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1 **Target animacy influences gorilla handedness**

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31 **Abstract**

32 We investigated the unimanual actions of a biological family group of twelve western lowland
33 gorillas (*Gorilla gorilla gorilla*) using a methodological approach designed to assess behavior
34 within social context from a bottom-up perspective. Measures of both the lateralization of
35 unimanual actions (left, right) and the target of the action (animate, inanimate) were assessed
36 during dual, synchronized video observations of naturalistic behavior. This paper demonstrates
37 a co-relationship between handedness and the animate quality of the target object. Analyses
38 demonstrated a significant interaction between lateralized unimanual actions and target
39 animacy, and a right-hand bias for actions directed towards inanimate targets. We suggest that
40 lateralized motor preference reflects the different processing capabilities of the left and right
41 hemispheres, as influenced by the emotive (animate) and/or functional (inanimate)
42 characteristics of the target, respectively.

43
44 **Keywords:** Handedness, Animacy, Hemispheric Specialization, Gorilla

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61 Introduction

62 Investigations of human action suggest that lateralized skilled motor action is not arbitrary, but rather
63 represents an evolutionary bias stemming from the asymmetric organization of underlying neural
64 function (Jackson 1898; Hellige 1993). The most prominent manifestation of lateralized motor
65 behavior in humans is right-handedness. Within an evolutionary context, it has been theorized that
66 handedness emerged through the evolution of articulated speech (Annett 2002), gestural language
67 (Corballis 2002), tool-use (Greenfield 1991), coordinated bimanual actions (MacNeilage, Studdert-
68 Kennedy and Lindblom 1987; Hopkins et al. 2003) and bipedalism (Braccini et al. 2010). While right-
69 handedness provides a highly reliable marker for the brain organization of left hemisphere language
70 function, the causal evolutionary link between handedness and language function remains highly
71 controversial (Corballis 2003; Vauclair 2004). Although the preponderance of studies of asymmetries
72 in behavior and neuroanatomical structure have focused on language, studies have also revealed a right
73 hemisphere lateralization in human processing of emotive stimuli (e.g. Borod, Haywood & Koff 1997)
74 with links to left lateralized motor behavior (e.g. stronger display of facial expressions on the left side
75 of the body for the processing of emotional stimuli; Alves, Fukusima & Casonova 2008).

76 Traditionally considered hallmarks of human evolution (Ettlinger 1988), population-level
77 behavioral and neuroanatomical brain asymmetries have now been found in a host of nonhuman
78 vertebrates including non-human primates (e.g. Vallortigara & Rogers 2005; Vallortigara et al. 2010).
79 In addition, structural neuroanatomical investigations (Cantalupo et al. 2003; Spocter et al. 2010) have
80 revealed homologous asymmetric language regions (larger left hemisphere) in the ape brain, providing
81 evidence for a common mechanism underlying communication processes in humans and apes. Whether
82 these brain asymmetries in apes translate into a population-level handedness bias remains highly
83 controversial Hopkins et al. 2003; Hopkins & Russell 2004; Hopkins et al. 2004).

84 While the human population exhibits an extreme preference for right-handedness (90%),
85 linked to an overwhelming dominance for language ability in the left hemisphere (95%) (Santrock
86 2008), great ape handedness data have been variable. Some ape studies have demonstrated a
87 generalized population-level right-handedness for specific species (chimpanzees, bonobos: Hopkins &
88 Russell 2004; Hopkins et al. 2004). Others have extended a population-level handedness bias to all ape
89 species for task-specific actions, for example: chimpanzee coordinated bimanual actions, (Hopkins
90 2006); gorilla skilled gathering tasks (Byrne & Byrne 1991); orangutan self-directed behaviors (Rogers

91 & Kaplan 1995) and chimpanzee and gorilla infant cradling (e.g. Damerose & Vauclair 2002). Others
92 still have discounted captive ape lateralized handedness as a byproduct of exposure to human culture
93 (McGrew & Marchant 1997). While a recent meta-analysis of 1524 apes suggests that some species of
94 great apes show population-level handedness (chimpanzees and bonobos, Hopkins 2006), nevertheless,
95 the bias for population-level right-handedness is significantly higher in humans compared with apes
96 (Braccini et al. 2010; Harrison & Nystrom 2010). The investigation of handedness linked with emotive
97 stimuli has seen little attention, however two great ape studies demonstrating left-handed bias for self-
98 touching suggest that if emotions are expressed more intensely on the left side of the face, then the left
99 hand may be employed by the right hemisphere as an index of heightened emotion (Dimond & Harries
100 1983; Rogers & Kaplan 1995).

101 Due to variable methods and measures, comparing human and ape handedness is problematic
102 and has concentrated on right hand biases in task-specific actions (Seltzer et al. 1990; Hopkins &
103 Cantalupo 2003). Some discrepancies in human and ape handedness findings may be the result of
104 methodological issues. Human handedness data have been derived from surveys focused exclusively on
105 object-use (e.g. Oldfield 1971). Although humans demonstrate a reliable right-hand dominance for
106 object manipulation, this measure is not representative of the spectrum of routine activities of modern
107 humans, ancestral humans or extant apes. Ape studies, though less clear-cut, provide a more
108 comprehensive picture of handedness in naturalistic behavior (e.g. tool-use, self-scratching, manual
109 gesturing; Harrison & Nystrom 2010).

110 We propose a broader evaluation of manual actions to elucidate the co-relationship between
111 hemispheric specialization and handedness. We present a fixed slice of manual action data, from an
112 underrepresented ape population sample, as revealed through the use of the multidimensional method
113 (MDM) (Forrester 2008). The over-arching objective of this research was to exploit the benefits of the
114 MDM, which allows for the assessment of naturalistic behavior from a bottom-up perspective. The
115 MDM unveils latent patterns of co-relationships between variables that would not be visible via
116 hypothesis-driven, task-specific investigations of lateralized action. The methodology employed
117 throughout this study is in compliance with the MDM guiding principles, and the data we present
118 emerged as a result of this alternative approach (Forrester 2008).

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120

121 **Material and Methods**

122 *Subjects*

123 Subjects were 12 western lowland gorillas (*Gorilla gorilla gorilla*) living in a peer-raised, semi
124 free-ranging, biological family group at Port Lympne Wild Animal Park, UK. The group consisted of 1
125 silverback, 7 adult females and 4 juveniles (see Table 1). Gorillas moved freely about the ‘Palace of the
126 Apes’, the world’s largest gorillarium.

127

128 *Data Capture*

129 Subjects were recorded during naturally occurring behavior based on a focal sampling paradigm
130 (Altmann 1974). Ten-minute focal-follows were conducted for each subject using synchronized digital
131 video cameras (Panasonic NVGS11B), capturing both the focal individual in full frame and a wide-
132 angle to encompass the subject, conspecifics and surroundings. Synchronization was established using
133 a flash bulb. Cameras were tripod mounted and followed gorilla activity using zoom, tilt and swivel to
134 optimize view. Synchronized video streams were compressed into a single file (15 frames per second)
135 viewed in a top/bottom format for subsequent coding.

136

137 **(Table-1)**

138

139 *Coding Categorization and Analyses*

140 OBSERVATRON software designed to run on the Mac OS X platform was used to code and
141 store action records (Forrester 2008). Unimanual actions were single-handed lateralized (left, right)
142 actions that acted upon (made physical contact) with an animate (conspecific, self) or inanimate target
143 (objects, ground, enclosure) while the other hand remained at rest. Rest was a state of physical
144 inactivity. All actions to targets were considered, including instances when the purpose of the action
145 was to shift the subject’s position or leveraging the body for motion. This type of action was recorded
146 for both animate (conspecific) and inanimate targets (e.g. cage, rope, tyre).

147 While some studies differentiate between self-directed actions (e.g. self-scratching, auto-
148 grooming) and actions towards conspecifics (e.g. Rogers & Kaplan 1995), we simply addressed the
149 gorillas’ choice of lateralized manual action based on the target’s animacy status (animate, inanimate).

150 Therefore, combining actions towards both the self and conspecifics was in keeping with the animate

151 quality of the target. To avoid confounds of postural positions on manual actions (e.g. tripedal and
152 bipedal positions, where one hand is used for support, allowing only one hand free for action,
153 Westergaard 1998; Braccini et al. 2010), we considered only unimanual actions. Furthermore, we only
154 considered unimanual actions when the gorilla had a choice of both hands. This meant that both hands
155 were inactive prior to the actions so that each hand was equally available to perform the action.

156 We used a 2(left and right hands) x2(animate and inanimate target) repeated measures analysis
157 of variance (ANOVA), with paired-sample t-tests for post-hoc analyses.. Coded observation times
158 varied between individuals as a result of animal visibility (see Table 1). To normalize data for
159 statistical analyses, frequency counts were converted into rates by dividing frequencies of manual
160 actions by the total number of minutes of observation, rendering a rate per minute. Analyses were
161 conducted under an exclusion criterion (only individuals with ≥ 25 responses per condition, Palmer
162 2002), as well as under a non-exclusion criterion ($n=12$).

163

164 **Results**

165 Under the exclusion criterion ($n=6$), the ANOVA revealed a significant interaction of hand-
166 use and target animacy, illustrated by a right-hand bias for actions upon inanimate objects, and bilateral
167 recruitment of hands for actions upon animate targets ($F_{1,5} = 10.207, p = 0.024$; see Figure 1). A main
168 effect of animacy ($F_{1,5} = 39.035, p < 0.002$), demonstrated a higher overall rate of actions upon
169 inanimate targets compared with animate targets. An overall trend for right-handedness was also
170 revealed ($F_{1,5} = 4.67, p = 0.083$), driven by the right-hand bias towards inanimate objects. Paired-
171 sample t-tests confirmed dominance for right-handed actions ($M=1.766, SE=0.191$) compared with
172 left-hand actions ($M=1.330, SE=0.247$) for inanimate targets; $t(5) = -2.726, p = .041$); however, no
173 significant difference between left-hand ($M=0.244, SD=0.513$) and right-hand ($M=0.214, SE=0.040$)
174 actions upon animate targets was found; $t(5) = 0.586, p = 0.583$). Results under the non-exclusion
175 criterion ($n=12$) remained unchanged, including more frequent right-handed use for right-handed
176 manual actions upon inanimate targets, although this finding emerged as not significant ($p = 0.054$).

177

178 (*Figure 1*)

179

180

181 **Discussion**

182 Gorilla handedness interacted with the animacy of a target object such that gorillas were
183 equally likely to use the left and right hands for actions upon animate targets, but biased towards using
184 the right hand for actions towards inanimate objects. In addition, a general trend for right-handedness
185 was found, however, post-hoc analyses revealed that right-hand dominance appeared to manifest *only*
186 for actions upon inanimate targets.

187 The results of our study reflect a highly controlled, unique subset of handedness data that
188 cannot be directly compared with previous studies of handedness tied to acts of communication or task-
189 specific actions. These studies do not assess the lateralized action of the hand towards the target, but
190 rather the type, or complexity of the action itself (e.g. communicative gestures tied to right hand
191 preference; Hopkins & Leavens 1998; Hopkins & Cantero 2003; Meguerditchian, Vauclair & Hopkins
192 2010). Therefore, we cannot claim that our results either complement or contradict previous findings.
193 We can, however address the choice of hand that was active based on the qualitative differences
194 between animate and inanimate targets. We speculate that inanimate targets would be reached towards
195 for a functional purpose with a relatively reduced emotive--perhaps more analytical--element (e.g.
196 manipulation, tool use, food preparation), whereas animate targets may be reached towards for either a
197 functional (e.g. climbing) and/or emotive purpose (e.g. play, parenting).

198 Our results revealed a right-hand dominance for actions towards inanimate objects. This result
199 could bolster theories proposing that object manipulation skills were a critical precursor to the
200 emergence of human language skills based on a shared, simple, syntactic structure (Greenfield 1991;
201 Hopkins et al. 2007). These findings may highlight an early categorical neural distinction between
202 objects that require functional manipulation and objects that require social manipulation, or both, that
203 emerged prior to the evolutionary split of extant apes and modern humans. Support for this
204 interpretation comes from a recent functional brain imaging (fMRI) study demonstrating an overlap in
205 brain activity for both perceiving language and tools-use in the homologous monkey region for Broca's
206 area (Higuchia et al. 2009).

207 Equal use of the left and right hands for actions towards animate targets could be the result of
208 the recruitment of both manipulative and emotive processes from the left and right hemispheres
209 respectively. However, the small sample size and low frequency counts for animate targets makes it
210 difficult to speculate about underlying mechanisms. Because it is impossible to determine if

211 hemispheric specialization evinced by any subject is the product of their ontogenetic or evolutionary
212 history, future investigations are required to assess the robustness of these findings within the current
213 population as well as across a spectrum of human and non-human primates. Furthermore, the flexible
214 nature of the MDM offers an opportunity to work towards a consistent experimental framework for
215 future studies of naturalistic human and ape behaviour, leading to both a better understanding of the
216 evolution and the development of hemispheric specialization.

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316

317 *Figure 1.* Interaction between hand use and target animacy

318

Table 1: Gender, status, frequencies and z-scores for target type and handedness and observation times in minutes.

subject	gender	status	left inanimate	right inanimate	z-score	left animate	right animate	z-score	total	observation (min)
**Dishi	male	juvenile	87	118	2.10*	26 (5)	11 (2)	-2.30*	242	90
**Djala	male	adult	78	137	3.96*	6 (0)	20 (1)	2.55*	241	90
**Emmie	female	adult	98	119	1.36	16 (7)	20 (16)	0.50	253	90
**Foufou	female	adult	101	198	5.55*	32 (22)	34 (22)	0.12	365	90
**Jaja	male	juvenile	225	219	-0.24	16 (9)	9 (9)	-1.20	469	90
Kibi	female	adult	90	88	-0.07	0 (0)	1 (1)	-	179	30
Kishi	female	adult	181	181	0.05	7 (2)	8 (2)	0.00	377	90
Kouni	male	juvenile	137	184	2.57*	3 (1)	11 (9)	1.87	335	90
Mumba	female	adult	48	44	-0.31	5 (1)	5 (0)	0.32	102	50
**Tamarilla	female	adult	144	181	2.00*	40 (11)	24 (3)	1.88	389	100
Tamki	female	adult	148	148	0.06	12 (1)	8 (0)	-0.67	316	90
Yene	female	juvenile	131	117	-0.83	5 (3)	6 (0)	0.00	259	80

Notes:

*Significant lateral asymmetry ($p < .05$).

**Individuals with ≥ 25 responses per condition [31].

Numbers in parentheses are the number of animate actions directed to the self.

