Structured Bimanual Actions and Hand Transfers Reveal Population-Level Right-Handedness in Captive Gorillas

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Word Count (5,922, excluding references)

Dear Dr. Held (Editor)

Thank you for accepting our manuscript for publication in Animal Behaviour, pending a revision based upon the itemised list below. We are very pleased for the opportunity to share our investigation of gorilla handedness with the wider scientific community, and consider our findings to be a significant contribution to the current body of literature regarding handedness in human and non-human primate populations. Based on your comments below, we have reformatted the manuscript to deal with the imbalance between the length of the introduction and discussion sections. As requested, the introduction poses a theoretical link between bimanual actions and the structure underling language processes, while the detailed consideration of our results, in light of this hypothesis, is now addressed within the discussion section. Additionally, we have amended the text to address formatting changes (items 1-3, 5-16 below) and have uploaded video files (item 4) to provide examples of bimanual actions and hand transfers (supplemental materials).

Thank you again for your decision to accept our manuscript for publication in Animal Behaviour.

Sincerely,

Gillian Forrester
Ernest Tabiowo (cc)

Date Revision Due Jul 19, 2013

Dear Authors -
I am happy to accept your paper for publication in Animal Behaviour, subject to revision. Your last revision convincingly addressed the reviewers' points but this has - partly - resulted in an imbalance between the introduction and discussion.
At eight pages the introduction, while an interesting read, is now far too long, and the discussion fails to discuss some to the interpretation points that should be made there. I therefore suggest you mention in the introduction the link between bimanual co-ordination and syntactic language as part of the rationale for your study, but leave its detailed discussion to the discussion. Your results can then be considered in context in the discussion.

In addition, please make the following formatting changes.

1. Add the abstract to the manuscript, followed by up to 10 keywords in alphabetical order including the common and scientific names of the study species.
2. Lists of citations in the text should be in chronological order.
3. Give the scientific names of species at first mention.
4. You refer to videos in the Methods but you have not yet uploaded any.
5. In statistics, write 'mean' in full. 'Mean' and 'SE' should not be in italics.
6. Change P<0.000 to P<0.001. Note that P should be in italics. throughout.
7. Put the figure legends after the reference list.
8. In the reference list, all journal titles must be written in full.
9. Do not italicise publishers' names and towns.
10. Provide more details for D'Ausilio & Fadiga 2011, such as a volume number and page numbers, or editors' names, publisher and town of publication.
11. Add page numbers for Dawkins 1976.
12. Update Hopkins 2013, at least with the online publication date.
13. Italicise scientific names in the reference list.
14. Do not include issue numbers after volume numbers.
15. Provide page numbers for Lashley 1951.
16. Ensure page numbers are complete, e.g. for Ott 2009 should 255-69 be 255-269?

HIGHLIGHTS

- The evolutionary origins of human handedness is poorly understood
- We assessed bimanual hand dominance and hand transfers in gorillas
- We found a significant population-level right-handed bias for both measures
- Results suggest that human right-handedness was inherited from a common ancestor
- We propose that bimanual actions and language processes share a basic structure

ABSTRACT

There is a common prevailing perception that humans possess a species-unique population-level right-hand bias that has evolutionary links with language. New theories suggest that an early evolutionary division of cognitive function gave rise to a left hemisphere bias for behaviours underpinned by structured sequences of actions. However, studies of great ape handedness have generated inconsistent results and considerable debate. Additionally, the literature places a heavy focus on chimpanzees, revealing a paucity of handedness findings from other great ape species, and thus limiting the empirical evidence with which we can evaluate evolutionary theory. We observed handedness during spontaneous naturalistic bimanual actions in a captive, biological group of 13 western lowland gorillas (*Gorilla gorilla gorilla*). Our results demonstrated a significant group-level right-handed bias for bimanual actions as well as for a novel measure of handedness: *hand transfer*. The two measures revealed similar patterns of handedness, such that a right-hand bias for the majority of individuals was found across both measures. Our findings suggest that human population-level right-handedness is a behavioural trait linked with left hemisphere dominance for the processing of structured sequences of actions, and was inherited by a common ancestor of both humans and apes.

Keywords: cerebral lateralisation, evolution, great apes, gorilla, *Gorilla gorilla gorilla*, handedness, language

INTRODUCTION

Historically, researchers have argued that population-level right-handedness is a human-unique behaviour, underpinned by an evolutionary link with left hemisphere neural regions dedicated to language processing (e.g. Broca 1865; Wernicke 1874). Approximately 90% of the human population are considered to be right-handed, (Porac & Coren 1981; Annett 1985). Additionally, about 95% of the right-handed population expresses language dominance in the left hemisphere of the brain (Santrock 2008). Specifically, the inferior frontal gyrus (Tomaiuolo et al. 1999; Robichon et al. 2000; Keller et al. 2009) and a portion of the posterior temporal lobe (planum temporale) are proportionately larger in the left hemisphere compared with the right hemisphere (Beaton 1997; Shapleske et al. 1999; Sommer et al. 2001; 2008), and coincide with the anatomical locations of Broca's and Wernicke's areas respectively (e.g. Horwitz et al. 2003). The commonality of the human left hemisphere bias for handedness and language processing has perpetuated a theory that lateralized motor action elicited by cerebral lateralisation for specific cognitive functions is unique to humans (Warren 1980; Ettlinger 1988; Crow 2004; Schoenemann 2006). Some have posited that handedness is directly linked with language capabilities, such as articulated speech (Annett 2002) or gesture (Corballis 2002). Others have suggested that handedness may have originated from tool use (Greenfield 1991), coordinated bimanual actions (Wundrum 1986; Hopkins et al. 2003), or bipedalism (Westergaard et al. 1998; Braccini et al. 2010). However, the emergence of handedness and its evolutionary relationship with language remains a controversial topic.

Lateralised motor action underpinned by cerebral lateralisation for specific cognitive processes has now been revealed across a range of vertebrate (Vallortigara & Rogers 2005; MacNeilage, et al. 2009; Rogers & Andrew 2002; Vallortigara et al. 2011) and invertebrate (Anfora et al. 2011; Frasnelli et al. 2012) species, and thus, is no longer considered human specific. For example, right hemisphere dominance has been identified for processing of social stimuli in chimpanzees (*Pan troglodytes*, Morris et al. 1993), rhesus monkeys (*Macca mulatta*, Guo et al. 2009), dogs (*Canis familiaris*, Guo et al. 2009) and sheep (*Ovis aries*, Peirce et al. 2000). Alternatively, the left hemisphere has been reported to be dominant for well-practiced sequences of actions, such as feeding tasks in pigeons (*Columbia livia*, Güntürkün & Kesh 1987), chicks (*Gallus gallus domesticus*, Rogers 1995) and toads (*B. bufo and B. marinus*, Robins & Rogers 2004), and in numeracy tasks in dolphins (*Tursiops truncates*, Killian et al. 2005). The result of such evidence, suggests that the right hemisphere of the brain evolved as dominant for controlling arousal levels in order to react quickly to the environment (e.g. predators), whilst the left hemisphere emerged as dominant for processing routine behaviours with structured sequences of actions (e.g. feeding) (Vallortigara et al. 2008, 2011; MacNeilage et al. 2009). An early evolutionary division of labour for these critical survival processes in the left and right hemispheres may have produced advantages for: increasing neural capacity, enabling parallel processing and deterring the simultaneous initiation of incompatible responses (e.g. Andrew 1991; Vallortigara 2000; Rogers 2002).

Based upon the evolutionary theory above, it is not surprising that hierarchically structured language processes are left hemisphere dominant for the majority of the human population. However, the precursor behaviours that language emerged from are poorly understood. For over half a century, theoretical parallels have been drawn between the cognitive processes underlying a left hemispheric specialisation for language and right-handed tool use in humans. While hierarchical structures are known to be a distinctive component of language (e.g. Hauser et al. 2002), it has been suggested that they also appear in non-linguistic domains such as object manipulation (for a review see Tettamanti 2003). Motor activity has been described as a hierarchy of structured sequence of behavioural units (Holloway 1969); and hierarchical action sequences are integral to tool use (e.g. Lashley 1951; Dawkins 1976; Byrne & Russon 1998). While some have argued that the sequences of actions supporting tool manufacture do not possess a linguistic type of syntax because the actions are based upon physical constraints rather than internal rules (e.g. Graves 1994; Wynn 1995), others have argued that some Paleolithic tool manufacturing methods do share abstract syntactical content with linguistic processes (e.g. Holloway 1981; Stout & Chaminade 2009). Additionally, evidence from prehistoric human tool use and manufacture suggests that human population-level right-handedness has origins that precede the emergence of modern human language. Specifically, archaeological data suggest that right biased asymmetries existed in the arm and hand bones at least by the stage of the genus *Homo*. Evidence from tool use production and cave art suggests that population-level right-handedness was established in Neanderthals (for a review see Cashmore et al. 2008), thus preceding human language, which is claimed to have emerged not earlier than 100,000 years ago (e.g. Ott 2009). One hypothesis is that right-handed tool use provided an evolutionary bridge between left hemisphere dominant action sequences and language processes (Hamzei et al. 2003).

Great apes are proven tool users in both wild and captive settings; and although they do not possess language, great apes demonstrate evidence of a neuroanatomical brain region that overlaps with Broca's regions and that, like in humans, is proportionately larger in the left hemisphere than in the right hemisphere (e.g. Cantalupo & Hopkins 2001; Hopkins et al. 2007). Therefore, great apes offer an excellent animal model to investigate the evolutionary link between handedness and human language. Early handedness studies achieved inconsistent results in both captive (e.g. Finch 1941; Marchant 1983; Annett & Annett 1991; Hopkins 1993) and wild ape populations (e.g. Boesch 1991; McGrew & Marchant 1992; Shafer 1993). However, traditional handedness coding methods may not have effectively revealed manual biases. Early behavioural studies of great ape handedness assessed unimanual actions, such as simple reaching or manipulation tasks. Unimanual actions can often be confounded by postural (e.g. one hand supporting posture) and situational elements (e.g. one hand occupied with an object) (Aruguete et al. 1992; Westergaard et al. 1998; Braccini et al. 2010). Additionally, it is now acknowledged that task complexity can influence the direction, magnitude and consistency of hand preference of both humans (e.g.

Perelle & Ehrman 1994; Marchant et al. 1995; Fagard 2001) and great apes (Boesch 1991; McGrew et al. 1999; O'Malley & McGrew 2006; Hopkins 2007). Therefore, unimanual actions may represent simplistic behaviours that do not necessarily demand the use of a dominant hand or hemisphere (Hopkins 1995).

More recently, studies have investigated bimanual actions, characterised by both hands cooperating in the manipulation or processing of the same item. During bimanual actions, one hand is used to support an item (the non dominant hand) while the other hand manipulates the item (dominant hand) (e.g. McGrew & Marchant 1997). Bimanual handedness is thought to represent more complex behaviours and is considered to be a more sensitive measure of hand dominance (e.g. Hopkins 2006; Vauclair & Meguerditichian 2007). Additionally, investigating bimanual actions minimises postural factors due to the necessity for the individual to appropriate a bipedal or seated posture in order for both hands to be available to engage in a bimanual task (Roney & King 1993). Laboratory studies that investigated the bimanual actions of large samples of chimpanzees have revealed evidence of population-level right-handedness (Hopkins & Russell 2004; Hopkins et al. 2004; for a review see: Hopkins 2006; 2007). Studies implemented a tube task that required chimpanzees to manipulate an object (tube) to retrieve food. Peanut butter was placed deep inside of poly-vinyl-chloride tubes such that the chimpanzees could not lick the contents, as successful retrieval of food required the insertion of fingers for extraction. Some have contended that captive ape handedness could be confounded from exposure to human behaviour (McGrew & Marchant 1997; Palmer 2002; 2003; Crow 2004), and queried methods of statistical analyses (Hopkins 1999, Hopkins & Cantalupo 2005). However, more recent studies, controlling for confounding factors, have also revealed population-level right-hand biases for bimanual tasks in naturalistically housed chimpanzees (Llorente et al. 2009; 2011). Conversely, observational studies of wild chimpanzee termite fishing have consistently revealed a left-handed bias (Lonsdorf & Hopkins 2005; Hopkins et al. 2009). However, it has been postulated that for this task, the less demanding action (dipping) is directed by the non-dominant left hand, such 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). In general, findings from chimpanzee bimanual actions studies contradict the traditional supposition that population-level right-handedness is a human unique characteristic, and support the hypothesis that right-handedness has been inherited from a last common ancestor, preceding the emergence of human language skills.

Compared with studies of chimpanzee, gorillas are largely neglected in the handedness literature. Whether or not gorillas demonstrate population-level handedness is debated due to limited and inconsistent findings across laboratories (e.g. McGrew & Marchant 1993). An early study investigating unimanual and bimanual actions of 10 captive gorillas found no population-level bias for unimanual reaching, but did report a left hand population bias for a bimanual spatial task requiring the alignment of two openings (Fagot & Vauclair 1988). The authors posited that the task might have probed mental rotation capabilities, widely considered to be a right-hemisphere dominant capability in humans (e.g. Jones & Anuza 1982). More recently, the tube task has been extended to bonobos (*Pan paniscus*), gorillas and orangutans (*Pongo pygmaeus*) (Hopkins et al. 2011). Results from these investigations demonstrated that like chimpanzees, bonobos and gorillas also revealed right-handed population biases when assessed for handedness during this specific bimanual coordinated activity. Only three studies, to date, have investigated the spontaneous bimanual behaviours of gorillas. Byrne & Byrne (1991) found a significant right hand bias for bimanual multi-stage sequences of food processing in a group of 44 mountain gorillas, where the strongest degree of hand preference was for processing food types in which leaves were protected by stings. Two more recent studies investigated naturalistic bimanual feeding behaviours of captive gorillas, but achieved varied results. Both studies assessed unimanual, simple reaching behaviours to food items and bimanual feeding behaviours in captive gorillas (Meguerditchian et al. 2010; Lambert 2012). Neither study reported a population-level bias for unimanual simple reaching actions, however Meguerditchian and colleagues (2010) revealed a significant right-hand population-level bias for bimanual feeding actions. While Lambert (2012) demonstrated stronger manual biases for bimanual feeding compared with unimanual simple reaching, bimanual actions were not found to be significantly right-handed. The author proposed that bimanual actions may vary in complexity and that assessing different grip morphologies may provide an alternate way to measure hand dominance. Specifically, precision grip, versus power grip, may signify more complex dextral action, and therefore elicit a dominant hand bias (e.g. Pouydebat et al. 2011).

Although inconsistent methodological approaches may be responsible for mixed results across laboratories, much of the research points to a right-handed bias in great apes during object manipulation. One possible interpretation of the literature is that right-handedness in humans is not a direct by-product of language capabilities, but rather the behavioural manifestation of left hemisphere dominance for processing structured sequences of actions. We hypothesise that this inherited cerebral lateralisation characteristic can be exploited in our closest living relatives, specifically during bimanual behaviours for object manipulation sequences. Therefore, in the present study we investigated the naturalistic spontaneous behaviours of a biological group of captive gorillas (*Gorilla gorilla gorilla*) performing bimanual object manipulation during: feeding (e.g. leaf stripping, nettle folding and honeypot dipping), tool use for food retrieval (preparing sticks for the honey pot, using sticks in the honey pot) and tools manufacture for food extraction (e.g. stripping sticks for use in honeypot). Additionally, we introduced a new measure of handedness that considers transfers of objects to the opposite hand prior to object manipulation. Hopkins (2006) noted that the tube task produced a right hand dominance even when controlling for the hand in which the chimpanzee received the tube. Specifically, the ‘hand transfer’ measure evaluated when an object was grasped by dominant hand and then transferred to the non-dominant hand, such that the dominant hand was free to perform manipulative actions upon the object. We hypothesised that the cost of transferring an object is outweighed by the increase of efficiency achieved through performing the manipulation with the dominant hand.

METHODS

Subjects

Data were collected on 13 (6 males), captive western lowland gorillas (*Gorilla gorilla*) living in a peer-raised, semi-free ranging, biological family group at Port Lympne Wild Animal Park, UK. The group was made up of one silverback, seven adult females, four juvenile males and one juvenile female (see Table 1) ranging in age from 2-36 years. Observational consent was granted by the John Aspinall Foundation. Due to the non-invasive nature of this study, further permits or ethical approvals were not required.

Housing and Enrichment

The 'Palace of the Apes' is the world's largest family gorilla house and is modeled on the habitat of wild gorillas. The gorillas are considered 'semi free ranging', in that they move freely about the large enclosure comprised of four composite parts: caged upper, caged lower, inside and garden. The two-tiered outside enclosure is fronted by toughened glass, and equipped with enrichment equipment including: ropes, nets and slides to encourage physical activity. Inside, there is a play area equipped with further enrichment equipment and 14 bedrooms with access to water. By way of the caged upper and lower areas of the enclosure, the gorillas have further access to a large garden equipped with climbing frames, trees, logs, a boundary stream and a large pile of boulders. The garden has viewing windows at ground level and unimpeded visual access from above the garden via a raised steel footpath. Both the caged area and the garden have food receptacles for enrichment purposes that require the gorillas to prepare sticks that fit the hole for retrieving the contents. Contents of the receptacle vary (e.g. honey, peanut butter, hummus, marmite). Further enrichment is regularly provided in the form of retrieving food from different types of cartons in order to cognitively challenge individuals and maintain high standards of animal welfare.

Nourishment

Gorillas receive six daily scatter feeds in order to stimulate natural foraging behaviours. A proportion of the scatter feeds are roof top dispersals of herbs and fruit that stimulate physical activity, requiring gorillas to brachiate. Gorillas receive up to 50 different varieties of fruits and vegetables, primarily organically grown. With seasonal variation, gorillas consume: apples, beans, blackberries, carrots, cauliflower, damsons, leeks, melon, oranges, pears, peppers, plums, raspberries, spinach, strawberries and sweet potatoes. Gorillas are also offered a large variety of woodland browse including bamboo and willow. Additionally, gorillas benefit from fresh herbs (e.g. parsley, thyme, rosemary and coriander), vitamin pellets, cheese, eggs, yoghurt and mealworms crickets. During the winter months, gorillas receive high-protein treats (e.g. lamb, sausages) to replace the protein that would be typically ingested by the way of insects within the foliage consumed in a wild setting.

Data Capture

From April 2004 to September 2006, subjects were video recorded during spontaneous naturalistic behaviour based on a counterbalanced focal sampling paradigm (Altmann 1974). Ten-minute focal follows were conducted for each animal. Due to low visibility of some gorillas, total focal follow time for each subject varied between 55–215 minutes (see Table 1). Synchronised digital video cameras (Panasonic NVGS11B) were employed to capture both the focal individual (camera 1: full frame) and encompass the focal subject within the context of any conspecifics and surroundings (camera 2: wide-angle) (see Multidimensional Method, Forrester 2008). Synchronization was established using a flash bulb. Cameras were tripod mounted and followed gorilla activity using zoom, tilt, and swivel to optimise view. Synchronised video streams were compressed into a single file (15 frames per second) viewed in a top/bottom format for subsequent coding using OBSERVATRON coding software (Forrester 2008).

Coding

Bimanual actions were defined in line with Meguerditchian et al. (2010) such that one hand holds an object (non-dominant 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 manipulating foods for ingestions (e.g. stripping and folding nettles, stripping leaves, and extracting nuts from their shells), using tools to extract food (e.g. dipping sticks in honey pot) and manufacturing tools to for food extraction (e.g. stripping sticks for use in honeypot). Bimanual actions began when one hand reached for an object for manipulation. The hand supporting the object was classified as the 'non-dominant' hand and was classified as left or right, whilst the hand used for manipulation of the object was classified as the 'dominant' hand was classified as the opposite hand (see Video 1 and Video 2 for examples of nettle folding and honeypot dipping bimanual actions). In the case of the honey dipping, the dominant hand manipulated the tool, while the non-dominant hand held the receptacle and simultaneously provided postural support.

Additionally, we coded the frequency of hand transfer events prior to object manipulation. Franz and colleagues (2002) demonstrated that the lead hand in a bimanual sequence does not necessarily signify the dominant hand (e.g. reaching for the object), but rather could be a consequence of posture (e.g. postural origins hypothesis; MacNeilage et al. 1987). For this measure we coded hand transfer events preceding bimanual object manipulation that involved the transfer of an object from one hand to the other such that the gorilla could employ the dominant hand for manipulation. For example, a locomoting gorilla may pick up a stick with the left hand on the way to the honeypot, but then transfers the stick to the right hand prior to dipping for honey. This action was coded as a transfer for right hand dominance such that the right hand could perform the dominant action. Furthermore, a gorilla might pick a nettle with the right hand, but then transfer it to the left hand such that the left hand can support the object while the right hand performs the actions of stripping and folding the nettles. This was also coded as a transfer for right hand dominance (see Video 3 for examples of hand transfers). Research into human handedness has shown that bilateral transfers can be used as a marker of hand dominance (Kumar & Mandal 2005).

For both 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. In the case of a hand transfer prior to manipulation, we first coded hand dominance and then coded the first manipulative action for hand dominance. A bout ended when the focal animal released the object. Although there has been some controversy in the literature whether events or bouts represent the most valid measure for evaluating hand dominance (McGrew & Marchant 1997; Hopkins et al. 2001), concerning a statistical bias that may result from the dependence of the data between each hand use response (e.g. pseudo-replication) (see Hurlburt 1984; Palmer 2003), a high correlation has been found between analyses of bouts and events, suggesting they are equally valid measures of handedness (e.g. Hopkins et al. 2005a).

Analyses

For both bimanual actions and hand transfer measures, we calculated frequencies, proportions, rates and Handedness Index (HI) scores for bouts. We employed a range of measures to demonstrate the consistency of the results across a range of statistical preferences throughout the literature. Specifically proportions and rates were used to equalise the weighting that each participant contributed to the data set. This is a critical evaluation process as to not let a single subject or non-significant group of subjects sway the group statistical test results. As each individual contributed a different number of bouts to the dataset, proportions were calculated by dividing the frequency of left or right hand actions by the total frequency of actions. Additionally, coded observation times varied between individuals as a result of animal visibility. Therefore, rates were calculated by dividing the frequency of bimanual actions by the total number of observational minutes per subject. Paired sample t-tests were used to compare bout group means for frequencies, proportions and rates for both hand dominance and hand transfers. A mean handedness index (MHI) score was also calculated for the group. Nonparametric Wilcoxon tests were also performed as a stricter test of difference. All statistical tests were two-tailed with alpha < 0.05.

In order to reveal individual patterns of hand dominance for bimanual actions and hand transfer measures, we calculated the z-scores, binomial approximations of the z-scores, and the individuals' strength of handedness using handedness index (HI) scores (see Tables 2 and 3). The direction of hand preference for each subject was calculated using z-scores such that gorillas were left handed when $z \leq -1.96$, right handed when $z \geq 1.96$ and ambiguously handed when $-19.6 < z < 1.96$. HI scores were calculated for each subject in for both measures to establish the degree of hand asymmetry. HI scores were calculated 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. When R=L, the HI is taken to be zero. 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. Two subjects were excluded from analyses for the measure of hand transfer due to low overall counts (total counts < 10). Excluded subjects are marked with a double asterisk (see Table 3). All statistical tests were two-tailed with alpha < 0.05.

RESULTS

Hand Dominance

The frequencies, proportions and rates of bouts along with their associated HI scores, z-scores and binomial approximations of the z-scores for the measures of hand dominance are displayed in Tables 2. A one sample t-test of the MHI scores for hand dominance (Mean = 0.62, SE = 0.07) indicated a significant population-level right-handedness, $t_{12} = 10.62$, $P < 0.001$.

A paired-sample t-test of frequencies demonstrated a significant bias for right hand dominance (Mean = 24.54, SE = 3.01), compared with left handed dominance (Mean = 6.08, SE = 1.48) for bimanual actions, $t_{12} = - 7.44$, $P < 0.001$. A paired-sample t-test of proportions demonstrated a significant right-handed dominance (Mean = 0.81, SE = 0.028), compared with left handed dominance (Mean = 0.19, SE = 0.028) for bimanual actions, $t_{12} = - 10.86$, $P < 0.001$. A paired-sample t-test of rates demonstrated a significant right-handed dominance (Mean = 0.21, SE = 0.04), compared with left-handed dominance (Mean = 0.05, SE = 0.01) for bimanual actions, $t_{12} = - 4.41$, $P = 0.001$ (Figure 1). Based on the *P*-values from the binomial approximations of the z-scores, ten of the thirteen gorillas (76.9%) demonstrated a significant right-handed dominance for bimanual actions. Three gorillas were ambiguously handed, however each of the three individuals' HI scores indicated a right-hand bias. Hand dominance measures were also calculated using the nonparametric Wilcoxon signed-ranks test. There was no change in the significant pattern of the results.

Hand Transfer

The frequencies, proportions and rates of bouts along with their associated HI scores, z-scores and binomial approximations of the z-scores for the measures of hand transfer are displayed in Tables 3. A one sample t-test of MHI scores for hand transfer (Mean = 0.71, SE = 0.09) indicated a significant population-level right hand dominance, $t_{10} = 10.00$, $P < 0.001$.

Under exclusion criteria (n=11 for counts > 10), a paired-sample t-test of frequencies demonstrated a significant bias for transfers from right hand to left hand (Mean = 18.64, SE = 2.33), compared with transfers from left hand to right hand (Mean = 3.45, SE = 1.22) for bimanual actions, $t_{10} = -6.63$, $P < 0.001$. Under the exclusion criteria, a paired-sample t-test of proportions demonstrated a significant bias for transfers from right hand to left hand (Mean = 0.86, SE = 0.44), compared with left hand to right hand (Mean = 0.15, SE = 0.44), for bimanual actions, $t_{10} = -8.14$, $P < 0.001$. Under exclusion criteria, a paired-sample t-test of rates demonstrated a significant bias for transfers from right hand to left hand (Mean = 0.13, SE = 0.02), compared with transfers from left hand to right hand (Mean = 0.03, SE = 0.01) for bimanual actions, $t_{10} = -6.18$, $P < 0.001$ (Figure 2). Based on the *P*-values from the binomial approximations of the z-scores, eight of the eleven gorillas (72.7%) demonstrated a significant bias for transfers from right hand to left hand for bimanual actions. Three gorillas were ambiguously handed, however individual HI scores maintained a preference for right-hand dominance. Hand transfer measures were also calculated using the nonparametric Wilcoxon signed ranks test. There was no change in the significant pattern of the results.

A paired sample t-test indicated that there was no significant difference between the HI scores for hand dominance and hand transfer $t_{10} = -0.995$, P = 0.343 (Figure 3).

DISCUSSION

The findings from this study demonstrated a significant population-level right-handed bias for the measures of bimanual actions and hand transfer. The majority of individual subjects demonstrated a significant right hand preference for both measures. There was no significant difference between the strength of hand preference when comparing the two measures, thus hand transfers may offer an alternative and/or complementary objective measure of hand dominance. Our finding of a population-level right hand bias for bimanual actions is consistent with previous studies of captive apes performing the tube task (e.g. Hopkins et al. 2011) as well as with studies the majority of studies investigating naturalistic bimanual feeding behaviours in captive (Meguerditchian et al. 2010) and wild gorillas (Byrne & Byrne 1991).

The implementation of the measure of hand transfer to investigate ape handedness appears to be a relevant marker of hand dominance. Like grip morphology, hand transfer may also prove to be sensitive to dextral complexity. Hand transfers were likely to have been performed when the sequence of object manipulation actions could not be efficiently or effectively performed with the non-dominant hand. In human children, planning abilities have been exploited through the measure of hand transfer tasks. Specifically, when one hand supports an object (non dominant) and the other hand (dominant) manipulates aspects of the object, infants under 2 years of age tend to transfer the object from the right to the left hand. Older children anticipate the requirement of the dominant hand and thus begin the bimanual task by grasping the object with the non-dominant hand (Potier, Meguerditchian & Fagard 2012), further suggesting that hand transfers may be a useful measure of individual handedness development during increasing task complexity.

There is growing evidence in humans that lateralised behaviours manifesting from contralateral domain specific neural processing extends beyond the association between population-level right-handedness and left hemisphere language regions. For example, the right hand has also shown a significant bias for communicative gesture (Corina et al. 1993), implicating a dominant left hemisphere control. Conversely, a left visual field/right hemisphere preference has been identified in face perception for exploring the left side of a centrally presented face when measured behaviourally (looking time; Burt & Perrett 1997) and with functional imaging (Kanwisher et al. 1998). As in humans, in addition to object manipulation, great apes have also demonstrated a right hand bias for communicative gestures in a range of chimpanzee populations (Hopkins & Leavens 1998; Hopkins et al. 2005b; Meguerditichian et al. 2009; 2012), suggesting left hemisphere dominant processing. Conversely, leftward action biases have been reported for social-emotional processing for self-directed face touching in orangutans (Rogers & Kaplan 1995), self-scratching (Leavens et al. 2004) and during increases in task complexity in chimpanzees (Leavens et al. 2001), potentially resulting from a rise in stress or arousal levels increasing right hemisphere processing. Another method that appears to probe cerebral lateralisation of domain specific processing involves assessing the type of target to which hand actions are directed. For example, chimpanzees demonstrated a right hand preference for touching their inanimate environments and ambi-preference for self-directed behaviours (Aruguete et al. 1992). Similarly, a unimanual right hand bias was found for actions towards inanimate objects, but ambi-preference for unimanual actions to animate targets (self and conspecifics) in gorillas (Forrester et al. 2011), chimpanzees (Forrester et al. 2012) and typically developing children (Forrester et al. 2013). These findings add to the mounting evidence that lateralised motor actions are markers of contralateral domain specific cerebral lateralisation, where the left hemisphere presides over structured sequences of actions, while the right hemisphere dominates social-emotional processing (e.g. MacNeilage 2009). The implications of such brain organisation is integral to the evolution and development of higher cognitive functions, as emergent functions are predicted to develop within the hemisphere that could support that function through the exaptation of neural regions for processing more elementary functions with similar underlying structure.

Some posit that Broca's area may be a supra-modal hierarchical processor, supporting a speculative hypothesis that language emerged from left hemisphere dominant neural regions originally evolved to cope with the hierarchical sequences of actions inherent in tool use (Pulvermüller & Fadiga 2010; Petersson et al. 2012). Action sequences for object manipulation (that are not random) were proposed to possess a rudimentary syntax (e.g. Tettamanti & Weniger 2006; Pastra & Aloimonos 2012). For example, in human infants, non-linguistic actions involving objects (e.g. self-feeding with a spoon) were seen to involve hierarchical sequence of actions (Connolly & Dagleish 1989; Greenfield 1991). Specifically, the activity in Broca's region has been shown to correlate with increasing hierarchical structural complexity (Bates & Dick 2002; Greenfield 1991). Broca's area is typically segmented into three regions: the pars triangularus (PTr), the pars orbitalus (PO) and the pars opercularis (POp). Recent neuroimaging studies demonstrated the Pop was activated for acquiring grammatical rules (i.e., having a hierarchical structure) (e.g. Tettamanti et al. 2002) and during complex grammar processing (Friederici et al. 2006), as opposed to an area posterior to POp has been recognised for tasks of simple grammar (Sakai 2005). Additionally, a transcranial magnetic stimulation study demonstrated that the POp was critical for the encoding of complex human action (Clerget, et al. 2009). Moreover, an fMRI investigation of healthy human adults evidenced an overlap of brain activity for perceiving language and using tools in this same region (POp), suggesting that language and tool use share a common neural generator for processing "complex hierarchical structures common to these two abilities" (Higuchi et al. 2009). This growing body of evidence suggests that the POp region of Broca's area may not be language-specific, but rather is active for disparate tasks (e.g. linguistic, cognitive, sensorimotor) that involve computational processing of hierarchical structure (Tettamanti & Weniger 2006) and that may also be present in other primate tool users.

Although limited data exists from brain imaging studies of great apes, Catalupo and Hopkins (2001) sampled 26 great apes and found a general leftward bias for the anatomical volume of the POp. A subsequent sample of chimpanzees (Hopkins et al. 2008), demonstrated a non-significant anatomical leftward bias, however the authors posit that differences in the boundaries placed upon POp may have contributed to inconsistent findings between the two studies. In fact, comparing the anatomical similarities of Broca's area in human and ape brains rely primarily on the surface area or volume of the POp because the PTr and the PO have not been reliably defined in the chimpanzee brain (e.g. Keller et al 2009; for a review see Hopkins 2013). Inconsistencies in anatomical boundaries of Broca's area may have also led to discrepancies in findings from cytoarchitectonic studies of human and ape brains (Amunts et al. 1999; Ziles & Amunts 2010). Nevertheless, imaging studies have reported in both humans (Foundas et al. 1995) and apes (Gilissen & Hopkins 2013) that a significantly greater proportion of right-handers demonstrate a left hemisphere POp asymmetry compared to left-handers, supporting a link between the neuroanatomical regions underpinning both manual and language asymmetries across species. Additionally, when hand biases from termite fishing, anvil use and simple reaching were assessed for neuroanatomical characteristics from the MRI scans of 22 chimpanzees, the authors found that right-handed chimpanzees had a significantly greater leftward asymmetry than non-right-handed subjects within a region of the inferior frontal gyrus, known to overlap with Broca's area (Hopkins et al. 2007), and also implicated in the processing of human language syntax (Peelle et al. 2004; Caplan et al. 2008). However, the correlation between right-handedness and left hemisphere asymmetry was not evident for a region of the chimpanzee brain considered to overlap with the Wernicke's area (see Hopkins & Cantalupo 2004 for planum temporale). These findings suggest that the neural regions associated with tool use and language production may overlap and be biased to the left hemisphere in right-handed individuals. From an evolutionary perspective, the overlap in neural function underlying tool use and language processes provides one possible example of neural exaptation (e.g. Gould & Vrba 1982; Iriki & Taoka 2012) supporting a hypothesis that language emerged from neural regions originally evolved to cope with the hierarchical sequences of actions inherent in tool use and manufacture. While the evolutionary emergence of population-level human right-handedness remains speculative, the development of lateralised markers of contralateral neural processing may unite studies of brain and behaviour and inform about the evolutionary emergence of higher cognitive functions.

CONCLUSIONS

The present study focused on dense data collection for a small sample of captive gorillas and assessed observed naturalistic hand dominance for bimanual object manipulation. Based on our findings, we argue that gorillas possess population-level right-handedness for object manipulation with a proportional split similar to that found in the human population. Assessing great ape handedness within specific domains, like object manipulation, is more in keeping with human handedness measures that *exclusively* focus on the routine sequences of structured actions for tool use (e.g. Edinburgh Handedness Inventory; Oldfield 1971), thus allowing for more direct intra-species comparisons. While we speculate an evolutionary link between tool use and the emergence of human language, at present, there is a paucity of behavioural and neuroanatomical finding to fully substantiate such a claim. Moreover, a consistent methodological approach across laboratories, and the investigation of larger and more diverse populations, are necessary progressions in order to generate reliable behavioural markers of cerebral lateralisation and thus facilitate the synthesis and generalisation of findings. Nevertheless, based on the results of the current study and those from the literature that span disparate species, not only can lateralised motor actions act as plausible markers of contralateral neural generators, they may also provide insight into the evolution of cognitive function.

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FIGURE LEGENDS

Figure 1. Demonstrates the difference in mean proportion for left and right hand dominance.

Figure 2. Demonstrates the difference in mean proportion for left and right hand dominant

hand transfers.

Figure 3. Demonstrates the strength of handedness using MHI scores for hand dominance and hand transfers.

ABSTRACT

There is a common prevailing perception that humans possess a species-unique population-level right-hand bias that has evolutionary links with language. New theories suggest that an early evolutionary division of cognitive function gave rise to a left hemisphere bias for behaviours underpinned by structured sequences of actions. However, studies of great ape handedness have generated inconsistent results and considerable debate. Additionally, the literature places a heavy focus on chimpanzees, revealing a paucity of handedness findings from other great ape species, and thus limiting the empirical evidence with which we can evaluate evolutionary theory. We observed handedness during spontaneous naturalistic bimanual actions in a captive, biological group of 13 western lowland gorillas (*Gorilla gorilla gorilla*). Our results demonstrated a significant group-level right-handed bias for bimanual actions as well as for a novel measure of handedness: *hand transfer*. The two measures revealed similar patterns of handedness, such that a right-hand bias for the majority of individuals was found across both measures. Our findings suggest that human population-level right-handedness is a behavioural trait linked with left hemisphere dominance for the processing of structured sequences of actions, and was inherited by a common ancestor of both humans and apes.

Keywords: cerebral lateralisation, evolution, great apes, gorilla, *Gorilla gorilla gorilla*, handedness, language

INTRODUCTION

Historically, researchers have argued that population-level right-handedness is a human-unique behaviour, underpinned by an evolutionary link with left hemisphere neural regions dedicated to language processing (e.g. Broca 1865; Wernicke 1874). Approximately 90% of the human population are considered to be right-handed, (Porac & Coren 1981; Annett 1985). Additionally, about 95% of the right-handed population expresses language dominance in the left hemisphere of the brain (Santrock 2008). Specifically, the inferior frontal gyrus (Tomaiuolo et al. 1999; Robichon et al. 2000; Keller et al. 2009) and a portion of the posterior temporal lobe (planum temporale) are proportionately larger in the left hemisphere compared with the right hemisphere (Beaton 1997; Shapleske et al. 1999; Sommer et al. 2001; 2008), and coincide with the anatomical locations of Broca's and Wernicke's areas respectively (e.g. Horwitz et al. 2003). The commonality of the human left hemisphere bias for handedness and language processing has perpetuated a theory that lateralized motor action elicited by cerebral lateralisation for specific cognitive functions is unique to humans (Warren 1980; Ettlinger 1988; Crow 2004; Schoenemann 2006). Some have posited that handedness is directly linked with language capabilities, such as articulated speech (Annett 2002) or gesture (Corballis 2002). Others have suggested that handedness may have originated from tool use (Greenfield 1991), coordinated bimanual actions (Wundrum 1986; Hopkins et al. 2003), or bipedalism (Westergaard et al. 1998; Braccini et al. 2010). However, the emergence of handedness and its evolutionary relationship with language remains a controversial topic.

Lateralised motor action underpinned by cerebral lateralisation for specific cognitive processes has now been revealed across a range of vertebrate (Vallortigara & Rogers 2005; MacNeilage, et al. 2009; Rogers & Andrew 2002; Vallortigara et al. 2011) and invertebrate (Anfora et al. 2011; Frasnelli et al. 2012) species, and thus, is no longer considered human specific. For example, right hemisphere dominance has been identified for processing of social stimuli in chimpanzees (*Pan troglodytes*, Morris et al. 1993), rhesus monkeys (*Macca mulatta*, Guo et al. 2009), dogs (*Canis familiaris*, Guo et al. 2009) and sheep (*Ovis aries*, Peirce et al. 2000). Alternatively, the left hemisphere has been reported to be dominant for well-practiced sequences of actions, such as feeding tasks in pigeons (*Columbia livia*, Güntürkün & Kesh 1987), chicks (*Gallus gallus domesticus*, Rogers 1995) and toads (*B. bufo and B. marinus*, Robins & Rogers 2004), and in numeracy tasks in dolphins (*Tursiops truncates*, Killian et al. 2005). The result of such evidence, suggests that the right hemisphere of the brain evolved as dominant for controlling arousal levels in order to react quickly to the environment (e.g. predators), whilst the left hemisphere emerged as dominant for processing routine behaviours with structured sequences of actions (e.g. feeding) (Vallortigara et al. 2008, 2011; MacNeilage et al. 2009). An early evolutionary division of labour for these critical survival processes in the left and right hemispheres may have produced advantages for: increasing neural capacity, enabling parallel processing and deterring the simultaneous initiation of incompatible responses (e.g. Andrew 1991; Vallortigara 2000; Rogers 2002).

Based upon the evolutionary theory above, it is not surprising that hierarchically structured language processes are left hemisphere dominant for the majority of the human population. However, the precursor behaviours that language emerged from are poorly understood. For over half a century, theoretical parallels have been drawn between the cognitive processes underlying a left hemispheric specialisation for language and right-handed tool use in humans. While hierarchical structures are known to be a distinctive component of language (e.g. Hauser et al. 2002), it has been suggested that they also appear in non-linguistic domains such as object manipulation (for a review see Tettamanti 2003). Motor activity has been described as a hierarchy of structured sequence of behavioural units (Holloway 1969); and hierarchical action sequences are integral to tool use (e.g. Lashley 1951; Dawkins 1976; Byrne & Russon 1998). While some have argued that the sequences of actions supporting tool manufacture do not possess a linguistic type of syntax because the actions are based upon physical constraints rather than internal rules (e.g. Graves 1994; Wynn 1995), others have argued that some Paleolithic tool manufacturing methods do share abstract syntactical content with linguistic processes (e.g. Holloway 1981; Stout & Chaminade 2009). Additionally, evidence from prehistoric human tool use and manufacture suggests that human population-level right-handedness has origins that precede the emergence of modern human language. Specifically, archaeological data suggest that right biased asymmetries existed in the arm and hand bones at least by the stage of the genus *Homo*. Evidence from tool use production and cave art suggests that population-level right-handedness was established in Neanderthals (for a review see Cashmore et al. 2008), thus preceding human language, which is claimed to have emerged not earlier than 100,000 years ago (e.g. Ott 2009). One hypothesis is that right-handed tool use provided an evolutionary bridge between left hemisphere dominant action sequences and language processes (Hamzei et al. 2003).

Great apes are proven tool users in both wild and captive settings; and although they do not possess language, great apes demonstrate evidence of a neuroanatomical brain region that overlaps with Broca's regions and that, like in humans, is proportionately larger in the left hemisphere than in the right hemisphere (e.g. Cantalupo & Hopkins 2001; Hopkins et al. 2007). Therefore, great apes offer an excellent animal model to investigate the evolutionary link between handedness and human language. Early handedness studies achieved inconsistent results in both captive (e.g. Finch 1941; Marchant 1983; Annett & Annett 1991; Hopkins 1993) and wild ape populations (e.g. Boesch 1991; McGrew & Marchant 1992; Shafer 1993). However, traditional handedness coding methods may not have effectively revealed manual biases. Early behavioural studies of great ape handedness assessed unimanual actions, such as simple reaching or manipulation tasks. Unimanual actions can often be confounded by postural (e.g. one hand supporting posture) and situational elements (e.g. one hand occupied with an object) (Aruguete et al. 1992; Westergaard et al. 1998; Braccini et al. 2010). Additionally, it is now acknowledged that task complexity can influence the direction, magnitude and consistency of hand preference of both humans (e.g.

Perelle & Ehrman 1994; Marchant et al. 1995; Fagard 2001) and great apes (Boesch 1991; McGrew et al. 1999; O'Malley & McGrew 2006; Hopkins 2007). Therefore, unimanual actions may represent simplistic behaviours that do not necessarily demand the use of a dominant hand or hemisphere (Hopkins 1995).

More recently, studies have investigated bimanual actions, characterised by both hands cooperating in the manipulation or processing of the same item. During bimanual actions, one hand is used to support an item (the non dominant hand) while the other hand manipulates the item (dominant hand) (e.g. McGrew & Marchant 1997). Bimanual handedness is thought to represent more complex behaviours and is considered to be a more sensitive measure of hand dominance (e.g. Hopkins 2006; Vauclair & Meguerditichian 2007). Additionally, investigating bimanual actions minimises postural factors due to the necessity for the individual to appropriate a bipedal or seated posture in order for both hands to be available to engage in a bimanual task (Roney & King 1993). Laboratory studies that investigated the bimanual actions of large samples of chimpanzees have revealed evidence of population-level right-handedness (Hopkins & Russell 2004; Hopkins et al. 2004; for a review see: Hopkins 2006; 2007). Studies implemented a tube task that required chimpanzees to manipulate an object (tube) to retrieve food. Peanut butter was placed deep inside of poly-vinyl-chloride tubes such that the chimpanzees could not lick the contents, as successful retrieval of food required the insertion of fingers for extraction. Some have contended that captive ape handedness could be confounded from exposure to human behaviour (McGrew & Marchant 1997; Palmer 2002; 2003; Crow 2004), and queried methods of statistical analyses (Hopkins 1999, Hopkins & Cantalupo 2005). However, more recent studies, controlling for confounding factors, have also revealed population-level right-hand biases for bimanual tasks in naturalistically housed chimpanzees (Llorente et al. 2009; 2011). Conversely, observational studies of wild chimpanzee termite fishing have consistently revealed a left-handed bias (Lonsdorf & Hopkins 2005; Hopkins et al. 2009). However, it has been postulated that for this task, the less demanding action (dipping) is directed by the non-dominant left hand, such 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). In general, findings from chimpanzee bimanual actions studies contradict the traditional supposition that population-level right-handedness is a human unique characteristic, and support the hypothesis that right-handedness has been inherited from a last common ancestor, preceding the emergence of human language skills.

Compared with studies of chimpanzee, gorillas are largely neglected in the handedness literature. Whether or not gorillas demonstrate population-level handedness is debated due to limited and inconsistent findings across laboratories (e.g. McGrew & Marchant 1993). An early study investigating unimanual and bimanual actions of 10 captive gorillas found no population-level bias for unimanual reaching, but did report a left hand population bias for a bimanual spatial task requiring the alignment of two openings (Fagot & Vauclair 1988). The authors posited that the task might have probed mental rotation capabilities, widely considered to be a right-hemisphere dominant capability in humans (e.g. Jones & Anuza 1982). More recently, the tube task has been extended to bonobos (*Pan paniscus*), gorillas and orangutans (*Pongo pygmaeus*) (Hopkins et al. 2011). Results from these investigations demonstrated that like chimpanzees, bonobos and gorillas also revealed right-handed population biases when assessed for handedness during this specific bimanual coordinated activity. Only three studies, to date, have investigated the spontaneous bimanual behaviours of gorillas. Byrne & Byrne (1991) found a significant right hand bias for bimanual multi-stage sequences of food processing in a group of 44 mountain gorillas, where the strongest degree of hand preference was for processing food types in which leaves were protected by stings. Two more recent studies investigated naturalistic bimanual feeding behaviours of captive gorillas, but achieved varied results. Both studies assessed unimanual, simple reaching behaviours to food items and bimanual feeding behaviours in captive gorillas (Meguerditchian et al. 2010; Lambert 2012). Neither study reported a population-level bias for unimanual simple reaching actions, however Meguerditchian and colleagues (2010) revealed a significant right-hand population-level bias for bimanual feeding actions. While Lambert (2012) demonstrated stronger manual biases for bimanual feeding compared with unimanual simple reaching, bimanual actions were not found to be significantly right-handed. The author proposed that bimanual actions may vary in complexity and that assessing different grip morphologies may provide an alternate way to measure hand dominance. Specifically, precision grip, versus power grip, may signify more complex dextral action, and therefore elicit a dominant hand bias (e.g. Pouydebat et al. 2011).

Although inconsistent methodological approaches may be responsible for mixed results across laboratories, much of the research points to a right-handed bias in great apes during object manipulation. One possible interpretation of the literature is that right-handedness in humans is not a direct by-product of language capabilities, but rather the behavioural manifestation of left hemisphere dominance for processing structured sequences of actions. We hypothesise that this inherited cerebral lateralisation characteristic can be exploited in our closest living relatives, specifically during bimanual behaviours for object manipulation sequences. Therefore, in the present study we investigated the naturalistic spontaneous behaviours of a biological group of captive gorillas (*Gorilla gorilla gorilla*) performing bimanual object manipulation during: feeding (e.g. leaf stripping, nettle folding and honeypot dipping), tool use for food retrieval (preparing sticks for the honey pot, using sticks in the honey pot) and tools manufacture for food extraction (e.g. stripping sticks for use in honeypot). Additionally, we introduced a new measure of handedness that considers transfers of objects to the opposite hand prior to object manipulation. Hopkins (2006) noted that the tube task produced a right hand dominance even when controlling for the hand in which the chimpanzee received the tube. Specifically, the ‘hand transfer’ measure evaluated when an object was grasped by dominant hand and then transferred to the non-dominant hand, such that the dominant hand was free to perform manipulative actions upon the object. We hypothesised that the cost of transferring an object is outweighed by the increase of efficiency achieved through performing the manipulation with the dominant hand.

METHODS

Subjects

Data were collected on 13 (6 males), captive western lowland gorillas (*Gorilla gorilla*) living in a peer-raised, semi-free ranging, biological family group at Port Lympne Wild Animal Park, UK. The group was made up of one silverback, seven adult females, four juvenile males and one juvenile female (see Table 1) ranging in age from 2-36 years. Observational consent was granted by the John Aspinall Foundation. Due to the non-invasive nature of this study, further permits or ethical approvals were not required.

Housing and Enrichment

The 'Palace of the Apes' is the world's largest family gorilla house and is modeled on the habitat of wild gorillas. The gorillas are considered 'semi free ranging', in that they move freely about the large enclosure comprised of four composite parts: caged upper, caged lower, inside and garden. The two-tiered outside enclosure is fronted by toughened glass, and equipped with enrichment equipment including: ropes, nets and slides to encourage physical activity. Inside, there is a play area equipped with further enrichment equipment and 14 bedrooms with access to water. By way of the caged upper and lower areas of the enclosure, the gorillas have further access to a large garden equipped with climbing frames, trees, logs, a boundary stream and a large pile of boulders. The garden has viewing windows at ground level and unimpeded visual access from above the garden via a raised steel footpath. Both the caged area and the garden have food receptacles for enrichment purposes that require the gorillas to prepare sticks that fit the hole for retrieving the contents. Contents of the receptacle vary (e.g. honey, peanut butter, hummus, marmite). Further enrichment is regularly provided in the form of retrieving food from different types of cartons in order to cognitively challenge individuals and maintain high standards of animal welfare.

Nourishment

Gorillas receive six daily scatter feeds in order to stimulate natural foraging behaviours. A proportion of the scatter feeds are roof top dispersals of herbs and fruit that stimulate physical activity, requiring gorillas to brachiate. Gorillas receive up to 50 different varieties of fruits and vegetables, primarily organically grown. With seasonal variation, gorillas consume: apples, beans, blackberries, carrots, cauliflower, damsons, leeks, melon, oranges, pears, peppers, plums, raspberries, spinach, strawberries and sweet potatoes. Gorillas are also offered a large variety of woodland browse including bamboo and willow. Additionally, gorillas benefit from fresh herbs (e.g. parsley, thyme, rosemary and coriander), vitamin pellets, cheese, eggs, yoghurt and mealworms crickets. During the winter months, gorillas receive high-protein treats (e.g. lamb, sausages) to replace the protein that would be typically ingested by the way of insects within the foliage consumed in a wild setting.

Data Capture

From April 2004 to September 2006, subjects were video recorded during spontaneous naturalistic behaviour based on a counterbalanced focal sampling paradigm (Altmann 1974). Ten-minute focal follows were conducted for each animal. Due to low visibility of some gorillas, total focal follow time for each subject varied between 55–215 minutes (see Table 1). Synchronised digital video cameras (Panasonic NVGS11B) were employed to capture both the focal individual (camera 1: full frame) and encompass the focal subject within the context of any conspecifics and surroundings (camera 2: wide-angle) (see Multidimensional Method, Forrester 2008). Synchronization was established using a flash bulb. Cameras were tripod mounted and followed gorilla activity using zoom, tilt, and swivel to optimise view. Synchronised video streams were compressed into a single file (15 frames per second) viewed in a top/bottom format for subsequent coding using OBSERVATRON coding software (Forrester 2008).

Coding

Bimanual actions were defined in line with Meguerditchian et al. (2010) such that one hand holds an object (non-dominant 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 manipulating foods for ingestions (e.g. stripping and folding nettles, stripping leaves, and extracting nuts from their shells), using tools to extract food (e.g. dipping sticks in honey pot) and manufacturing tools to for food extraction (e.g. stripping sticks for use in honeypot). Bimanual actions began when one hand reached for an object for manipulation. The hand supporting the object was classified as the 'non-dominant' hand and was classified as left or right, whilst the hand used for manipulation of the object was classified as the 'dominant' hand was classified as the opposite hand (see Video 1 and Video 2 for examples of nettle folding and honeypot dipping bimanual actions). In the case of the honey dipping, the dominant hand manipulated the tool, while the non-dominant hand held the receptacle and simultaneously provided postural support.

Additionally, we coded the frequency of hand transfer events prior to object manipulation. Franz and colleagues (2002) demonstrated that the lead hand in a bimanual sequence does not necessarily signify the dominant hand (e.g. reaching for the object), but rather could be a consequence of posture (e.g. postural origins hypothesis; MacNeilage et al. 1987). For this measure we coded hand transfer events preceding bimanual object manipulation that involved the transfer of an object from one hand to the other such that the gorilla could employ the dominant hand for manipulation. For example, a locomoting gorilla may pick up a stick with the left hand on the way to the honeypot, but then transfers the stick to the right hand prior to dipping for honey. This action was coded as a transfer for right hand dominance such that the right hand could perform the dominant action. Furthermore, a gorilla might pick a nettle with the right hand, but then transfer it to the left hand such that the left hand can support the object while the right hand performs the actions of stripping and folding the nettles. This was also coded as a transfer for right hand dominance (see Video 3 for examples of hand transfers). Research into human handedness has shown that bilateral transfers can be used as a marker of hand dominance (Kumar & Mandal 2005).

For both 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. In the case of a hand transfer prior to manipulation, we first coded hand dominance and then coded the first manipulative action for hand dominance. A bout ended when the focal animal released the object. Although there has been some controversy in the literature whether events or bouts represent the most valid measure for evaluating hand dominance (McGrew & Marchant 1997; Hopkins et al. 2001), concerning a statistical bias that may result from the dependence of the data between each hand use response (e.g. pseudo-replication) (see Hurlburt 1984; Palmer 2003), a high correlation has been found between analyses of bouts and events, suggesting they are equally valid measures of handedness (e.g. Hopkins et al. 2005a).

Analyses

For both bimanual actions and hand transfer measures, we calculated frequencies, proportions, rates and Handedness Index (HI) scores for bouts. We employed a range of measures to demonstrate the consistency of the results across a range of statistical preferences throughout the literature. Specifically proportions and rates were used to equalise the weighting that each participant contributed to the data set. This is a critical evaluation process as to not let a single subject or non-significant group of subjects sway the group statistical test results. As each individual contributed a different number of bouts to the dataset, proportions were calculated by dividing the frequency of left or right hand actions by the total frequency of actions. Additionally, coded observation times varied between individuals as a result of animal visibility. Therefore, rates were calculated by dividing the frequency of bimanual actions by the total number of observational minutes per subject. Paired sample t-tests were used to compare bout group means for frequencies, proportions and rates for both hand dominance and hand transfers. A mean handedness index (MHI) score was also calculated for the group. Nonparametric Wilcoxon tests were also performed as a stricter test of difference. All statistical tests were two-tailed with alpha < 0.05.

In order to reveal individual patterns of hand dominance for bimanual actions and hand transfer measures, we calculated the z-scores, binomial approximations of the z-scores, and the individuals' strength of handedness using handedness index (HI) scores (see Tables 2 and 3). The direction of hand preference for each subject was calculated using z-scores such that gorillas were left handed when $z \leq -1.96$, right handed when $z \geq 1.96$ and ambiguously handed when $-19.6 < z < 1.96$. HI scores were calculated for each subject in for both measures to establish the degree of hand asymmetry. HI scores were calculated 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. When R=L, the HI is taken to be zero. 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. Two subjects were excluded from analyses for the measure of hand transfer due to low overall counts (total counts < 10). Excluded subjects are marked with a double asterisk (see Table 3). All statistical tests were two-tailed with alpha < 0.05.

RESULTS

Hand Dominance

The frequencies, proportions and rates of bouts along with their associated HI scores, z-scores and binomial approximations of the z-scores for the measures of hand dominance are displayed in Tables 2. A one sample t-test of the MHI scores for hand dominance (Mean = 0.62, SE = 0.07) indicated a significant population-level right-handedness, $t_{12} = 10.62$, $P < 0.001$.

A paired-sample t-test of frequencies demonstrated a significant bias for right hand dominance (Mean = 24.54, SE = 3.01), compared with left handed dominance (Mean = 6.08, SE = 1.48) for bimanual actions, t_{12} = - 7.44, $P < 0.001$. A paired-sample t-test of proportions demonstrated a significant right-handed dominance (Mean = 0.81, SE = 0.028), compared with left handed dominance (Mean = 0.19, SE = 0.028) for bimanual actions, t_{12} = - 10.86, $P < 0.001$. A paired-sample t-test of rates demonstrated a significant right-handed dominance (Mean = 0.21, SE = 0.04), compared with left-handed dominance (Mean = 0.05, SE = 0.01) for bimanual actions, t_{12} = - 4.41, $P = 0.001$ (Figure 1). Based on the *P*-values from the binomial approximations of the z-scores, ten of the thirteen gorillas (76.9%) demonstrated a significant right-handed dominance for bimanual actions. Three gorillas were ambiguously handed, however each of the three individuals' HI scores indicated a right-hand bias. Hand dominance measures were also calculated using the nonparametric Wilcoxon signed-ranks test. There was no change in the significant pattern of the results.

Hand Transfer

The frequencies, proportions and rates of bouts along with their associated HI scores, z-scores and binomial approximations of the z-scores for the measures of hand transfer are displayed in Tables 3. A one sample t-test of MHI scores for hand transfer (Mean = 0.71, SE = 0.09) indicated a significant population-level right hand dominance, $t_{10} = 10.00$, $P < 0.001$.

Under exclusion criteria (n=11 for counts > 10), a paired-sample t-test of frequencies demonstrated a significant bias for transfers from right hand to left hand (Mean = 18.64, SE = 2.33), compared with transfers from left hand to right hand (Mean = 3.45, SE = 1.22) for bimanual actions, $t_{10} = -6.63$, $P < 0.001$. Under the exclusion criteria, a paired-sample t-test of proportions demonstrated a significant bias for transfers from right hand to left hand (Mean = 0.86, SE = 0.44), compared with left hand to right hand (Mean = 0.15, SE = 0.44), for bimanual actions, $t_{10} = -8.14$, $P < 0.001$. Under exclusion criteria, a paired-sample t-test of rates demonstrated a significant bias for transfers from right hand to left hand (Mean = 0.13, SE = 0.02), compared with transfers from left hand to right hand (Mean = 0.03, SE = 0.01) for bimanual actions, $t_{10} = -6.18$, $P < 0.001$ (Figure 2). Based on the *P*-values from the binomial approximations of the z-scores, eight of the eleven gorillas (72.7%) demonstrated a significant bias for transfers from right hand to left hand for bimanual actions. Three gorillas were ambiguously handed, however individual HI scores maintained a preference for right-hand dominance. Hand transfer measures were also calculated using the nonparametric Wilcoxon signed ranks test. There was no change in the significant pattern of the results.

A paired sample t-test indicated that there was no significant difference between the HI scores for hand dominance and hand transfer $t_{10} = -0.995$, P = 0.343 (Figure 3).

DISCUSSION

The findings from this study demonstrated a significant population-level right-handed bias for the measures of bimanual actions and hand transfer. The majority of individual subjects demonstrated a significant right hand preference for both measures. There was no significant difference between the strength of hand preference when comparing the two measures, thus hand transfers may offer an alternative and/or complementary objective measure of hand dominance. Our finding of a population-level right hand bias for bimanual actions is consistent with previous studies of captive apes performing the tube task (e.g. Hopkins et al. 2011) as well as with studies the majority of studies investigating naturalistic bimanual feeding behaviours in captive (Meguerditchian et al. 2010) and wild gorillas (Byrne & Byrne 1991).

The implementation of the measure of hand transfer to investigate ape handedness appears to be a relevant marker of hand dominance. Like grip morphology, hand transfer may also prove to be sensitive to dextral complexity. Hand transfers were likely to have been performed when the sequence of object manipulation actions could not be efficiently or effectively performed with the non-dominant hand. In human children, planning abilities have been exploited through the measure of hand transfer tasks. Specifically, when one hand supports an object (non dominant) and the other hand (dominant) manipulates aspects of the object, infants under 2 years of age tend to transfer the object from the right to the left hand. Older children anticipate the requirement of the dominant hand and thus begin the bimanual task by grasping the object with the non-dominant hand (Potier, Meguerditchian & Fagard 2012), further suggesting that hand transfers may be a useful measure of individual handedness development during increasing task complexity.

There is growing evidence in humans that lateralised behaviours manifesting from contralateral domain specific neural processing extends beyond the association between population-level right-handedness and left hemisphere language regions. For example, the right hand has also shown a significant bias for communicative gesture (Corina et al. 1993), implicating a dominant left hemisphere control. Conversely, a left visual field/right hemisphere preference has been identified in face perception for exploring the left side of a centrally presented face when measured behaviourally (looking time; Burt & Perrett 1997) and with functional imaging (Kanwisher et al. 1998). As in humans, in addition to object manipulation, great apes have also demonstrated a right hand bias for communicative gestures in a range of chimpanzee populations (Hopkins & Leavens 1998; Hopkins et al. 2005b; Meguerditichian et al. 2009; 2012), suggesting left hemisphere dominant processing. Conversely, leftward action biases have been reported for social-emotional processing for self-directed face touching in orangutans (Rogers & Kaplan 1995), self-scratching (Leavens et al. 2004) and during increases in task complexity in chimpanzees (Leavens et al. 2001), potentially resulting from a rise in stress or arousal levels increasing right hemisphere processing. Another method that appears to probe cerebral lateralisation of domain specific processing involves assessing the type of target to which hand actions are directed. For example, chimpanzees demonstrated a right hand preference for touching their inanimate environments and ambi-preference for self-directed behaviours (Aruguete et al. 1992). Similarly, a unimanual right hand bias was found for actions towards inanimate objects, but ambi-preference for unimanual actions to animate targets (self and conspecifics) in gorillas (Forrester et al. 2011), chimpanzees (Forrester et al. 2012) and typically developing children (Forrester et al. 2013). These findings add to the mounting evidence that lateralised motor actions are markers of contralateral domain specific cerebral lateralisation, where the left hemisphere presides over structured sequences of actions, while the right hemisphere dominates social-emotional processing (e.g. MacNeilage 2009). The implications of such brain organisation is integral to the evolution and development of higher cognitive functions, as emergent functions are predicted to develop within the hemisphere that could support that function through the exaptation of neural regions for processing more elementary functions with similar underlying structure.

Some posit that Broca’s area may be a supra-modal hierarchical processor, supporting a speculative hypothesis that language emerged from left hemisphere dominant neural regions originally evolved to cope with the hierarchical sequences of actions inherent in tool use (Pulvermüller & Fadiga 2010; Petersson et al. 2012). Action sequences for object manipulation (that are not random) were proposed to possess a rudimentary syntax (e.g. Tettamanti & Weniger 2006; Pastra & Aloimonos 2012). For example, in human infants, non-linguistic actions involving objects (e.g. self-feeding with a spoon) were seen to involve hierarchical sequence of actions (Connolly & Dagleish 1989; Greenfield 1991). Specifically, the activity in Broca's region has been shown to correlate with increasing hierarchical structural complexity (Bates & Dick 2002; Greenfield 1991). Broca's area is typically segmented into three regions: the pars triangularus (PTr), the pars orbitalus (PO) and the pars opercularis (POp). Recent neuroimaging studies demonstrated the Pop was activated for acquiring grammatical rules (i.e., having a hierarchical structure) (e.g. Tettamanti et al. 2002) and during complex grammar processing (Friederici et al. 2006), as opposed to an area posterior to POp has been recognised for tasks of simple grammar (Sakai 2005). Additionally, a transcranial magnetic stimulation study demonstrated that the POp was critical for the encoding of complex human action (Clerget, et al. 2009). Moreover, an fMRI investigation of healthy human adults evidenced an overlap of brain activity for perceiving language and using tools in this same region (POp), suggesting that language and tool use share a common neural generator for processing "complex hierarchical structures common to these two abilities" (Higuchi et al. 2009). This growing body of evidence suggests that the POp region of Broca's area may not be language-specific, but rather is active for disparate tasks (e.g. linguistic, cognitive, sensorimotor) that involve computational processing of hierarchical structure (Tettamanti & Weniger 2006) and that may also be present in other primate tool users.

Although limited data exists from brain imaging studies of great apes, Catalupo and Hopkins (2001) sampled 26 great apes and found a general leftward bias for the anatomical volume of the POp. A subsequent sample of chimpanzees (Hopkins et al. 2008), demonstrated a non-significant anatomical leftward bias, however the authors posit that differences in the boundaries placed upon POp may have contributed to inconsistent findings between the two studies. In fact, comparing the anatomical similarities of Broca's area in human and ape brains rely primarily on the surface area or volume of the POp because the PTr and the PO have not been reliably defined in the chimpanzee brain (e.g. Keller et al 2009; for a review see Hopkins 2013). Inconsistencies in anatomical boundaries of Broca's area may have also led to discrepancies in findings from cytoarchitectonic studies of human and ape brains (Amunts et al. 1999; Ziles & Amunts 2010). Nevertheless, imaging studies have reported in both humans (Foundas et al. 1995) and apes (Gilissen & Hopkins 2013) that a significantly greater proportion of right-handers demonstrate a left hemisphere POp asymmetry compared to left-handers, supporting a link between the neuroanatomical regions underpinning both manual and language asymmetries across species. Additionally, when hand biases from termite fishing, anvil use and simple reaching were assessed for neuroanatomical characteristics from the MRI scans of 22 chimpanzees, the authors found that right-handed chimpanzees had a significantly greater leftward asymmetry than non-right-handed subjects within a region of the inferior frontal gyrus, known to overlap with Broca's area (Hopkins et al. 2007), and also implicated in the processing of human language syntax (Peelle et al. 2004; Caplan et al. 2008). However, the correlation between right-handedness and left hemisphere asymmetry was not evident for a region of the chimpanzee brain considered to overlap with the Wernicke's area (see Hopkins & Cantalupo 2004 for planum temporale). These findings suggest that the neural regions associated with tool use and language production may overlap and be biased to the left hemisphere in right-handed individuals. From an evolutionary perspective, the overlap in neural function underlying tool use and language processes provides one possible example of neural exaptation (e.g. Gould & Vrba 1982; Iriki & Taoka 2012) supporting a hypothesis that language emerged from neural regions originally evolved to cope with the hierarchical sequences of actions inherent in tool use and manufacture. While the evolutionary emergence of population-level human right-handedness remains speculative, the development of lateralised markers of contralateral neural processing may unite studies of brain and behaviour and inform about the evolutionary emergence of higher cognitive functions.

CONCLUSIONS

The present study focused on dense data collection for a small sample of captive gorillas and assessed observed naturalistic hand dominance for bimanual object manipulation. Based on our findings, we argue that gorillas possess population-level right-handedness for object manipulation with a proportional split similar to that found in the human population. Assessing great ape handedness within specific domains, like object manipulation, is more in keeping with human handedness measures that *exclusively* focus on the routine sequences of structured actions for tool use (e.g. Edinburgh Handedness Inventory; Oldfield 1971), thus allowing for more direct intra-species comparisons. While we speculate an evolutionary link between tool use and the emergence of human language, at present, there is a paucity of behavioural and neuroanatomical finding to fully substantiate such a claim. Moreover, a consistent methodological approach across laboratories, and the investigation of larger and more diverse populations, are necessary progressions in order to generate reliable behavioural markers of cerebral lateralisation and thus facilitate the synthesis and generalisation of findings. Nevertheless, based on the results of the current study and those from the literature that span disparate species, not only can lateralised motor actions act as plausible markers of contralateral neural generators, they may also provide insight into the evolution of cognitive function.

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FIGURE LEGENDS

Figure 1. Demonstrates the difference in mean proportion for left and right hand dominance.

Figure 2. Demonstrates the difference in mean proportion for left and right hand dominant

hand transfers.

Figure 3. Demonstrates the strength of handedness using MHI scores for hand dominance and hand transfers.

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Figure 1 - Hand Dominance

Figure 2 - Hand Transfers

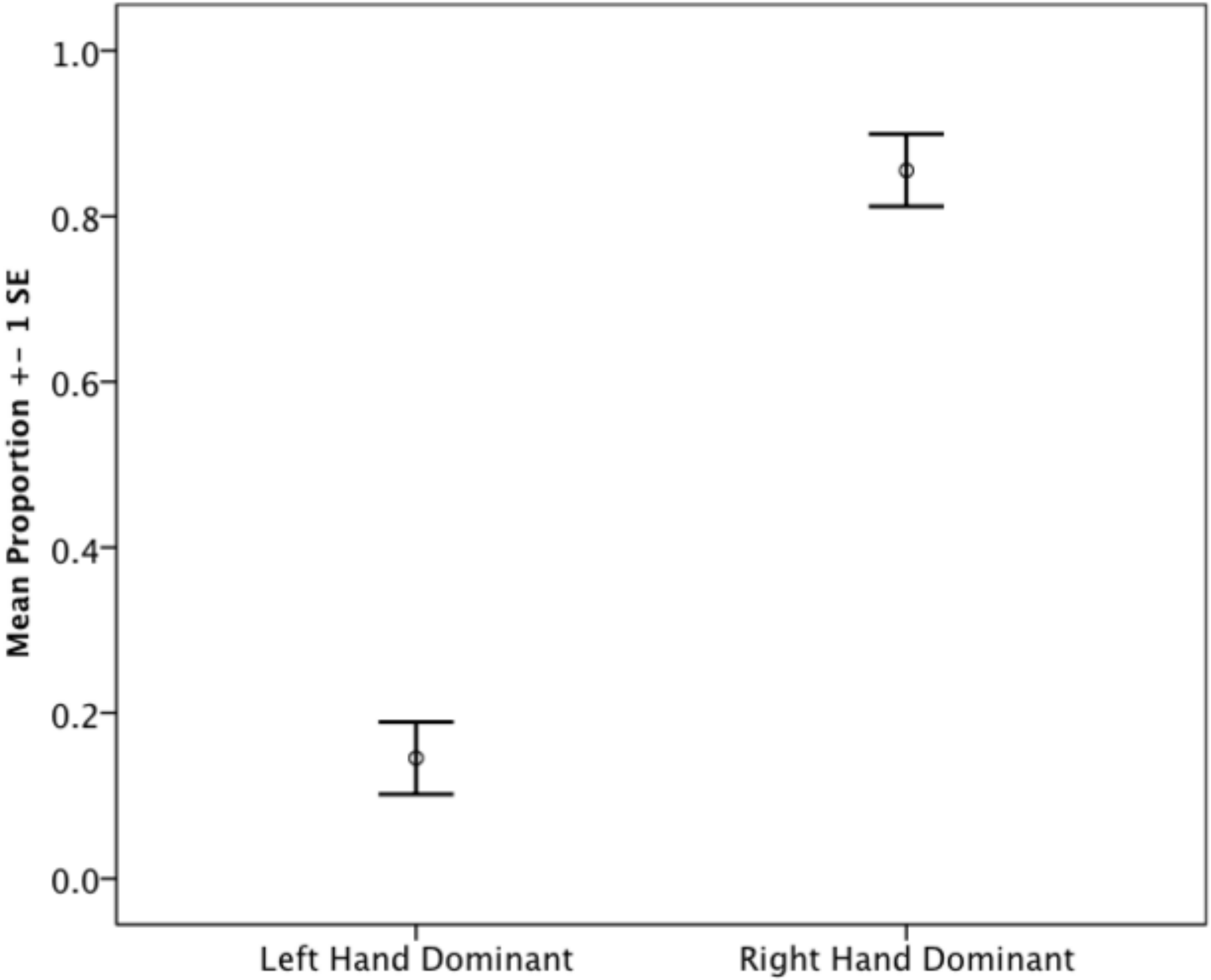

Figure 3 - MHI HD & HT

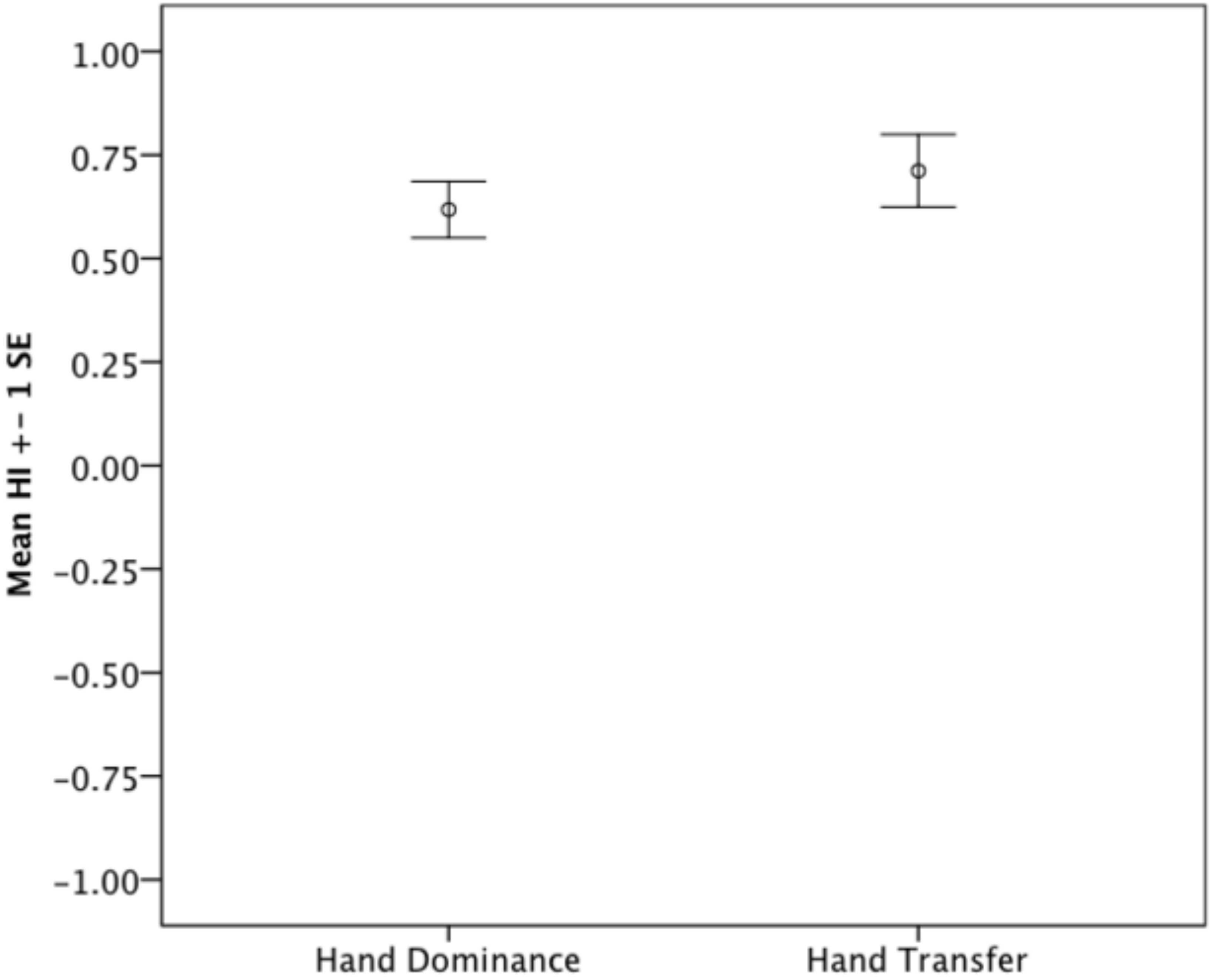

Table 1

Table 1. Gender, status and number of minutes of sampled behaviour.

Subject	Gender	Status	Sample (min)
Dishi	Male	Juvenile	143
Djala	Male	Adult	171
Emmie	Female	Adult	175
Foufou	Female	Adult	250
Jaja	Male	Juvenile	200
Kibi	Female	Adult	55
Kishi	Female	Adult	176
Kouni	Male	Juvenile	158
M’Passa	Male	Juvenile	26
Mumba	Female	Adult	63
Tamarilla	Female	Adult	215
Tamki	Female	Adult	140
Yene	Female	Juvenile	165

Table 2

Table 2. Z-scores, binomial approximation of z-scores and HI Scores based on frequencies, proportions and rates of direction for bimanual hand dominance.

Subject	Left dominant			Right dominant			Z-score	P-value	HI score
	F	P	R	F	P	R			
Dishi	6	0.27	0.04	16	0.73	0.11	-1.92	0.055	0.46
Djala	1	0.03	0.01	37	0.97	0.22	-5.68*	<0.001*	0.95
Emmie	3	0.20	0.02	12	0.80	0.07	-2.07*	0.038*	0.60
Foufou	21	0.29	0.08	51	0.71	0.20	-3.42*	0.001*	0.42
Jaja	10	0.25	0.05	30	0.72	0.15	-3.00*	0.003*	0.50
Kibi	8	0.33	0.15	16	0.67	0.29	-1.43	0.153	0.33
Kishi	3	0.09	0.02	30	0.91	0.17	-4.53*	<0.001*	0.82
Kouni	3	0.10	0.02	27	0.90	0.17	-4.20*	<0.001*	0.80
M'Passa	3	0.15	0.12	17	0.85	0.66	-2.91*	0.004*	0.70
Mumba	1	0.06	0.02	17	0.94	0.27	-3.54*	<0.001*	0.89
Tamarilla	8	0.33	0.04	16	0.67	0.07	-1.43	0.153	0.33
Tamki	4	0.14	0.03	25	0.86	0.18	-3.71*	<0.001*	0.72
Yene	8	0.24	0.05	25	0.76	0.15	-2.65*	0.005*	0.52

alpha $P < 0.05$* ; F=frequency, P=proportion (L/L+R, R/L+R), R=rate (minutes/frequency)

Table 3

Table 3. Z-scores, binomial approximation of z-scores and HI Scores based on frequencies, proportions and rates of direction of transfer for bimanual actions.

Subject	Left dominant			Right dominant			Z-score	P-value	HI score
	F	P	R	F	P	R			
Dishi**	1	0.14	0.01	6	0.86	0.04	**	**	**
Djala	1	0.03	0.01	33	0.97	0.19	-5.32*	<0.001*	0.94
Emmie	0	0.00	0.00	14	1.00	0.08	-3.47*	<0.001*	1.00
Foufou	13	0.28	0.05	33	0.72	0.13	-2.80*	0.005*	0.44
Jaja	6	0.29	0.03	15	0.71	0.07	-1.75	0.08	0.43
Kibi	7	0.37	0.13	12	0.63	0.22	-0.92	0.358	0.26
Kishi	1	0.06	0.01	17	0.94	0.10	-3.54*	<0.001*	0.89
Kouni	0	0.00	0.00	19	1.00	0.12	-4.13*	<0.001*	1.00
M’Passa**	0	0.00	0.00	5	1.00	0.19	**	**	**
Mumba	0	0.00	0.00	14	1.00	0.22	-3.47*	<0.001*	1.00
Tamarilla	5	0.33	0.02	10	0.67	0.05	-1.03	0.303	0.33
Tamki	3	0.13	0.02	21	0.88	0.15	-3.47*	<0.001*	0.75
Yene	2	0.11	0.01	17	0.89	0.10	-3.21*	0.001*	0.79

alpha $P < 0.05$* ; F=frequency, P=proportion (L/L+R, R/L+R), R=rate (minutes/frequency)
**excluded from analyses due to low counts

Video 1 - Nettle Processing

Video 2 - Honey Dipping

Video 3 - Hand Transfers

Thumbnail Video 1

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