Target animacy influences chimpanzee handedness

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Abstract

We assessed the unimanual actions to animate and inanimate targets during naturalistic behaviorof a group of nine captive, zoo-housed chimpanzees (*Pan troglodytes*). The main aim of this study was to expand on our previous study on gorillas (*Gorilla gorilla gorilla*), which demonstrated a right-hand unimanual bias to inanimate target objects compared with animate target objects (Forrester, Quaresmini, Leavens and Vallortigara 2011). Measures of unimanual actions (left hand, right hand) directed to target objects (animate: self, social partner; inanimate: object, environment, enclosure) were assessed from focal follow video observations at the Parco Natura Viva, Italy. The results from this study demonstrate a significant interaction between handedness and the animacy of the target object. The pattern of results and post hoc tests revealed a significant right-hand bias for actions directed towards inanimate targets and no significant preference for use of the left or right hand for actions directed towards animate targets, thus exhibiting the same pattern for the chimpanzees that we previously found for gorillas. We postulate that this distinct pattern of lateralized motor preference reflects the differential processing capabilities of the left and right hemispheres, as influenced by the emotive (animate) and/or functional (inanimate) characteristics of the target, respectively. We further speculate that right-handed hierarchical object manipulation may have served as a precursor to modern human language skills.

Keywords: Handedness, Animacy, Hemispheric Specialization, Chimpanzee

Introduction

Historically, behavioral lateralization driven by dominant contralateral neural regions was considered unique to the human species. The most notable example of this phenomenon in humans is right-handedness correlated with left-hemisphere language regions (e.g. Broca 1865, Hellige 1993). For the vast majority of the population, both language function and right-handedness are hosted by the left hemisphere (e.g. Hellige 1993; Santrock 2008). The human population exhibits 90% right-handedness (McManus 2002) and within this population approximately 95% of individuals have language-processing regions situated in the left hemisphere of the brain (Foundas Leonard and Heilman 1995; Pujol, Deus, Losilla and Capdevila, 1999; Lurito and Dzemidzic, 2001). This association has led scientists to hypothesize that hemispheric specialization for language and right-handedness are linked with one another in ways that may reveal clues about the evolution of human language skills (MacNeilage Studdert-Kennedy and Lindblom 1987; Corballis, 1992, 2002; Annett, 2002; McManus, 2002). However, the causal link between the emergence of right-handedness and language evolution is hotly debated (Corballis 2003; Vauclair 2004).

Today, research demonstrates that lateralized motor action, underpinned by contralateral neural regions, is not human-specific, and occurs across a wide range of vertebrates (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; MacNeilage, Rogers and Vallortigara, 2009; Vallortigara, Chiandetti and Sovrano 2011) and invertebrates (e.g. Frasnelli, Vallortigara, and Rogers, 2010). However, the extent to which a significant majority of any other species shows a bias in lateralized limb action (e.g. right-handedness) for any given task (e.g. language) akin to humans remains questionable (MacNeilage Studdert-Kennedy and Lindblom 1987; McGrew and Marchant, 1997; Hopkins, 1999; Palmer, 2002; Hopkins and Cantalupo, 2005; Papademetriou, Sheu and Michel2005; Cashmore Uomini and Chapelain 2008; Uomini, 2009).

There are multiple disparate theories linking right-handedness with left hemisphere language function in humans. Holder (1997) argues that the high rate of human right-handedness suggests a genetic component, and Annett (1998) further postulates that both processes, language and right-handedness, are driven by a single common gene. Within an evolutionary context, it has been suggested that right-handedness emerged as a result of speech (Annett, 2002), gestural language (Corballis, 2002; Hopkins,

Russell, Freeman, Buehler, Reynolds, and Schapiro, 2005), tool use (Breuer, Ndoundou-Hockemba, Fishlock, 2005; Greenfield 1991), coordinated bimanual actions (Wundrum, 1986; Hopkins, Hook, Braccini and Schapiro, 2003) posture (MacNeilage Studdert-Kennedy and Lindblom 1987) and bipedalism (Westergaard, Kuhn and Suomi 1998; Braccini, Lambeth, Schapiro and Fitch 2010). However, while handedness studies demonstrate a strong correlation between right-handedness and left hemisphere language dominance, a *causal* relationship between the two remains hypothesized rather than empirically supported.

At face value, human right-handedness appears to be a robust and universal finding (Perelle and Ehrman, 1994; Raymond and Pontier, 2004). However these data are not without methodological concerns or limitations. Data revealing a 90% right-handed and 10% left-handed population split are mainly derived from self-report questionnaires in literate populations (e.g. Oldfield 1971; Hardyck, Goldman and Petrinovich 1975; McManus 1981). Furthermore, questionnaires rely primarily on measures of precision tool-use. In the limited literature where sampling methods are altered to include a more ethological range of factors, handedness patterns become more complex and right-handedness can vary between 70-90% (Annett 1985). For instance, Dimond and Harries (1984) reported a human left-hand preference for the self-directed behavior of face touching, in individuals who were otherwise right-handed, suggesting that the right-hemisphere's dominance for emotional processing (e.g. Borod, Haywood and Koff 1997; Borod et al. 1998) may influence these manual actions. A subsequent study demonstrated that a left-hand preference for face-touching was present in native English, but not in native Japanese speakers (Hatta and Nakatsuka 1976), suggesting that handedness is also subject to socio-cultural influences. Marchant, McGrew and Eibl-Eibesfeldt (1995) noted that a range of manual behaviors, barring tool use, were missing from handedness surveys (e.g. Edinburgh Handedness Inventory; Oldfield 1971) and argued for handedness measurements to be captured during observations of naturalistic behavior. By tracking naturalistic handedness across three different preliterate populations they noted that while there was an overall 'consistent but weak right hand dominance', individuals were mixed-handed for all actions across a 'comprehensive range of ethological measures' with the exception for tool-use, which was distinctly right-handed. Further studies demonstrated that the percentage left-handedness fluctuated (3-27%) in traditional cultures (Faurie and Raymond 2005). Moreover, Knecht and colleagues (2000) reported that 70% of left-handers still exhibit a left-hemisphere

dominance for language functions, calling into question that a bias in handedness serves as a reliable marker of hemispheric specialization for language. Some argue that the dominant hand for manual gesture may, in fact constitute a more accurate marker of language lateralized brain regions (Vauclair and Meguerditchian 2008).

Although the general perception is that the human population is strongly right-hand dominant, this finding is derived from a limited set of questionnaire data. From the few studies that look outside of object manipulation, there is evidence that handedness can vary across tasks, cultures and levels of literacy. Therefore, it could be argued that the very high percentage of human right-handedness (90%) is selectively generated from tasks for object manipulation and highlights tasks that are specifically tied to the neural resources of the left hemisphere. Reports of varying handedness across environmental factors calls into question the strict classification of individuals as: right-handed, left-handed or ambidextrous, as these labels do not appear to be representative of a comprehensive range of natural human manual actions. Furthermore, this type of over-generalization is not only problematic for understanding how handedness is specialized for specific tasks or types of stimuli, it also causes concerns for inter- and intra-species comparisons. In fact, Annett (1985) argues that hand preference should be treated as a continuous variable that correlates strength of handedness for specific tasks, rather than a dichotomized right/left bias, because only a small proportion of the human population manifests an extreme right- or left-hand preference for daily activities. However, it should be noted that regardless of culture or literacy abilities a right-hand bias for interaction with objects appears reliable across diverse human populations and may shed light on the evolution of human language capabilities.

In order to reveal information about the evolutionary relationship between human right-handedness and language skills, archeologists investigate human fossils and ancient tool kits. Unfortunately, human fossils provide limited clues about how our ancestors communicated with one another, but they have been helpful for revealing information about the handedness of our preliterate ancestors. Archeologists believe that human population-level right-handedness dates back more than 2 million years (Cashmore, 2009; Uomini 2009). Interestingly, evidence suggests that human right-handedness is linked specifically to tool-use from as far back as 2.5 million years (Bradshaw and Rogers, 1993; Toth 1985; McManus 2002). The evidence suggesting that right-handedness preceded language

makes tool-use a strong candidate for further research into the evolution of human communication skills. This is not the first time that tool-use has been implicated in the evolution of human language skills. In fact, Byrne and Byrne (1993); Corballis, (2002); Foucart et al, (2005); Weiss and Newport, (2006); Mercader, Barton and Gillespie (2007) and Greenfield (1991) have all suggested that object manipulation for actions related to tool-use, manufacture and even food preparation have common features to modern language and therefore serve as a likely precursor to language. Some scientists postulate that language evolved as an extension of right hand and left hemisphere ability to produce temporal sequences of motor activity derived from tool use (Bradshaw and Nettleton, 1982; Corballis, 1991; Morgan and Corballis 1978; Hewes, 1973; Kimura, 1993; MacNeilage, Studdert0Kennedy and Lindblom 1987). While each investigator has their own manner of theorizing a causal relationship between handedness and language-like skills, theories require testing for validation.

Great apes represent a functional model to study handedness 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, Corp and Byrne 2001), the ability to occasionally locomote bipedally (Videan and McGrew, 2002) and the capacity to exhibit intentionally communicative gestures (e.g. Savage-Rumbaugh, McDonald, Sevcik, Hopkins, and Rubert, 1986; Bard 1992; Leavens and Hopkins 1998; Hobaiter and Byrne 2011). Great apes do not only share musculoskeletal characteristics with humans. The organization of the great apes brains shares many structural and processing capabilities with that of the human brain. Recent neuroimaging studies have indicated that all four species of great apes display homologous human Broca's (Cantalupo, Pilcher and Hopkins 2003) and Wernicke's (Spocter et al. 2010) areas that are asymmetrically larger in the left hemisphere of all species of great apes. Moreover, Higuchia, Chaminadeb, Imamizua and Kawatoa (2009) found that the homologous Broca's and Wernicke's areas were active (fMRI) in the ape brain during tool use and, furthermore, that there is an overlap of neural activation for both language perception and tool-use in humans within Broca's area. Other neuroimaging studies corroborate a left-hemisphere specialization for tool-use in apes demonstrating an overlap with brain regions associated with language-like skills in humans (Binkofski et al. 1999a,b; Binkofski and Buccino 2004).

Until recently, handedness has been extensively explored in great apes, but not in a systematic way

that is useful to make direct comparisons between human and non-human primates. Researchers have explored bimanual and unimanual handedness directed at inanimate objects to a range of different actions and tasks with varying levels of complexity. Historically, with only one exception (Boleda, Chincilla, Valls and Pastor 1975), results suggested that great apes did not express a right-hand population bias exhibited similar to humans (e.g. Finch 1941; Marchant and Steklis 1986). These early investigations of handedness in great apes focused on manipulative motor behaviors in both wild and captive subjects and showed inconsistent patterns of population-level handedness according to species, sample size and complexity of manual tasks (McGrew and Marchant, 1997; Papademetriou, Sheu, and Michel, 2005; Hopkins, Russell and Cantalupo 2007). However, it should be noted that methodologies between laboratories differed significantly, confounding interpretations of results and comparisons between laboratories.

More recently, systematic investigations with large sample sizes have reported great ape right-hand biases in captive chimpanzees (*Pan troglodytes*), related to complex manual tasks such as bimanual feeding, coordinated bimanual actions, bipedal reaching and throwing (for reviews, see Hopkins 2006, 2007), and in captive gorillas (*Gorilla gorilla)* (Byrne and Byrne, 1991; Meguerditchian, Calcutt, Lonsdorf, Ross and Hopkins, 2010) for bimanual coordinated actions. These initial reports were criticized for being based upon single laboratory samples (McGrew and Marchant, 1997; Papademetriou, Sheu and Michel 2005 for reviews), methodological and theoretical grounds (McGrew and Marchant, 1997; Palmer, 2002, 2003; Crow, 2004) and the suggestion that apes' exposure to human culture might have induced a bias of hand use in manual actions (e.g. McGrew and Marchant 1997). However skepticism over these findings have largely been dispelled as newly obtained data in support of a right hand bias continues to mount from an increasing number of great ape species for a range of manual actions (e.g. Hopkins, Wesley, Izard, Hook and Schapiro 2004; Meguerditchian et al. 2010; Meguerditchian, Vauclair and Hopkins 2010; Llorente, Mosquera and Fabre´ 2009; Llorente et al. 2011) across captive and wild settings (Llorente et al. 2011; Lonsdorf and Hopkins, 2005).

Along with object use, there has been a recent interest in great ape handedness for social communication to evaluate theories of language origins linked to hemispheric specialization (Shafer 1993; Hopkins and Leavens 1998; Hopkins et al. 2005; Meguerditchian, Vauclair, Hopkins, 2010; Hopkins and Vauclair, in press). While great apes apparently do not possess human-like language skills, scientists argue

that communicative gestures may represent a unique behavior, similar to humans, and may be important for drawing a causal link between the evolution of communication and handedness (Falk 1987; Hewes 1973; Kimura 1993). Evidence suggests that great apes communicate by gestures across a variety of different social contexts (e.g., Call and Tomasello, 2007; Goodall, 1986; Pika, Leibal, Call and Tomasello 2005). Group-level right-handedness for gestural communication has been reported in small samples of captive bonobos and gorillas (Shafer 1993; Hopkins and de Waal, 1995). Although as with studies of object manipulation, studies reporting a right hand bias (e,g. Hopkins et al. 2005) have been criticized for exclusively coding chimpanzee gestures directed towards human experimenters (e.g. McGrew and Marchant, 1997). However, a further study (Meguerditchiana, Vauclair Hopkins 2010) revealed significant right hand dominance regardless of whether the receiver was a conspecific or human, diminishing concerns that ape handedness is biased by enculturation.

Although the evidence is limited, it has recently been suggested that there may be an even higher rate of right-handedness in great ape communicative gesture compared with actions directed upon inanimate objects (Hopkins et al. 2011). The authors argue that communicative gestures may be the result of different underlying neural generators from those employed during object manipulation. However, it could also be argued that handedness tied to both object interaction and gestural communication are highly right-lateralized behaviors because they both exploit the left hemisphere's functional capabilities to produce hierarchical temporal sequences of events to reach a goal state. In great apes, communicative gestures may represent an evolutionary step towards language skills, extending the left hemisphere's specialized processing derived from tool use. This line of reasoning would suggest that this step occurred prior to our evolutionary split from great apes and may be unique to humans and great apes. Based on the review above, great ape handedness appears to be present for interactions with objects and during communicative gestures, expressing a similar pattern of handedness with humans and reinforcing the ape model for the evolution of language. This is consistent with recent characterizations of apes' gestures as a kind of social tool use (Bard 1990, 1992; Gomez 2007; Leavens, Hopkins, and Bard 2005). Limited handedness data have also been collected during observational studies of self-directed behaviors in great apes. Similar to the limited human data, studies have not revealed a right-hand bias. In the handful of studies, a few have revealed both equal frequency use of both hands for self-directed behaviors, (Aruguete, Ely and King 1992;

Hopkins and de Waal, 1995; Marchant and McGrew, 1996; Forrester et al. 2011) while others observed a left-hand bias for face-touching in orangutans (*Pongo pygmaeus*) (Rogers and Kaplan 1995) and gorillas (*Gorilla gorilla*) (Dimond and Harries 1983).

Interestingly, all studies of self-directed behaviors report a larger contribution of the left hand, compared with manual actions involving inanimate objects. Similar to the human research, scientists propose a greater involvement of the left side of the body during social arousing situations compared with non-emotive stimuli may be due to the right hemisphere's dominant role in perceiving emotion, with differential effects on primary cutaneous afferents across the left and right hemispaces of the integument (e.g. Hopkins, Russell, Freeman, Reynolds, Griffis, and Leavens, 2006). Behavioral asymmetries tied to emotive stimuli have also been reported for perception and production of facial expressions in both apes and humans. These studies are consistent with the right-hemisphere dominance for emotive stimuli and report an earlier activation of the left side of the face (e.g. Fernandez-Carriba, Loches, and Hopkins, 2002; Borod, Koff, Perlman Lorch, Nicholas, 1986).

It is clear from a review of the literature that there are large discrepancies in the way we collect handedness data from human and nonhuman primate populations that cause confounds for direct comparisons both within and between species. However, even with these methodological confounds, there are striking similarities in the handedness patterns for humans and apes for interactions with inanimate objects, communicative gestures and self-directed manual actions potentially highlighting the different processing capabilities of the left and right hemispheres. While we are not the first authors to raise the issue of inconsistencies in handedness measurements across species (e.g. Aurgete, Ely and King 1992), we highlight the need for a consistent investigative framework under which to assess naturalistic handedness across a range of behaviors in order to make valid comparisons both within and between species

Previous work with gorillas sought to investigate differences in hand preference to animate and inanimate target stimuli for spontaneous behaviors in captive, semi-free-ranging lowland gorillas (Forrester et al. 2011). That study took into account a comprehensive range of interactions with both social (animate) and non-social (inanimate) targets employing a Multidimensional Method (MDM) that systematically captures, codes and analyzes naturalistic behavior for the purpose of allowing valid comparisons across human and nonhuman primate species (Forrester 2008). In that study, we did not categorize or code

actions towards conspecifics as communicative gestures and therefore did not test the right-hand social communication hypothesis. However, we hypothesized that the bilateral use of both arms for self-directed and conspecific-directed actions combined, may represent an increased participation of the right hemisphere for targets with social-emotional components (e.g. conspecific) compared with non-emotive targets (e.g. inanimate objects). The findings demonstrated that when we teased apart animate targets from inanimate tasks, a right-handed bias for inanimate target objects was revealed. We postulated that these data give credence to the theory that there is a causal relationship between left hemisphere language centers in humans and right-handedness that is inherited from the last common ancestor whose right-handed actions for tool-use was underpinned by left-hemisphere specialized areas for orchestrating hierarchical sequences of events to reach a goal state. We further speculated that sequences of actions to reach a goal could be described as a very basic syntax, and that these types of activities may have paved the way for the evolution of language skills. Therefore, it brings into question whether tests of complex bimanual action are required to observe individual and population-level right-handedness. Rather, we ask, can the animacy of the target object be enough to bias the hand of use? The anticipation of a manipulation may draw on the left hemisphere processing resources. If so, it can be argued that right-handedness may be the result of a long-standing left hemisphere neural bias whose processing abilities were molded from our ancient ancestors' interactions with tools. Since that time, we have extended the hierarchical sequencing abilities of the left hemisphere to evolve language like skills.

The main objective of our current investigation is to see if the pattern of handedness found in gorillas can be extended a group of captive chimpanzees. Specifically, we sought to investigate if the animacy of the target object influenced the handedness of the chimpanzees, thus either supporting or contradicting the theory that interactions with inanimate objects have been a critical predecessor to the evolution of language. As in our investigation of gorilla handedness, we employed the use of the Multidimensional Method (MDM), during observations of naturalistic behavior (Forrester 2008, Forrester et al 2011).

Material and methods

Subjects and housing

This study included a group of nine captive chimpanzees (*Pan troglodyte*) hosted at the Garda Zoological Park Parco Natura Viva, in Verona (Italy). The group included: 2 males, 5 adult females and 2 juveniles. The individuals were institutionalized animals with a variety of rearing histories. The enclosure (only accessible by motor vehicle) was split into different segments comprised of a smaller round indoor room linked to a large outdoor island (2113 m^2) accessed through a mesh corridor. The island was furnished with two vertical wood towers, linked by ropes, a small branch and two caves. The island was surrounded by water (9 m wide). Chimpanzees slept and ate in the indoor enclosure. Daily nourishment consisted of mainly fruits and vegetables. Enrichment activities were provided on a daily basis in order to increase the manifestation of natural behaviors and maintain high standards of animal welfare.

Data capture

In order to ensure reliable chimpanzee identification, and allow for the subject groups to adapt to the presence of the experimenter and experimental equipment, a familiarization period was necessary. This process involved taking video samples for each subject and their daily natural behaviors and activities in the outdoor enclosure using a focal animal sampling method. Once reliable identification was achieved, a continuous focal sampling was initiated where each recording session lasted 10 minutes, counterbalanced over day the time of the observation (e.g. Altman 1974). Data sets consisted of 9 sessions for each focal sampling, equating to 90 minutes per subject. While we were unable to perform dual-synchronized video recording as prescribed by the MDM method (Forrester et al 2011), the view of the video camera was wide enough to include not only the focal subject but also the social context within which the focal individual was behaving. Video footage was captured using a Sony digital video camera, which was subsequently streamed and saved on a Macintosh computer for off-line coding and analysis.

Coding categorization

The Multidimensional Method (MDM) was employed for variable categorization, coding and analyses to facilitate direct comparisons with previous our previous investigations (Forrester 2008; Forrester et al. 2011). Specifically, we identified the laterality of each unimanual action towards an external target as left or right. This coding procedure referred to the hand used to conduct the action rather than the direction of

the action. In addition, we coded the animacy of the target object. The target was deemed animate when the hand was directed towards and made contact with either the self or a conspecific. Targets were identified as inanimate when the hand was directed towards, and made contact with, an object, the enclosure or the environment (e.g. tapping the ground). Frequencies of inanimate targets excluded locomotion. In line with Forrester et al. (2011), in order to avoid postural confounds, unimanual actions towards animate and inanimate targets were considered only when both hands were equally available to perform the task (Aruguete, Ely and King 1992; Westergaard, Kuhn and Suomi 1998; Braccini et al. 2010) (see Table 1). Therefore, in cases where one hand reached towards a target object but the other hand was used for postural support or a separate manual activity, the action was excluded from analyses.

- Insert Table 1 -

Analyses

Data were analyzed using a 2 (left hand, right hand) x 2 (animate target, inanimate target) repeated measures analysis of variance (ANOVA), with paired-sample t-tests for post-hoc analyses. All subject data were based on 90 minutes of observation time and analyses were all based on frequencies. Normalization by rate (rate = number of frequency counts/ observation time in minutes) was not required because all subjects were observed for the same amount of time. However, a second method of standardization was established to equalize the effect of each subject on the data set. To equalize the weighting that each subject contributed to the data set, we calculated proportions for each subject of each response type in relation to the total number of actions for that subject. 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 by proportions, and exactly reproduced the statistical patterns originally reported on only 6 gorillas. In the reanalysis, 11 of the 12 gorillas were included. One exclusion was made for a adult female (Kibi) who only produced 1 animate response.

Results

Gorillas

A reanalysis of gorilla data from the previous study (Forrester et al. 2011) yielded the following results: a non-significant trend for hand, ($F_{1,10} = 4.13$, $P = 0.07$) (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 stronger significant interaction than previously reported between hand and target animacy, ($F_{1,10} = 6.309$, $P = 0.032$), such that the right hand was significantly more often directed towards inanimate targets, in comparison to animate targets.

Chimpanzees

The 2 (left hand, right hand) x 2 (animate target, inanimate target) ANOVA (proportion and frequency) revealed significant interactions of lateralized unimanual action and target animacy (frequency: $F_{1,8} = 8.813$, $P = 0.018$; proportions: $F_{1,8} = 11.902$, $P = 0.009$) (see Figure 1). Main effects of target type (animate, inanimate) demonstrated higher overall rates of actions towards inanimate targets versus actions directed towards animate targets (frequency: $F_{1,8} = 28.19$, $P < 0.001$; proportion: $F_{1,8} = 46.60$, $P < 0.001$). Main effects of hand (left, right) were also identified (frequency: $F_{1,8} = 10.250$, $P = 0.013$; proportion: $F_{1,8} = 8.306$, $P = 0.020$) indicating a higher frequency of right-handed actions compared to left handed actions. Post-hoc analyses were conducted using paired-sample t-tests to test the dominance of right-handed actions (frequency: $M = 37$, SE = 4.19; proportion: $M = .444$, SE = .015) compared with left-handed actions (frequency: $M = 27.1$, SE = 3.88; proportion: $M = .313$, SE = .327) for inanimate targets only, (frequency: $t(8) = -4.080$, $P = .004$; proportion: $t(8) = -3.817$, $P = 0.005$). We also compared right-handed actions (frequency: $M = 9.66$, SE = 2.39; proportion: $M = .129$, SE = .030) with left-handed actions (frequency: $M = 9.66$, SE = 1.51; proportion: $M = .1142$, SE = .012) for animate targets only, (frequency: $t(8) = .000$, $P = 1.000$; proportion: $t(8) = -.566$, $P = 0.587$) which demonstrated no such significant difference.

- Insert Figure 1 -

Figure 1. Hand by animacy interaction in chimpanzees

Discussion

Results demonstrated a significant interaction between handedness and target animacy, where the right hand was more influenced by the animacy of the target than the left hand. Post-hoc t-tests revealed a significant bias for the right hand for actions directed towards inanimate objects, whereas both hands were used with equal frequency for actions directed towards animate targets. These findings are identical to the unimanual handedness pattern that we reported for captive semi-free ranging western lowland gorillas (Forrester et al. 2011). This pattern was also demonstrated by Aruguete and colleagues (1992), but was not discussed in light of underlying neural generators.

With respect to the previous literature, it is not surprising that we identified a right hand bias for manual actions in a group of captive apes. What is interesting is that the right hand bias was only significant for actions directed towards inanimate target objects regardless of task type, complexity or social context. This implies a dominance for left hemisphere processing of external inanimate stimuli. This finding is not in conflict with either the human or ape handedness data that we have reviewed, but our interpretation of the results reflects a causal relationship between tool use and the evolution of language like skills. We propose that interactions with inanimate objects require a sequence of hierarchical actions to create a valid goal state. The hierarchical sequence of manual events leading up to a goal state could be comparable to a simple or proto-syntax, similar to that which underpinned an early human proto-language. Interactions with objects (and ultimately tool-use) may have extended the left hemisphere's temporal-sequential processing abilities (originally selected for external stimuli) to a language-based syntax (internal stimuli).

We postulate that the left hemisphere has a preference for either manipulating and/or *predicting* manipulations required by the engagement with the object. We also considered the scenario where the left hemisphere *predicts* or *plans* for manipulation based on the inanimate characteristics afforded by the external object, thus electing the right hand for action towards the object. At this time we cannot distinguish if it is the animacy of the target object that biases the neural processing of external stimuli and thus the hand that is employed or, if it is the predicted tasks afforded by the external stimuli. It may be more likely that an inanimate object requires manipulation to reach a goal state compared with an animate object. For

example, tools require manipulation in order to achieve a goal. On the other hand, emotive interactions with conspecifics (excluding communicative gestures) and the self may require perseverative actions to fulfill a social requirement, but no immediate goal state (e.g. grooming).

To address the equal use of the left and right hands to animate target objects, we argue that there was also an evolutionary selection for hemispheric dominance in the control and processing of emotive external stimuli. Our mixed-handed findings for self-directed behaviors and conspecific-directed manual actions are not inconsistent with previous studies of great ape handedness (e.g. Aruguete, Ely and King1992). These interactions demonstrate a greater involvement of right hemisphere/left hand compared with actions to inanimate objects. However, if animate objects require an increase in right hemisphere processing compared with inanimate objects, or if inanimate objects require an increase left hemisphere processing compared with animate objects is yet to be determined.

We concede that it is difficult to draw a definitive causal relationship between hemispheric specialization for language and handedness based on our simplistic coding of unimanual actions directed towards animate and inanimate target objects. This investigation does not account for task complexity, goal states, bimanual actions, sequences of actions or different types of grips and postures, all which have been shown to influence great ape handedness. Nevertheless, we can debate claims that only particular tasks with varying complexities, particularly bimanual tasks (e.g. Hopkins and Rabinowitz 1997), are necessary to influence the manifestation of preferential hand use in non-human primates. We may also contest that simple manual actions are a poor measure of handedness and will fail to elicit a bias (Meguerditchian et al. 2010), as our study will have certainly had a mix of all types of tasks with varying complexities. In fact, our study brings into questions whether it is the task that influences handedness or the animacy of the object that influences handedness.

Our findings indicate a right-hand dominance for actions towards inanimate objects, consistent with theories that implicate tool-use as a critical precursor to language like skills. Further evidence that great ape communicative gesture also demonstrates a right hand bias suggests that it dines on the same left hemisphere neural resources as object manipulation. This is interesting because it supposes that communicative gesture is underpinned by neural regions for hierarchical structured sequences (like human language) rather than processing of emotion, creating a causal link between tool use and communication

skills in great apes (see Meguerditchian, Vauclair and Hopkins 2010, for evidence that laterality of communicative gestures is not correlated with laterality of self-directed behaviors in chimpanzees). While further research is required to distinguish between communicative gestures and other animate interactions with conspecifics, our bottom-up approach using the MDM to investigate great ape handedness has now revealed the same significant interaction of hand and animacy across two independent species of captive great apes. We argue that this pattern of results is associated with the specialization of cerebral hemisphere processing for the two external animate and inanimate target objects, and that a dissociation for processing these stimuli existed prior to our evolutionary split from great apes.

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Table

Table 1. Frequencies of left and right manual actions towards animate and inanimate target objects

Subject	Gender	Left inanimate	Right inanimate	Left animate	Right animate	Total	Observation (min)
Camilla	F	33	50	16	6	105	90
Davidino	M	42	43	9	5	99	90
Giorgina	F	26	28	4	7	65	90
Guidy	F	18	36	15	20	89	90
Jacky	M	19	33	13	24	89	90
Luisa	F	4	12	3	6	25	90
Mary	F	35	45	10	8	98	90
Samy	F	35	53	10	4	102	90
Valentina	F	32	33	7	7	79	90

Figure
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