observed in primates, and theoretically, the absence of these alleles allows for the expression of individual variability in handedness. Axon elimination plays a large role in cerebral lateralization, and genetic factors may influence the course of regressive events within the brain, therefore shaping callosal morphology as well as other anatomical regions, including right-left cortical asymmetries (Witelson, 1991). Two candidate genes have been investigated: the imprinted gene LRRTMI, first identified by Franks et al. (2003), and the autosomal protocadherin gene PCDHXY. LRRTMI is significantly associated with both schizophrenia and left-handedness, but there is no actual data showing any linkage or association of the pseudo-autosomal protocadherin gene PCDHXY with handedness or brain asymmetry (Francks, 2009).

Francks et al. (2007) performed the first genome-wide linkage scan for a quantitative measure of human handedness and suggested LRRTM1, an identical imprinted gene in both humans and chimpanzees. Most autosomal genes contain two duplicate alleles, one inherited from the mother and the other from the father. Usually, both are transcribed or expressed equally in the offspring, however imprinted genes are the exception to this rule. The word ‘imprint’ is used to describe when one allele is silenced via epigenetic mechanisms (depending on the parental origin of the allele) while the other is fully expressed, and is completely unrelated to classical ‘filial imprinting’ used to describe ethological behavior patterns (Davies et al., 2004). Davies et al. (2004) describes the dominant theory regarding the origins and maintenance of imprinting, which pits the maternal and paternal genomes against each other in an evolutionary battle of the sexes, where conflicting interests between the parental sexes in relation to the outcome of lateralized brain development in their offspring leads to the development of imprinting.

Genomic imprinting is common in polygamous mating systems, where parental investment is disproportionately distributed between the sexes (Franks et al., 2007). Paternally inherited alleles of imprinted genes often sequester more maternal resources than do maternally inherited alleles, especially when influencing fetal growth, and the corresponding maternal down-regulation of these genes may
significantly influence development, as in the case of LRRTM1, where specific forebrain structures affecting neuronal differentiation and connectivity are involved (Francks et al., 2007). The data suggest that allelic variation upstream of LRRTM1 may influence the gene’s expression, which is functionally relevant for brain asymmetry when inherited on the active paternal chromosome but not on the relatively inactive maternal chromosome, at certain locations and time points during human brain development (Francks et al., 2007). This may account for the variation observed in lateralization phenotypes described earlier by Knecht et al. (2000), with regards to the association between hemispheric dominance and handedness. This gene-model describes a measure of developmental plasticity, admitting that epigenetic environmental experiences may regulate the expression of this gene via several different mechanisms early in development. Two aspects of this model, derived from Francks (2007) extensive observations, are very interesting and deserve consideration. The first relates to a non-coding region downstream from LRRTM1 that displays accelerated evolution in the human lineage although it’s role in relation to LRRTM1 is unknown. Does it somehow regulate the expression of this gene, accounting for the pronounced lateralization observed in humans as opposed to other non-human hominid lineages? The second relates to the mechanism by which imprinting actually occurs in this gene, since Francks (2007) failed to detect any sort of increased methylation on LRRTM1, which is standard in most cases of genomic imprinting. What selective forces were acting on this gene in order for this imprinting to evolve? By which molecular pathway does imprinting actually occur if methylation is not responsible for it?

LRRTM1 is also a candidate gene for involvement in several common neurodevelopmental disorders (including schizophrenia, bi-polar disorder, autism, and language impairment), which may have developed due to subtle abnormalities in the central nervous system that could have influenced neuronal differentiation and intracellular trafficking in axons (Francks et al., 2007). Because there is an association between LRRTM1 and behavioral lateralization, understanding the evolution of this
gene and how it interacts with certain risk factors in the environment to predispose individuals to neuropsychiatric dysfunctions is of great clinical importance.

A competing perspective is that genes may indeed influence the predisposition of an individual to lateralize, but it does not actually influence the direction of handedness directly. Valotiagarra (2005) argues that the one-locus genetic model may determine the presence of lateralization and handedness in the individual, but not the alignment of the direction of lateralization, which therefore prevents the predictability of behavior. This plasticity may be important in predator-prey interactions. If the entire population of a species is strongly lateralized in one direction, then the behavioral response of that species would become more predictable and thereby exploitable, and hence disadvantageously affect individual fitness. This might account for the flexibility observed during the development of handedness in response to epigenetic cues in the environment, and also the ability of left or right handed people to shift their preference based on cultural demands. The alignment of the direction of laterality in the population (i.e. significant right and left-hand biases observed in many species of primates) may be simply the by-product of the expression of genes determining somatic asymmetry, which is not uncommon in vertebrate morphologies. Organisms are rarely symmetrical, especially in terms of organ development and the brain may not be exceptional in this regard. Which aspects of laterality are governed innately, and which are under the influence of epigenetic stimulus are largely unknown, and conflicting evidence makes it difficult to either support or refute a genetic basis for handedness. In an attempt to compare and analyze handedness in great apes while addressing rearing history (captive vs. wild), Hopkins (2006) evaluated the distribution of handedness using a common index of hand use. Mid-parent handedness scores were derived by averaging the sire and dam handedness scores, and there was a significant positive correlation found between the offspring and dam handedness values. For maternal hand preference, offspring were 2.24 times more likely to be right handed if born to a right handed compared with a left-handed dam. Offspring usually exhibit patterns of hand preference more similar to their biological parents compared with offspring who have been either adopted or raised by
step-parents (Hopkins, 2006). Based on this study, it can be assumed that hand preferences run in great ape families with a relatively strong maternal effect on handedness. Paternal handedness, on the other hand, had no significant influence on the handedness index of the infant. Studies in twins also indicate that concordance rates in hand preference are higher in monozygotic compared with dizygotic individuals, supporting a genetic basis for handedness (Hopkins, 2006). These findings are in stark contrast to the recent findings of Chamberlain & Hogervorst (2009), who found that a majority of bonobo mother-infant pairs showed different hand preferences, and only a 50% match between siblings.

Medland et al (2009) studied human fraternal vs. identical twin dyads and provided perhaps the most convincing evidence to date supporting the presence of genetic effects on handedness and laterality. The identical (monozygotic) twin pairs had significantly different concordance rates in regards to handedness when compared to the non-identical (dizygotic) twins. The magnitude of the dizygotic co-twin correlations observed suggested genetic effects are the primary source of familial resemblance, or aggregation, for hand preference, and familial aggregation for hand preference was found to be consistent with additive genetic effects, which accounted for about a quarter of the variation in the trait (Medland et al., 2009).

Lastly, genetic anomalies may provide some insight into the genetic mechanisms influencing lateralized handedness and brain organization. Two examples, involving cases characterized by lower levels of sex hormones, including testosterone in both sexes of the human population, are informative. Men with Klinefelter syndrome, characterized by an XXY genotype, were found to have 30% more left-handedness, less functional asymmetry on various left-hemisphere dependent tasks, and lower levels of testosterone, than the general population (Witelson, 1991). Women with Turner syndrome, characterized by an XO genotype, also demonstrate lower levels of sex hormones, perform poorly on various tests of spatial cognition, and also demonstrate atypical functional asymmetry. Neuropathological studies on women with Turner syndrome revealed structural abnormalities in right temporo-parietal regions, a part of the brain which mediates
spatial cognition (Witelson, 1991). The lower levels of sex hormones present during critical developmental phases may interrupt normal patterns of axon elimination associated with the fine-tuning of lateralized functions in these individuals. These cases demonstrate a genetic basis for lower levels of androgens, and a corresponding loss of lateralized function, which is reflected in a behavioral (handedness) phenotype.
B.IX: Mother-Infant Interaction Asymmetries, Nipple Preference and cradling

Based on evidence suggesting the role of posture on the development of handedness, it seems logical to suggest a model coupling the potential genetic mechanisms governing lateralized behavior with epigenetic pressures influencing these traits. A gene-environment interaction, as opposed to a gene vs. environment dichotomy, may explain the heritability in handedness while taking into account the significance of posture during the development of handedness. We know that both behavioral laterality and handedness develop prenatally in humans, possibly between 9-10 weeks gestation (Medland et al., 2009), which is consistent with the time estimate Francks et al. (2007) suggested for the activation and expression of the LRRTM1 gene based on the development of population-level morphological asymmetries of the cerebral cortex. Lateralization has also been linked to the prenatal development of the ear and labyrinth (Previc, 1991). In light of evidence which suggests a critical time period in the development of lateralization within each individual infant, it seems feasible that the causal mechanisms influencing these behavioral asymmetries may not have occurred exclusively over an evolutionary time frame, as interpreted by the postural origin/ bipedalism hypothesis, but rather during a much smaller period during early development and/ or throughout the lifetime of a single individual. Rather, the individual posture of the infant influences the dynamic process of lateralization which develops and changes throughout the maturation process. Some non-human primates studies have suggested that laterality may increase with age (McGrew & Marchant, 1997), with immature individuals exhibiting weaker or less consistent preferences than adults, in chimpanzees (Hook & Rogers, 2000; Hopkins, 1994, 1995), bush babies and ring tailed lemurs (Milliken et al., 1991), baboons (Vauclair & Fagot, 1987), capuchins and rhesus macaques (Westergaard & Suomi, 1996; Westergaard et al., 1997).

In rodents it has been shown that the direction and the amount of change in asymmetry observed during adulthood can be modulated by temporally remote and brief neonatal environmental alterations, which is significantly correlated with short-
term social recognition memory (Tang et al., 2004). Rats that experienced brief (3 min per day) neonatal novelty exposure during the first three weeks of life displayed a left-shift in paw preference during adulthood, which presumably reflects a central right-shift in the hippocampal volumetric asymmetry and a selective right-sided enhancement in hippocampal synaptic plasticity (Tang et al., 2004). Only animals that experienced neonatal novelty exposure displayed experience-dependent changes in brain asymmetry while the matched control animals did not, indicating that plasticity in functional lateralization may be dependent on very specific environmental conditions during the course of the brains maturation (Tang et al., 2003). This result is consistent with research on humans, for neonatal head orientation preference was found to be a significant predictor of consistent hand-use preferences for reaching at 16-22 weeks after birth, and again later when re-measured during a 3-18 month age period (Michel & Harkins, 1985). Infants who preferred to orient their heads toward their left side during their first two months showed left hand-use preferences for reaching whereas infants with a rightward head orientation preference showed right hand-use preferences. To explain this phenomenon, Michel & Harkins (1988) proposed that the differential visual experience and differential activity of the hands, induced by the infant’s head orientation preference, contribute to the mechanism linking head orientation preference to hand-use preference.

Interestingly, Tang et al. (2003) found that these induced behavioral, anatomical, and physiological asymmetries in rats reflected enhanced learning and memory performance in a variety of tasks, including spatial and non-spatial, positive and negative reinforcement, social and non-social, and different stress level tasks. Therefore, early developmental stimulation may be linked to the social development of an individual along with the management of stress during adulthood. It is appropriate to assume that the interaction between the regulatory forces of social learning, genetics, and postural constraints on functional lateralization may be considered dynamic rather than static or simply innate. Tang et al. (2003) showed empirically that asymmetric brain activation is not constant state of mind but rather highly plastic, where short-term experience-dependence may greatly influences the
long-term experience-dependent plasticity previously reported for other aspects of brain lateralization. Building from this evidence, Hopkins (2004) argues that phylogenetic and individual differences in hand preference, including intra- and inter-familial variation, might be explained rather by asymmetries in early mother-infant interactions, specifically related to maternal cradling bias, infant head position and infant nipple preference. These interactions may provide the novel stimulation during early development that influence the lateralization of both behavior and handedness in primates, complimentary to the rodent study performed by Tang et al (2003). He also suggested that mother-infant interactions between births can influence the concordance rates in offspring hand preference and that a prolongation of inter-birth intervals in higher primates led to greater consistency in asymmetries in mother-infant interactions between offspring, resulting in consistency in hand use within families.

In 1960 Salk first noticed that most mothers carried their infants with their left arm, and when he asked subjects why they preferred their left side while carrying their children, right-handers argued that it left their dominant hand free to respond to the environment. Left-handers, on the other hand, justified their bias based on the fact that the left hand was dominant and therefore more sensitive. Salk did not think there was a relationship between handedness and cradling bias in primates, rather he championed the idea that the position of the mother’s heart was the main factor influencing this phenomenon. His theory proposed that the mother positioned the baby closer to her own beating heart, which served to soothe the baby, easing the transition from the prenatal to postnatal environment. If this hypothesis were true, it would make sense that other primates also share this behavior. In support of Salk’s hypothesis, Hopkins et al. (2004) found that female chimpanzees and gorillas show a left-sided cradling bias, and infants also appear to show a left-sided positional bias on and a left nipple preference, just like humans. In macaques this trend was also observed, and was particularly strong in younger infants, which is consistent with Salk’s hypothesis because proximity to the heart may be especially important early in life (Tomaszycki et al., 1998). The idea is that if females use their left hand to carry infants, the head orientation of the child is correspondingly right sided, generally facing inwards.
towards rather than away from the mother. Sieratzki & Woll (2002) implicate emotional communication and behavioral intent to explain this left-cradling bias in primates and inward facing of the infant, suggesting a left visual field (right hemisphere) advantage for mothers monitoring an infant’s facial expressions of distress. They introduced the concept of a “speech melody”, i.e. a series of smiles, signals, and stroking, which mothers use to interact with their infants, which is optimally soothing to the infants cradled on the left and optimally stimulating when cradled on the right side. Similarly, left-side cradling enables the mother process information with her right hemisphere (implicated during emotional response) by monitoring her infant with her left eye and ear (Manning and Chamberlain, 1990, 1991). This unique positional asymmetry in the infant could theoretically lead to differential stimulation in hand-eye coordination for the right hand and eye and have a transient effect on handedness (Hopkins, 2004).

Although Salk’s original hypothesis is supported by evidence in some primate lineages, it was refuted by evidence in others, for no population-level biases for maternal cradling or nipple preferences have been detected in orangutans, nor the Cercopithecinae, Platyrhini and Prosimii lineages (Hopkins, 2004). If Salk’s hypothesis were correct, then based on the anatomy of all primate species, this trend would be consistent within all primate lineages. The argument against Salk’s hypothesis is further reinforced by two studies on Old World monkey twins. Rogers and Kaplan (1998) investigated mother-infant interactions in common marmosets (Callithrix jacchus jacchus) during the first 60 days post parturition. Twin teat preference was compared to hand preference and all infants, except one, exhibited strong preferences for one of the mother's teats. Preference for a teat was maintained when twins suckled separately as well as together, and as expected, there was a significant correlation between teat preference and the side of being carried by the mother, although there was no significant relationship between teat preference and hand preference in this species (Rogers & Kaplan, 1998). The discordance in nipple preference is intuitively advantageous because it would reduce competition between twins for the same food source and allows for an equal distribution of maternal
resources, although why it would be advantageous for twins to adopt different hand-preferences is much less obvious. In support of the minimization of competition between twins, Nakamishi (1983) published results on the behavioral development of infant twin Japanese monkeys in a free-ranging group during the first year of life. This study also showed that twins maintained a clear nipple preference, and that twins spent much time in contact with and proximity to each other and their interactions were peaceful no dominance relations were assumed. If Salk’s hypothesis were valid, then we’d expect both twins to compete for the left nipple, which would obviously reduce the individual fitness of both infants-, which is neither adaptive nor logical. Therefore, the left-cradling bias in apes and humans, which is seemingly related to the development of hand preference, may not be explained by the position of the heart and it’s soothing effect on infant primates, although other lateralized advantages may exist that support mother-infant communication may account for this phenomenon in certain lineages.

Hopkins (2006) found a significantly inverse relationship between maternal cradling bias and infant hand preference in both bonobos and chimpanzees. In other words, females that cradle their infants on the left side have right-handed offspring for simple reaching and females that cradle their offspring on the right side have left-handed offspring. The maternal cradling bias appears to be the only variable that predicts the outcome of infant hand preference (Hopkins, 2006). If this is so, we’d expect that twins would have opposite hand-preferences, due to a mirror-imaging effect related to maternal cradling. Interestingly, Medland et al. (2009) found no evidence supporting mirror imaging effects on handedness in a human twin study, which would have led to an increased prevalence of left handedness in monozygotic (identical) twins. Nonetheless, the other primate studies seem to suggest that early cradling bias (related to nipple preference) govern the development in handedness in primate infants. The next step would be to actually study nipple preference in human twin dyads in relation to handedness. If handedness were governed by social learning, historical constraints on posture, or under exclusively innate control, we’d expect twins to show the same nipple preference and hand preference. We can also discount
the possibility that one breast versus the other is a better source of food, because infant
nipple preferences seem unrelated to the yield or composition of milk produced by the
preferred vs. nonpreferred nipple (Tomaszycki et al., 1998), and hand preference
between siblings is not always consistent. Building from this evidence, Hopkins
(2004) reconfigured the extant models of lateralization and factored in the effect of
mother-infant interaction asymmetries, depicting maternal cradling bias, infant head
position and infant nipple preference as novel stimuli during early development that
somehow influences the lateralization of both behavior and handedness in primates.
The dextral bias observed in some primate populations therefore can be explained in
context of these mother-infant interactions. The concordance rates in offspring hand
preference and the prolongation of inter-birth intervals in higher primates led to
greater consistency in asymmetries in mother-infant interactions between offspring,
resulting in consistency in hand use within families (Hopkins, 2004). This model
emphasizing the epigenetic role of maternal cradling and corresponding infant nipple
preference is the only model, that I am aware of, that accounts for the discordance
between non-human twin nipple preferences, while simultaneously supporting
population level-handedness trends in hominids and some species of monkey.

Hopkins (2006) also examined the relationship between the mother’s age and
the parity of the offspring to assess whether age or previous experience with offspring
influenced nipple preferences or handedness of the offspring. Some theories proposed
that the cradling bias of the mother was a function of experience, and new mothers
generally started cradling with the more dominant hand and then eventually switched
to the less dominant hand as she gained more experience carrying an infant. This
would mean that mothers would impose lateralized interactions unto her offspring.
Correspondingly, infants would adopt different lateral biases (i.e. nipple preferences)
and hand preferences based on parity. It could be that the mother imposes a cradling
bias unto the offspring or that the offspring imposes a nipple preferences on the
mother, but evidence in macaques suggests that the left-side cradling bias actually
reflects a bias in the infant’s nipple preference rather than a bias maintained by
maternal behavior (Tomasyzcki et al., 1998). A weak, yet positive correlation between
the cradling bias and maternal experience (as measured by the number of previous offspring) was found in macaques but this finding was interpreted as reinforcing the idea that experience would enable mothers to recognize their infant’s nipple preference and adjust their cradling behavior to facilitate the expression of such preferences rather than as a shift in maternal behavior which forces the offspring into one lateralized pattern versus the other (Tomaszycki et al., 1998). According to Hopkins (2004) birth order does have a significant effect on handedness, although it is not really the likely factor influencing this system, but reflects other kinds of pregnancy risk variables, such as maternal age, gestational age of the offspring, birth stress, or birth trauma.

Hopkins (2006) found a significant association between perinatal risk and maternal handedness, which was related to the observation that laterality in cradling inversely predicted the subsequent handedness of offspring tested four years later. Rather than see these early dyadic interactions as a dichotomy, the mother having complete control over the development of the infant or the infant directly controlling the carrying preference of the mother, it is quite possible that there is a two-way interaction that is dynamic and flexible, accounting for the variation that we frequently observe in rearing styles. Hopkins found that neither maternal age nor the parity of offspring correlated with nipple preferences and therefore handedness in chimpanzees or bonobos, confirming the idea that neither party within the dyad has complete control over the other. These results agreed with previous findings in macaques, where lateralized nipple preferences, carrying, cradling, and retrieval were independent maternal age or dominance rank (Tomaszycki et al., 1998). Studies in human twins also support this, for there was no differences found in the prevalence of left-handedness between first and second born twins (Medland et al., 2009).

Hopkins (2006) also found that there was also no significant difference in nipple preferences between the infants of captive bred or wild-caught bonobos or chimpanzees, although the strength of lateral bias seems stronger in the offspring of captive born individuals. This finding may reflect some sort of selective pressure acting on captive populations towards lateralization.
### Appendix C: Data & Video Archives

**Table 17**: 1996-1997 videotape archive. Group includes Congo (C), Lolita (O), and Laverne (V). Video reviewed by Rebecca Dai is indicated by “R” and video reviewed by Elysa Everson is indicated by “E” in the last column.

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References


LRRTM1 on chromosome 2p12 is a maternally suppressed gene that is associated paternally with handedness and schizophrenia. Molecular Psychiatry 12(8): 1–11.

Francks, C. 2009. Understanding the genetics of behavioral and psychiatric traits will only be achieved through a realistic assessment of their complexity. Laterality 14(1): 11–16.


