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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

1 ABSTRACT

2

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

19

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

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29 INTRODUCTION

30

31 Historically, researchers have argued that population-level right-handedness is a human-
32 unique behaviour, underpinned by an evolutionary link with left hemisphere neural regions
33 dedicated to language processing (e.g. Broca 1865; Wernicke 1874). Approximately 90% of
34 the human population are considered to be right-handed, (Porac & Coren 1981; Annett
35 1985). Additionally, about 95% of the right-handed population expresses language
36 dominance in the left hemisphere of the brain (Santrock 2008). Specifically, the inferior
37 frontal gyrus (Tomaiuolo et al. 1999; Robichon et al. 2000; Keller et al. 2009) and a portion
38 of the posterior temporal lobe (planum temporale) are proportionately larger in the left
39 hemisphere compared with the right hemisphere (Beaton 1997; Shapleske et al. 1999;
40 Sommer et al. 2001; 2008), and coincide with the anatomical locations of Broca's and
41 Wernicke's areas respectively (e.g. Horwitz et al. 2003). The commonality of the human left
42 hemisphere bias for handedness and language processing has perpetuated a theory that
43 lateralized motor action elicited by cerebral lateralisation for specific cognitive functions is
44 unique to humans (Warren 1980; Ettliger 1988; Crow 2004; Schoenemann 2006). Some
45 have posited that handedness is directly linked with language capabilities, such as articulated
46 speech (Annett 2002) or gesture (Corballis 2002). Others have suggested that handedness
47 may have originated from tool use (Greenfield 1991), coordinated bimanual actions
48 (Wundrum 1986; Hopkins et al. 2003), or bipedalism (Westergaard et al. 1998; Braccini et
49 al. 2010). However, the emergence of handedness and its evolutionary relationship with
50 language remains a controversial topic.

51

52 Lateralised motor action underpinned by cerebral lateralisation for specific cognitive
53 processes has now been revealed across a range of vertebrate (Vallortigara & Rogers 2005;
54 MacNeilage, et al. 2009; Rogers & Andrew 2002; Vallortigara et al. 2011) and invertebrate
55 (Anfora et al. 2011; Frasnelli et al. 2012) species, and thus, is no longer considered human
56 specific. For example, right hemisphere dominance has been identified for processing of

57 social stimuli in chimpanzees (*Pan troglodytes*, Morris et al. 1993), rhesus monkeys (*Macca*
58 *mulatta*, Guo et al. 2009), dogs (*Canis familiaris*, Guo et al. 2009) and sheep (*Ovis aries*,
59 Peirce et al. 2000). Alternatively, the left hemisphere has been reported to be dominant for
60 well-practiced sequences of actions, such as feeding tasks in pigeons (*Columbia livia*,
61 Güntürkün & Kesh 1987), chicks (*Gallus gallus domesticus*, Rogers 1995) and toads (*B.*
62 *bufo* and *B. marinus*, Robins & Rogers 2004), and in numeracy tasks in dolphins (*Tursiops*
63 *truncatus*, Killian et al. 2005). The result of such evidence, suggests that the right
64 hemisphere of the brain evolved as dominant for controlling arousal levels in order to react
65 quickly to the environment (e.g. predators), whilst the left hemisphere emerged as dominant
66 for processing routine behaviours with structured sequences of actions (e.g. feeding)
67 (Vallortigara et al. 2008, 2011; MacNeilage et al. 2009). An early evolutionary division of
68 labour for these critical survival processes in the left and right hemispheres may have
69 produced advantages for: increasing neural capacity, enabling parallel processing and
70 deterring the simultaneous initiation of incompatible responses (e.g. Andrew 1991;
71 Vallortigara 2000; Rogers 2002).

72

73 Based upon the evolutionary theory above, it is not surprising that hierarchically structured
74 language processes are left hemisphere dominant for the majority of the human population.
75 However, the precursor behaviours that language emerged from are poorly understood. For
76 over half a century, theoretical parallels have been drawn between the cognitive processes
77 underlying a left hemispheric specialisation for language and right-handed tool use in
78 humans. While hierarchical structures are known to be a distinctive component of language
79 (e.g. Hauser et al. 2002), it has been suggested that they also appear in non-linguistic
80 domains such as object manipulation (for a review see Tettamanti 2003). Motor activity has
81 been described as a hierarchy of structured sequence of behavioural units (Holloway 1969);
82 and hierarchical action sequences are integral to tool use (e.g. Lashley 1951; Dawkins 1976;
83 Byrne & Russon 1998). While some have argued that the sequences of actions supporting
84 tool manufacture do not possess a linguistic type of syntax because the actions are based

85 upon physical constraints rather than internal rules (e.g. Graves 1994; Wynn 1995), others
86 have argued that some Paleolithic tool manufacturing methods do share abstract syntactical
87 content with linguistic processes (e.g. Holloway 1981; Stout & Chaminade 2009).
88 Additionally, evidence from prehistoric human tool use and manufacture suggests that
89 human population-level right-handedness has origins that precede the emergence of modern
90 human language. Specifically, archaeological data suggest that right biased asymmetries
91 existed in the arm and hand bones at least by the stage of the genus *Homo*. Evidence from
92 tool use production and cave art suggests that population-level right-handedness was
93 established in Neanderthals (for a review see Cashmore et al. 2008), thus preceding human
94 language, which is claimed to have emerged not earlier than 100,000 years ago (e.g. Ott
95 2009). One hypothesis is that right-handed tool use provided an evolutionary bridge between
96 left hemisphere dominant action sequences and language processes (Hamzei et al. 2003).
97
98 Great apes are proven tool users in both wild and captive settings; and although they do not
99 possess language, great apes demonstrate evidence of a neuroanatomical brain region that
100 overlaps with Broca's regions and that, like in humans, is proportionately larger in the left
101 hemisphere than in the right hemisphere (e.g. Cantalupo & Hopkins 2001; Hopkins et al.
102 2007). Therefore, great apes offer an excellent animal model to investigate the evolutionary
103 link between handedness and human language. Early handedness studies achieved
104 inconsistent results in both captive (e.g. Finch 1941; Marchant 1983; Annett & Annett 1991;
105 Hopkins 1993) and wild ape populations (e.g. Boesch 1991; McGrew & Marchant 1992;
106 Shafer 1993). However, traditional handedness coding methods may not have effectively
107 revealed manual biases. Early behavioural studies of great ape handedness assessed
108 unimanual actions, such as simple reaching or manipulation tasks. Unimanual actions can
109 often be confounded by postural (e.g. one hand supporting posture) and situational elements
110 (e.g. one hand occupied with an object) (Aruguete et al. 1992; Westergaard et al. 1998;
111 Braccini et al. 2010). Additionally, it is now acknowledged that task complexity can
112 influence the direction, magnitude and consistency of hand preference of both humans (e.g.

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

117

118 More recently, studies have investigated bimanual actions, characterised by both hands
119 cooperating in the manipulation or processing of the same item. During bimanual actions,
120 one hand is used to support an item (the non dominant hand) while the other hand
121 manipulates the item (dominant hand) (e.g. McGrew & Marchant 1997). Bimanual
122 handedness is thought to represent more complex behaviours and is considered to be a more
123 sensitive measure of hand dominance (e.g. Hopkins 2006; Vauclair & Meguerditichian
124 2007). Additionally, investigating bimanual actions minimises postural factors due to the
125 necessity for the individual to appropriate a bipedal or seated posture in order for both hands
126 to be available to engage in a bimanual task (Roney & King 1993). Laboratory studies that
127 investigated the bimanual actions of large samples of chimpanzees have revealed evidence
128 of population-level right-handedness (Hopkins & Russell 2004; Hopkins et al. 2004; for a
129 review see: Hopkins 2006; 2007). Studies implemented a tube task that required
130 chimpanzees to manipulate an object (tube) to retrieve food. Peanut butter was placed deep
131 inside of poly-vinyl-chloride tubes such that the chimpanzees could not lick the contents, as
132 successful retrieval of food required the insertion of fingers for extraction. Some have
133 contended that captive ape handedness could be confounded from exposure to human
134 behaviour (McGrew & Marchant 1997; Palmer 2002; 2003; Crow 2004), and queried
135 methods of statistical analyses (Hopkins 1999, Hopkins & Cantalupo 2005). However, more
136 recent studies, controlling for confounding factors, have also revealed population-level right-
137 hand biases for bimanual tasks in naturalistically housed chimpanzees (Llorente et al. 2009;
138 2011). Conversely, observational studies of wild chimpanzee termite fishing have
139 consistently revealed a left-handed bias (Lonsdorf & Hopkins 2005; Hopkins et al. 2009).

140 However, it has been postulated that for this task, the less demanding action (dipping) is

141 directed by the non-dominant left hand, such that the more demanding range of actions (e.g.
142 bridging termites to the mouth, grasp termites outside the mound) can be conducted by the
143 dominant right hand (Bogart et al. 2012). In general, findings from chimpanzee bimanual
144 actions studies contradict the traditional supposition that population-level right-handedness
145 is a human unique characteristic, and support the hypothesis that right-handedness has been
146 inherited from a last common ancestor, preceding the emergence of human language skills.

147

148 Compared with studies of chimpanzee, gorillas are largely neglected in the handedness
149 literature. Whether or not gorillas demonstrate population-level handedness is debated due to
150 limited and inconsistent findings across laboratories (e.g. McGrew & Marchant 1993). An
151 early study investigating unimanual and bimanual actions of 10 captive gorillas found no
152 population-level bias for unimanual reaching, but did report a left hand population bias for a
153 bimanual spatial task requiring the alignment of two openings (Fagot & Vauclair 1988). The
154 authors posited that the task might have probed mental rotation capabilities, widely
155 considered to be a right-hemisphere dominant capability in humans (e.g. Jones & Anuza
156 1982). More recently, the tube task has been extended to bonobos (*Pan paniscus*), gorillas
157 and orangutans (*Pongo pygmaeus*) (Hopkins et al. 2011). Results from these investigations
158 demonstrated that like chimpanzees, bonobos and gorillas also revealed right-handed
159 population biases when assessed for handedness during this specific bimanual coordinated
160 activity. Only three studies, to date, have investigated the spontaneous bimanual behaviours
161 of gorillas. Byrne & Byrne (1991) found a significant right hand bias for bimanual multi-
162 stage sequences of food processing in a group of 44 mountain gorillas, where the strongest
163 degree of hand preference was for processing food types in which leaves were protected by
164 stings. Two more recent studies investigated naturalistic bimanual feeding behaviours of
165 captive gorillas, but achieved varied results. Both studies assessed unimanual, simple
166 reaching behaviours to food items and bimanual feeding behaviours in captive gorillas
167 (Meguerditchian et al. 2010; Lambert 2012). Neither study reported a population-level bias
168 for unimanual simple reaching actions, however Meguerditchian and colleagues (2010)

169 revealed a significant right-hand population-level bias for bimanual feeding actions. While
170 Lambert (2012) demonstrated stronger manual biases for bimanual feeding compared with
171 unimanual simple reaching, bimanual actions were not found to be significantly right-
172 handed. The author proposed that bimanual actions may vary in complexity and that
173 assessing different grip morphologies may provide an alternate way to measure hand
174 dominance. Specifically, precision grip, versus power grip, may signify more complex
175 dextral action, and therefore elicit a dominant hand bias (e.g. Pouydebat et al. 2011).
176
177 Although inconsistent methodological approaches may be responsible for mixed results
178 across laboratories, much of the research points to a right-handed bias in great apes during
179 object manipulation. One possible interpretation of the literature is that right-handedness in
180 humans is not a direct by-product of language capabilities, but rather the behavioural
181 manifestation of left hemisphere dominance for processing structured sequences of actions.
182 We hypothesise that this inherited cerebral lateralisation characteristic can be exploited in
183 our closest living relatives, specifically during bimanual behaviours for object manipulation
184 sequences. Therefore, in the present study we investigated the naturalistic spontaneous
185 behaviours of a biological group of captive gorillas (*Gorilla gorilla gorilla*) performing
186 bimanual object manipulation during: feeding (e.g. leaf stripping, nettle folding and
187 honeypot dipping), tool use for food retrieval (preparing sticks for the honey pot, using
188 sticks in the honey pot) and tools manufacture for food extraction (e.g. stripping sticks for
189 use in honeypot). Additionally, we introduced a new measure of handedness that considers
190 transfers of objects to the opposite hand prior to object manipulation. Hopkins (2006) noted
191 that the tube task produced a right hand dominance even when controlling for the hand in
192 which the chimpanzee received the tube. Specifically, the ‘hand transfer’ measure evaluated
193 when an object was grasped by dominant hand and then transferred to the non-dominant
194 hand, such that the dominant hand was free to perform manipulative actions upon the object.
195 We hypothesised that the cost of transferring an object is outweighed by the increase of
196 efficiency achieved through performing the manipulation with the dominant hand.

197

198 METHODS

199

200 *Subjects*

201

202 Data were collected on 13 (6 males), captive western lowland gorillas (*Gorilla gorilla*)

203 living in a peer-raised, semi-free ranging, biological family group at Port Lympne Wild

204 Animal Park, UK. The group was made up of one silverback, seven adult females, four

205 juvenile males and one juvenile female (see Table 1) ranging in age from 2-36 years.

206 Observational consent was granted by the John Aspinall Foundation. Due to the non-

207 invasive nature of this study, further permits or ethical approvals were not required.

208

209 *Housing and Enrichment*

210

211 The ‘Palace of the Apes’ is the world’s largest family gorilla house and is modeled on the

212 habitat of wild gorillas. The gorillas are considered ‘semi free ranging’, in that they move

213 freely about the large enclosure comprised of four composite parts: caged upper, caged

214 lower, inside and garden. The two-tiered outside enclosure is fronted by toughened glass,

215 and equipped with enrichment equipment including: ropes, nets and slides to encourage

216 physical activity. Inside, there is a play area equipped with further enrichment equipment

217 and 14 bedrooms with access to water. By way of the caged upper and lower areas of the

218 enclosure, the gorillas have further access to a large garden equipped with climbing frames,

219 trees, logs, a boundary stream and a large pile of boulders. The garden has viewing windows

220 at ground level and unimpeded visual access from above the garden via a raised steel

221 footpath. Both the caged area and the garden have food receptacles for enrichment purposes

222 that require the gorillas to prepare sticks that fit the hole for retrieving the contents. Contents

223 of the receptacle vary (e.g. honey, peanut butter, hummus, marmite). Further enrichment is

224 regularly provided in the form of retrieving food from different types of cartons in order to

225 cognitively challenge individuals and maintain high standards of animal welfare.

226

227 *Nourishment*

228

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

240

241 *Data Capture*

242

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

253 viewed in a top/bottom format for subsequent coding using OBSERVATRON coding
254 software (Forrester 2008).

255

256 *Coding*

257

258 Bimanual actions were defined in line with Meguerditchian et al. (2010) such that one hand
259 holds an object (non-dominant hand) while the opposite hand performs any manipulations of
260 the object and brings it to the mouth in the case of feeding (dominant hand). Bimanual
261 actions consisted of manipulating foods for ingestions (e.g. stripping and folding nettles,
262 stripping leaves, and extracting nuts from their shells), using tools to extract food (e.g.
263 dipping sticks in honey pot) and manufacturing tools to for food extraction (e.g. stripping
264 sticks for use in honeypot). Bimanual actions began when one hand reached for an object for
265 manipulation. The hand supporting the object was classified as the ‘non-dominant’ hand and
266 was classified as left or right, whilst the hand used for manipulation of the object was
267 classified as the ‘dominant’ hand was classified as the opposite hand (see Video 1 and Video
268 2 for examples of nettle folding and honeypot dipping bimanual actions). In the case of the
269 honey dipping, the dominant hand manipulated the tool, while the non-dominant hand held
270 the receptacle and simultaneously provided postural support.

271

272 Additionally, we coded the frequency of hand transfer events prior to object manipulation.
273 Franz and colleagues (2002) demonstrated that the lead hand in a bimanual sequence does
274 not necessarily signify the dominant hand (e.g. reaching for the object), but rather could be a
275 consequence of posture (e.g. postural origins hypothesis; MacNeilage et al. 1987). For this
276 measure we coded hand transfer events preceding bimanual object manipulation that
277 involved the transfer of an object from one hand to the other such that the gorilla could
278 employ the dominant hand for manipulation. For example, a locomoting gorilla may pick up
279 a stick with the left hand on the way to the honeypot, but then transfers the stick to the right
280 hand prior to dipping for honey. This action was coded as a transfer for right hand

281 dominance such that the right hand could perform the dominant action. Furthermore, a
282 gorilla might pick a nettle with the right hand, but then transfer it to the left hand such that
283 the left hand can support the object while the right hand performs the actions of stripping
284 and folding the nettles. This was also coded as a transfer for right hand dominance (see
285 Video 3 for examples of hand transfers). Research into human handedness has shown that
286 bilateral transfers can be used as a marker of hand dominance (Kumar & Mandal 2005).

287

288 For both measures of handedness, we calculated the frequency of dominant hand actions for
289 bouts. Bouts began when one hand reached for an object for manipulation. Once the item
290 was gathered, only the first manipulative action was coded for hand dominance. In the case
291 of a hand transfer prior to manipulation, we first coded hand dominance and then coded the
292 first manipulative action for hand dominance. A bout ended when the focal animal released
293 the object. Although there has been some controversy in the literature whether events or
294 bouts represent the most valid measure for evaluating hand dominance (McGrew &
295 Marchant 1997; Hopkins et al. 2001), concerning a statistical bias that may result from the
296 dependence of the data between each hand use response (e.g. pseudo-replication) (see
297 Hurlburt 1984; Palmer 2003), a high correlation has been found between analyses of bouts
298 and events, suggesting they are equally valid measures of handedness (e.g. Hopkins et al.
299 2005a).

300

301 *Analyses*

302

303 For both bimanual actions and hand transfer measures, we calculated frequencies,
304 proportions, rates and Handedness Index (HI) scores for bouts. We employed a range of
305 measures to demonstrate the consistency of the results across a range of statistical
306 preferences throughout the literature. Specifically proportions and rates were used to
307 equalise the weighting that each participant contributed to the data set. This is a critical
308 evaluation process as to not let a single subject or non-significant group of subjects sway the

309 group statistical test results. As each individual contributed a different number of bouts to
310 the dataset, proportions were calculated by dividing the frequency of left or right hand
311 actions by the total frequency of actions. Additionally, coded observation times varied
312 between individuals as a result of animal visibility. Therefore, rates were calculated by
313 dividing the frequency of bimanual actions by the total number of observational minutes per
314 subject. Paired sample t-tests were used to compare bout group means for frequencies,
315 proportions and rates for both hand dominance and hand transfers. A mean handedness
316 index (MHI) score was also calculated for the group. Nonparametric Wilcoxon tests were
317 also performed as a stricter test of difference. All statistical tests were two-tailed with alpha
318 < 0.05 .

319

320 In order to reveal individual patterns of hand dominance for bimanual actions and hand
321 transfer measures, we calculated the z-scores, binomial approximations of the z-scores, and
322 the individuals' strength of handedness using handedness index (HI) scores (see Tables 2
323 and 3). The direction of hand preference for each subject was calculated using z-scores such
324 that gorillas were left handed when $z \leq -1.96$, right handed when $z \geq 1.96$ and ambiguously
325 handed when $-1.96 < z < 1.96$. HI scores were calculated for each subject in for both
326 measures to establish the degree of hand asymmetry. HI scores were calculated using the
327 formula $[HI = (R-L)/(R+L)]$, with R and L being the frequency counts for right and left hand
328 dominance in bimanual actions. When $R=L$, the HI is taken to be zero. HI values vary on a
329 continuum between -1.0 and +1.0, where the sign indicates the direction of hand preferences.
330 Positive values reflect a right hand preference while negative values reflect a left hand
331 preference. Two subjects were excluded from analyses for the measure of hand transfer due
332 to low overall counts (total counts < 10). Excluded subjects are marked with a double
333 asterisk (see Table 3). All statistical tests were two-tailed with alpha < 0.05 .

334

335

336

337 RESULTS

338

339 *Hand Dominance*

340

341 The frequencies, proportions and rates of bouts along with their associated HI scores, z-
342 scores and binomial approximations of the z-scores for the measures of hand dominance are
343 displayed in Tables 2. A one sample t-test of the MHI scores for hand dominance (Mean =
344 0.62, SE = 0.07) indicated a significant population-level right-handedness, $t_{12} = 10.62$, $P <$
345 0.001.

346

347 A paired-sample t-test of frequencies demonstrated a significant bias for right hand
348 dominance (Mean = 24.54, SE = 3.01), compared with left handed dominance (Mean = 6.08,
349 SE = 1.48) for bimanual actions, $t_{12} = -7.44$, $P < 0.001$. A paired-sample t-test of
350 proportions demonstrated a significant right-handed dominance (Mean = 0.81, SE = 0.028),
351 compared with left handed dominance (Mean = 0.19, SE = 0.028) for bimanual actions, $t_{12} =$
352 -10.86 , $P < 0.001$. A paired-sample t-test of rates demonstrated a significant right-handed
353 dominance (Mean = 0.21, SE = 0.04), compared with left-handed dominance (Mean = 0.05,
354 SE = 0.01) for bimanual actions, $t_{12} = -4.41$, $P = 0.001$ (Figure 1). Based on the P -values
355 from the binomial approximations of the z-scores, ten of the thirteen gorillas (76.9%)
356 demonstrated a significant right-handed dominance for bimanual actions. Three gorillas
357 were ambiguously handed, however each of the three individuals' HI scores indicated a
358 right-hand bias. Hand dominance measures were also calculated using the nonparametric
359 Wilcoxon signed-ranks test. There was no change in the significant pattern of the results.

360

361 *Hand Transfer*

362

363 The frequencies, proportions and rates of bouts along with their associated HI scores, z-
364 scores and binomial approximations of the z-scores for the measures of hand transfer are

365 displayed in Tables 3. A one sample t-test of MHI scores for hand transfer (Mean = 0.71, SE
366 = 0.09) indicated a significant population-level right hand dominance, $t_{10} = 10.00$, $P < 0.001$.

367

368 Under exclusion criteria (n=11 for counts > 10), a paired-sample t-test of frequencies
369 demonstrated a significant bias for transfers from right hand to left hand (Mean = 18.64, SE
370 = 2.33), compared with transfers from left hand to right hand (Mean = 3.45, SE = 1.22) for
371 bimanual actions, $t_{10} = - 6.63$, $P < 0.001$. Under the exclusion criteria, a paired-sample t-test
372 of proportions demonstrated a significant bias for transfers from right hand to left hand
373 (Mean = 0.86, SE = 0.44), compared with left hand to right hand (Mean = 0.15, SE = 0.44),
374 for bimanual actions, $t_{10} = - 8.14$, $P < 0.001$. Under exclusion criteria, a paired-sample t-test
375 of rates demonstrated a significant bias for transfers from right hand to left hand (Mean =
376 0.13, SE = 0.02), compared with transfers from left hand to right hand (Mean = 0.03, SE =
377 0.01) for bimanual actions, $t_{10} = - 6.18$, $P < 0.001$ (Figure 2). Based on the P -values from
378 the binomial approximations of the z-scores, eight of the eleven gorillas (72.7%)
379 demonstrated a significant bias for transfers from right hand to left hand for bimanual
380 actions. Three gorillas were ambiguously handed, however individual HI scores maintained
381 a preference for right-hand dominance. Hand transfer measures were also calculated using
382 the nonparametric Wilcoxon signed ranks test. There was no change in the significant
383 pattern of the results.

384

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

387

388 DISCUSSION

389

390 The findings from this study demonstrated a significant population-level right-handed bias
391 for the measures of bimanual actions and hand transfer. The majority of individual subjects
392 demonstrated a significant right hand preference for both measures. There was no significant

393 difference between the strength of hand preference when comparing the two measures, thus
394 hand transfers may offer an alternative and/or complementary objective measure of hand
395 dominance. Our finding of a population-level right hand bias for bimanual actions is
396 consistent with previous studies of captive apes performing the tube task (e.g. Hopkins et al.
397 2011) as well as with studies the majority of studies investigating naturalistic bimanual
398 feeding behaviours in captive (Meguerditchian et al. 2010) and wild gorillas (Byrne & Byrne
399 1991).

400

401 The implementation of the measure of hand transfer to investigate ape handedness appears to
402 be a relevant marker of hand dominance. Like grip morphology, hand transfer may also
403 prove to be sensitive to dextral complexity. Hand transfers were likely to have been
404 performed when the sequence of object manipulation actions could not be efficiently or
405 effectively performed with the non-dominant hand. In human children, planning abilities
406 have been exploited through the measure of hand transfer tasks. Specifically, when one hand
407 supports an object (non dominant) and the other hand (dominant) manipulates aspects of the
408 object, infants under 2 years of age tend to transfer the object from the right to the left hand.
409 Older children anticipate the requirement of the dominant hand and thus begin the bimanual
410 task by grasping the object with the non-dominant hand (Potier, Meguerditchian & Fagard
411 2012), further suggesting that hand transfers may be a useful measure of individual
412 handedness development during increasing task complexity.

413

414 There is growing evidence in humans that lateralised behaviours manifesting from
415 contralateral domain specific neural processing extends beyond the association between
416 population-level right-handedness and left hemisphere language regions. For example, the
417 right hand has also shown a significant bias for communicative gesture (Corina et al. 1993),
418 implicating a dominant left hemisphere control. Conversely, a left visual field/right
419 hemisphere preference has been identified in face perception for exploring the left side of a
420 centrally presented face when measured behaviourally (looking time; Burt & Perrett 1997)

421 and with functional imaging (Kanwisher et al. 1998). As in humans, in addition to object
422 manipulation, great apes have also demonstrated a right hand bias for communicative
423 gestures in a range of chimpanzee populations (Hopkins & Leavens 1998; Hopkins et al.
424 2005b; Meguerditichian et al. 2009; 2012), suggesting left hemisphere dominant processing.
425 Conversely, leftward action biases have been reported for social-emotional processing for
426 self-directed face touching in orangutans (Rogers & Kaplan 1995), self-scratching (Leavens
427 et al. 2004) and during increases in task complexity in chimpanzees (Leavens et al. 2001),
428 potentially resulting from a rise in stress or arousal levels increasing right hemisphere
429 processing. Another method that appears to probe cerebral lateralisation of domain specific
430 processing involves assessing the type of target to which hand actions are directed. For
431 example, chimpanzees demonstrated a right hand preference for touching their inanimate
432 environments and ambi-preference for self-directed behaviours (Aruguete et al. 1992).
433 Similarly, a unimanual right hand bias was found for actions towards inanimate objects, but
434 ambi-preference for unimanual actions to animate targets (self and conspecifics) in gorillas
435 (Forrester et al. 2011), chimpanzees (Forrester et al. 2012) and typically developing children
436 (Forrester et al. 2013). These findings add to the mounting evidence that lateralised motor
437 actions are markers of contralateral domain specific cerebral lateralisation, where the left
438 hemisphere presides over structured sequences of actions, while the right hemisphere
439 dominates social-emotional processing (e.g. MacNeilage 2009). The implications of such
440 brain organisation is integral to the evolution and development of higher cognitive functions,
441 as emergent functions are predicted to develop within the hemisphere that could support that
442 function through the exaptation of neural regions for processing more elementary functions
443 with similar underlying structure.

444

445 Some posit that Broca's area may be a supra-modal hierarchical processor, supporting a
446 speculative hypothesis that language emerged from left hemisphere dominant neural regions
447 originally evolved to cope with the hierarchical sequences of actions inherent in tool use
448 (Pulvermüller & Fadiga 2010; Petersson et al. 2012). Action sequences for object

449 manipulation (that are not random) were proposed to possess a rudimentary syntax (e.g.
450 Tettamanti & Weniger 2006; Pastra & Aloimonos 2012). For example, in human infants,
451 non-linguistic actions involving objects (e.g. self-feeding with a spoon) were seen to involve
452 hierarchical sequence of actions (Connolly & Dagleish 1989; Greenfield 1991). Specifically,
453 the activity in Broca's region has been shown to correlate with increasing hierarchical
454 structural complexity (Bates & Dick 2002; Greenfield 1991). Broca's area is typically
455 segmented into three regions: the pars triangularis (PTr), the pars orbitalis (PO) and the
456 pars opercularis (POp). Recent neuroimaging studies demonstrated the Pop was activated for
457 acquiring grammatical rules (i.e., having a hierarchical structure) (e.g. Tettamanti et al.
458 2002) and during complex grammar processing (Friederici et al. 2006), as opposed to an
459 area posterior to POp has been recognised for tasks of simple grammar (Sakai 2005).
460 Additionally, a transcranial magnetic stimulation study demonstrated that the POp was
461 critical for the encoding of complex human action (Clerget, et al. 2009). Moreover, an fMRI
462 investigation of healthy human adults evidenced an overlap of brain activity for perceiving
463 language and using tools in this same region (POp), suggesting that language and tool use
464 share a common neural generator for processing "complex hierarchical structures common
465 to these two abilities" (Higuchi et al. 2009). This growing body of evidence suggests that the
466 POp region of Broca's area may not be language-specific, but rather is active for disparate
467 tasks (e.g. linguistic, cognitive, sensorimotor) that involve computational processing of
468 hierarchical structure (Tettamanti & Weniger 2006) and that may also be present in other
469 primate tool users.

470

471 Although limited data exists from brain imaging studies of great apes, Catalupo and Hopkins
472 (2001) sampled 26 great apes and found a general leftward bias for the anatomical volume of
473 the POp. A subsequent sample of chimpanzees (Hopkins et al. 2008), demonstrated a non-
474 significant anatomical leftward bias, however the authors posit that differences in the
475 boundaries placed upon POp may have contributed to inconsistent findings between the two
476 studies. In fact, comparing the anatomical similarities of Broca's area in human and ape

477 brains rely primarily on the surface area or volume of the POp because the PTr and the PO
478 have not been reliably defined in the chimpanzee brain (e.g. Keller et al 2009; for a review
479 see Hopkins 2013). Inconsistencies in anatomical boundaries of Broca's area may have also
480 led to discrepancies in findings from cytoarchitectonic studies of human and ape brains
481 (Amunts et al. 1999; Ziles & Amunts 2010). Nevertheless, imaging studies have reported in
482 both humans (Foundas et al. 1995) and apes (Gilissen & Hopkins 2013) that a significantly
483 greater proportion of right-handers demonstrate a left hemisphere POp asymmetry compared
484 to left-handers, supporting a link between the neuroanatomical regions underpinning both
485 manual and language asymmetries across species. Additionally, when hand biases from
486 termite fishing, anvil use and simple reaching were assessed for neuroanatomical
487 characteristics from the MRI scans of 22 chimpanzees, the authors found that right-handed
488 chimpanzees had a significantly greater leftward asymmetry than non-right-handed subjects
489 within a region of the inferior frontal gyrus, known to overlap with Broca's area (Hopkins et
490 al. 2007), and also implicated in the processing of human language syntax (Peelle et al.
491 2004; Caplan et al. 2008). However, the correlation between right-handedness and left
492 hemisphere asymmetry was not evident for a region of the chimpanzee brain considered to
493 overlap with the Wernicke's area (see Hopkins & Cantalupo 2004 for planum temporale).
494 These findings suggest that the neural regions associated with tool use and language
495 production may overlap and be biased to the left hemisphere in right-handed individuals.
496 From an evolutionary perspective, the overlap in neural function underlying tool use and
497 language processes provides one possible example of neural exaptation (e.g. Gould & Vrba
498 1982; Iriki & Taoka 2012) supporting a hypothesis that language emerged from neural
499 regions originally evolved to cope with the hierarchical sequences of actions inherent in tool
500 use and manufacture. While the evolutionary emergence of population-level human right-
501 handedness remains speculative, the development of lateralised markers of contralateral
502 neural processing may unite studies of brain and behaviour and inform about the
503 evolutionary emergence of higher cognitive functions.

504

505 CONCLUSIONS

506 The present study focused on dense data collection for a small sample of captive gorillas and
507 assessed observed naturalistic hand dominance for bimanual object manipulation. Based on
508 our findings, we argue that gorillas possess population-level right-handedness for object
509 manipulation with a proportional split similar to that found in the human population.

510 Assessing great ape handedness within specific domains, like object manipulation, is more
511 in keeping with human handedness measures that *exclusively* focus on the routine sequences
512 of structured actions for tool use (e.g. Edinburgh Handedness Inventory; Oldfield 1971),
513 thus allowing for more direct intra-species comparisons. While we speculate an evolutionary
514 link between tool use and the emergence of human language, at present, there is a paucity of
515 behavioural and neuroanatomical finding to fully substantiate such a claim. Moreover, a
516 consistent methodological approach across laboratories, and the investigation of larger and
517 more diverse populations, are necessary progressions in order to generate reliable
518 behavioural markers of cerebral lateralisation and thus facilitate the synthesis and
519 generalisation of findings. Nevertheless, based on the results of the current study and those
520 from the literature that span disparate species, not only can lateralised motor actions act as
521 plausible markers of contralateral neural generators, they may also provide insight into the
522 evolution of cognitive function.

523

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1000 **FIGURE LEGENDS**

1001

1002 **Figure 1.** Demonstrates the difference in mean proportion for left and right hand dominance.

1003

1004 **Figure 2.** Demonstrates the difference in mean proportion for left and right hand dominant

1005 hand transfers.

1006

1007 **Figure 3.** Demonstrates the strength of handedness using MHI scores for hand dominance

1008 and hand transfers.

1009

1 ABSTRACT

2

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

19

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

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29 INTRODUCTION

30

31 Historically, researchers have argued that population-level right-handedness is a human-
32 unique behaviour, underpinned by an evolutionary link with left hemisphere neural regions
33 dedicated to language processing (e.g. Broca 1865; Wernicke 1874). Approximately 90% of
34 the human population are considered to be right-handed, (Porac & Coren 1981; Annett
35 1985). Additionally, about 95% of the right-handed population expresses language
36 dominance in the left hemisphere of the brain (Santrock 2008). Specifically, the inferior
37 frontal gyrus (Tomaiuolo et al. 1999; Robichon et al. 2000; Keller et al. 2009) and a portion
38 of the posterior temporal lobe (planum temporale) are proportionately larger in the left
39 hemisphere compared with the right hemisphere (Beaton 1997; Shapleske et al. 1999;
40 Sommer et al. 2001; 2008), and coincide with the anatomical locations of Broca's and
41 Wernicke's areas respectively (e.g. Horwitz et al. 2003). The commonality of the human left
42 hemisphere bias for handedness and language processing has perpetuated a theory that
43 lateralized motor action elicited by cerebral lateralisation for specific cognitive functions is
44 unique to humans (Warren 1980; Ettliger 1988; Crow 2004; Schoenemann 2006). Some
45 have posited that handedness is directly linked with language capabilities, such as articulated
46 speech (Annett 2002) or gesture (Corballis 2002). Others have suggested that handedness
47 may have originated from tool use (Greenfield 1991), coordinated bimanual actions
48 (Wundrum 1986; Hopkins et al. 2003), or bipedalism (Westergaard et al. 1998; Braccini et
49 al. 2010). However, the emergence of handedness and its evolutionary relationship with
50 language remains a controversial topic.

51

52 Lateralised motor action underpinned by cerebral lateralisation for specific cognitive
53 processes has now been revealed across a range of vertebrate (Vallortigara & Rogers 2005;
54 MacNeilage, et al. 2009; Rogers & Andrew 2002; Vallortigara et al. 2011) and invertebrate
55 (Anfora et al. 2011; Frasnelli et al. 2012) species, and thus, is no longer considered human
56 specific. For example, right hemisphere dominance has been identified for processing of

57 social stimuli in chimpanzees (*Pan troglodytes*, Morris et al. 1993), rhesus monkeys (*Macca*
58 *mulatta*, Guo et al. 2009), dogs (*Canis familiaris*, Guo et al. 2009) and sheep (*Ovis aries*,
59 Peirce et al. 2000). Alternatively, the left hemisphere has been reported to be dominant for
60 well-practiced sequences of actions, such as feeding tasks in pigeons (*Columbia livia*,
61 Güntürkün & Kesh 1987), chicks (*Gallus gallus domesticus*, Rogers 1995) and toads (*B.*
62 *bufo* and *B. marinus*, Robins & Rogers 2004), and in numeracy tasks in dolphins (*Tursiops*
63 *truncatus*, Killian et al. 2005). The result of such evidence, suggests that the right
64 hemisphere of the brain evolved as dominant for controlling arousal levels in order to react
65 quickly to the environment (e.g. predators), whilst the left hemisphere emerged as dominant
66 for processing routine behaviours with structured sequences of actions (e.g. feeding)
67 (Vallortigara et al. 2008, 2011; MacNeilage et al. 2009). An early evolutionary division of
68 labour for these critical survival processes in the left and right hemispheres may have
69 produced advantages for: increasing neural capacity, enabling parallel processing and
70 deterring the simultaneous initiation of incompatible responses (e.g. Andrew 1991;
71 Vallortigara 2000; Rogers 2002).

72

73 Based upon the evolutionary theory above, it is not surprising that hierarchically structured
74 language processes are left hemisphere dominant for the majority of the human population.
75 However, the precursor behaviours that language emerged from are poorly understood. For
76 over half a century, theoretical parallels have been drawn between the cognitive processes
77 underlying a left hemispheric specialisation for language and right-handed tool use in
78 humans. While hierarchical structures are known to be a distinctive component of language
79 (e.g. Hauser et al. 2002), it has been suggested that they also appear in non-linguistic
80 domains such as object manipulation (for a review see Tettamanti 2003). Motor activity has
81 been described as a hierarchy of structured sequence of behavioural units (Holloway 1969);
82 and hierarchical action sequences are integral to tool use (e.g. Lashley 1951; Dawkins 1976;
83 Byrne & Russon 1998). While some have argued that the sequences of actions supporting
84 tool manufacture do not possess a linguistic type of syntax because the actions are based

85 upon physical constraints rather than internal rules (e.g. Graves 1994; Wynn 1995), others
86 have argued that some Paleolithic tool manufacturing methods do share abstract syntactical
87 content with linguistic processes (e.g. Holloway 1981; Stout & Chaminade 2009).
88 Additionally, evidence from prehistoric human tool use and manufacture suggests that
89 human population-level right-handedness has origins that precede the emergence of modern
90 human language. Specifically, archaeological data suggest that right biased asymmetries
91 existed in the arm and hand bones at least by the stage of the genus *Homo*. Evidence from
92 tool use production and cave art suggests that population-level right-handedness was
93 established in Neanderthals (for a review see Cashmore et al. 2008), thus preceding human
94 language, which is claimed to have emerged not earlier than 100,000 years ago (e.g. Ott
95 2009). One hypothesis is that right-handed tool use provided an evolutionary bridge between
96 left hemisphere dominant action sequences and language processes (Hamzei et al. 2003).
97
98 Great apes are proven tool users in both wild and captive settings; and although they do not
99 possess language, great apes demonstrate evidence of a neuroanatomical brain region that
100 overlaps with Broca's regions and that, like in humans, is proportionately larger in the left
101 hemisphere than in the right hemisphere (e.g. Cantalupo & Hopkins 2001; Hopkins et al.
102 2007). Therefore, great apes offer an excellent animal model to investigate the evolutionary
103 link between handedness and human language. Early handedness studies achieved
104 inconsistent results in both captive (e.g. Finch 1941; Marchant 1983; Annett & Annett 1991;
105 Hopkins 1993) and wild ape populations (e.g. Boesch 1991; McGrew & Marchant 1992;
106 Shafer 1993). However, traditional handedness coding methods may not have effectively
107 revealed manual biases. Early behavioural studies of great ape handedness assessed
108 unimanual actions, such as simple reaching or manipulation tasks. Unimanual actions can
109 often be confounded by postural (e.g. one hand supporting posture) and situational elements
110 (e.g. one hand occupied with an object) (Aruguete et al. 1992; Westergaard et al. 1998;
111 Braccini et al. 2010). Additionally, it is now acknowledged that task complexity can
112 influence the direction, magnitude and consistency of hand preference of both humans (e.g.

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

117

118 More recently, studies have investigated bimanual actions, characterised by both hands
119 cooperating in the manipulation or processing of the same item. During bimanual actions,
120 one hand is used to support an item (the non dominant hand) while the other hand
121 manipulates the item (dominant hand) (e.g. McGrew & Marchant 1997). Bimanual
122 handedness is thought to represent more complex behaviours and is considered to be a more
123 sensitive measure of hand dominance (e.g. Hopkins 2006; Vauclair & Meguerditichian
124 2007). Additionally, investigating bimanual actions minimises postural factors due to the
125 necessity for the individual to appropriate a bipedal or seated posture in order for both hands
126 to be available to engage in a bimanual task (Roney & King 1993). Laboratory studies that
127 investigated the bimanual actions of large samples of chimpanzees have revealed evidence
128 of population-level right-handedness (Hopkins & Russell 2004; Hopkins et al. 2004; for a
129 review see: Hopkins 2006; 2007). Studies implemented a tube task that required
130 chimpanzees to manipulate an object (tube) to retrieve food. Peanut butter was placed deep
131 inside of poly-vinyl-chloride tubes such that the chimpanzees could not lick the contents, as
132 successful retrieval of food required the insertion of fingers for extraction. Some have
133 contended that captive ape handedness could be confounded from exposure to human
134 behaviour (McGrew & Marchant 1997; Palmer 2002; 2003; Crow 2004), and queried
135 methods of statistical analyses (Hopkins 1999, Hopkins & Cantalupo 2005). However, more
136 recent studies, controlling for confounding factors, have also revealed population-level right-
137 hand biases for bimanual tasks in naturalistically housed chimpanzees (Llorente et al. 2009;
138 2011). Conversely, observational studies of wild chimpanzee termite fishing have
139 consistently revealed a left-handed bias (Lonsdorf & Hopkins 2005; Hopkins et al. 2009).

140 However, it has been postulated that for this task, the less demanding action (dipping) is

141 directed by the non-dominant left hand, such that the more demanding range of actions (e.g.
142 bridging termites to the mouth, grasp termites outside the mound) can be conducted by the
143 dominant right hand (Bogart et al. 2012). In general, findings from chimpanzee bimanual
144 actions studies contradict the traditional supposition that population-level right-handedness
145 is a human unique characteristic, and support the hypothesis that right-handedness has been
146 inherited from a last common ancestor, preceding the emergence of human language skills.

147

148 Compared with studies of chimpanzee, gorillas are largely neglected in the handedness
149 literature. Whether or not gorillas demonstrate population-level handedness is debated due to
150 limited and inconsistent findings across laboratories (e.g. McGrew & Marchant 1993). An
151 early study investigating unimanual and bimanual actions of 10 captive gorillas found no
152 population-level bias for unimanual reaching, but did report a left hand population bias for a
153 bimanual spatial task requiring the alignment of two openings (Fagot & Vauclair 1988). The
154 authors posited that the task might have probed mental rotation capabilities, widely
155 considered to be a right-hemisphere dominant capability in humans (e.g. Jones & Anuza
156 1982). More recently, the tube task has been extended to bonobos (*Pan paniscus*), gorillas
157 and orangutans (*Pongo pygmaeus*) (Hopkins et al. 2011). Results from these investigations
158 demonstrated that like chimpanzees, bonobos and gorillas also revealed right-handed
159 population biases when assessed for handedness during this specific bimanual coordinated
160 activity. Only three studies, to date, have investigated the spontaneous bimanual behaviours
161 of gorillas. Byrne & Byrne (1991) found a significant right hand bias for bimanual multi-
162 stage sequences of food processing in a group of 44 mountain gorillas, where the strongest
163 degree of hand preference was for processing food types in which leaves were protected by
164 stings. Two more recent studies investigated naturalistic bimanual feeding behaviours of
165 captive gorillas, but achieved varied results. Both studies assessed unimanual, simple
166 reaching behaviours to food items and bimanual feeding behaviours in captive gorillas
167 (Meguerditchian et al. 2010; Lambert 2012). Neither study reported a population-level bias
168 for unimanual simple reaching actions, however Meguerditchian and colleagues (2010)

169 revealed a significant right-hand population-level bias for bimanual feeding actions. While
170 Lambert (2012) demonstrated stronger manual biases for bimanual feeding compared with
171 unimanual simple reaching, bimanual actions were not found to be significantly right-
172 handed. The author proposed that bimanual actions may vary in complexity and that
173 assessing different grip morphologies may provide an alternate way to measure hand
174 dominance. Specifically, precision grip, versus power grip, may signify more complex
175 dextral action, and therefore elicit a dominant hand bias (e.g. Pouydebat et al. 2011).
176
177 Although inconsistent methodological approaches may be responsible for mixed results
178 across laboratories, much of the research points to a right-handed bias in great apes during
179 object manipulation. One possible interpretation of the literature is that right-handedness in
180 humans is not a direct by-product of language capabilities, but rather the behavioural
181 manifestation of left hemisphere dominance for processing structured sequences of actions.
182 We hypothesise that this inherited cerebral lateralisation characteristic can be exploited in
183 our closest living relatives, specifically during bimanual behaviours for object manipulation
184 sequences. Therefore, in the present study we investigated the naturalistic spontaneous
185 behaviours of a biological group of captive gorillas (*Gorilla gorilla gorilla*) performing
186 bimanual object manipulation during: feeding (e.g. leaf stripping, nettle folding and
187 honeypot dipping), tool use for food retrieval (preparing sticks for the honey pot, using
188 sticks in the honey pot) and tools manufacture for food extraction (e.g. stripping sticks for
189 use in honeypot). Additionally, we introduced a new measure of handedness that considers
190 transfers of objects to the opposite hand prior to object manipulation. Hopkins (2006) noted
191 that the tube task produced a right hand dominance even when controlling for the hand in
192 which the chimpanzee received the tube. Specifically, the ‘hand transfer’ measure evaluated
193 when an object was grasped by dominant hand and then transferred to the non-dominant
194 hand, such that the dominant hand was free to perform manipulative actions upon the object.
195 We hypothesised that the cost of transferring an object is outweighed by the increase of
196 efficiency achieved through performing the manipulation with the dominant hand.

197

198 METHODS

199

200 *Subjects*

201

202 Data were collected on 13 (6 males), captive western lowland gorillas (*Gorilla gorilla*)

203 living in a peer-raised, semi-free ranging, biological family group at Port Lympne Wild

204 Animal Park, UK. The group was made up of one silverback, seven adult females, four

205 juvenile males and one juvenile female (see Table 1) ranging in age from 2-36 years.

206 Observational consent was granted by the John Aspinall Foundation. Due to the non-

207 invasive nature of this study, further permits or ethical approvals were not required.

208

209 *Housing and Enrichment*

210

211 The ‘Palace of the Apes’ is the world’s largest family gorilla house and is modeled on the

212 habitat of wild gorillas. The gorillas are considered ‘semi free ranging’, in that they move

213 freely about the large enclosure comprised of four composite parts: caged upper, caged

214 lower, inside and garden. The two-tiered outside enclosure is fronted by toughened glass,

215 and equipped with enrichment equipment including: ropes, nets and slides to encourage

216 physical activity. Inside, there is a play area equipped with further enrichment equipment

217 and 14 bedrooms with access to water. By way of the caged upper and lower areas of the

218 enclosure, the gorillas have further access to a large garden equipped with climbing frames,

219 trees, logs, a boundary stream and a large pile of boulders. The garden has viewing windows

220 at ground level and unimpeded visual access from above the garden via a raised steel

221 footpath. Both the caged area and the garden have food receptacles for enrichment purposes

222 that require the gorillas to prepare sticks that fit the hole for retrieving the contents. Contents

223 of the receptacle vary (e.g. honey, peanut butter, hummus, marmite). Further enrichment is

224 regularly provided in the form of retrieving food from different types of cartons in order to

225 cognitively challenge individuals and maintain high standards of animal welfare.

226

227 *Nourishment*

228

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

240

241 *Data Capture*

242

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

253 viewed in a top/bottom format for subsequent coding using OBSERVATRON coding
254 software (Forrester 2008).

255

256 *Coding*

257

258 Bimanual actions were defined in line with Meguerditchian et al. (2010) such that one hand
259 holds an object (non-dominant hand) while the opposite hand performs any manipulations of
260 the object and brings it to the mouth in the case of feeding (dominant hand). Bimanual
261 actions consisted of manipulating foods for ingestions (e.g. stripping and folding nettles,
262 stripping leaves, and extracting nuts from their shells), using tools to extract food (e.g.
263 dipping sticks in honey pot) and manufacturing tools to for food extraction (e.g. stripping
264 sticks for use in honeypot). Bimanual actions began when one hand reached for an object for
265 manipulation. The hand supporting the object was classified as the ‘non-dominant’ hand and
266 was classified as left or right, whilst the hand used for manipulation of the object was
267 classified as the ‘dominant’ hand was classified as the opposite hand (see Video 1 and Video
268 2 for examples of nettle folding and honeypot dipping bimanual actions). In the case of the
269 honey dipping, the dominant hand manipulated the tool, while the non-dominant hand held
270 the receptacle and simultaneously provided postural support.

271

272 Additionally, we coded the frequency of hand transfer events prior to object manipulation.
273 Franz and colleagues (2002) demonstrated that the lead hand in a bimanual sequence does
274 not necessarily signify the dominant hand (e.g. reaching for the object), but rather could be a
275 consequence of posture (e.g. postural origins hypothesis; MacNeilage et al. 1987). For this
276 measure we coded hand transfer events preceding bimanual object manipulation that
277 involved the transfer of an object from one hand to the other such that the gorilla could
278 employ the dominant hand for manipulation. For example, a locomoting gorilla may pick up
279 a stick with the left hand on the way to the honeypot, but then transfers the stick to the right
280 hand prior to dipping for honey. This action was coded as a transfer for right hand

281 dominance such that the right hand could perform the dominant action. Furthermore, a
282 gorilla might pick a nettle with the right hand, but then transfer it to the left hand such that
283 the left hand can support the object while the right hand performs the actions of stripping
284 and folding the nettles. This was also coded as a transfer for right hand dominance (see
285 Video 3 for examples of hand transfers). Research into human handedness has shown that
286 bilateral transfers can be used as a marker of hand dominance (Kumar & Mandal 2005).

287

288 For both measures of handedness, we calculated the frequency of dominant hand actions for
289 bouts. Bouts began when one hand reached for an object for manipulation. Once the item
290 was gathered, only the first manipulative action was coded for hand dominance. In the case
291 of a hand transfer prior to manipulation, we first coded hand dominance and then coded the
292 first manipulative action for hand dominance. A bout ended when the focal animal released
293 the object. Although there has been some controversy in the literature whether events or
294 bouts represent the most valid measure for evaluating hand dominance (McGrew &
295 Marchant 1997; Hopkins et al. 2001), concerning a statistical bias that may result from the
296 dependence of the data between each hand use response (e.g. pseudo-replication) (see
297 Hurlburt 1984; Palmer 2003), a high correlation has been found between analyses of bouts
298 and events, suggesting they are equally valid measures of handedness (e.g. Hopkins et al.
299 2005a).

300

301 *Analyses*

302

303 For both bimanual actions and hand transfer measures, we calculated frequencies,
304 proportions, rates and Handedness Index (HI) scores for bouts. We employed a range of
305 measures to demonstrate the consistency of the results across a range of statistical
306 preferences throughout the literature. Specifically proportions and rates were used to
307 equalise the weighting that each participant contributed to the data set. This is a critical
308 evaluation process as to not let a single subject or non-significant group of subjects sway the

309 group statistical test results. As each individual contributed a different number of bouts to
310 the dataset, proportions were calculated by dividing the frequency of left or right hand
311 actions by the total frequency of actions. Additionally, coded observation times varied
312 between individuals as a result of animal visibility. Therefore, rates were calculated by
313 dividing the frequency of bimanual actions by the total number of observational minutes per
314 subject. Paired sample t-tests were used to compare bout group means for frequencies,
315 proportions and rates for both hand dominance and hand transfers. A mean handedness
316 index (MHI) score was also calculated for the group. Nonparametric Wilcoxon tests were
317 also performed as a stricter test of difference. All statistical tests were two-tailed with alpha
318 < 0.05 .

319

320 In order to reveal individual patterns of hand dominance for bimanual actions and hand
321 transfer measures, we calculated the z-scores, binomial approximations of the z-scores, and
322 the individuals' strength of handedness using handedness index (HI) scores (see Tables 2
323 and 3). The direction of hand preference for each subject was calculated using z-scores such
324 that gorillas were left handed when $z \leq -1.96$, right handed when $z \geq 1.96$ and ambiguously
325 handed when $-1.96 < z < 1.96$. HI scores were calculated for each subject in for both
326 measures to establish the degree of hand asymmetry. HI scores were calculated using the
327 formula $[HI = (R-L)/(R+L)]$, with R and L being the frequency counts for right and left hand
328 dominance in bimanual actions. When $R=L$, the HI is taken to be zero. HI values vary on a
329 continuum between -1.0 and +1.0, where the sign indicates the direction of hand preferences.
330 Positive values reflect a right hand preference while negative values reflect a left hand
331 preference. Two subjects were excluded from analyses for the measure of hand transfer due
332 to low overall counts (total counts < 10). Excluded subjects are marked with a double
333 asterisk (see Table 3). All statistical tests were two-tailed with alpha < 0.05 .

334

335

336

337 RESULTS

338

339 *Hand Dominance*

340

341 The frequencies, proportions and rates of bouts along with their associated HI scores, z-
342 scores and binomial approximations of the z-scores for the measures of hand dominance are
343 displayed in Tables 2. A one sample t-test of the MHI scores for hand dominance (Mean =
344 0.62, SE = 0.07) indicated a significant population-level right-handedness, $t_{12} = 10.62$, $P <$
345 0.001.

346

347 A paired-sample t-test of frequencies demonstrated a significant bias for right hand
348 dominance (Mean = 24.54, SE = 3.01), compared with left handed dominance (Mean = 6.08,
349 SE = 1.48) for bimanual actions, $t_{12} = -7.44$, $P < 0.001$. A paired-sample t-test of
350 proportions demonstrated a significant right-handed dominance (Mean = 0.81, SE = 0.028),
351 compared with left handed dominance (Mean = 0.19, SE = 0.028) for bimanual actions, $t_{12} =$
352 -10.86 , $P < 0.001$. A paired-sample t-test of rates demonstrated a significant right-handed
353 dominance (Mean = 0.21, SE = 0.04), compared with left-handed dominance (Mean = 0.05,
354 SE = 0.01) for bimanual actions, $t_{12} = -4.41$, $P = 0.001$ (Figure 1). Based on the P -values
355 from the binomial approximations of the z-scores, ten of the thirteen gorillas (76.9%)
356 demonstrated a significant right-handed dominance for bimanual actions. Three gorillas
357 were ambiguously handed, however each of the three individuals' HI scores indicated a
358 right-hand bias. Hand dominance measures were also calculated using the nonparametric
359 Wilcoxon signed-ranks test. There was no change in the significant pattern of the results.

360

361 *Hand Transfer*

362

363 The frequencies, proportions and rates of bouts along with their associated HI scores, z-
364 scores and binomial approximations of the z-scores for the measures of hand transfer are

365 displayed in Tables 3. A one sample t-test of MHI scores for hand transfer (Mean = 0.71, SE
366 = 0.09) indicated a significant population-level right hand dominance, $t_{10} = 10.00$, $P < 0.001$.

367

368 Under exclusion criteria (n=11 for counts > 10), a paired-sample t-test of frequencies
369 demonstrated a significant bias for transfers from right hand to left hand (Mean = 18.64, SE
370 = 2.33), compared with transfers from left hand to right hand (Mean = 3.45, SE = 1.22) for
371 bimanual actions, $t_{10} = -6.63$, $P < 0.001$. Under the exclusion criteria, a paired-sample t-test
372 of proportions demonstrated a significant bias for transfers from right hand to left hand
373 (Mean = 0.86, SE = 0.44), compared with left hand to right hand (Mean = 0.15, SE = 0.44),
374 for bimanual actions, $t_{10} = -8.14$, $P < 0.001$. Under exclusion criteria, a paired-sample t-test
375 of rates demonstrated a significant bias for transfers from right hand to left hand (Mean =
376 0.13, SE = 0.02), compared with transfers from left hand to right hand (Mean = 0.03, SE =
377 0.01) for bimanual actions, $t_{10} = -6.18$, $P < 0.001$ (Figure 2). Based on the P -values from
378 the binomial approximations of the z-scores, eight of the eleven gorillas (72.7%)
379 demonstrated a significant bias for transfers from right hand to left hand for bimanual
380 actions. Three gorillas were ambiguously handed, however individual HI scores maintained
381 a preference for right-hand dominance. Hand transfer measures were also calculated using
382 the nonparametric Wilcoxon signed ranks test. There was no change in the significant
383 pattern of the results.

384

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

387

388 DISCUSSION

389

390 The findings from this study demonstrated a significant population-level right-handed bias
391 for the measures of bimanual actions and hand transfer. The majority of individual subjects
392 demonstrated a significant right hand preference for both measures. There was no significant

393 difference between the strength of hand preference when comparing the two measures, thus
394 hand transfers may offer an alternative and/or complementary objective measure of hand
395 dominance. Our finding of a population-level right hand bias for bimanual actions is
396 consistent with previous studies of captive apes performing the tube task (e.g. Hopkins et al.
397 2011) as well as with studies the majority of studies investigating naturalistic bimanual
398 feeding behaviours in captive (Meguerditchian et al. 2010) and wild gorillas (Byrne & Byrne
399 1991).

400

401 The implementation of the measure of hand transfer to investigate ape handedness appears to
402 be a relevant marker of hand dominance. Like grip morphology, hand transfer may also
403 prove to be sensitive to dextral complexity. Hand transfers were likely to have been
404 performed when the sequence of object manipulation actions could not be efficiently or
405 effectively performed with the non-dominant hand. In human children, planning abilities
406 have been exploited through the measure of hand transfer tasks. Specifically, when one hand
407 supports an object (non dominant) and the other hand (dominant) manipulates aspects of the
408 object, infants under 2 years of age tend to transfer the object from the right to the left hand.
409 Older children anticipate the requirement of the dominant hand and thus begin the bimanual
410 task by grasping the object with the non-dominant hand (Potier, Meguerditchian & Fagard
411 2012), further suggesting that hand transfers may be a useful measure of individual
412 handedness development during increasing task complexity.

413

414 There is growing evidence in humans that lateralised behaviours manifesting from
415 contralateral domain specific neural processing extends beyond the association between
416 population-level right-handedness and left hemisphere language regions. For example, the
417 right hand has also shown a significant bias for communicative gesture (Corina et al. 1993),
418 implicating a dominant left hemisphere control. Conversely, a left visual field/right
419 hemisphere preference has been identified in face perception for exploring the left side of a
420 centrally presented face when measured behaviourally (looking time; Burt & Perrett 1997)

421 and with functional imaging (Kanwisher et al. 1998). As in humans, in addition to object
422 manipulation, great apes have also demonstrated a right hand bias for communicative
423 gestures in a range of chimpanzee populations (Hopkins & Leavens 1998; Hopkins et al.
424 2005b; Meguerditichian et al. 2009; 2012), suggesting left hemisphere dominant processing.
425 Conversely, leftward action biases have been reported for social-emotional processing for
426 self-directed face touching in orangutans (Rogers & Kaplan 1995), self-scratching (Leavens
427 et al. 2004) and during increases in task complexity in chimpanzees (Leavens et al. 2001),
428 potentially resulting from a rise in stress or arousal levels increasing right hemisphere
429 processing. Another method that appears to probe cerebral lateralisation of domain specific
430 processing involves assessing the type of target to which hand actions are directed. For
431 example, chimpanzees demonstrated a right hand preference for touching their inanimate
432 environments and ambi-preference for self-directed behaviours (Aruguete et al. 1992).
433 Similarly, a unimanual right hand bias was found for actions towards inanimate objects, but
434 ambi-preference for unimanual actions to animate targets (self and conspecifics) in gorillas
435 (Forrester et al. 2011), chimpanzees (Forrester et al. 2012) and typically developing children
436 (Forrester et al. 2013). These findings add to the mounting evidence that lateralised motor
437 actions are markers of contralateral domain specific cerebral lateralisation, where the left
438 hemisphere presides over structured sequences of actions, while the right hemisphere
439 dominates social-emotional processing (e.g. MacNeilage 2009). The implications of such
440 brain organisation is integral to the evolution and development of higher cognitive functions,
441 as emergent functions are predicted to develop within the hemisphere that could support that
442 function through the exaptation of neural regions for processing more elementary functions
443 with similar underlying structure.

444

445 Some posit that Broca's area may be a supra-modal hierarchical processor, supporting a
446 speculative hypothesis that language emerged from left hemisphere dominant neural regions
447 originally evolved to cope with the hierarchical sequences of actions inherent in tool use
448 (Pulvermüller & Fadiga 2010; Petersson et al. 2012). Action sequences for object

449 manipulation (that are not random) were proposed to possess a rudimentary syntax (e.g.
450 Tettamanti & Weniger 2006; Pastra & Aloimonos 2012). For example, in human infants,
451 non-linguistic actions involving objects (e.g. self-feeding with a spoon) were seen to involve
452 hierarchical sequence of actions (Connolly & Dagleish 1989; Greenfield 1991). Specifically,
453 the activity in Broca's region has been shown to correlate with increasing hierarchical
454 structural complexity (Bates & Dick 2002; Greenfield 1991). Broca's area is typically
455 segmented into three regions: the pars triangularis (PTr), the pars orbitalis (PO) and the
456 pars opercularis (POp). Recent neuroimaging studies demonstrated the Pop was activated for
457 acquiring grammatical rules (i.e., having a hierarchical structure) (e.g. Tettamanti et al.
458 2002) and during complex grammar processing (Friederici et al. 2006), as opposed to an
459 area posterior to POp has been recognised for tasks of simple grammar (Sakai 2005).
460 Additionally, a transcranial magnetic stimulation study demonstrated that the POp was
461 critical for the encoding of complex human action (Clerget, et al. 2009). Moreover, an fMRI
462 investigation of healthy human adults evidenced an overlap of brain activity for perceiving
463 language and using tools in this same region (POp), suggesting that language and tool use
464 share a common neural generator for processing "complex hierarchical structures common
465 to these two abilities" (Higuchi et al. 2009). This growing body of evidence suggests that the
466 POp region of Broca's area may not be language-specific, but rather is active for disparate
467 tasks (e.g. linguistic, cognitive, sensorimotor) that involve computational processing of
468 hierarchical structure (Tettamanti & Weniger 2006) and that may also be present in other
469 primate tool users.

470

471 Although limited data exists from brain imaging studies of great apes, Catalupo and Hopkins
472 (2001) sampled 26 great apes and found a general leftward bias for the anatomical volume of
473 the POp. A subsequent sample of chimpanzees (Hopkins et al. 2008), demonstrated a non-
474 significant anatomical leftward bias, however the authors posit that differences in the
475 boundaries placed upon POp may have contributed to inconsistent findings between the two
476 studies. In fact, comparing the anatomical similarities of Broca's area in human and ape

477 brains rely primarily on the surface area or volume of the POp because the PTr and the PO
478 have not been reliably defined in the chimpanzee brain (e.g. Keller et al 2009; for a review
479 see Hopkins 2013). Inconsistencies in anatomical boundaries of Broca's area may have also
480 led to discrepancies in findings from cytoarchitectonic studies of human and ape brains
481 (Amunts et al. 1999; Ziles & Amunts 2010). Nevertheless, imaging studies have reported in
482 both humans (Foundas et al. 1995) and apes (Gilissen & Hopkins 2013) that a significantly
483 greater proportion of right-handers demonstrate a left hemisphere POp asymmetry compared
484 to left-handers, supporting a link between the neuroanatomical regions underpinning both
485 manual and language asymmetries across species. Additionally, when hand biases from
486 termite fishing, anvil use and simple reaching were assessed for neuroanatomical
487 characteristics from the MRI scans of 22 chimpanzees, the authors found that right-handed
488 chimpanzees had a significantly greater leftward asymmetry than non-right-handed subjects
489 within a region of the inferior frontal gyrus, known to overlap with Broca's area (Hopkins et
490 al. 2007), and also implicated in the processing of human language syntax (Peelle et al.
491 2004; Caplan et al. 2008). However, the correlation between right-handedness and left
492 hemisphere asymmetry was not evident for a region of the chimpanzee brain considered to
493 overlap with the Wernicke's area (see Hopkins & Cantalupo 2004 for planum temporale).
494 These findings suggest that the neural regions associated with tool use and language
495 production may overlap and be biased to the left hemisphere in right-handed individuals.
496 From an evolutionary perspective, the overlap in neural function underlying tool use and
497 language processes provides one possible example of neural exaptation (e.g. Gould & Vrba
498 1982; Iriki & Taoka 2012) supporting a hypothesis that language emerged from neural
499 regions originally evolved to cope with the hierarchical sequences of actions inherent in tool
500 use and manufacture. While the evolutionary emergence of population-level human right-
501 handedness remains speculative, the development of lateralised markers of contralateral
502 neural processing may unite studies of brain and behaviour and inform about the
503 evolutionary emergence of higher cognitive functions.

504

505 CONCLUSIONS

506 The present study focused on dense data collection for a small sample of captive gorillas and
507 assessed observed naturalistic hand dominance for bimanual object manipulation. Based on
508 our findings, we argue that gorillas possess population-level right-handedness for object
509 manipulation with a proportional split similar to that found in the human population.

510 Assessing great ape handedness within specific domains, like object manipulation, is more
511 in keeping with human handedness measures that *exclusively* focus on the routine sequences
512 of structured actions for tool use (e.g. Edinburgh Handedness Inventory; Oldfield 1971),
513 thus allowing for more direct intra-species comparisons. While we speculate an evolutionary
514 link between tool use and the emergence of human language, at present, there is a paucity of
515 behavioural and neuroanatomical finding to fully substantiate such a claim. Moreover, a
516 consistent methodological approach across laboratories, and the investigation of larger and
517 more diverse populations, are necessary progressions in order to generate reliable
518 behavioural markers of cerebral lateralisation and thus facilitate the synthesis and
519 generalisation of findings. Nevertheless, based on the results of the current study and those
520 from the literature that span disparate species, not only can lateralised motor actions act as
521 plausible markers of contralateral neural generators, they may also provide insight into the
522 evolution of cognitive function.

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999

1000 **FIGURE LEGENDS**

1001

1002 **Figure 1.** Demonstrates the difference in mean proportion for left and right hand dominance.

1003

1004 **Figure 2.** Demonstrates the difference in mean proportion for left and right hand dominant

1005 hand transfers.

1006

1007 **Figure 3.** Demonstrates the strength of handedness using MHI scores for hand dominance

1008 and hand transfers.

1009

ACKNOWLEDGMENTS

We thank Phil Ridges and the Aspinall Foundation for observational access to their gorillas, Roberta Herrick for assistance with data collection, David A. Leavens for comments on the drafted manuscript and for advice on statistical analyses and Hazel Dewart and Angela Clow for promoting active research through the PPSS. This study was funded in part by the University of Westminster PPSS, the Daphne Jackson Trust and the Gatsby Charitable Foundation.

Figure 1 - Hand Dominance
[Click here to download high resolution image](#)

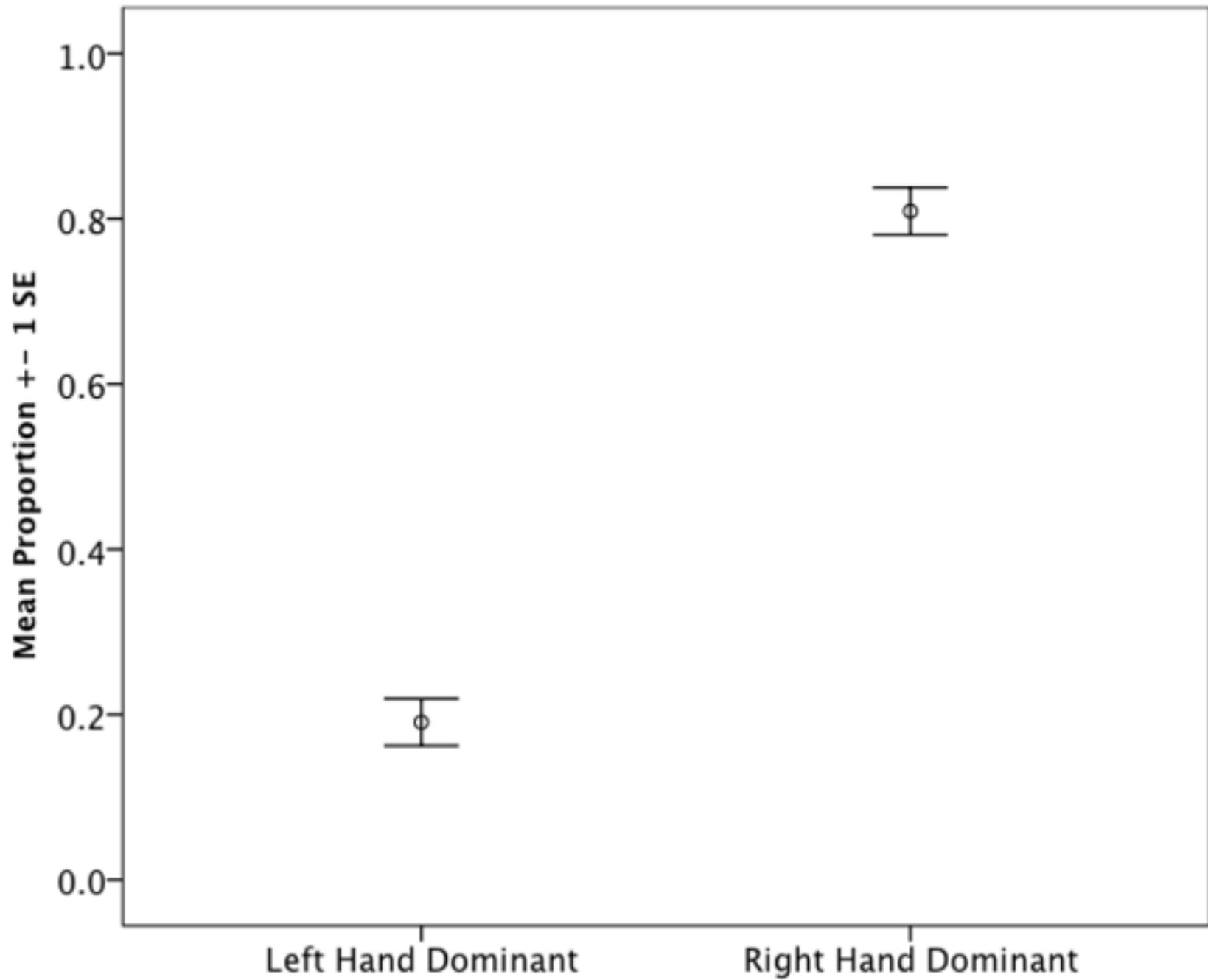


Figure 2 - Hand Transfers
[Click here to download high resolution image](#)

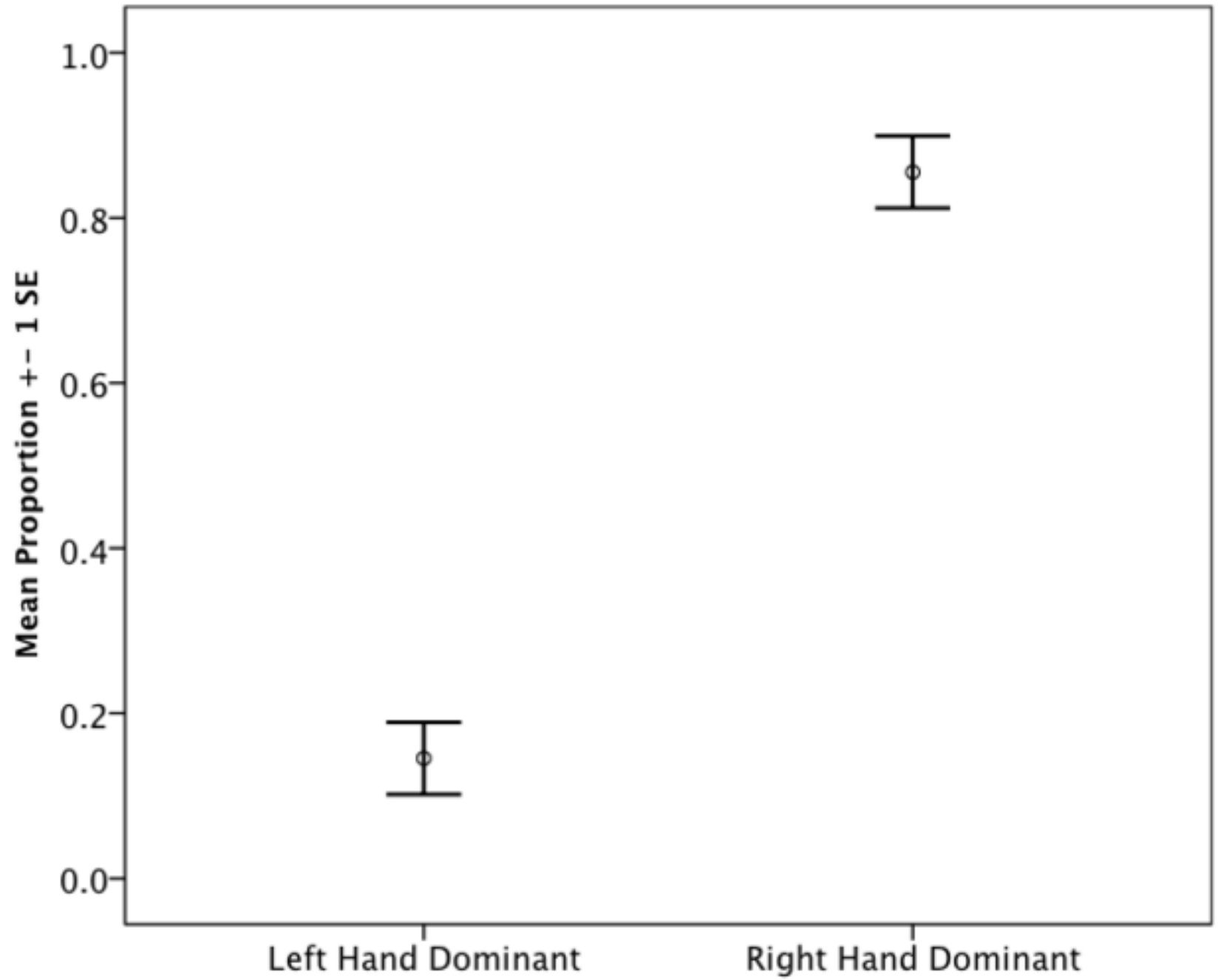


Figure 3 - MHI HD & HT
[Click here to download high resolution image](#)

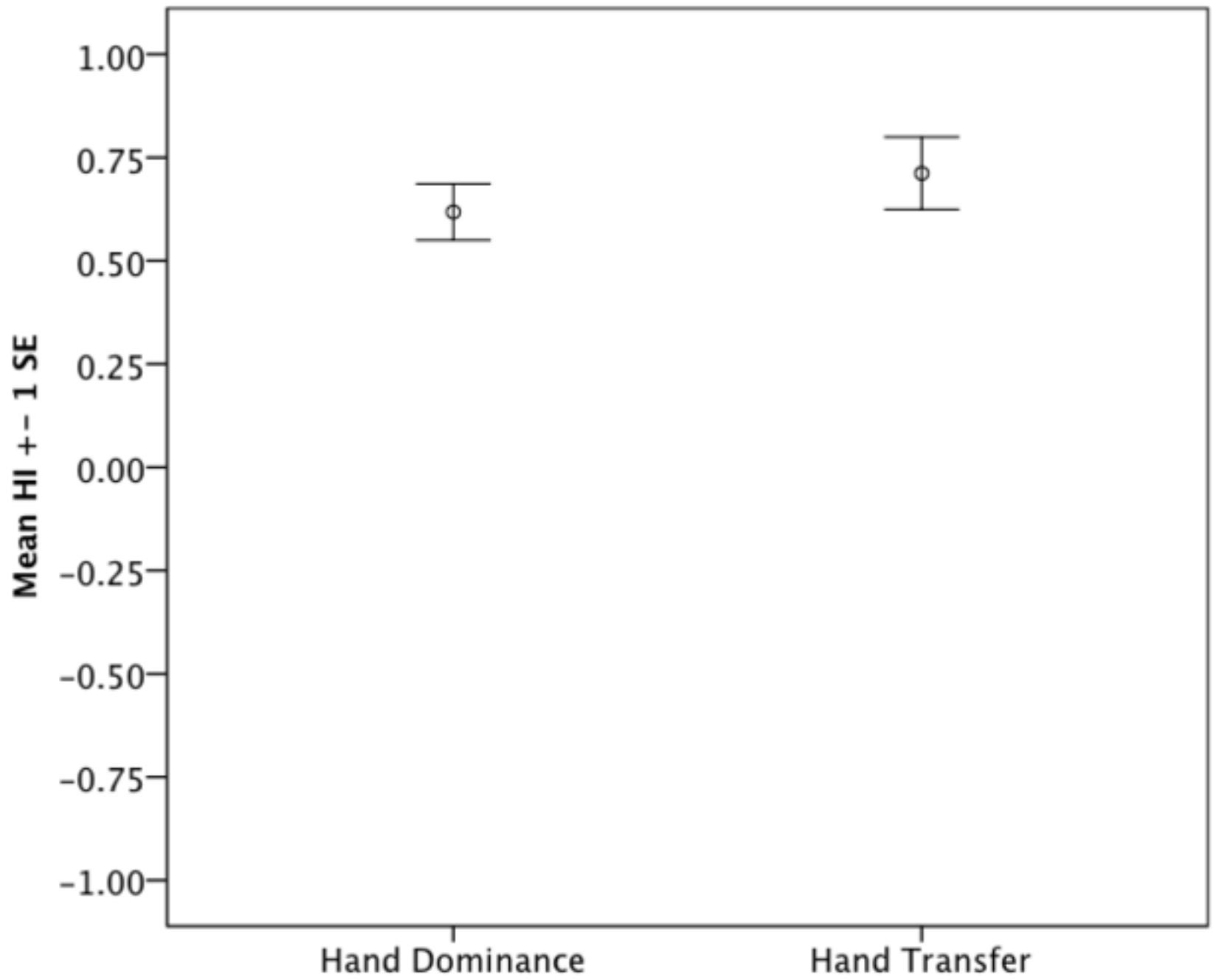


Table 1. Gender, status and number of minutes of sampled behaviour.

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. 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. 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

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Video 2 - Honey Dipping

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Video 3 - Hand Transfers

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