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Target animacy influences chimpanzee handedness

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Abstract We employed a bottom-up, quantitative method
to investigate great ape handedness. Our previous investi-
gation of gorillas (*Gorilla gorilla gorilla*) demonstrated that
contextual information influenced an individual's handed-
ness toward target objects. Specifically, we found a signif-
icant right-hand bias for unimanual actions directed toward
inanimate target objects but not for actions directed to
animate target objects (Forrester et al. in Anim Cogn
14(6):903–907, 2011). Using the identical methodological
technique, we investigated the spontaneous hand actions of
nine captive chimpanzees (*Pan troglodytes*) during natu-
ralistic, spontaneous behavior. We assessed both the fre-
quencies and proportions of lateralized hand actions
directed toward animate and inanimate targets employing
focal follow video sampling. Like the gorillas, the chim-
panzees demonstrated a right-handed bias for actions
directed toward inanimate targets, but not toward animate
targets. This pattern was evident at the group level and for
the majority of subjects at the individual level. We postulate
that a right-hand bias for only inanimate targets reflects the
left hemisphere's dominant neural processing capabilities
for objects that have functional properties (inanimate
objects). We further speculate that a population-level right-
hand bias is not a human-unique characteristic, but one that
was inherited from a common human-ape ancestor.

Introduction

Historically, behavioral lateralization driven by dominant
contralateral neural regions was considered to be unique to
the human species. The most salient example of this phe-
nomenon is human right-handedness correlated with left-
hemisphere language regions (e.g., Broca 1865; Hellige
1993). For the majority of the population, both language
function and right-handedness are controlled by the left
hemisphere (e.g., Hellige 1993; Santrock 2008). The
human population exhibits 90 % right-handedness (McM-
anus 2002), and within this population, approximately
95 % of individuals have language-processing regions sit-
uated in the left hemisphere of the brain (Foundas et al.
1995; Lurito and Dzemidzic 2001; Pujol et al. 1999). These
data support the hypothesis that hemispheric specialization
for language and human right-handedness are linked in a
unique way that could reveal clues about the evolution of
language (Annett 2002; Corballis 1992, 2002; MacNeilage
et al. 1987; McManus 2002).

Today, research demonstrates that lateralized motor
action, underpinned by contralateral neural regions, is not
human specific and occurs across a wide range of verte-
brates (MacNeilage et al. 2009; Rogers and Andrew 2002;
Vallortigara et al. 2011; Vallortigara and Rogers 2005) and

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invertebrates (e.g., Frasnelli et al. 2012). However, it remains questionable if any other species demonstrates a degree of bias in lateralized motor action akin to humans (Cashmore et al. 2008; Hopkins 1999; Hopkins and Cantalupo 2005; MacNeilage et al. 1987; McGrew and Marchant 1997; Palmer 2002; Papademetriou et al. 2005; Uomini 2009). Additionally, the causal link between the emergence of right-handedness and language evolution remains a hotly debated topic (Corballis 2003; Vauclair 2005).

Within an evolutionary context, it has been suggested that right-handedness emerged as a result of speech (Annett 2002), gestural language (Corballis 2002; Hopkins et al. 2005), tool use (Breuer et al. 2005; Greenfield 1991), coordinated bimanual actions (Hopkins et al. 2003; Wundrum 1986), posture (MacNeilage et al. 1987) and bipedalism (Braccini et al. 2010; Westergaard et al. 1998). To investigate these evolutionary hypotheses, many researchers study the behaviors of our closest living biological relatives. Great apes represent a functional model to study the evolution of both handedness and human cognition, not only because of their phylogenetic proximity to humans, but also because they display clear anatomical human-like features, such as the morphology and the manipulative skills of hands (Byrne et al. 2001), the ability to occasionally locomote bipedally (Videan and McGrew 2002) and the capacity to exhibit intentionally communicative gestures (e.g., Bard 1992; Hobaiter and Byrne 2011; Leavens and Hopkins 1998; Savage-Rumbaugh et al. 1986). Great apes not only share musculoskeletal characteristics with humans, the organization of the great apes' brains share many structural and processing capabilities with the human brain. For example, recent neuroimaging studies have indicated that all four species of great apes display homologous human Broca's (Cantalupo et al. 2003) and Wernicke's (Spocter et al. 2010) areas that are asymmetrically larger in the left hemisphere, similar to humans.

Handedness has been extensively explored in great apes; however, to date, there is no consensus in the literature regarding a population-level right-handed bias. While a range of studies find no clear evidence of species-level manual lateralization (e.g., Finch 1941; Fletcher and Weghorst 2005; Heestand 1986; Marchant and McGrew 2007; Marchant and Steklis 1986; McGrew and Marchant 2001), others have reported right-hand biases in chimpanzees (*Pan troglodytes*) for bimanual feeding, coordinated bimanual actions, bipedal reaching and throwing (for reviews, see Hopkins 2006, 2007), and in captive gorillas for bimanual feeding (Meguerditchian et al. 2010a).

Some findings, particularly related to chimpanzees, have been challenged on methodological grounds. For example, findings for chimpanzee population-level right-hand bias related to bimanual tasks were derived almost exclusively from one group of institutionalized chimpanzees, creating the possibility that the finding was unique to the group (Palmer 2002). This group also received regular exposure to human behavior, creating a second confound related to cultural learning (McGrew and Marchant 1997).

More recently, systematic investigations of ape handedness employing larger sample sizes have attempted to clarify confounds in earlier studies. Hopkins et al. (2004) investigated the influences of rearing histories on handedness, while Llorente et al. (2009, 2011) tested the influence of bimanual and unimanual tasks on handedness. Although no ape study has revealed a manual bias with a similar degree of lateralization compared with the human population, each of the above investigations did return a right-hand bias using their own methodological assessment.

Although it is not yet clear if great apes share a human-like right-hand bias for manual actions, it is clear that the different methods for testing handedness across laboratories are making it difficult to assess handedness in an objective manner. Based on discrepancies in the laboratory methods for data collection, coding and analysis, it is difficult to discern if apes truly lack population-level handedness, or if the pattern is masked by discordant methods. While we are not the first authors to raise methodological inconsistencies in handedness measurements for both humans and non-human primates (e.g., Aruguete et al. 1992), we highlight the urgency for a consistent investigative framework across a range of ethologically valid behaviors, in order to facilitate comparisons both within and between species.

A recent increase in data storage capabilities has facilitated the development of new bottom-up, quantitative techniques for systematically capturing, coding and analyzing fine-grained components of naturalistic behavior. This has been hugely successful, for example, in the field of language development (e.g., Roy et al. 2006) using corpus data from small subject samples. Forrester (2008) developed a corpus technique called the multidimensional method (MDM) that makes use of frequencies of discrete body actions, within context, to reveal patterns that would not otherwise be available to the naked eye. Piloted on a captive family group of western lowland gorillas with over 3,000 data points, the MDM revealed a significant right-handed bias for unimanual actions directed toward inanimate target objects, but not for actions toward animate objects (Forrester et al. 2011). We posited that an early categorical neural distinction exists between objects that require functional manipulation and those that do not. Specifically, the results suggest that the left hemisphere is more involved in hand actions directed toward inanimate objects compared with animate objects. This finding suggests that the link between right-handedness and left-hemisphere neural processing may have been forged prior

to the emergence of language, and was shared by a common human-ape ancestor. The finding is also in line with the 'tool theory' which posits that tool use was critical for the emergence of language skills because the acquired structured sequences of actions required for object manipulation was, in effect, a physical proto-syntax which acted a catalyst for the emergence of a human language syntax (Greenfield 1991; Hopkins et al. 2007b).

Data obtained in the present study allow for a direct comparison of the handedness patterns in chimpanzees with those found previously in gorillas. The following investigation tests the capabilities of the corpus method to deal with different animal species and further extends the investigation of the evolutionary link between handedness and left-hemisphere specialization for human language. Specifically, we investigated whether the animacy of the target object influenced the handedness of chimpanzees during observations of naturalistic behavior.

Materials and methods

Subjects and housing

Subjects were nine captive chimpanzees (*Pan troglodyte*) housed at the Garda Zoological Park Parco Natura Viva, Italy. The group consisted of 2 adult males, 5 adult females and 2 female juveniles aged 2–36 years, with a variety of rearing histories (see Table 1). The enclosure (only accessible by motor vehicle) consisted of a round indoor room with access to a large outdoor island (2,113 m^2) accessed through a mesh corridor. The island, surrounded by water (9 m wide), was furnished with two caves and two wooden towers linked together with ropes. Chimpanzees moved freely about the entire enclosure, but slept and ate in the indoor enclosure. Daily nourishment consisted of

mainly fruits (e.g., bananas, apples, sliced pineapple) and a range of vegetables. Enrichment activities, for example, retrieving food from cartons, bags or paper rolls, were provided daily to elicit natural behaviors and maintain high standards of animal welfare.

Data capture

To ensure reliable chimpanzee identification, and allow for the subject groups to habituate to the experimenter and camera equipment, a familiarization period was conducted. Video samples for each subject were taken during natural, spontaneous activities in the outdoor enclosure. Subsequent experimental data collection involved 10-min continuous focal sampling sessions, counterbalanced such that each subject's data represented behaviors throughout a typical day (e.g., Altmann 1974). Data consisted of 9 focal sessions for each chimpanzee, equating to 90 min per subject. Dual-synchronized video recording, as prescribed by the MDM for fine motor actions (e.g., eye gaze), was not conducted because gross manual motor actions, within context, were visible within a single wide-angle video perspective. A digital video camera (Sony DCR-TRV900E) was tripod-mounted, but mobile, and followed chimpanzee activity using zoom, tilt and swivel to optimize view. Video footage was collected at 24 frames per second and saved off-line for subsequent statistical analysis and coding.

Coding categorization

The MDM's OBSERVATRON software, designed to run on Mac OS X platform, was used to code and store unimanual actions and to facilitate direct comparisons with previous investigations (Forrester 2008; Forrester et al. 2011). Unimanual actions were single-handed lateralized

Table 1 Frequencies, *z*-scores and binomial results of unimanual lateralized hand actions

Subject	Sex	Age in years	Rearing history	Animate left	Animate right	Inanimate left	Inanimate right	Total freq.	*z*-Score animate	*P* value animate	*z*-Score inanimate	*P* value inanimate
Camilla	F	10	CB	16	6	33	50	105	1.76	0.0758	−1.92	0.0392*
Davidino	M	8	CB	9	5	42	43	99	0.00	0.2120	−0.80	0.5000
Giorgina	F	6	CB	4	7	26	28	65	0.14	0.2744	0.60	0.4460
Giudy	F	36[a]	WB	15	20	18	36	89	2.31	0.2498	0.68	0.0198*
Jacky	M	19[a]	U	13	24	19	33	89	1.80	0.0490*	1.64	0.0352*
Luisa	F	35[a]	WB	3	6	4	12	25	1.75	0.0730	0.67	0.0384*
Mary	F	18[a]	U	10	8	35	45	98	1.01	0.4073	−0.24	0.1572
Samy	F	36[a]	WB	10	4	35	53	102	1.81	0.0898	−1.34	0.0347*
Valentina	F	2	CB	7	7	32	33	79	0.00	0.6047	0.27	0.5000

Asterisks denote statistical results in which $P < 0.05$, one-tailed

[a] Ages are approximations due to uncertain rearing histories. *CB* captive born, *U* unknown, *WB* Likely to have been wild born

(left, right) actions that were directed toward, and made physical contact with, animate (conspecific, self) or inanimate (objects, ground, enclosure) target objects, while the other hand remained physically inactive. In order to avoid postural confounds, unimanual actions were considered only when both hands were equally available to perform the task (Aruguete et al. 1992; Braccini et al. 2010; Westergaard et al. 1998) (see Table 1). Therefore, in cases where one hand reached toward a target object but the other hand was used for postural support, locomotion or a separate manual activity, the action was excluded from analyses. We assessed handedness based on the frequency of unimanual events, which has been demonstrated to have similar statistical outcomes to analyses considering bouts (Hopkins et al. 2007a). However, since both hands were required to be at rest prior to a unimanual action, each event in our data set was independent of prior events and furthermore did not include events related to perseverative actions.

Analyses

Data were analyzed using a 2 (left hand, right hand) $\times$ 2 (animate target, inanimate target) repeated-measures analysis of variance (ANOVA) and paired-sample t tests. Alpha was set at 0.05, and all tests were two-tailed, except where otherwise noted. All subject data were based on 90 min of observation time, and analyses were all based on frequencies. Data in figures are reported in rates (freq./min.) to facilitate comparison with previously published and future work. A second method of standardization was established to equalize the weight that each subject contributed to the data set. Along with frequencies, proportions were calculated for each subject within each condition. To further investigate the patterns of handedness at the individual subject level, one-tailed binomial tests were conducted (see Table 1). To facilitate direct comparisons between the present study and our previously published data on gorillas (Forrester et al. 2011), we re-analyzed the gorilla data also by proportions (they were originally analyzed by rates). These results exactly reproduced the statistical patterns originally reported on 6 gorillas and can be extended to a further 5 of the 12 gorillas. One adult female gorilla (Kibi) was excluded from the analysis for low animate responses (she displayed only 1 animate response).

Results

Gorillas

A re-analysis of gorilla data ($n = 11$) from the previous study (Forrester et al. 2011) yielded the following results: a non-
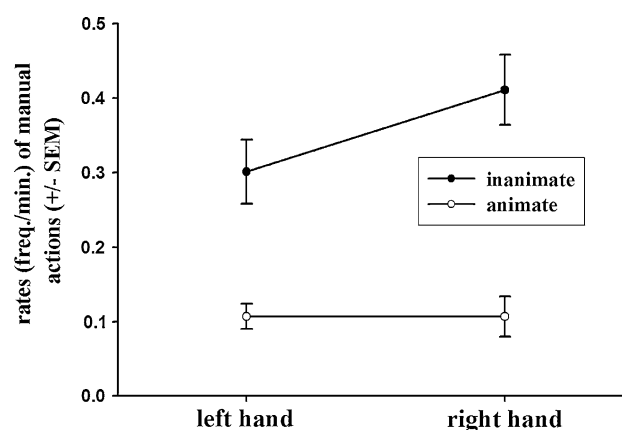

Fig. 1 Interaction between chimpanzee lateralized manual action and animacy of target

significant trend for general handedness ($F_{1,10} = 4.13$, $P = 0.07$) (favoring the right hand), a main effect of target animacy ($F_{1,10} = 606.61$, $P < 0.001$) (indicating a higher frequency of inanimate events) and a significant interaction between hand and target animacy ($F_{1,10} = 6.31, P = 0.032$), such that the right hand was directed with greater proportion to inanimate targets compared to animate targets.

Chimpanzees

The 2 (left hand, right hand) $\times$ 2 (animate target, inanimate target) ANOVA (proportion and frequency) revealed significant interactions of lateralized unimanual action and target animacy (frequency: $F_{1,8} = 8.81$, $P = 0.018$; proportions: $F_{1,8} = 11.90$, $P = 0.009$) (see Fig. 1). Main effects of target type (animate, inanimate) demonstrated higher overall rates of actions toward inanimate targets versus actions directed toward animate targets (frequency: $F_{1,8} = 28.19$, $P < 0.001$; proportion: $F_{1,8} = 46.60$, $P < 0.001$). A main effect of hand (left, right) was also identified (frequency: $F_{1,8} = 10.25$, $P = 0.013$; proportion: $F_{1,8} = 8.31$, $P = 0.020$) indicating a higher frequency of right-handed actions compared to left-handed actions. Paired-sample t tests were used to assess the dominance of right-handed actions (frequency: $M = 37$, SE = 4.19; proportion: $M = 0.444$, SE = 0.015) compared with left-handed actions (frequency: $M = 27.1$, SE = 3.88; proportion: $M = 0.313$, SE = 0.327) for inanimate targets only (frequency: $t(8) = -4.08$, $P = 0.004$; proportion: $t(8) = -3.82$, $P = 0.005$). We also compared right-handed actions (frequency: $M = 9.66$, SE = 2.39; proportion: $M = 0.129$, SE = 0.030) with left-handed actions (frequency: $M = 9.66$, SE = 1.51; proportion: $M = 0.114$, SE = 0.012) for animate targets only (frequency: $t(8) = 0.00$, $P = 1.00$; proportion: $t(8) = -0.57$, $P = 0.59$) which demonstrated no such significant difference.

Binomial tests revealed that five of the nine chimpanzees replicated the group pattern of a right-hand dominance within the inanimate target condition, but not within the animate target condition. The four chimpanzees that did not demonstrate an individual right-hand bias within the inanimate condition did not manifest a left-hand bias either.

Discussion

Results indicated a significant interaction between handedness and target animacy where the right hand was more influenced by the animacy of the target than the left. There was a significant group right-hand bias for actions toward inanimate objects, but no significant difference in the frequency or proportion of left- and right-hand actions to animate targets. More than 170 animate actions contributed to our analyses, extinguishing concerns that the pattern revealed may have been generated by a 'floor effect'. Additional binomial tests confirmed that the pattern held true for the majority of individual subjects.

These findings match the unimanual handedness pattern previously reported for a captive, biological family group of western lowland gorillas (Forrester et al. 2011) and indicate that context influences manual behavior, which may act as an indirect marker of the neural generators that underpin lateralized actions. From an evolutionary perspective, one interpretation of our finding is that the animacy of objects influencing lateralized manual behaviors represents an early, categorical hemisphere distinction for objects that require functional manipulation as ordered sequences of actions to reach a goal state, and those that do not. These findings are consistent with the '*tool theory*', which argues that object manipulation shares common features with modern human language such that they both require the production of temporal sequences of actions and thus suggests tool use to be a possible precursor and catalyst for the emergence of a language proto-syntax (Corballis 2002; Greenfield 1991).

This interpretation would help to explain why some ape studies demonstrate a right-hand bias for communicative gestures (Hopkins et al. 2005; Meguerditchian et al. 2010b, 2012). In great apes, communicative gestures may represent an evolutionary step toward language skills, extending the left hemisphere's dominance for temporal sequences of structured actions. In handedness for objects, this manifests as structured manipulation of the object to achieve a function. In handedness for gesture, this manifests as the structured sequences of manual actions to achieve the manipulation of a social partner. This interpretation is consistent with recent characterizations of apes' gestures as

a kind of social tool use (Bard 1990, 1992; Gomez 2007; Hopkins et al. 2012; Leavens et al. 2005).

These data also help to clarify why recent neuroimaging studies reveal that all four species of great apes (all known to be tool users in both captivity and in the wild) possess neuroanatomical left-hemisphere asymmetries consistent with language areas in humans (Cantalupo et al. 2003; Spocter et al. 2010), yet do not possess human-like language capabilities. These data also facilitate the interpretation of recent brain-imaging studies that indicate a high correlation between brain areas responsible for tool use in great apes and those that process language in humans (Higuchi et al. 2009; Hopkins et al. 2007b).

Manual actions to animate targets (self and conspecifics) revealed no lateralized bias at the group level, and only one of the nine subjects demonstrated a significant right-hand bias in this condition. One interpretation of this finding is that, like humans, apes exhibit a greater involvement of the left side of the body during social arousing situations compared with non-emotive stimuli due to a right-hemisphere dominant role for perceiving emotion. This has been evident in both human (Borod et al. 1986) and ape studies of perception and production of facial expressions, where authors report an earlier activation of the left side of the face for responses to emotive stimuli (e.g., Fernández-Carriba et al. 2002). In light of handedness investigations, studies of self-directed behaviors have also revealed a left-side bias, suggesting that the right hemisphere plays a more dominant role in the processing of social and emotional stimuli. For example, self-scratching associated with high levels of stress was seen to occur significantly more frequently on the left side of the body (e.g., Hopkins et al. 2006).

Based on our relatively small sample size, it is difficult to know how well our findings will generalize to other populations, as there may be a relatively high contribution of individual variability. However, balanced against this limitation is the fact that this corpus technique evaluated a large number of data points, and additionally, both the methods and findings were very similar to our previous study in gorillas. Nevertheless, the generalizability of our findings is, at present, uncertain and the question regarding whether or not the context of the target influences ape handedness warrants further investigation.

In conclusion, we demonstrate that quantitative, corpus methods are effective for comparative studies investigating the evolutionary basis of behavior. The MDM is just one example of a new corpus technique that has the capability to reveal context-specific behavioral patterns across disparate animal species. We extend our previous findings on gorillas, providing evidence that a second species of great ape's (chimpanzee) handedness is influenced by the context of target objects. One interpretation of this finding is

that the pattern is associated with the specialization of cerebral dominance for processing functional and emotive stimuli. The theoretical implication of our result is consistent with the 'tool theory', which speculates that human right-handedness derived from object use, prior to its involvement with language, and thus was inherited from an ancestor shared with extant great apes.

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