An analysis of bimanual actions in natural feeding of semi-wild chimpanzees

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Running Head: Natural feeding behavior in chimpanzees

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Abstract

Objective

The objective of the current study was to investigate the lateral dominance for a bimanually coordinated natural feeding behavior in semi-wild chimpanzees.

Materials and Methods

We investigated *strychnos* spp. fruit consumption behaviors in semi-wild chimpanzees as an ecologically comparable feeding behavior to those found in cerebral lateralization studies of non-primate species. Video recordings of thirty-three chimpanzees were assessed while they consumed hard-shelled strychnos fruits. We explored statistical and descriptive measures of hand dominance to highlight lateralized patterns.

Results

Statistical evaluation of feeding bouts revealed a group-level right-handed bias for bimanual coordinated feeding actions, however few individuals were statistically lateralized. Descriptive analyses revealed that the majority of individuals were lateralized and possessed a right-handed bias for strychnos feeding behavior.

Discussion

The results provide empirical evidence in supports of an early evolutionary delineation of function for the right and left hemispheres. The present findings suggest that great apes express an intermediate stage along the phylogenetic trajectory of human manual lateralization.

Introduction

Whether any non-human animal expresses lateral biases in motor action akin to that of *Homo sapiens* is a growing debate. It is commonly reported that the human population exhibits approximately 90% right-handedness (e.g. McManus, 2002). Moreover, the majority of individuals within this population (95%) have language-processing regions situated in the left hemisphere of the brain (Foundas, Leonard and Heilman, 1995). However, a causal relationship between language function and human handedness appears too simplistic.

In addition to evolutionary links with language (Annett, 2002), human right-handedness has demonstrated links with tool use (e.g. Greenfield, 1991; Bruer Ndoundou-Kockemba and Fishlock, 2005), coordinated bimanual actions (Wundrum, 1986; Hopkins, Hook, Braccini and Schapiro, 2003) and gesture (Corballis, 2002; Meguerditchian, Vauclair and Hopkins, 2010; Hobaiter and Byrne, 2013). Human right-handedness may precipitate from a division of labor between the left and right hemispheres dating back 500 million years ago. A growing body of evidence across a range of species suggests that the right hemisphere emerged dominant for processing novel and urgent stimuli (e.g. approach-avoidance behavior). The left hemisphere, in turn, became dominant for executing top-down behaviors related to routine sequences of actions (e.g. feeding behavior) (Vallortigara and Rogers, 2005; MacNeilage, Rogers and Vallortigara, 2009; Rogers, Vallortigara and Andrew, 2013). For instance, studies report right hemisphere/left visual field dominance for monitoring conspecifics, for example in fish **(**Sovrano, Bisazza, and Vallortigara, 2001), toads (Robins, Lippolis, Bisazza, Vallortigara, and Rogers, 1998) lizards (Deckel, 1995; Hews and Worthington, 2001), pigeons (Nagy, Àkos, Biro and Vicsek, 2010), chicks (e.g. Vallortigara, 1992; Vallortigara and Andrew, 1991), beluga whales (Karenina et al., 2010) and gorillas (Quaresmini, Forrester, Spiezio and Vallortigara, 2014). Conversely, studies report left hemisphere/right motor action dominant behaviors during prey capture in fish and toads, during foraging and manipulating food items in birds (Alonso, 1998) and for object manipulation in birds (Rutlidge and Hunt, 2003), monkeys (e.g. Westergaard and Suomi, 1996) and apes (e.g. Hopkins, 2007; Forrester, Quaresmini, Leavens, Mareschal and Thomas, 2013). Hemispheric specialization of function may have provided advantages such as increased neural capacity through the enabling of parallel processing. In turn, non-replication of function across both hemispheres would deter the simultaneous incompatible responses (e.g. Vallortigara, 2000; Rogers, 2002). Based on such evidence, it is unlikely that human right-handedness is a species unique trait. Human population-level right-handedness is more likely to have been inherited from a last common ancestor that exhibited left hemisphere dominance for structured sequences of actions (Forrester et al., 2013).

Great apes represent a functional model to study the evolution of handedness and human cognition, not only because of their phylogenetic proximity to humans, but because they display clear anatomical humanlike features, like the morphology and manipulative skills of hands (Byrne, Corp and Byrne, 2001). Historically, captive and wild non-human primate studies of hand dominance revealed no clear evidence of species-level manual lateralization (e.g. Finch, 1941; Marchant and Steklis, 1986; Parnell, 2001; Fletcher and Weghorst, 2005; Marchant and McGrew, 2007). However, the processes for controlling experimental parameters (e.g. terminology, behavioral tasks, rearing histories, analysis procedures) varied across laboratories, potentially contributing to disparate findings (e.g. McGrew and Marchant, 1997; Palmer, 2002; 2003; Cashmore et al., 2008; Hopkins, 2013; Marchant and McGrew, 2013). Moreover, self-report and survey methods for testing human hand dominance (e.g. Edinburgh Handedness Inventory; Oldfield, 1971) inhibit direct cross-species comparisons. A recent set of studies employed identical experimental parameters across humans and non-human primates to investigate unimanual dominance during spontaneous object manipulation in great apes and children. These studies reported population-level right manual biases in gorillas and chimpanzees (e.g. Forrester et al., 2011; Forrester et al., 2012) that were similar in pattern (but not equal in strength) to that reported in children (Forrester et al., 2013). More research taking such an approach is warranted to provide further clarity on the similarities and differences across species.

Studies that have focused on the context of subsistence tool use in captive apes have also reported population-level right-handedness in great apes (see for a review, Hopkins, 2007). These experimental investigations employed the ‘tube task’ whereby subjects obtained a food reward from inside a plastic tube by gripping the tube with one hand and using the fingers to extract the reward from inside the tube. The task requires coordinated bimanual actions, which, compared with unimanual actions, is considered to be a more sensitive measure of hand dominance (e.g. Hopkins, 2006; Vauclair and Meguerditchian, 2007). Bimanual actions tend to minimize postural factors, as the individual must adopt a bipedal or seated posture in order to maintain the freedom of both hands (Roney and King, 1993). Population-level right-handedness has since been replicated across multiple investigations employing bimanual coordinated actions (e.g. Hopkins et al., 2005; Hopkins, 2006; Meguerditchian, Calcutt, Lonsdorf, Ross and Hopkins, 2010; Meguerditchian, Gardner, Schapiro and Hopkins, 2012). Moreover, the robust pattern has been consistent in apes across a variety of rearing histories, suggesting that exposure to humans does not significantly impact population-level right-handedness (Hopkins, Wesley, Izard, Hook and Shapiro, 2004; Llorente et al., 2011). The findings support the evolutionary position that sequences of coordinated bimanual actions are dominantly controlled by left hemisphere processing.

Non-human primate studies have rarely considered lateral motor dominance in natural behaviors. This is an important omission because natural behaviors are likely to be the conditions under which hemispheric specialization for motor dominance evolved. Therefore, the investigation of lateral biases of natural behaviors provides a necessary element of ecological validity. A few studies have investigated the influence of cerebral lateralization on motor action during approach-avoidance behaviors. These studies have reported a left orienting preference (right hemisphere dominance) during aggressive encounters in gelada baboons (Casperd and Dunbar, 1996), in a zoo-housed group of mangabeys during spontaneous approach behaviors (Baraud, Buytet, Bec and Blois-Heulin, 2009), and during conspecific monitoring in both gorillas and chimpanzees (Quaresmini et al., 2014). These findings suggest that urgent environmental stimuli requiring approach-avoidance behaviors, are dominantly processed by the right hemisphere (Vallortigara and Rogers, 2005; MacNeilage et al., 2009). However, there is a paucity of empirical evidence from cross-species studies that focus on natural behaviors comprised of routine sequences of motor actions.

Natural food preparation and feeding sequences of apes provide an excellent opportunity to investigate the evolution of human cerebral lateralization. To date, reported findings have been inconsistent. Some studies have found hand biases only at the individual level in wild chimpanzees for food consumption (e.g. Sugiyama, Fushimi, Sakuro and Matsuzawa, 1993) and anvil use (McGrew, Marchant, Wrangham and Klein, 1999), while others report no lateral bias for non-tool using feeding behaviors (e.g. Marchant and McGrew, 1996; Parnell, 2001). Studies focusing on sustenance tool use or object manipulation in wild apes have also failed to reveal any evidence of population-level lateral biases (Boesch, 1991; Matsuzawa, 1996; McGrew and Marchant, 1996). However, the vast array of observed behaviors, coding criteria and assessment parameters make direct comparisons difficult across species and laboratories. Additionally, only a few investigations have evaluated bimanually coordinated sequences of actions. Of these studies, one investigation demonstrated a right-handed population-level preference for nettle processing in mountain gorillas (Byrne and Byrne, 1991). Two further studies of captive gorillas also noted a population-level right-hand preference for bimanual foraging behaviors (Meguerditchian, Calcutt, Lonsdorf, Ross and Hopkins, 2010, but see Lambert, 2012) and in bimanually coordinated honey-dipping and nettle processing (e.g. Tabiowo and Forrester, 2013). Although chimpanzee termite fishing has historically been considered a population-level left-handed biased motor activity (e.g. McGrew and Marchant, 1992; Lonsdorf and Hopkins, 2005), recent evidence suggests that during termite fishing, the less demanding action (dipping) is directed by the nondominant left hand, so that the more demanding range of actions (e.g. bridging termites to the mouth, grasp termites outside the mound) can be conducted by the dominant right hand (Bogart et al., 2012). These investigations point to an emergent pattern in context-specific natural behaviors that requires further exploration.

The current study investigated the bimanual feeding behaviors of *Strychnos spinosa* fruit consumption in semi-wild chimpanzees. We focuses on the bimanual sequences of actions during the extraction of fruit for ingestion, once the shell of the fruit had already been weakened, in order to control for the variety of methods used to chimpanzees to open strychnos fruits (e.g. biting the fruit or striking the fruit against rocks and trees: Rawlings, Davila-Ross and Boysen, 2014). Based on previous cross-species evidence of left hemisphere dominance for routine sequences of motor actions, we predicted a right-hand population-level bias for this naturally occurring feeding behavior in semi-wild chimpanzees.

Materials and Methods

Subjects: Subjects were 33 chimpanzees (12 males, 21 females) housed in three stable multi-male-multi-female colonies at Chimfunshi Wildlife Orphanage, Zambia. Ages of chimpanzees were based on time of final collection (mean = 18.25 years; range = 5-31). Subjects consisted of a sampling of individuals from the three separate colonies that were housed in three large outdoor enclosures (25-77 hectares), with the largest colony living in the largest enclosure and the smallest colony living in the smallest enclosure. Each enclosure contained naturally developed forests, fruit groves and grassland in a miombo forest. Enclosures were separated by walls, trees and fencing preventing inter-group interaction. Each colony comprised a mixture of wild-born chimpanzees and chimpanzees born at the sanctuary. At the time of final data collection, Colony 1 comprised 46 chimpanzees (14 males, 32 females; 15 immature, 31 adolescent/adult), Colony 2 comprised 25 chimpanzees (12 males, 13 females; 9 immature, 16 adolescent/adult) and Colony 3 comprised 11 chimpanzees

(8 males, 3 females; 2 immature, 9 adolescent/adult) For a detailed description of the colony demographics from 2007 (see Rawlings et al., 2014).

Strychnos spinosa (Loganiaceae)

The *Strychnos spinosa* (Loganiaceae) is a spherical fruit commonly eaten by large primates and typically ranging in size from 5cm to 12cm in diameter. Strychnos fruits are consumed by wild chimpanzees throughout Africa, including Senegal (Bertolani and Pruetz, 2011), Tanzania (McGrew et al., 1999), Ivory Coast (Matsuzawa and Yamakoshi, 1996), Uganda (Tweheyo, Lye and Weladji, 2004) and Guinea (Matsuzawa and Yamakoshi, 1996). They are deep yellow to yellow-brown when ripe and have a smooth exterior and hard woody rind, 3-4mm thick (Sitrit et al., 2003). The inside of a ripe fruit is a sweet-sour edible pulp that can be scooped or sucked, but the seeds are toxic (Philippe et al., 2004) and are spat out. To access the edible fruit, an individual must first find a way through the tough woody exterior. Some chimpanzees use a 'cup hold' grip (Marzke and Wullstein, 1996) and employ an overarm action to smash the fruit against an anvil, or against another fruit (Rawlings et al., 2014). This produces a crack or weakness in the fruit, which is further compromised by the canines and/or the fingers of the individual to split the fruit. The present study considered only the flesh extraction and ingestion regardless of fruit-opening strategy.

Data Collection

The following research was compiled in line with all protocols and adhered to the legal requirements of the country in which the research was conducted. As the study was of a non-invasive observational nature, approval by the institutional animal care committee was not required. The data collection at Chimfunshi was based on observational methods, approved by the University of Portsmouth Psychology Research Ethics Committee and thus complies with all regulations regarding the ethical treatment of research subjects including the American Association of Physical Anthropologists Code of Ethics, as it pertains to extant human and nonhuman subjects.

The strychnos fruits were bought from local farmers and they were given to the chimpanzees 0-7 times per week during the main feeding times (between 13:30 and 14:30 pm). Video recordings of 9 strychnos feeding sessions were collected over a two-month period in 2007 (June-August), 10 sessions from a single month in 2011 (August), 10 sessions from a single month in 2012 (August) and 37 sessions over a three-month period in 2013 (July-September). An opportunity sampling method was adopted with the objective of recording as many subjects as possible (Rawlings et al., 2014). Thus, the data set is comprised of coded behaviors from individuals who were visibly observable during periods of data collection. Over the entire data collection periods (2007, 2011, 2012, 2013), 23 subjects were recorded over more than one year, with a mean of 1.94 separate years (SD = 0.72) across all subjects.

Data Coding:

Bimanual actions were defined in line with Meguerditchian et al., (2010) such that one hand holds an object (nondominant hand) while the opposite hand performs any manipulations of the object and brings it to the mouth in the case of feeding (dominant hand). Bimanual actions consisted of a sequence of actions related to manipulating foods for ingestion that began with holding and/or manipulating the fruit and bringing it to the mouth to further manipulate with the teeth or hands for ingestion. When considering these sequences of bimanual actions, there is a clear distinction of hand dominance: one hand manipulates the fruit (dominant) while the other maintains its stability (nondominant) (Figure 1).

Analyses:

For measures of handedness, we calculated the frequency of dominant hand actions for bouts. Bouts began when one hand reached for an object for manipulation. Once the item was gathered, only the first manipulative action was coded for hand dominance. A bout ended when the focal animal released the object. There is on-going discussion in the literature regarding whether events or bouts represent the most valid measure for evaluating hand dominance (McGrew and Marchant, 1997; Hopkins et al., 2001). While some purport a statistical bias may result from the dependence of the data between each hand use response (e.g. pseudo-replication; see Hurlburt, 1984; Palmer, 2003), others have demonstrated a high correlation between analyses of bouts and events, suggesting they are equally valid measures of handedness (e.g. Hopkins et al., 2005; Hopkins, 2013). The present study employed bouts rather than events (e.g. Llorente et al, 2011), as they are commensurate with studies that have been previously investigated naturalistic manual behaviors (e.g. Forrester et al., 2011; 2012; 2013; Tabiowo and Forrester 2013). Bimanual actions were coded by three researchers, demonstrating an inter-coder reliability, Kappa = .95, based on a random sampling of 65 action bouts. To analyze bouts, we employed a range of statistical and descriptive measures to illustrate patterns of lateral biases.

For bimanual hand actions, we calculated individual frequencies, and proportions of bouts (see Table 1). Proportions were assessed to equalize the weighting that each subject contributed to the data set. Proportions were calculated by dividing the frequency of left and right hand actions by the total frequency of actions, respectively. Subjects with less than five bouts were excluded from analysis. To reveal individual patterns of hand dominance, we calculated the z-scores, binomial approximations of the z-scores and the individuals' strength of handedness using HI (Handedness Index) scores (Table 1). The direction of hand preference for each subject was calculated using z-scores such that chimpanzees were left handed when $z \leq -1.96$, right handed when $z \geq 1.96$ and ambiguously handed when $-1.96 < z < 1.96$. HI scores were calculated for each subject to establish the degree of hand asymmetry, using the formula [$HI = (R - L)/(R + L)$], with R and L being the frequency counts for right- and left hand dominance in bimanual actions. HI values vary on a continuum between -1.0 and +1.0, where the sign indicates the direction of hand preferences. Positive values reflect a right hand preference while negative values reflect a left hand preference. When R = L, the HI is taken to be zero. Mean Handedness Index scores (MHI) were calculated for group analyses. Absolute Handedness was also calculated for strength of handedness not considering direction of laterality (ABHI). One-sample t-tests were used to evaluate group-level handedness using HI scores. Additionally, paired-sample t-tests were employed to test for significant differences in the frequencies and proportions of left- and right-handed dominant bouts of fruit opening. A Mann-Whitney U test was used to evaluate similarity of HI scores of left and right lateralized individuals. All statistical tests were two-tailed with alpha < 0.05.

Results

A total of 327 bimanual bouts of fruit opening were recorded by 33 individuals, of which 124 37.92% (*n* = 124) were left hand dominant and 62.08% (*n* = 203) were right hand dominant. Binomial tests of individual bouts revealed that 26 individuals were not statistically lateralized, 5 were right lateralized and 2 were left lateralized. The MHI is 0.220 (± SE= 0.092). The ABHI for all subjects was 0.500 (± SE = 0.046). The ABHI for right-handed (mean = 0.540 ± SE 0.055) and left-handed (mean = 0.462 ± SE 0.078) were similar (*U* = 91.500; P = 0.449).

Table 1. Bimanual hand frequencies, proportions, HI scores, hand bias classification, z-scores and P values.

[Table 1 here]

A one-sample t-test of HI values indicated a significant right-handed preference for *strychnos* fruit opening (mean = 0.220 ± SE 0.092); (t_{32} = 2.40, P = 0.022). Additionally, an evaluation of raw frequencies showed a significant bias for bimanual right-handed fruit opening dominance (mean = 6.150 ± SE 0.699) compared with left hand fruit opening dominance (mean = 3.760 ± SE 0.486), (t_{32} = 2.579, P = 0.015). Likewise, proportions demonstrated a significant right-handed bias (mean = 0.610 ± SE 0.046) compared with left-handed dominance (mean = 0.390 ± SE 0.046) for bimanual actions (t_{32} = 2.422, P = 0.021) (Figure 2).

There was no significant difference in HI scores between sexes (females: mean = 0.099 ± SE = 0.120; males: mean = 0.430 ± SE 0.121), (U = 84.00; P = 0.115). Additionally, there was no significant difference in strength of handedness (ABHI) for sex (females: mean = 0.480 ± SE 0.058; males: mean = 0.530 ± SE 0.078), (U = 113.00; P = 0.625). However, binomial tests where ABHI divided into equal bins ($-1 \leq L \leq -.33 \leq A \leq .33 \leq R \leq +1$), indicated that 24 of 33 (72.7%) individuals were lateralized either left or right (P = 0.013). Of the lateralized individuals, 17 of 24 (70.8%) demonstrated a right hand preference (binomial test, P = 0.064).

Discussion

The aim of the current study was to consider manual laterality during an ecologically valid behaviour in semi-wild chimpanzees. This study is in the minority of investigations that have specifically focused on coordinated bimanual actions in natural feeding behaviors in wild apes (e.g. Boesch, 1991; Bryne and Byrne, 1991; McGrew and Marchant, 1992; Sugiyama et al., 1993; McGrew et al., 1999; Byrne et al., 2001; Parnell, 2001; Lonsdorf, 2005). At the individual level, few subjects demonstrated a significant manual bias (left or right). It is likely that the high percentage of non-lateralized subjects is based on too few observations and the use of z-scores with the critical value set at 1.96. However, ABHI scores revealed that a significant number of individuals were lateralized either left or right. Of the lateralized individuals, a non-significant majority of individuals demonstrated a right hand preference. Future studies may consider the coding of events in addition to bouts in order to increase the statistical power for observed behavior and allow for a deeper level of analysis of motor action. At the population-level, a one-sample t-test of HI values and two-sample t-tests of bout frequencies and proportions, all revealed significant right hand dominant coordinated bimanual actions for fruit consumption.

The current results differ from two previous investigations that did not reveal evidence of population-level right-handedness for bimanual behaviors in wild chimpanzees (e.g. McGrew and Marchant 1996; 2001). However, these earlier studies did not isolate a specific behavior to evaluate. Instead, a combination of the 15 most frequent behaviors were pooled and assessed for hand dominance. While 'eat' was one behavior, other behaviors evaluated within the dataset were isolated actions such as: scratch, nose wipe and pick up. Recent human and great ape studies indicate that the context of the manual task influences hand choices (Forrester, Leavens, Quaresmini and Vallortigara, 2011; Forrester, Quaresmini, Leavens, Spiezio and Vallortigara, 2012; Forrester, Quaresmini, Leavens, Spiezio and Vallortigara, 2013). Therefore, the pooling of different behaviors may obscure a pattern that exists for a specific behavior. The findings of the present study are consistent with investigations that have strictly focused on bimanual coordinated feeding behavior in wild gorillas (Bynre and Byrne, 1991) and in captive gorillas (Meguerditchian et al., 2010).

The strength of handedness found in the present study is not equivalent to that reported in studies of human handedness (e.g. 90% right-handed at the population-level, e.g. McManus, 2002). However, disparate testing methods make direct comparisons between human and non-human primates difficult. Because human handedness results typically stem from self-reported tool use (e.g. Oldfield, 1971), the strength of human handedness for non-tool coordinated bimanual actions is not known. Additionally, studies of non-human primate laterality indicate that hand dominance is not a rigid nominal variable, but can vary in strength based on the choice of measurement such as: subjects and tasks (hand bias congruence), within subject and task (hand preference), within subject, across task (manual specialization), across subjects, within task (task specialization) (Marchant and McGrew, 2013). It is possible that once thoroughly investigated, we will find no significant difference between humans and ape handedness, indicating that a left hemisphere dominant trait for routine sequences of actions was well established prior a common last ancestor. However, it is also possible that great ape hand dominance represents an intermediate stage along the phylogenetic trajectory of human manual lateralization. Great ape handedness may represent hand strength inherited by a last common ancestor before sophisticated tool use and modern language skills may have exaggerated the extreme manual laterality found in our own evolutionary lineage (Marchant and McGrew, 2013). In order to address these questions, future investigations should consider a systematic methodology for assessing handedness across species to enable direct comparisons that can elucidate the evolutionary trajectory of cerebral dominance (Cashmore et al., 2008).

Disparate evaluation of behavior across laboratories is a significant issue across species. Data collection and analyses approaches for motor actions show striking inconsistencies. For example, chick feeding laterality has been assessed by comparing left or right frequency means in experimental conditions (Rogers, Zucca and Vallortigara, 2004), or by tallying events in natural contexts and assessing probability (Grace and Craig 2008). Some research investigating fish cerebral lateralization has applied binomial tests of feeding bouts (Takeuchi, Hori and Oda, 2012), while others have employed a laterality index system. However, these laterality indices were based on data obtained at temporal intervals within and across individuals (Sovrano, 2003), or data from individual bouts (Roche et al., 2013). Moreover, assessment of toads have also been inconsistent, with some researchers applying a laterality index (Robins, Lippolis, Bisazza, Vallortigara and Rogers, 1998), and others tallying left and right responses for statistical comparison (Robins and Rogers 2004). Finally, tool-based foraging behaviors in New Caledonian crows have been measured using binomial tests of individual bouts (Rutlidge and Hunt, 2003). While there is no single or perfect way to measure lateral motor actions, without the adoption of a standardized system for data processing we are unlikely to unveil a phylogenetic progression of manual specialization towards modern human right-handedness.

The findings from the present study demonstrate a robust population-level right-handed bias in a group of chimpanzees. The novelty of this investigation is that the findings represent data from semi-wild chimpanzees engaged in a naturally occurring behaviour. The findings complement laterality investigations from non-primate animals, supporting an early evolutionary delineation of function in the right and left hemispheres (e.g. MacNeilage et al., 2009). Moreover, this research contributes to a growing body of evidence suggesting that human right-handedness was inherited from a last common ancestor of humans and apes, underpinned by a dominant left hemisphere control of structured sequences of actions (e.g. Forrester et al., 2013). The experimental parameters employed in this study are ecologically valid and readily transferrable across species to facilitate evolutionary investigations of cerebral dominance of motor action.

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Figure Legend

Figure 1.

Bimanual coordinated feeding behaviour by a chimpanzee (Kambo) at Chimfunshi
(Photo by: Davila Ross)

Figure 2.

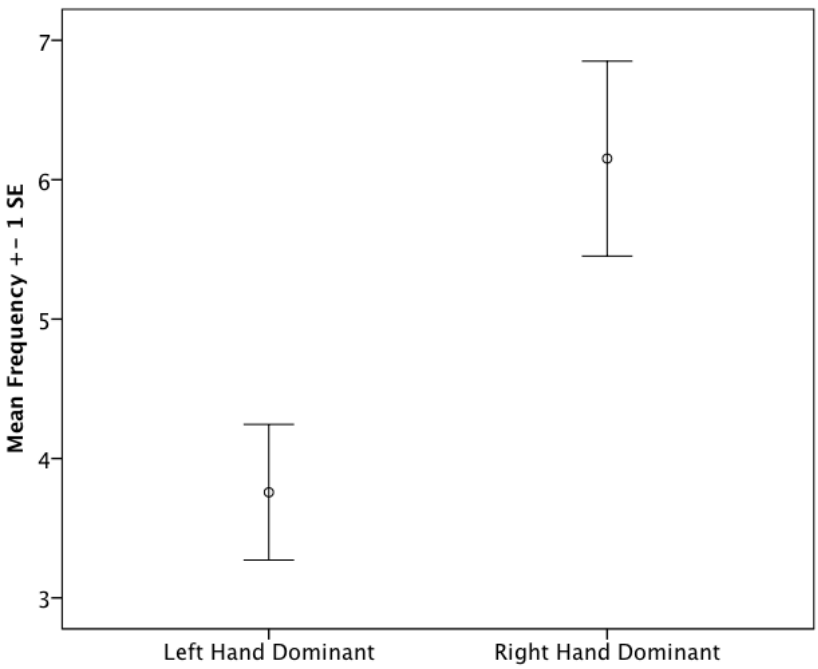

Figure 2 illustrates mean frequencies of left and right hand dominance