Target animacy influences gorilla handedness

Gillian S. Forrester\textsuperscript{a,b,*}, David A. Leavens\textsuperscript{b}, Caterina Quaresmini\textsuperscript{c}, Giorgio Vallortigara\textsuperscript{c}

\textsuperscript{a}Department of Psychology, University of Westminster, 309 Regent Street, London, W1B 2UW
\textsuperscript{b}School of Psychology, University of Sussex, Falmer, BN1 9QH
\textsuperscript{c}Center for Mind/Brain Sciences, University of Trento, Rovereto, Italy

Corresponding Author:
Gillian S. Forrester
Email-g.forrester@westminster.ac.uk
Tel +44 (0)7814704884
Abstract
We investigated the unimanual actions of a biological family group of twelve western lowland gorillas (*Gorilla gorilla gorilla*) using a methodological approach designed to assess behavior within social context from a bottom-up perspective. Measures of both the lateralization of unimanual actions (left, right) and the target of the action (animate, inanimate) were assessed during dual, synchronized video observations of naturalistic behavior. This paper demonstrates a co-relationship between handedness and the animate quality of the target object. Analyses demonstrated a significant interaction between lateralized unimanual actions and target animacy, and a right-hand bias for actions directed towards inanimate targets. We suggest that lateralized motor preference reflects the different processing capabilities of the left and right hemispheres, as influenced by the emotive (animate) and/or functional (inanimate) characteristics of the target, respectively.

**Keywords:** Handedness, Animacy, Hemispheric Specialization, Gorilla
Introduction

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

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

While the human population exhibits an extreme preference for right-handedness (90%), linked to an overwhelming dominance for language ability in the left hemisphere (95%) (Santrock 2008), great ape handedness data have been variable. Some ape studies have demonstrated a generalized population-level right-handedness for specific species (chimpanzees, bonobos: Hopkins & Russell 2004; Hopkins et al. 2004). Others have extended a population-level handedness bias to all ape species for task-specific actions, for example: chimpanzee coordinated bimanual actions, (Hopkins 2006); gorilla skilled gathering tasks (Byrne & Byrne 1991); orangutan self-directed behaviors (Rogers
& Kaplan 1995) and chimpanzee and gorilla infant cradling (e.g. Damerose & Vauclair 2002). Others still have discounted captive ape lateralized handedness as a byproduct of exposure to human culture (McGrew & Marchant 1997). While a recent meta-analysis of 1524 apes suggests that some species of great apes show population-level handedness (chimpanzees and bonobos, Hopkins 2006), nevertheless, the bias for population-level right-handedness is significantly higher in humans compared with apes (Braccini et al. 2010; Harrison & Nystrom 2010). The investigation of handedness linked with emotive stimuli has seen little attention, however two great ape studies demonstrating left-handed bias for self-touching suggest that if emotions are expressed more intensely on the left side of the face, then the left hand may be employed by the right hemisphere as an index of heightened emotion (Dimond & Harries 1983; Rogers & Kaplan 1995).

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

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

Subjects

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

Data Capture

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

Coding Categorization and Analyses

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

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

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

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

Results

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

(Figure 1)
Discussion

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

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

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

Equal use of the left and right hands for actions towards animate targets could be the result of the recruitment of both manipulative and emotive processes from the left and right hemispheres respectively. However, the small sample size and low frequency counts for animate targets makes it difficult to speculate about underlying mechanisms. Because it is impossible to determine if
hemispheric specialization evinced by any subject is the product of their ontogenetic or evolutionary history, future investigations are required to assess the robustness of these findings within the current population as well as across a spectrum of human and non-human primates. Furthermore, the flexible nature of the MDM offers an opportunity to work towards a consistent experimental framework for future studies of naturalistic human and ape behaviour, leading to both a better understanding of the evolution and the development of hemispheric specialization.

References

pp. 306-362.


tool use in chimpanzees (*Pan troglodytes*): implication for theories on the evolution of language. Psychol Sci 18:971–977


26. Jackson JH (1898) Remarks on the relations of different divisions of the central nervous system to one another and to parts of the body. British Medical Journal 1:65-69


Interdisciplinary Reviews: Cognitive Science

38. Vauclair J (2004) Lateralization of communicative signals in nonhuman primates and the
hypothesis of the gestural origin of language. Interact Stud 5:365–86

Humans and Other Primates. J Comp Psychol 112:56–63

Acknowledgements

We thank Phil Ridges and the Aspinall Foundation for research access to gorillas, Kim Bard for
discussions on methodological design, JointSoftware for software development and Roberta Herrick
for assistance with data collection. This study was funded in part by the Daphne Jackson Trust and the
Gatsby Charitable Foundation.

Figure 1. Interaction between hand use and target animacy
Table 1: Gender, status, frequencies and z-scores for target type and handedness and observation times in minutes.

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

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.