Handedness as a Product of Cerebral Lateralization: The Evolutionary Adaptations Behind Hand Preference in Gorillas, Siamangs and Wild Ring-Tailed Lemurs

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An Honors Thesis
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The Department of Anthropology
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by
Kyleen Breslin
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Approved:____________________________

Date:________________________________

Honor Pledge

On my honor, I have neither given, nor received, any unauthorized aid on this honors thesis. Honor Code upheld.

Kyleen Breslin

Acknowledgements

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Abstract

In humans, a species-wide right hand bias is well documented but hand preference is not as well understood in other primate species. Although many studies have examined handedness within individual primates populations, few have compared the levels of handedness between species. This study explores whether there is a spectrum of handedness in primate species; a spectrum that mirrors the neural development of symbolic language comprehension. Similar to Peter MacNeilage's (1987) "postural origins" theory, this study investigates the hypothesis that handedness developed alongside neurological capabilities. As the left side of the brain grew to accommodate the neurons needed for speech, the right side of the body became dominant. I hypothesize that the degree of right handedness will increase in species that rely heavily on kinship and communication for survival. For this reason, it was hypothesized that gorillas (*Gorilla gorilla)* and ring-tail lemurs (*Lemur catta)* should show a higher degree of handedness than siamangs (*Symphalangus syndactylus),* whose brains are more specialized for locomotion. This hypothesis was not fully supported and reasons underlying the unexpected results are explored.

Data were collected on captive gorillas and siamangs at the Cheyenne Mountain Zoo in Colorado Springs, Colorado. Wild ring-tail lemurs were observed over a period of 1.5 months at Beza Mahafaly Special Reserve in Madagascar. All of these populations were observed for hand preference using continuous focal sampling. Population-wide handedness trends were found. Gorillas demonstrated the most pronounced right handed bias using their right hand for 55.6% of hand usages. Siamangs did not show a handedness bias and used both of their hands for 38.6% of actions. The wild ring-tailed lemur population showed a left hand biases, using their left hand for 39.1% of actions. The implications and reasons behind handedness theories are discussed.

Introduction

It is a well-documented fact that worldwide human populations favor their right hand (Coren 1977, Hopkins 2001, Leliveld et al. 2008, Masataka 1989, McManus 2004). But until the 1970s, handedness remained a cultural phenomena, untouched by scientific studies. Early implications of such a prominent bias caused a cultural backlash against left handedness. In 1977 when Stanley Coren published his novel, *The Left-Hander Syndrome*, the Oxford English Dictionary was still defining left handedness as "crippled," "ill-omened," and "illegitimate" (Coren 1977: 2). Cultural suspicions about why some people were left handed ran the gamut from possession by an evil spirit to the notion that left handers lacked a full mental capacity (Coren 1977, McManus 2004). When the problem of handedness began to be addressed by the scientific community, these myths were quickly dispelled. Even the earliest handedness studies showed that left handed people were just as mentally capable and generally good natured as right handed people (Annett, 1985, Harris 1980, McManus 2004). Instead, scientists began to ask questions about just how widespread right-handedness is and why it occurs so readily in humans (Hardyck 1977, Oldfield 1970). Very quickly, handedness studies took on a life of their own. Are females more left handed than males? Are Americans more right handed than foreigners? Does handedness occur in the womb or later in life? Questions like these held the attentions of early handedness researchers. It was soon established that humans, regardless of race, sex or age, show a 90% bias towards right handedness (Hardyck 1977, Hopkins 2001, Leliveld et al. 2008, Masataka 1989, Oldfield, 1970, Riehl 2010). By the early 1980's, right handedness was widely regarded as a natural phenomenon resulting from an evolutionary process known as “cerebral lateralization” (Annett 1985, Geschwind 1974,1982, 1985,1987, Hardyck 1977, Kinsbourne 1972).

My interest in the origins of right and left handedness stem from my own personal experience as a lefty. My earliest memories of the handedness debate come from listening to my grandfather talk about how the nuns at his Catholic school “beat the left-handedness out of him” in an attempt to rid him of his mischievous behavior. This made me wonder if left handedness was biologically associated with bad behavior. Did my hand preference doom me to a life of crime? Also in early childhood, I learned that my mom is left handed and yet her twin sister is right handed. This caused me to question whether handedness is determined more by nature or by nurture. Am I left handed only because of my mother? What unseen differences between my mom and my aunt determined their hand preferences? Simple internet searches provided as many questions as answers and it wasn’t until I found the field of primatology that I discovered a more appropriate medium through which to explored my curiosities.

Cerebral lateralization, better known as brain asymmetry, is the theory that the different hemispheres of the brain evolved separately and at different speeds based on the selective pressures influencing the neurons contained within them (Annett, 1985, Geschwind and Galaburda 1987, Riehl 2010). Geshwind and Galaburda (1987) examined evidence ranging from fetal brain development to learning disorders to suggest that the hemispheres of the human brain evolved under different selective pressures. Geschwind concluded that, “In most people there is dominance of the left hemisphere for language and of the right side for certain spatial functions” (1982: 5097). This assertion was supported by later studies suggesting that lesions in the “posterior portion of the left temporal lobe” caused the most harm to language production mechanisms (Hopkins et al. 2003: 425). As further brain studies were conducted and connections between brain and behavior were established, handedness came to light as one of the most convincing lines of evidence for cerebral lateralization in humans. After the research done by Geschwind and Galaburda, it was surmised that since humans relied so heavily on language for survival, the left side of their brain evolved to be dominant resulting in a population-wide trend of right handedness (Annett 1985, Geschwind and Galaburda 1987, Hopkins et al. 2003, Molfese and Morse 1991). The notion that handedness and language are related is supported by the close proximity of the hand and language control centers in the brain (Annett 1985, Geschwind 1985). Figure 1 illustrates the proximity within the brain of the neurons needed for the control of the hands and fingers near the mechanisms needed for speech.

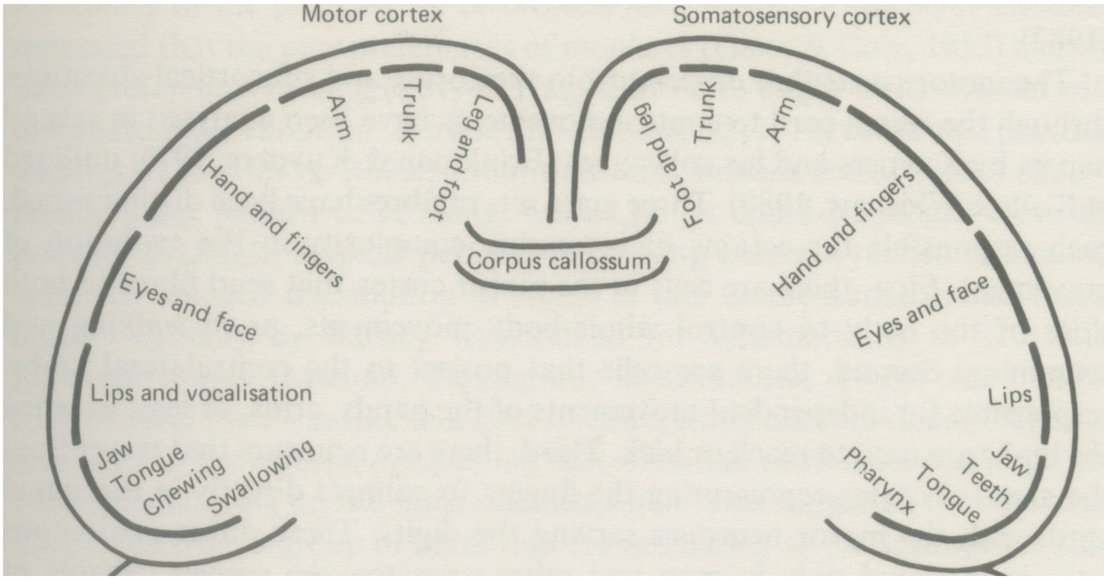


Figure 1: The representation of the body at the motor and somatosensory cortex. Based on Penfield & Jasper, 1954 (Annett 1985: 25)

The conclusion that language and handedness were related led to speculation that language and right handedness developed in humans simultaneously (Annett 1985, Geschwind and Galaburda 1985, McManus 2004, Riehl 2010). The right side of the body is controlled by the left side of the brain suggesting that if the left hemisphere is dominant, so too is the right hand (Annett 1985, Riehl 2010). The reason for the cross-control of the brain is unknown but it appears to have happened early in primate evolution and seems to have been aided by the specialization of different lobes for different functions (Annett 1985). As the hemispheres specialized, the left hemisphere's strength became speech and communication while the right hemisphere specialized in visual behaviors (Annett 1985, Geschwind and Galaburda 1985, Hopkins et al. 2003, Leca et al. 2010, Molfese and Morse 1991, Parr and Maestripieri 2003, Owren et al 2003). This cross hemisphere phenomena is demonstrated in Figure 2 which details the behaviors controlled by each lobe and the degree of their lateralization. This figure demonstrates the crossing of the optic nerve that causes the body to be controlled by the opposite hemisphere. It also shows that the left side of the brain controls speech, writing and language while the right hemisphere controls spatial abilities and nonverbal functions.

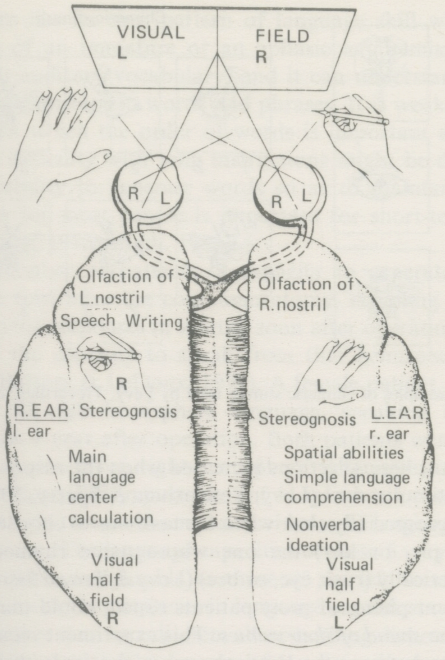


FIG. 6.1. Sperry's 1974 schema summarising inferences about cerebral specialisation.

Figure 2: Inferences about cerebral specialization (Annett 1985:107).

The anthropocentric assumption that only humans showed evidence of handedness remained unquestioned until 1987 when the field of primatology entered the handedness debate. Led by Peter MacNeilage, primatologists began monitoring non-human primates for evidence of handedness and drawing conclusions about what this must mean for the development of the primate brain (Bower 1989, Dodson et al. 1992, Fagot et al. 1991, Ward et al. 1990). They were especially interested in exploring when and why cerebral lateralization occurred on the evolutionary timeline. MacNeilage (1987) found that non-human primates also show population-wide handedness trends; these findings have spawned the research forays into primate handedness that continue today. MacNeilage was the first researcher to propose a comprehensive theory about why non-human primates might be lateralized for handedness. MacNeilage (1987) suggests that as humans evolved from arboreal to terrestrial habitats, the hemispheres of the brain lateralized to maximize habitat-specific fitness potential. This specialized lateralization resulted in bodily asymmetries (MacNeilage 1987). The neurons needed to complete the visually guided movements crucial to an arboreal lifestyle are housed within the right hemisphere of the brain (Annett 1985, Geschwind and Galaburda 1985, MacNeilage 1987). MacNeilage (1987) hypothesized that since the right hemisphere controls the mechanisms needed to survive arboreally, tree-bound primates would favor their left hands for reaching and foraging behaviors. This asymmetrical hand use was amplified as primates began to move to terrestrial habitats and heavily rely on the completion of dexterous behaviors such as tool use and hunting (MacNeilage 1987). Since the right hemisphere of the brain had specialized for visualized motions, the left hemisphere specialized to contain the neurons necessary for the completion of complex tasks. In this study I test the implications of MacNeilage's theory by hypothesizing that the capacity to complete dexterous tasks aided the evolution of the neurological foundations necessary for living in social groups. Using MacNeilage's (1987) theory as a backdrop, I examine the behavioral differences associated with arboreal and terrestrial lifestyles and hypothesize that living terrestrially is one of the main reasons humans are predominately right handed.

Although much research has been done on the origins of handedness in primates, very few studies compare handedness rates across species. This motivated me to conduct a study that examined the earliest assumptions suggested by Norman Geshwind (1985): are primates that rely on language or other communicative strategies more right handed? I hypothesized that different species will show different rates of handedness in accordance with their reliance on kinship and communication for survival due to the neural development associated with these skills. The importance of social behavior in the history of primate evolution is a growing topic with many implications for brain development (Hawkes 2004, Kappeler 2005, Roney and Maestripieri 2003, Silk 2005, Shettleworth 1998). This study works towards investigating whether a growing reliance on kinship, living in social groups, and communication increased cerebral lateralization therefore producing higher levels of handedness. In order to better understand how and why I developed this hypothesis, one must understand the influence that kinship, living in permanent social groups, and communication has had on primate brain development.

An understanding of the importance of kinship and the formation of permanent social groups is vital to the discussion of cerebral lateralization because the creation and sustainment of relationships requires highly evolved neurological capabilities (Call and Tomasello 2003, Roney and Maestripieri 2003, Bering and Pvinelli 2003). The survival of individuals within a population is aided by and often dependent on their social behavior, mainly the formation and maintenance of complex relationships (Call and Tomasello 2003, Kappeler 2005, Silk 2005, Roney and Maestripieri 2003). These relationships are altruistic, mutually beneficial and work to increase evolutionary fitness by providing protection from predators, the opportunities to learn from others, and the ability to protect vital resources (Roney and Maestripieri 2003, Shettleworth 1998). Studies conducted on humans have shown that social interactions requiring cooperation activate different areas of the brain than social interactions requiring deception or deceit (Roney and Maestripieri 2003). This suggests that the primate brain has specific, compartmentalized adaptations developed for socialization and that some areas of the brain may be more highly evolved than others depending on necessity (Annett 1985, Shettleworth 1998, Roney and Maestripieri 2003). A socially influenced, compartmentalized theory of brain development supports Geshwind and Galaburda's (1987) notions about cerebral lateralization as well as MacNeilage's (1987) postural origins theory. Kinship specific brain development can be applied on a species level to suggest that different social mechanisms have caused primate species to diverge on their evolutionary paths (Annett 1985, Bering and Povinelli 2003). Annett (1985) explains how the importance of different social behaviors may have caused primate brains to develop differently:

> Rheses [sic] monkey genes expect that an instruction to 'cling tightly to that warm hairy thing' will lead to all the interactions between monkey mother and infant that lead to normal development and socialisation [sic] into monkey society. Human babies prefer to look at roundish face-like shapes and to listen to sounds in the human voice range (Annett 1985: 16).

As Annett suggests, the neural development of rhesus monkeys (*Macaca mulatta*) specialized to select for tactile communication and survival skills such as clinging while human neural development focused on verbal communication. When thinking about the implications that this observation has for cerebral lateralization and handedness, one could hypothesize that rhesus monkeys will show a higher degree of left handedness than humans because their left hemisphere is not as specialized for language. This hypothesis is supported by a study conducted by Molfese and Morse (1991) that found the right hemisphere of the rhesus monkey brain more likely to respond to vocalizations by family members than the left meaning that, unlike humans, the right hemisphere is more actively involved in social behaviors. This suggests that the ability to adapt new survival skills based on environment and social structure evolved early in the primate lineage and influenced which brain hemisphere became dominant (Bering and Povinelli 2003, Molfese and Morse 1991). Bering and Povinelli suggest that what seem to be uniquely human forms of social interaction come from "ancestral psychological systems" that are shared with even the earliest primate ancestors (2003: 223). If one redefines the unique neurological systems of primates to be byproducts of social interactions necessary for survival, then the importance of kinship to brain development becomes clear. My hypothesis, that right handedness can be associated with higher degrees of communicative socialization, stems from the idea that socialization promoted communication which, in turn, promoted the growth of the left hemisphere of the brain.

Although living in social groups was an important behavioral adaptation for primates, the acquisition of communication skills created the neurological changes that manifested themselves as cerebral lateralization (Bering and Povinelli 2003, Geshwind 1974, Gregg 1971, Hawkes 2005, Hopkins et al. 2003, Molfese and Morse 1991, Rumbaugh et al. 2003, Shettleworth 1998, Studdert-Kennedy 1991). For some primates, inter-species communication means subtle, nonverbal tools while for humans, communication has evolved into the development of speech

(Hawkes 2004, Owren et al. 2003, Parr and Maestripieri 2003, Rumbaugh et al. 2003). Although no other species has developed as complex methods of communication as humans, language comprehension has still influenced non-human brain development (Bering and Povinelli 2003, Geshwind 1974, Gregg 1971, Hawkes 2005, Hopkins et al. 2003, Molfese and Morse 1991, Rumbaugh et al. 2003, Shettleworth 1998, Studdert-Kennedy 1991). Hawkes explains how the lack of language in non-human primates caused the importance of communication in brain development to be overlooked:

> While language reveals aspects of experience that can only be appreciated in humans, other dimensions can be studied in comparable ways in both human and nonhuman animals [...] The many physiological and specifically neurological and endochronological processes we share with other primates are a foundation for the emotional architecture that shapes behavior in us all (Darwin [1872] 1965, Hrdy 1999). Similarities between us and other animals can correct erroneous conclusions about the uniqueness of human patterns (Hawkes 2004: 455).

Hawkes demonstrates the importance of recognizing broad themes of communication to understanding neurology. This assertion is supported by a study conducted on speakers of American Sign Language. This study found that although there is no sound involved in ASL communication, signers use the same left hemisphere areas of their brains as verbal speakers (Hopkins et al. 2003). This suggests that it is not vocalizations that give human communication meaning but rather the ability to grasp knowledge from seemingly arbitrary social cues (Owren et al. 2003, Parr and Maestripieri 2003). Owren et al. (2003) support this hypothesis by suggesting that language stems from a combination of genes and socialization. Owren et al. write, “most nonverbal communications in human and nonhuman primates probably results from an interaction between species-typical genetic predispositions and processes of individual and social learning” (2003: 357). The concept of “species-typical” communication was important when developing my hypotheses since I strive to support the theory that lateralization occurred because primate species developed communication tools suited to their habitats and social stimuli. Much like Bering and Povinelli's suggestion that kinship and familial loyalty come from "ancestral psychological systems," Hawkes suggests that the neurological processes necessary for human speech find their roots in the physiology of our early ancestors (2004: 455).

Although every species communicates in some way, this study looks at the neurological ability to understand the structures that give speech meaning as the driving factor behind brain lateralization. This hypothesis does not suggest that verbal communication and lateralization are correlated but rather that there is a relationship between lateralization and the capacity to derive meaning from the symbolic actions of others (Hopkins et al. 2007, Owren et al. 2003, Parr and Maestripieri 2003, Rumbaugh et al. 1991). Norman Geshwind (1974) purposed that the human capacity for speech evolved from an ability to connect one stimuli to another in order to derive meaning. Since this definition, language has been viewed as a highly evolved process involving much more than just the capacity to produce sounds (Hopkins et al. 2003, Owren et al. 2003, Rumbaugh et al. 1991). Owren et al. described the production of language as "paradoxical" because it is controlled by "non linguistic systems" (2003:393). Although these "systems" make the studying of language acquisition difficult, they also suggest that primates who do not have the capacity for speech may have evolved a similar system of understanding. Studies conducted on a variety of primates suggest that the ability to understand language systems varies between species (Hopkins et al. 2003, Owren et al. 2003, Parr and Maestripieri 2003, Rumbaugh et al. 1991). Studies on gorilla language comprehension found that gorillas contain the neurological ability to use "iconic, indexical and symbolic" gestures and that "gestural communication in humans and in the great apes share some [...] cognitive underpinnings" (Parr and Maestripieri 2003: 354-355). Conversely, studies conducted on species that use visual forms of communication, like facial expression recognition, found that this type of social knowledge uses neurological skills vastly different from those employed by language comprehension (Hopkins et al 2003, Owren et al. 2003, Parr and Maestripieri 2003). Studies conducted on rhesus monkeys found the right hemisphere of their brain to be highly engaged in the recognition of kin (Hopkins et al 2003, Owren et al. 2003, Parr et al. 1999). Comparative studies found that rhesus monkeys were better at identifying social cues from unfamiliar members of their own species while chimpanzees (*Pan troglodytes*) were more likely to misread the expressions of strange chimps (Parr and Maestripieri 2003). This suggests that chimpanzee communication is dependent on social learning and familiarity rather than instinctual visual tools (Parr and Maestripieri 2003). These studies imply that language comprehension and communication is a complex system that has evolved to facilitate kinship on a species dependent level.

After examining the influence of communication, kinship and socialization on the primate brain, I developed several species specific expectations for the findings of this study:

1) Primate species that rely heavily on symbolic communication will display a population-wide right hand bias. I define the capacity for symbolic communication as the ability to be taught survival skills by members of a social group *a priori* and to then use those skills to maximize individual gain or fitness. The ability to communicate symbolically is assessed through simple behaviors, such as gesturing, as well as more complex behaviors, like the ability to maintain complex relationships based on abstract ideas like dominance.

2) Species that rely heavily on visually specialized locomotion (specifically brachiation) will show a population-wide left hand bias.

3) Species adapted to a terrestrial lifestyle will show a more pronounced degree of handedness than species that are arboreally adapted because their brains contain a

higher degree of lateralization in accordance with the postural origins theory (MacNeilage 1985).

4) Gorillas and ring-tailed lemurs will show a high degree of right handedness because they live terrestrially in large social groups while siamangs will demonstrate a left hand preference because they are dependent on the visual mechanisms associated with brachiation.

Methods

Study Species

Three species were observed to test the expectations of this study. The species monitored were western lowland gorillas (*Gorilla gorilla),* siamangs (*Hylobates syndactylus)* and ring-tailed lemurs (*Lemur catta)*. These species were chosen because each represents a different set of evolutionary pressures that influenced primate neural development. Gorillas were chosen because of their close evolutionary relationship to humans (Annett 1985, Hopkins et al. 2003) . Since gorillas rely heavily on social groups for survival, their neural development operated under selective pressures that favored socialization (Hopkins 2003 et al. , Falk 2000). Siamangs were observed because of their unique form of locomotion. Specialized for brachiation, the siamang brain evolved to process visual, spacial connections (Morino 2011). Ring-tailed lemurs were studied due to their unique evolutionary history. Being isolated on the island of Madagascar, lemurs adapted to selective pressures not faced by other primates and did so without heavy competition from other mammal species (Falk 2000). By comparing the levels of handedness found in these species, and what those biases imply about neural development, this study gives insight into the development of the human brain and the relationship between brain development and behavior. Figures 3-7 illustrate the observed populations and their habitats.


Figure 3

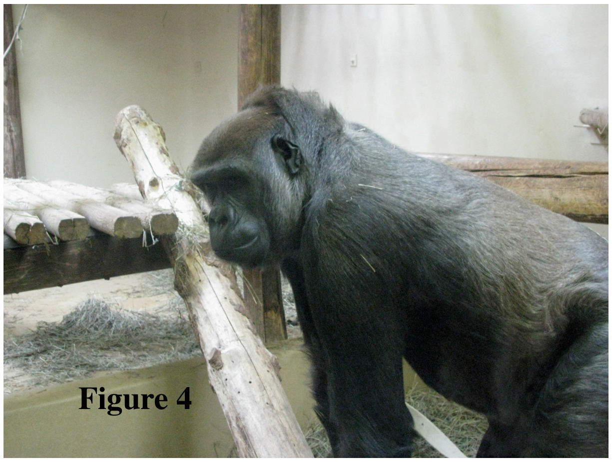


Figure 4

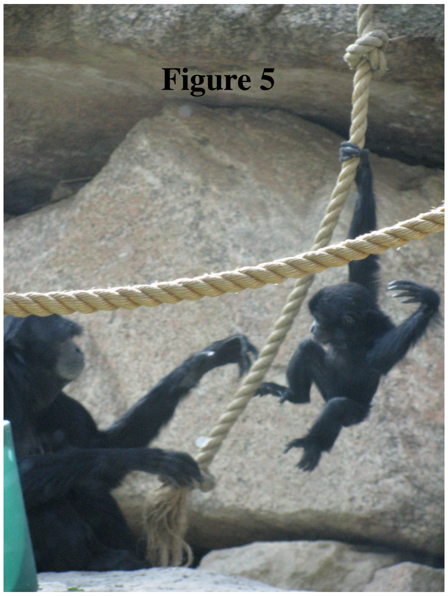


Figure 5

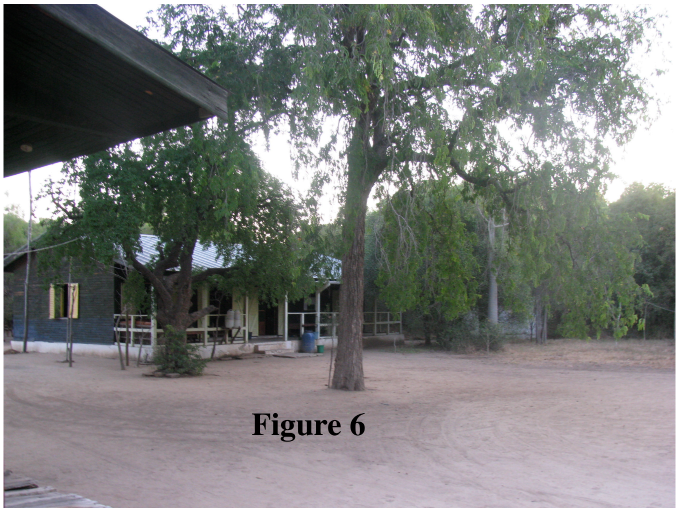


Figure 6

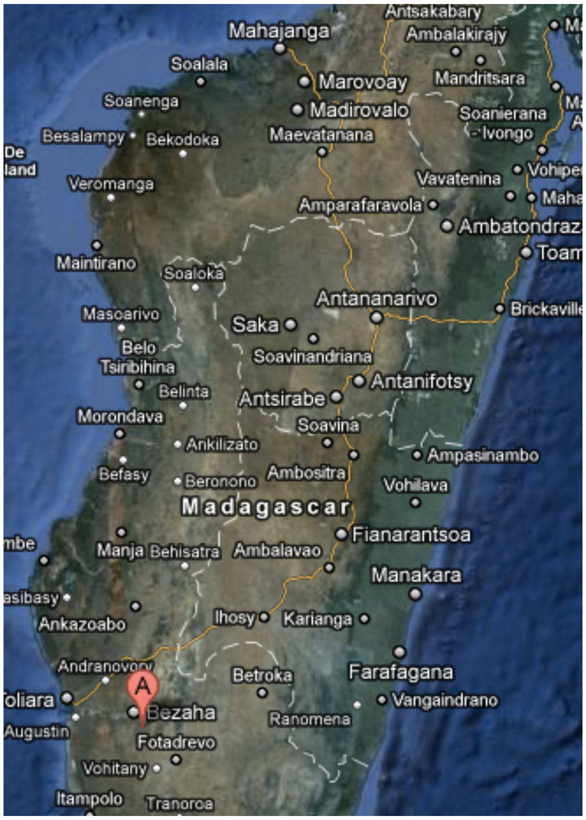

Figure 7

Figure 3 and **Figure 4**: Gorillas in their indoor and outdoor habitats at the Cheyenne Mountain Zoo. (Photo credit: Kyleen Breslin)
Figure 5: Siamang population at Cheyenne Mountain Zoo. Note: this photo was taken in 2008, the juvenile is now significantly older. (Photo credit: Kyleen Breslin)
Figure 6 and **Figure 7**: Human-influenced habitat of lemurs at Beza Mahafaly Special Reserve. (Photo credit: Kyleen Breslin)

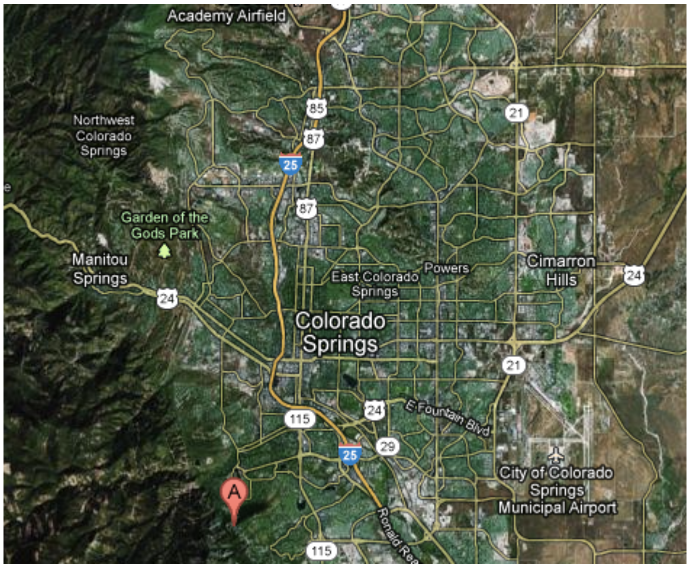
Each of these species was originally chosen because of their differing habitats but the differing social organizations are also an important component of this study. Gorillas traditionally live social groups composed of one male and multiple females (Falk 2000). Male gorillas, also known as silverbacks, are dominate within the social group and will sometimes fight other silverbacks for access to groups of females (Falk 2000). Some studies have shown that in 40% of mountain gorilla populations there are multiple males in one group (Falk 2000). Often these males are related and have formed an alliance to give them an advantage over one male groups (Falk 2000). In adulthood, female gorillas migrate away from their familiar groups and spend the majority of their lives amongst unrelated males and females (Falk 2000). Siamangs live in mated pairs and these lifelong bonds helped garnered their reputation as one of the few monogamous primates (Falk 2000). Living with up to four offspring, siamangs pairs establish and defend well established territories from other familial units (Falk 2000). The role of the male and female siamang varies from pair to pair but often male siamangs play prominent roles in caring for offspring and female siamangs actively participate in the formation of social alliances and forage for resources (Falk 2000). Ring-tailed lemurs live in groups of about 15-25 individuals, often these groups have a femal-sex bias (Krista Fish email to author March 12, 2012). These groups, also known as troops, and are led by a dominant female and her offspring (Falk 2000). Dominance is passed down through female kinship lineages while males migrate from troop to troop throughout their lives (Falk 2000). Although this study does not test the influence of social organization on behavior, these differing social structures represent different evolutionary strategies. Gorillas and lemurs favor large social groups for protection and resource acquisition while siamangs favor kinship based groups for the maximization of fitness potential.

Study Sites

The observations for this research took place both at Beza Mahafaly Special Reserve in Southern Madagascar (-23.680136, 44.583139) and the Cheyenne Mountain Zoo in Colorado Springs, CO.



Map 1: Beza Mahafaly Special Reserve located in Southern Madagascar. Marked with an “A” this map shows the location of Beza Mahafaly within the larger context of the island (© 2012 Google).



Map 2: Cheyenne Mountain Zoo in Colorado Springs, CO. Marked with an “A” this map shows the location of the Cheyenne Mountain Zoo in respect to the greater Colorado Springs area (© 2012 Google).

For ten non-consecutive days during the dry season of June and July 2011, I observed the wild ring-tailed lemur population of the Beza Mahafaly Special Reserve, Madagascar. The population I observed was well habituated because they have been studied by scientists since the early 1980s (Gould et al. 2003, Loudon et al. 2006, Sauther 1989, Sauther 1991, Sussman 1991, Yamashita 2002). Their diet and behaviors were altered by the presence of humans on the reserve. They ate foods not available to lemurs in undisturbed habitats (such as bananas, yams and other food waste) and their water supply was subsidized by the reserve's well.

During January and February of 2012, I observed the captive populations of gorillas and siamangs at the Cheyenne Mountain Zoo. The gorilla troop at the Cheyenne Mountain Zoo consists of six individuals but only four were observed for handedness (the dominate male, the male juvenile and two randomly selected adult females). One of the females is the mother of the juvenile also observed in this population. The Cheyenne Mountain Zoo has three siamangs, a male, a female and their juvenile female offspring. All three were studied for handedness.

Study Methods

During this study, a total of 58 primates were observed for handedness. Fifty-one members of the sample population were wild ring-tailed lemurs (*Lemur catta)*, four were captive gorillas (*Gorilla gorilla)* and three were captive siamangs (*Hylobates syndactylus).* Thirty-four adults and 24 juveniles were observed. Within the sample population, 17 primates were identified as female and 12 were identified as male. The sex of 29 of the wild ring-tailed lemurs was unable to be determined (22 of the unsexed primates were juveniles). Although 51 periods of observation took place with the wild ring-tailed lemurs, this study may contain data from less than 51 individuals because it is unknown whether some lemurs were observed multiple times.

Sixteen individuals were able to be identified using the number collared system developed by Dr. Michelle Sauther (1991).

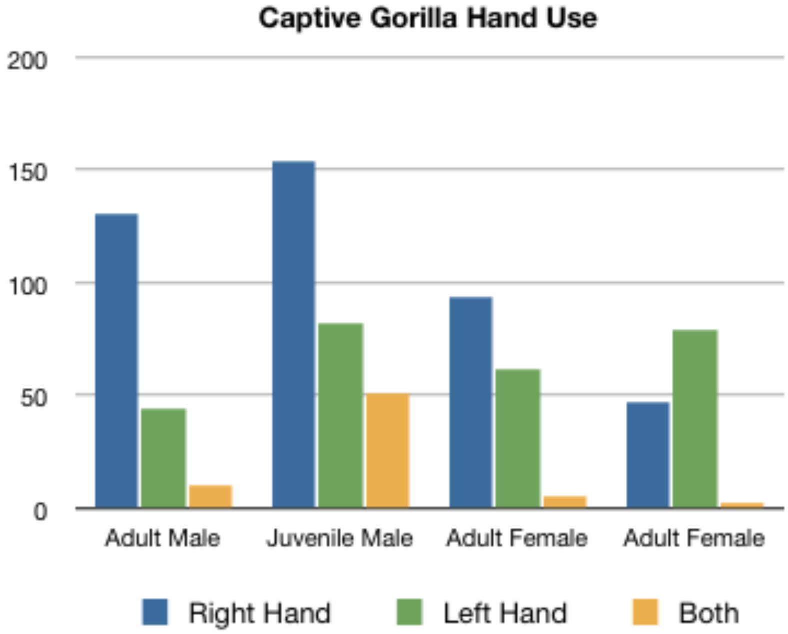
Using continuous focal sampling (Altmann 1974), captive individuals were observed over one hour increments. In some cases, these time increments had to be shortened because the primates moved out of sight or began a long period of rest. For the wild population, continuous focal sampling was used but the observation incriminates were shorter. The wild population moved in and out of the Beza Mahafaly Special Reserve limiting times of observation to around midday when the group entered camp to feed. During sampling periods, each instance of hand usage was recorded. It was also noted whether the right hand, left hand or both hands were used. For the ring-tailed lemurs, actions completed with the aid of the mouth were also noted. Although all behaviors requiring the use of hands were recorded, the majority of observed actions fell into the categories of eating, locomotion or grooming. After data on all three species were collected, graphs showing the hand usage of each individual were created in order to facilitate analysis. Graphs were created using Apple’s iWork ’08 version of Numbers. Hand preference in primates of captive populations was assessed on an individual level while data from the wild lemurs were used to determine population level trends.

Results

Gorillas

Within the western lowland gorilla population of the Cheyenne Mountain Zoo, a population level right hand bias was observed (Figure 8). Three of the individuals showed decisive right hand biases while one individual appeared to favor her left side. The adult male gorilla completed 70% of actions with his right hand, 24% with his left hand and 5.9% of actions with both hands. The juvenile male completed 53.5% of his actions with his right hand, 28.8% of actions with the left hand and 17.7% of actions with both hands. The right-hand-favoring adult female completed 58% of tasks with her right hand, 38.3% of tasks with her left hand and 3.7% of tasks with both hands. The female who favored her left hand (the mother of the juvenile in this study) used her right hand 36.6% of the time, her left hand 61% of the time, and both hands for 2.3% of all hand related actions.

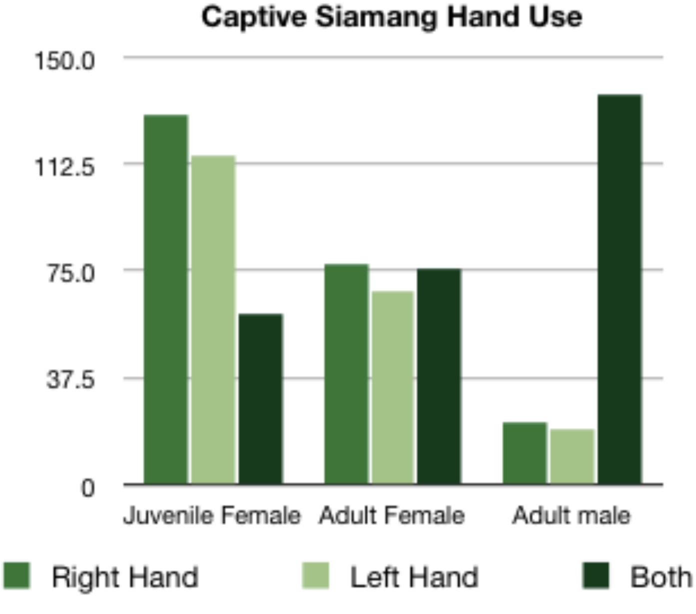
Figure 8:



Siamangs

The captive population of siamangs did not show a decisive level of handedness (Figure 9). The juvenile favored her right hand but the adults used both hands for a large proportion of their actions. Although neither adult showed pointed degrees of handedness, both showed a slight favoring of right hand over left. The juvenile siamang used her right hand for 42.5% of actions, her left hand for 37.9%, and both hands for 19.6% observed actions. The female showed the most evenly distributed hand preference of all studied primates. She completed 35.1% of actions with her right hand, 30.6% of actions with her left hand and 34.2% of actions with both hands. The male showed a low degree of handedness using his right hand 12.3% of the time, his left hand 11.2% and both hands for 76.5% of actions.

Figure 9:

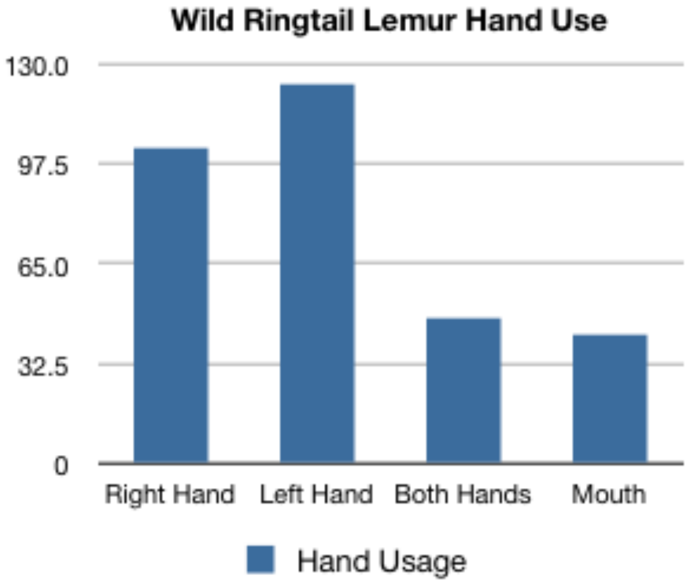


Although the behaviors of each of these primates is influenced by their captivity, I believe the male siamang showed a higher degree of abnormal, captivity associated behaviors than the other observed siamangs (Garner 2008). During observation periods, the male displayed signs of compulsive and aberrant repetitive behavior often associated with captivity and boredom (Garner 2005). One specific pattern of locomotion, a combination of brachiation and bipedal running which took place in the same clockwise pattern around the enclosure, constituted 29.9% of all observed behaviors.

Wild Ring-Tailed Lemurs

The ring-tailed lemurs of the Beza Mahafaly Special Reserve in Madagascar showed a slight population level left-hand bias (Figure 10). Of all actions completed by the observed ring-tail lemur population, 32.5% were done with the right hand, 39.1% with the left, 15.1% with both hands and 13.2% with the mouth. Preliminary observations of lemurs suggested that these primates often use their mouths to assist them with grooming and gathering food. Although mouth usage has not yet been correlated with brain lateralization, it does suggest an adaptive strategy used by lemurs that could reveal selective pressures not experienced by other primates.

Figure 10:



Discussion

The results differed somewhat from my expected outcomes. I hypothesized that the siamangs, because of their arboreal habitat, would demonstrate a prominent left hand bias. Instead, the data suggest that siamang hand preference is dependent on age and sex. I also hypothesized that ring-tailed lemurs would show a degree of right handedness because of their social organization, but the wild population at Beza Mahafaly Special Reserve showed a slight left hand preference. The data on captive gorilla handedness supports my hypothesis, but the level of individual variation speaks to the broader issue of why some primates are left handed. The following discussion examines the theories behind primate handedness and what my results suggest about these theories. In addition, it endeavors to provide an explanation regarding why my data differed from my hypothesis and what these deviations imply for our understanding of cerebral lateralization.

Postural Origins and Other Theories on Handedness

Many theories exist concerning why non-human primates show differing degrees of handedness, but the one most closely supported by my data is the “postural origins” theory (MacNeilage 1987). Although I do not believe that this theory provides a finite conclusion to why cerebral lateralization occurred, it gives important insight into why handedness levels may differ between species. The necessity of conducting this cross-species study became evident after reading Peter MacNeilage’s theory. In 1987, MacNeilage defiantly claimed that population-wide handedness was evident in non-human primates (1997: 59). Prior to MacNeilage, handedness was believed to be a uniquely human trait, having developed because of tool use and verbal language (1991: 165). MacNeilage (1987) challenged this belief by suggesting that non-human primates also demonstrate handedness because of the asymmetry associated with evolving from an arboreal to terrestrial habitat (Bower 1989, Hansbury et al. 2010, Hopkins et al. 2003, Rigamonti et al. 2005). MacNeilage (1987) suggests that when primates lived in trees, the left hand was primarily used for foraging since visual mechanisms are controlled by the right hemisphere. This meant that the right hand was used for more dexterous tasks allowing the left hemisphere to become specialized for complex neurological processes, thereby laying the foundations necessary for language comprehension (Hopkins et al. 2007, Leca et al. 2010, MacNeilage 1987, Morino 2011, Phillips and Sherwood 2005, Zhao et al. 2010). He elaborated on this theory to argue that both hemispheres of the primate brain underwent specialization to develop behaviors that would increase fitness within species specific environments of evolutionary adaptiveness. MacNeilage writes:

> It is argued that not only the left-hemisphere specializations of modern humans but also the right-hemisphere specializations, revealed in visual-spatial functions, may have taken a major formative step in the development of lateralized control of whole body postural organization, as an adaptation to the inherently asymmetrical arboreal habitat of early primates, perhaps as early as 50 million years ago (1991: 165).

MacNeilage suggests that while the left side of the brain specialized to support the capacity for language in humans, the right side of the brain specialized to accommodate the "visual-spacial functions" crucial to the survival of other primate species. The following flowchart visualizes the components MacNeilage suggests influence cerebral lateralization (as expressed by handedness). Habitat specific skills and their neurological correlates are identified to demonstrate how social behaviors impacted the evolution of asymmetry.

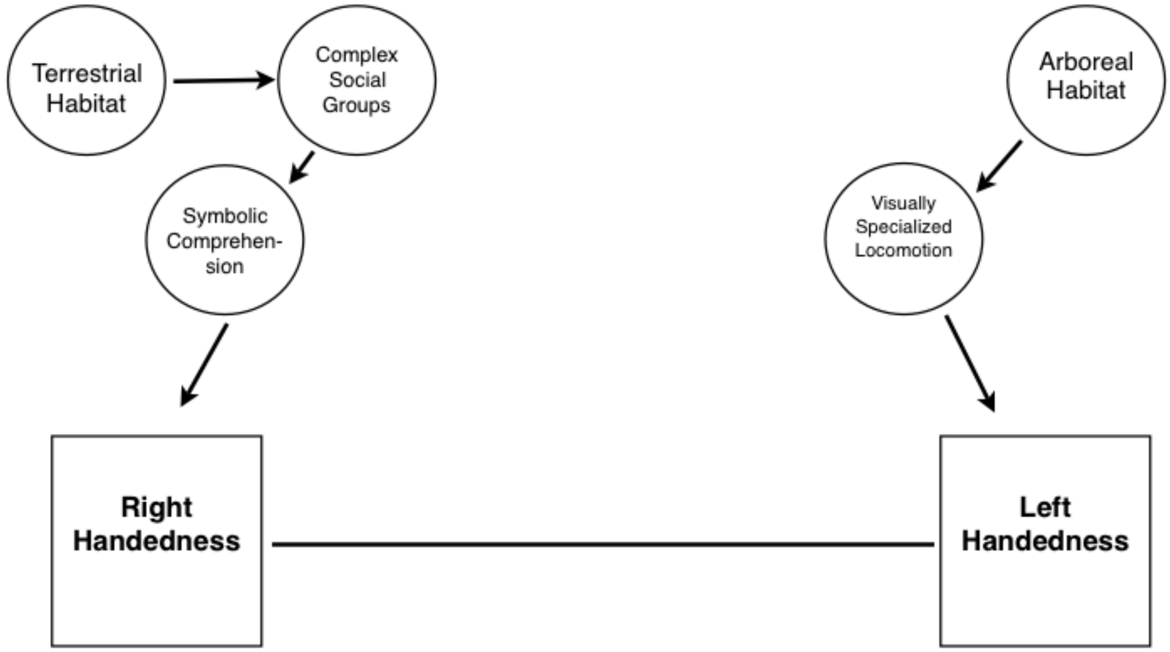


Figure 11: MacNeilage's Postural
Origins Theory

MacNeilage's theory shook the way that primatologists had been thinking about brain evolution and spawned decades of research focused on the causes and effects of cerebral lateralization. If the primate brain evolved to accommodate habitat specific adaptations, then behavioral differences must also be present. Subsequent studies conducted with the postural origins theory as a backdrop suggested that this theory was plausible but also more complicated then once assumed (Hopkins et al. 2003, Hanbury et al. 2010, Rigamonti et al. 2005). Further complications were introduced when handedness studies were conducted on species that use appendages other than their hands. For example, studies focused on prosimians, primates with fewer advanced adaptations than humans or great apes, suggested that bodily manifestations of cerebral lateralization can be observed in behaviors other than handedness. Prosimian studies indicate that non-handedness indicators of lateralization can also occur on a species specific scale with some species, like Garnett's bushbaby (*Otolemur garnettii),* showing higher degrees of tail wrapping and turning asymmetry than other prosimians (Hanbury et al. 2010, Rigamonti et al. 2005). Since the tails of bushbabies are prehensile, this behavior can be viewed as the equivalent of handedness in prosimians. Indications of the complexity of using handedness as an indicator of lateralization drove researchers to divide primate hand usage into categories, such as habitual, dexterous and bimanual. Habitual behaviors were defined as actions done with statistically significant levels of regularity while bimanual behaviors required the use of both hands (Hopkins et al. 2003, Hanbury et al. 2010, Rigamonti et al. 2005). Dividing seemingly indistinguishable instances of hand usage into these categories helped researchers to quantify levels of dexterity and notice subtle handedness variations between the species.

Despite a growing body of support, a number of primatological studies tested the postural origins theory and found that their results do not fully support MacNeilage's initial proposal. Most of these contradictory studies were focused on prosimian behaviors suggesting that lateralization developed later in the timeline of primate evolution, perhaps around the strepsirhine-haplorhine split about 55 million years ago (Dodson et al. 1992, Falk 2000, Scheumann et al. 2011). Late onset lateralization supports my hypothesis that complex social behaviors lead to hemispherical asymmetries because relationship networks requiring symbolic communication, multigenerational alliance maintenance and individually fluctuating levels of dominance are only seen in more recent evolutionary offshoots of the primate order (Parr and Maestripieri 2003). Figure 12 is a diagram outlining possible trends that may have occurred during primate evolution. This figure demonstrates how apes and humans diverged more recently than humans and lemurs. It also demonstrates the continuum thought to exist within the primate order.

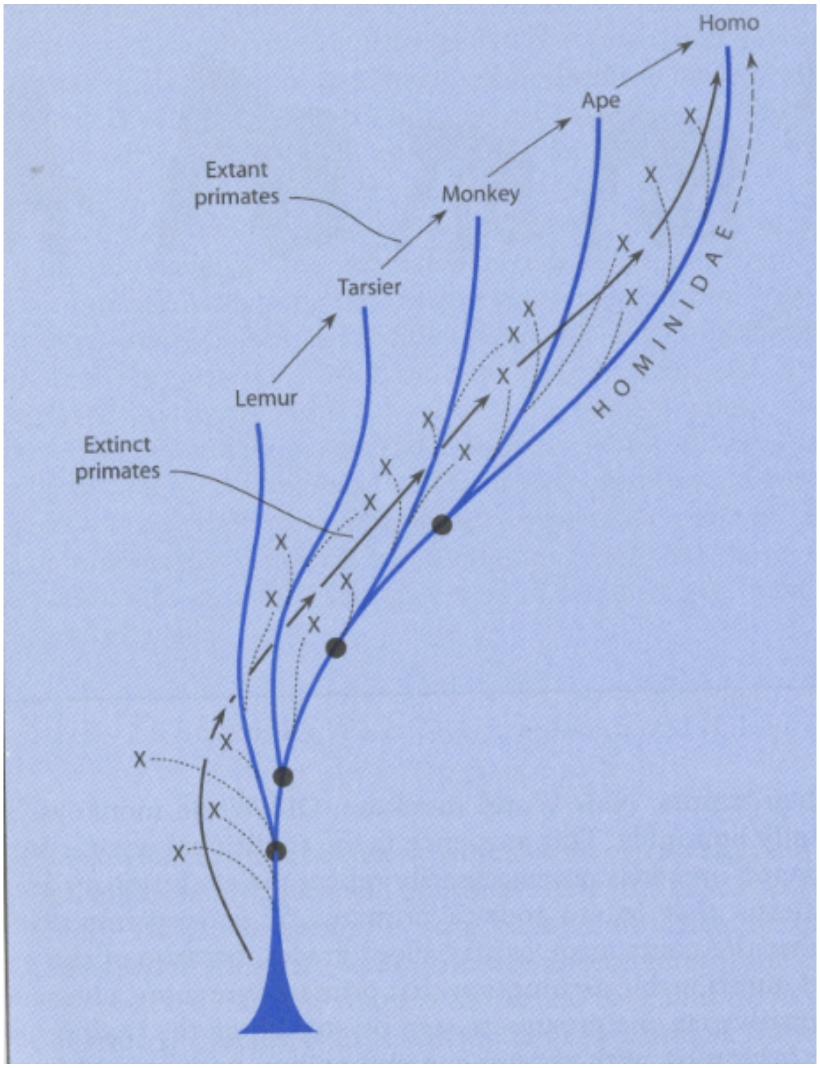


Figure 12: Trends in Primate Evolution. This diagram shows probable trends within the primate order and demonstrates how some living primates are more closely related than others (Falk 2000).

A study that contradicts the postural origins theory was conducted by Scheumann et al. (2011). This study monitored the behavior of grey mouse lemurs (*Microcebus murinus)* and determined that they prefer to forage with their mouths over either hand. Scheumann et al. (2011) suggests that the theory of the left hand specializing for balance and the right hand specializing for dexterity could not have played a role in the evolution of early primates since these mouse-lemur-like ancestors preferred to use their feet for support and their mouths for gathering (2011). Another contradictory study suggested that bipedalism rather than socialization had a direct influence on lateralization levels (Dodson et al. 1992). Focused on mouse lemurs (*Microcebus murinus)* and galagos (*Galago moholi)*, this study found that the galagos completed more motions in a bipedal posture than mouse lemurs and also showed a higher degree of lateralization (Dodson et al. 1992). This conclusion challenges MacNeilage's theory by suggesting that significant lateralization trends developed alongside bipedal tendencies rather than arboreal ones. Mouse lemurs and galagos are bipedal in their arboreal environment because their brains have evolved to favor the visually guided, agile motions that allow them to move on two limbs when necessary. Although these species have the ability to move bipedally, they do not have the capacity to complete complex tasks requiring dexterity. The presence of bipedality in prosimian species suggests that bipedalism evolved as an adaptive strategy rather than acting as a selective pressure and that bipedal tendencies found within the primate species evolved covergently. Both of these studies base their methods on the postural origins theory, but their conclusions are a reminder that an all encompassing explanation of handedness has not been reached. These findings challenge MacNeilage's (1987) assumptions but support the idea that language and socialization influenced lateralization because they were conducted using the primate species that depend the least on symbolic socialization.

Although the postural origins theory remains the most widely accepted explanation of handedness, several other purposed theories look to explain bodily asymmetries without addressing neurology. Some of these theories directly contradict MacNeilage's theory while others suggest that looking at non-behavioral adaptations will provide more conclusive answers about the development of cerebral lateralization. The majority of non-postural origin theories that have emerged suggest that researchers should look towards the morphological adaptations of modern primate species to better understand their evolutionary history (Kelly 2001, Lazenby 2002, Scheumann et al. 2011, Dodson et al. 1992). Richard Lazenby argues that the handedness debate is incomplete and misunderstood because it fails to incorporate archaeology and material culture (2002). Lazenby suggests that through a system of skeletal remodeling and a close study of skeletal remains, the origins of human and non-human handedness can be observed through changes in bone structure (2002). This article outlines methodologies that could be used to firmly establish the degrees of lateralization found in early human ancestors, but it does not provide theories as to why lateralization occurred in the first place (Lazenby 2002). Lazenby writes:

> Addressing the origins of laterality- which is both interesting and important and a very different problem than demonstrating which living primates exhibit hand preferences- falls legitimately, though perhaps not easily, to skeletal biology (2002: 131).

Lazeby discredits the insights gained through studying living primates by suggesting that only material remains can illuminate the origins of handedness. Unfortunately, Lazenby has failed to recognize that species-specific adaptations hold a record of evolutionary history and can be studied to understand what selective pressures caused lateralization to occur. Lazenby classifies the origins of lateralization as “the basic evolutionary question underlying all others” yet he proposes a methodology unsupported by theory (Lazenby 136:2002). Although this methodology could provide interesting new insights into human handedness, the practicality of finding enough early primate skeletons, even fossilized ones, to create a spectrum of change renders it impractical.

A similar theory suggests that an influential, albeit brief, form of locomotion used by early human ancestors led to today's marked levels of handedness (Kelly 2001). This theory suggests that early humans locomoted using an asymmetrical, hunched form of locomotion known as "tripedal knuckle-walking" (Kelly 2001:333). Overtime, our early ancestors grew strong on the side that was carrying tools or gathering food while the supportive knuckle side atrophied (Kelly 2001). This created a bodily asymmetry in humans and, according to the claims of this study, explains why handedness is more prominent in humans than apes who never evolved through a tripedal stage (Kelly 2001). This theory marks a decided deviation from the postural origins theory by suggesting that our behavior influenced our cerebral structure rather than our cerebral structure influencing our behavior. This theory seems to disregard the advancements made in the handedness debate by the field of primatology. If non-human primates never evolved through the tripedal stage, why do they show any evidence of handedness? This theory also provides no reasoning for why humans favor their right side to such a statistically significant degree. What about knuckle walking and tool carrying caused whole populations of early human ancestors to spontaneously use their right hands for heavy lifting?

Out of the plethora of theories intended to explain handedness, MacNeilage's postural origins theory best explains the data gathered during this study. Trends in the handedness biases of gorillas, siamangs, and ring-tailed lemurs suggest that the postural origins theory is supported by the behaviors of these observed primate populations. Gorillas demonstrate a right hand bias because they are social and terrestrial. Siamang hand preference is complicated by age and sex but can ultimately be explained by the necessity of both hands for arboreal locomotion. Although ring-tailed lemur hand preference deviated from my hypothesized results, the data, when combined with the findings of other studies, support the postural origins theory. Studies on ring-tailed lemurs suggest that perhaps the neuro-chemical mechanisms used to regulate social relations, like scent marking, were a more forceful selective pressure than the neurological adaptations that promote symbolic communication (Mertl-Millhollen 2007). This implies that strepsirhines experienced different evolutionary pressures leading to the specialization of other forms of communication such as olfaction.

Gorilla handedness

In accordance with theories on cerebral lateralization and handedness, gorillas should show a marked degree of handedness that is greater than other species, a hypothesis supported by this and other studies (Hopkins et al. 2003, Parr and Maestripieri 2003, Rumbaugh et al. 1991, Westergaard et al. 1998). A study conducted by Westergaard et al. found “a gradual increase in the degree of right-handedness in species more closely related to humans” for behaviors conducted in a bipedal position (Hopkins et al. 2003: 442). The Westergaard et al. study reaches a conclusion similar to my purposed hypothesis: that right handedness will increase with neurological similarity to humans. A relationship between lateralization and evolutionary closeness to humans is supported by studies that demonstrate that lateralization increases with brain size ending with humans showing the highest degrees of lateralization (Hopkins et al. 2003). Although the handedness levels of the gorillas most clearly matched my expectations, these results are contrary to studies conducted on other gorilla populations. The captive gorilla population at the Cheyenne Mountain Zoo demonstrated what appeared to be a population-wide right hand bias but I feel as though this result may have been skewed by the small sample size. The presence of one adult female who favored her left hand suggests that hand preference may be determined on an individual level in gorillas. This conclusion has been supported by other studies which have shown that gorillas showed a "nonsignificant" trend towards population-wide right handedness and that only individual hand preferences can be analyzed with certainty (Annett 1991, Hopkins et al. 2003). Hopkins et al. (2003) conducted the only other cross-species handedness study and determined that gorillas demonstrated a tendency to use their right hand but that this preference was insignificant when compared to the handedness biases demonstrated by chimpanzees and orangutans (2003: 6). Hopkins et al. suggest that while gorillas may lack a population-wide hand preference, their hand usage still lends support to MacNeilage's postural origins theory. Hopkins et al. write:

> If [the postural origins theory] is applied to the natural positional behavior of great apes, then orangutans should be more left-handed than either gorillas or chimpanzees because they are more arboreal in terms of habitat use. Because gorillas are considered to be the most terrestrial great ape, the postural origin theory would propose that they would be more right-handed (2003: 3).

Hopkins et al. (2003) demonstrate the importance of conducting cross-species studies because they are able to establish a spectrum of handedness throughout the great ape family. This spectrum, when compared to MacNeilage's theory, becomes powerful evidence for the argument that handedness developed due to shifting habitats and selective pressures. Although establishing an irrefutable population-wide handedness trend amongst gorillas may be impossible, comparing their handedness levels to that of other great apes provides insight to when and why cerebral lateralization occurred. Chimpanzee lateralization studies are similar to those conducted on gorillas and imply that certain lateralization trends exist in the great ape family. Multiple studies conducted on chimpanzees suggest that a population-wide right hand bias can be established (Hopkins et al. 2003, Hopkins et al. 2007, Cantalupo 2008). Despite this clear population-wide trend, these studies found that this bias becomes more pronounced with an increase in the complexity of behavior (Hopkins et al. 2003, Hopkins et al. 2007, Cantalupo 2008). Although the data were not presented in a way that would allow this degree of analysis, I hypothesize that during the Hopkins et al. (2003) cross-species study, chimpanzees performed a wider variety of dexterous tasks than gorillas. It is well known that chimpanzees show the highest levels of dexterous behavior found in non-human primate populations (Falk 2000, Hopkins et al. 2003, Hopkins et al. 2007). An increased right hand bias in chimpanzees follows the logic of the postural origins theory by implying that the right hand specialized for complex tasks (Falk 2000, Hopkins et al. 2003, Hopkins et al. 2007, Cantalupo 2008). The complexity of hand preference in the great ape family is the most closely related to the complexities of hand biases found in human populations. For example, the presence of individual left handed gorilla complicates gorilla hand preference and implies that this species' lateralization is similar to that of humans. Studying why some gorillas are left handed can give us clues about the mechanisms that sustain left hand selection in humans.

Left Hand Maintenance in Human Populations

Gorillas provide an interesting foray into the neurological reasons behind population wide left hand maintenance. No conclusive theory has been produced to explain why some individuals are left handed, but studies have linked left handedness with a variety of traits (Annett 1985, Corballis 1980, Deutsch 1980, Geschwind and Galaburda 1985, Harris 1980, Mebert and Michel 1980, Raymond et al. 1996). Studies on ancient human remains suggest that the population-wide distribution of handedness has remained consistent throughout human evolution with about 90% of the population being right hand and 10% being left (Annett 1985, Raymond et al. 1996). This suggests that a purposeful selection for left handedness has kept this trait in human morphology. The most common theories about the methods behind left hand maintenance suggest that a combination of genetic and environmental factors produce this abnormal trait at fairly regulated levels (Annett 1985, Corballis 1980, Harris 1980). Annett's (1985) "right shift theory" provides the most in depth look at the factors leading to left handedness. Annett (1985) found that asymmetry can be detected when humans are still in the womb suggesting that left handedness cannot be caused by completely environmental factors. She also found that incidents of left handedness increase within genetically related families implying that genetics play a role in creating a hemispherical right shift (1985). Annett sums up the factors that influence left handedness by saying, "[...] the expression of left-and right-handedness can be modified by factors associated with sex, physical disruptions of normal development, and training for socially significant actions" (1985: 79).

Annett (1985) provides interesting theories about how handedness has been maintained in human populations, but most left handed studies focus on how this abnormal asymmetry influences behavior and brain composition. Geschwind and Galaburda (1985) found that left handedness is associated with higher rates of migraines, auto immune disorders, allergies, and developmental disorders. They also found that left handed people are more likely to hold highly skilled jobs (Geschwind and Galaburda 1985). The good and bad traits associated with left handedness come from higher rates of "anomalous dominance" in the left handed brain (Geschwind and Galaburda 1985). Anomalous dominance is the deviation from normal patterns of brain organization that results in equal or more specialized brain function (Geschwind and Galaburda 1985). This trait is expressed in 30% of the population, meaning that it is not unique to left handers (Geschwind and Galaburda 1985). Theories behind anomalous dominance suggest that this pattern of brain development allows for the specialization of certain beneficial skills (Deutsch 1980, Mebert and Michel 1980, Raymond et al. 1996). Improved memory, tonal recognition and artistic skill have all shown to be correlated with left handedness and abnormal brain patterning (Deutsch 1980, Mebert and Michel 1980). A study conducted by Raymond et al. (1996) tested the hypothesis that left handedness has been maintained in human populations because it gives lefties an advantage in fights over right handed competitors. Raymond et al. (1996) supported this hypothesis by demonstrating that there is a statistically significant increase in left handed athletes who play sports requiring combat-like skills. The implications that stem from left handed studies suggest that population wide trends are difficult to establish and that multiple factors influence hand choice.

Task Complexity and Lateralization

One complicating factor at play in primate hand preference is the issue of whether or not the complexity of a task influences lateralization. Although Hopkins et al. (2003) doubt that gorillas demonstrate handedness, other studies have found population-wide handedness trends by looking at behaviors in terms of complexity (Fagot et al. 1988, Meguerditchian et al. 2010). Some studies do this by classifying gorilla hand behaviors into two categories: unimanual or bimanual (Fagot et al. 1988, Meguerditchian et al. 2010). These studies concluded that gorillas showed a more pronounced degree of handedness for bimanual tasks than for unimanual tasks and support the theory that handedness is related to task complexity (Bryne et al. 1991, Fagot et al. 1988, Meguerditchian et al. 2010). In 2010, a study found that while no population-wide bias was found for tasks involving one hand, a significant population-wide right hand bias was found for two handed tasks (Meguerditchian et al. 2010). Bimanual tasks often require more dexterity and complex thought suggesting that the left side of the brain evolved to control problem-oriented tasks, a mental capability on par with communication (Bryne et al. 1991, Fagot et al. 1988).

Patterns suggesting that task complexity and lateralization are correlated have also been found in other species (Hopkins et al. 2007, Leca et al. 2010, Morino 2011, Phillips and Sherwood 2005, Zhao et al. 2010). Studies on capuchin monkeys (*Cebus apella*) suggest that the thought processes required for dexterous tasks may have contributed to brain asymmetry by "causing a gross anatomical lengthening" in certain areas of the brain (Phillips and Sherwood 2005: 1703). Studies on wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana)* found that population level handedness biases occurred much more regularly when animals were involved in complex bimanual behaviors (Zhao et al. 2010). The relationship between task complexity and increased levels of asymmetry suggest that there is a relationship between human and non-human patterns of lateralization (Fagot et al. 1988). Researchers believe that the roots of the neurological capability for language can be found in complex tasks such as throwing or tool use (Hopkins et al. 2007). Finding that these behaviors are highly lateralized suggests a strong link between the ability to complete complex tasks and the ability to create symbolic meaning from social interactions (Hopkins et al. 2007).

Siamang Handedness

The siamang population observed during this study did not demonstrate a population-wide hand preference, but their tendency to use both hands is consistent with their prolific use of brachiation. The age and sex differences noted during this study were consistent with the other handedness studies conducted on this species (Stafford et al. 1990). Siamangs are a fairly unstudied species in terms of handedness and many lateralization studies focus on the effect of vocalizations or complex tasks on hand usage (Morino 2011, Redmond 2004). The first study conducted on the handedness of wild siamangs found that siamangs showed a population-wide preference of their left hand for complex, dexterous tasks (Morino 2011). This finding supports the postural origins theory because it suggests that the left hand is more widely used in species dependent on “visually guided movements” (Morino 2011: 793). The Cheyenne Mountain Zoo population did not contain a sufficient number of individuals to establish a definite population-wide standard of handedness but the results of the wild siamang study support my expectation that visually oriented species will demonstrate a degree of left handedness. Siamang support for the postural origins theory is furthered by studies that suggest that right hand usage increases with vocalization (Redmond 2004). This suggests that while the left hand is relied upon for dexterous tasks, the left side of the brain is more actively engaged in actions that require verbal communication.

The Influence of Age and Sex on Handedness

Although siamang studies support the postural origins theory, they also suggest that factors such as age and sex may influence lateralization. In studies which monitored siamang hand usage for tasks involving food reaching and brachiation, sex and age were found to influence hand usage (Stafford et al. 1990, Redmond 2004). The Cheyenne Mountain Zoo data also suggested that sex and age influenced siamang hand usage. Several studies, including my own, found that males demonstrate far lower levels of handedness than females or juveniles (Stafford et al.1990, Redmond 2004). Stafford et al. (1990: 407) found that:

> “Adult females were very strongly right hand preferent, where as adult males had no across group consistent preference. Within the female group there was a strong correlation between age and strength of right handedness.”

Another study described juvenile siamang hand preference as “highly variable” (Morino 2011: 793). These findings were similar to my results which showed the male with no hand preference and the young female with a strong right hand preference. The highly variable hand usage patterns found in juvenile siamangs suggest that perhaps the neurological systems that result in lateralization take time to develop just as humans must mature in order to acquire the ability to speak (Morino 2011). This suggestion is supported by studies conducted on ring-tailed lemur populations that found that juveniles do not adapt adult hand usage patterns until they are three years old (Ward et al. 1990). Although the postural origins theory does not explain why such a division would occur across sexes, I noted that the male spent more of his time brachiating than the females causing his use of both hands to far exceed his unimanual tasks. His hand usage was a direct result of his arboreally specialized method of locomotion. This suggests that, like the gorillas, more than one factor influences the hand preference of individual siamangs.

Differing levels of lateralization between males and females have been discovered in other species not included in this study as well. A study on the white matter of chimpanzee brains found that males demonstrated higher rates of handedness and asymmetry (Hopkins et al. 2007). This study represents a different approach to the study of handedness because it uses brain composition, rather than behavior, as supporting evidence yet it still finds similar trends in hand preference (Hopkins et al. 2007). Lateralization studies on mouse lemurs found that males demonstrate a “right ear-left hemisphere bias” when responding to communication sounds associated with negative emotions (Scheumann and Zimmerman 2008: 1). This suggests that communication and the left hemisphere are related. Although these studies did not speculate about why males may show “greater leftward asymmetries,” they suggest that the male and female brains are products of different selective pressures (Hopkins et al. 2007: 2570). Multiple studies conducted on ring-tailed lemurs found that neurochemical changes created different levels of asymmetry between males and females (Shaw et al. 2004, Ward et al. 1990). One study found male ring-tailed lemurs to be more lateralized than females suggesting that discrepancies in testosterone levels may be responsible for different levels of lateralization between the sexes (Ward et al. 1990). Subsequent studies have shown that testosterone is more influential in the left hemisphere than the right providing insight into why males and females might show differing lateralization patterns (Shaw et al. 2004, Ward et al. 1990). These studies were not the first suggests that testosterone had an influence on cerebral lateralization. Geshwind (1985) also proposed theories concerning testosterone levels in the brain suggesting that perhaps high levels of testosterone caused left handedness in humans.

Wild Ring-Tailed Lemur Handedness

The wild ring-tailed lemurs deviated most from expected outcomes demonstrating a population-wide left hand bias. In accordance with the postural origins theory and its implications for cerebral lateralization, a left hand bias for ring-tailed lemurs suggests that lemurs evolved to favor visual and olfactory forms of communication rather than symbolic. Findings of left handedness in ring-tailed lemurs are not unique to this study and have interesting implications for our understanding of primate brain development (Masataka 1989, Mertl-Millhollen 2007, Shaw 2004, Ward et al. 1990). It has been suggested that ring-tail lemur handedness differs from patterns found in other primate species because there is the possibility that studied lemur populations are influenced by the founder effect (Ward et al. 1990). This would suggest that hand preferences in lemurs have been influenced by generations of similar genetics more so than the environment of evolutionary adaptation (Ward et al. 1990). Other studies suggest hand preference is highly variable and that an individual lemur's preference may shift over the course of a lifetime (Shaw et al. 2004, Ward et al. 1990). The explanation for ring-tailed lemur left handedness that best supports the postural origins theory is the suggestion that levels of lateralization among ring-tailed populations are influenced by the emotional variance of a behavior (Mertl-Millhollen 2007). Studies on male ring-tailed lemur scent marking patterns suggest that males are highly lateralized for this activity (Mertl-Millhollen 2007). Mertl-Millhollen suggests that perhaps lemurs favor their left side for this behavior because they have evolved "a right cerebral hemisphere bias to the processing of perceptions with an emotional content" (2007: 635). This theory is consistent with Geshwind and Galaburda's (1985) theory that the right hemisphere specialized to control emotions.

Potential Error Sources

This study was conducted in adherence to scientific methodology, but when collecting data on trends as variable as animal behavior, there are numerous opportunities for error. Errors most likely occurred in the form of discrepancies between the behaviors of captive and wild primates. I was able to collect more data about the behaviors of captive primates since their habitats are constructed to ensure almost constant visibility. This allowed me to be able to look at handedness trends on individual and population-wide levels. In the wild, observing one primate for extended amounts of time is difficult, making population-wide trends the only level of analysis. Despite the higher amounts of data available on captive primates, results may also be skewed by the influence of captivity on primates' behavior. Gorillas were observed regurgitating and reingesting their food, a behavior highly associated with captivity (Akers and Schildkraut 1985). The behavior was performed regularly and with the same hand. The gorilla who regurgitated her food the most was the female who showed a left hand tendency. She regurgitated her food into her left hand then ingested it from her left palm. Although she also favored her left hand in non-stress related settings, behavior that was influenced by her captivity may have skewed my results. In addition, the male siamang performed repetitive behaviors that seemed to be associated with boredom and captivity (Gould 2003). These behaviors mostly included the use of brachiation which may have skewed data. This study could have benefitted from a comparison between the behaviors of wild and captive primates of the same species. Unfortunately, a set back in the introduction of two new male lemurs to the Cheyenne Mountain Zoo population caused them to be off display for several months and precluded this aspect of analysis.

Conclusion

Handedness in primates is a complex neurological web influenced by a multitude of environmental and genetic forces. Beginning with authors like Geschwind and Galaburda (1985), Annett (1985) and MacNeilage (1987), discussions about handedness in human and non-human primate populations have become important to our understanding of brain structure and development. Although data from this study did not support all expected outcomes, it supports trends purposed by the "postural origins" theory (MacNeilage 1987).

The right hand bias found in the Cheyenne Mountain Zoo gorilla population is consistent with other studies suggesting that gorillas demonstrate a slight population-wide left hemisphere bias (Annett 1991, Cantalupo 2008, Hopkins et al. 2003, Paar and Maestripieri 2003, Rumbaugh et al. 1991, Westergaard et al. 1998). This trend is consistent with my hypothesis that handedness evolved as indicator of complex social interactions regulated by symbolic meanings. The presence of individual left handed gorillas is similar the presence of left handed humans suggesting that gorilla and human lateralization trends have been maintained by similar mechanisms (Annett 1985). This study is consistent with other studies conducted on gorilla handedness which found that cerebral lateralization is influenced by task complexity and that the necessity of performing dexterous tasks influenced brain composition (Bryne et al. 1991, Fagot et al. 1988, Meguerditchian et al. 2010). Comparing the levels of dexterous lateralization in great apes to that of lesser primate species suggests that the neural pathways needed for dexterous behaviors laid the foundation for the neural pathways needed for speech comprehension (Hopkins et al. 2007, Owren et al. 2003).

The fluctuating hand preference of siamang populations suggest that age and sex play a role in determining bodily asymmetry even in species that are highly specialized for their environment (Stafford et al. 1990, Redmond 2004, Ward et al. 1990). Lesser degrees of handedness in younger primates suggest that the complex neurological processes that cause cerebral lateralization take time to develop (Morino 2011). Although siamangs did not show the expected left-hand bias, their use of both hands can be attributed to their abundant use of brachiation. Population-wide handedness studies, as well as studies that look for trends between vocalization and hand preference, suggest that siamangs prefer their left hands for certain behaviors (Morino 2011, Redmond 2004). This supports the postural origins theory by suggesting that arboreal habitats and left handedness are correlated.

The wild ring-tailed lemur population demonstrated a notable left hand bias suggesting that lateralization has also been influenced by olfactory and neurochemical specializations (Masataka 1989, Mertl-Millhollen 2007, Shaw et al. 2004, Ward et al. 1990). This trend also supports the postural origins theory by suggesting that the right hemisphere specialized for emotionally related behaviors (Geschwind and Galaburda 1987).

Although the origins of handedness are still not completely understood, this cross-species study suggests that cerebral lateralization may have occurred around the time of the strepsirhine-haplorhine split around 55 million years ago (Falk 2000). It also suggests that more research is needed on the origins of language comprehension to fully understand why some species rely on symbolic communication more than others. Primatologists have noted the presence of symbolic communication in chimpanzees but have not proposed new theories as to why this ability is seen in so few primates (Rumbaugh et al 2003). This study also provides a definite conclusion that non-human primates show evidence of cerebral lateralization. Hand preference may seem like a subconscious and even trivial behavioral oddity, but this understated action is regulated by complex neural mechanisms that have been nuanced throughout the evolution of the primate linage.

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