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1 **Target animacy influences chimpanzee handedness**

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29 **Abstract**

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

46 **Keywords:** Handedness, Animacy, Hemispheric Specialization, Chimpanzee

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4 **57 Introduction**

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8 **59** Historically, behavioral lateralization driven by dominant contralateral neural regions was  
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10 **60** considered unique to the human species. The most notable example of this phenomenon in humans is right-  
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12 **61** handedness correlated with left-hemisphere language regions (e.g. Broca 1865, Hellige 1993). For the vast  
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14 **62** majority of the population, both language function and right-handedness are hosted by the left hemisphere  
15  
16 **63** (e.g. Hellige 1993; Santrock 2008). The human population exhibits 90% right-handedness (McManus  
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18 **64** 2002) and within this population approximately 95% of individuals have language-processing regions  
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20 **65** situated in the left hemisphere of the brain (Foundas Leonard and Heilman 1995; Pujol, Deus, Losilla and  
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22 **66** Capdevila, 1999; Lurito and Dziedzic, 2001). This association has led scientists to hypothesize that  
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24 **67** hemispheric specialization for language and right-handedness are linked with one another in ways that may  
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26 **68** reveal clues about the evolution of human language skills (MacNeilage Studdert-Kennedy and Lindblom  
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28 **69** 1987; Corballis, 1992, 2002; Annett, 2002; McManus, 2002). However, the causal link between the  
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30 **70** emergence of right-handedness and language evolution is hotly debated (Corballis 2003; Vauclair 2004).

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32 **71** Today, research demonstrates that lateralized motor action, underpinned by contralateral neural  
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34 **72** regions, is not human-specific, and occurs across a wide range of vertebrates (Rogers and Andrew, 2002;  
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36 **73** Vallortigara and Rogers, 2005; MacNeilage, Rogers and Vallortigara, 2009; Vallortigara, Chiandetti and  
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38 **74** Sovrano 2011) and invertebrates (e.g. Frasnelli, Vallortigara, and Rogers, 2010). However, the extent to  
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40 **75** which a significant majority of any other species shows a bias in lateralized limb action (e.g. right-  
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42 **76** handedness) for any given task (e.g. language) akin to humans remains questionable (MacNeilage Studdert-  
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44 **77** Kennedy and Lindblom 1987; McGrew and Marchant, 1997; Hopkins, 1999; Palmer, 2002; Hopkins and  
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46 **78** Cantalupo, 2005; Papademetriou, Sheu and Michel 2005; Cashmore Uomini and Chapelain 2008; Uomini,  
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48 **79** 2009).

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50 **80** There are multiple disparate theories linking right-handedness with left hemisphere language  
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52 **81** function in humans. Holder (1997) argues that the high rate of human right-handedness suggests a genetic  
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54 **82** component, and Annett (1998) further postulates that both processes, language and right-handedness, are  
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56 **83** driven by a single common gene. Within an evolutionary context, it has been suggested that right-  
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58 **84** handedness emerged as a result of speech (Annett, 2002), gestural language (Corballis, 2002; Hopkins,  
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85 Russell, Freeman, Buehler, Reynolds, and Schapiro, 2005), tool use (Breuer, Ndoundou-Hockemba,  
86 Fishlock, 2005; Greenfield 1991), coordinated bimanual actions (Wundrum, 1986; Hopkins, Hook,  
87 Braccini and Schapiro, 2003) posture (MacNeilage Studdert-Kennedy and Lindblom 1987) and bipedalism  
88 (Westergaard, Kuhn and Suomi 1998; Braccini, Lambeth, Schapiro and Fitch 2010). However, while  
89 handedness studies demonstrate a strong correlation between right-handedness and left hemisphere  
90 language dominance, a *causal* relationship between the two remains hypothesized rather than empirically  
91 supported.

92           At face value, human right-handedness appears to be a robust and universal finding (Perelle and  
93 Ehrman, 1994; Raymond and Pontier, 2004). However these data are not without methodological concerns  
94 or limitations. Data revealing a 90% right-handed and 10% left-handed population split are mainly derived  
95 from self-report questionnaires in literate populations (e.g. Oldfield 1971; Hardyck, Goldman and  
96 Petrinovich 1975; McManus 1981). Furthermore, questionnaires rely primarily on measures of precision  
97 tool-use. In the limited literature where sampling methods are altered to include a more ethological range of  
98 factors, handedness patterns become more complex and right-handedness can vary between 70-90%  
99 (Annett 1985). For instance, Dimond and Harries (1984) reported a human left-hand preference for the self-  
100 directed behavior of face touching, in individuals who were otherwise right-handed, suggesting that the  
101 right-hemisphere’s dominance for emotional processing (e.g. Borod, Haywood and Koff 1997; Borod et al.  
102 1998) may influence these manual actions. A subsequent study demonstrated that a left-hand preference for  
103 face-touching was present in native English, but not in native Japanese speakers (Hatta and Nakatsuka  
104 1976), suggesting that handedness is also subject to socio-cultural influences. Marchant, McGrew and Eibl-  
105 Eibesfeldt (1995) noted that a range of manual behaviors, barring tool use, were missing from handedness  
106 surveys (e.g. Edinburgh Handedness Inventory; Oldfield 1971) and argued for handedness measurements to  
107 be captured during observations of naturalistic behavior. By tracking naturalistic handedness across three  
108 different preliterate populations they noted that while there was an overall ‘consistent but weak right hand  
109 dominance’, individuals were mixed-handed for all actions across a ‘comprehensive range of ethological  
110 measures’ with the exception for tool-use, which was distinctly right-handed. Further studies demonstrated  
111 that the percentage left-handedness fluctuated (3-27%) in traditional cultures (Faurie and Raymond 2005).  
112 Moreover, Knecht and colleagues (2000) reported that 70% of left-handers still exhibit a left-hemisphere

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4 113 dominance for language functions, calling into question that a bias in handedness serves as a reliable  
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6 114 marker of hemispheric specialization for language. Some argue that the dominant hand for manual gesture  
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8 115 may, in fact constitute a more accurate marker of language lateralized brain regions (Vauclair and  
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10 116 Meguerditchian 2008).

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12 117 Although the general perception is that the human population is strongly right-hand dominant, this  
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14 118 finding is derived from a limited set of questionnaire data. From the few studies that look outside of object  
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16 119 manipulation, there is evidence that handedness can vary across tasks, cultures and levels of literacy.  
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18 120 Therefore, it could be argued that the very high percentage of human right-handedness (90%) is selectively  
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20 121 generated from tasks for object manipulation and highlights tasks that are specifically tied to the neural  
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22 122 resources of the left hemisphere. Reports of varying handedness across environmental factors calls into  
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24 123 question the strict classification of individuals as: right-handed, left-handed or ambidextrous, as these labels  
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26 124 do not appear to be representative of a comprehensive range of natural human manual actions. Furthermore,  
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28 125 this type of over-generalization is not only problematic for understanding how handedness is specialized for  
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30 126 specific tasks or types of stimuli, it also causes concerns for inter- and intra-species comparisons. In fact,  
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32 127 Annett (1985) argues that hand preference should be treated as a continuous variable that correlates  
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34 128 strength of handedness for specific tasks, rather than a dichotomized right/left bias, because only a small  
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36 129 proportion of the human population manifests an extreme right- or left-hand preference for daily activities.  
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38 130 However, it should be noted that regardless of culture or literacy abilities a right-hand bias for interaction  
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40 131 with objects appears reliable across diverse human populations and may shed light on the evolution of  
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42 132 human language capabilities.

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44 133 In order to reveal information about the evolutionary relationship between human right-  
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46 134 handedness and language skills, archeologists investigate human fossils and ancient tool kits.  
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48 135 Unfortunately, human fossils provide limited clues about how our ancestors communicated with one  
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50 136 another, but they have been helpful for revealing information about the handedness of our preliterate  
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52 137 ancestors. Archeologists believe that human population-level right-handedness dates back more than 2  
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54 138 million years (Cashmore, 2009; Uomini 2009). Interestingly, evidence suggests that human right-  
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56 139 handedness is linked specifically to tool-use from as far back as 2.5 million years (Bradshaw and Rogers,  
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58 140 1993; Toth 1985; McManus 2002). The evidence suggesting that right-handedness preceded language  
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4 141 makes tool-use a strong candidate for further research into the evolution of human communication skills.  
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6 142 This is not the first time that tool-use has been implicated in the evolution of human language skills. In fact,  
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8 143 Byrne and Byrne (1993); Corballis, (2002); Foucart et al, (2005); Weiss and Newport, (2006); Mercader,  
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10 144 Barton and Gillespie (2007) and Greenfield (1991) have all suggested that object manipulation for actions  
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12 145 related to tool-use, manufacture and even food preparation have common features to modern language and  
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14 146 therefore serve as a likely precursor to language. Some scientists postulate that language evolved as an  
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16 147 extension of right hand and left hemisphere ability to produce temporal sequences of motor activity derived  
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18 148 from tool use (Bradshaw and Nettleton, 1982; Corballis, 1991; Morgan and Corballis 1978; Hewes, 1973;  
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20 149 Kimura, 1993; MacNeilage, Studdert0Kennedy and Lindblom 1987). While each investigator has their own  
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22 150 manner of theorizing a causal relationship between handedness and language-like skills, theories require  
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24 151 testing for validation.

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26 152 Great apes represent a functional model to study handedness not only because of their  
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28 153 phylogenetic proximity to humans, but also because they display clear anatomical human-like features,  
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30 154 such as the morphology and the manipulative skills of hands (Byrne, Corp and Byrne 2001), the ability to  
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32 155 occasionally locomote bipedally (Videan and McGrew, 2002) and the capacity to exhibit intentionally  
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34 156 communicative gestures (e.g. Savage-Rumbaugh, McDonald, Sevcik, Hopkins, and Rubert, 1986; Bard  
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36 157 1992; Leavens and Hopkins 1998; Hobaiter and Byrne 2011). Great apes do not only share  
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38 158 musculoskeletal characteristics with humans. The organization of the great apes brains shares many  
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40 159 structural and processing capabilities with that of the human brain. Recent neuroimaging studies have  
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42 160 indicated that all four species of great apes display homologous human Broca's (Cantalupo, Pilcher and  
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44 161 Hopkins 2003) and Wernicke's (Spocter et al. 2010) areas that are asymmetrically larger in the left  
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46 162 hemisphere of all species of great apes. Moreover, Higuchia, Chaminadeb, Imamizua and Kawatoa (2009)  
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48 163 found that the homologous Broca's and Wernicke's areas were active (fMRI) in the ape brain during tool  
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50 164 use and, furthermore, that there is an overlap of neural activation for both language perception and tool-use  
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52 165 in humans within Broca's area. Other neuroimaging studies corroborate a left-hemisphere specialization for  
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54 166 tool-use in apes demonstrating an overlap with brain regions associated with language-like skills in humans  
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56 167 (Binkofski et al. 1999a,b; Binkofski and Buccino 2004).

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59 168 Until recently, handedness has been extensively explored in great apes, but not in a systematic way  
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4 169 that is useful to make direct comparisons between human and non-human primates. Researchers have  
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6 170 explored bimanual and unimanual handedness directed at inanimate objects to a range of different actions  
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8 171 and tasks with varying levels of complexity. Historically, with only one exception (Boleda, Chincilla, Valls  
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10 172 and Pastor 1975), results suggested that great apes did not express a right-hand population bias exhibited  
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12 173 similar to humans (e.g. Finch 1941; Marchant and Steklis 1986). These early investigations of handedness  
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14 174 in great apes focused on manipulative motor behaviors in both wild and captive subjects and showed  
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16 175 inconsistent patterns of population-level handedness according to species, sample size and complexity of  
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18 176 manual tasks (McGrew and Marchant, 1997; Papademetriou, Sheu, and Michel, 2005; Hopkins, Russell and  
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20 177 Cantalupo 2007). However, it should be noted that methodologies between laboratories differed  
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22 178 significantly, confounding interpretations of results and comparisons between laboratories.

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24 179 More recently, systematic investigations with large sample sizes have reported great ape right-hand  
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26 180 biases in captive chimpanzees (*Pan troglodytes*), related to complex manual tasks such as bimanual  
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28 181 feeding, coordinated bimanual actions, bipedal reaching and throwing (for reviews, see Hopkins 2006,  
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30 182 2007), and in captive gorillas (*Gorilla gorilla*) (Byrne and Byrne, 1991; Meguerditchian, Calcutt, Lonsdorf,  
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32 183 Ross and Hopkins, 2010) for bimanual coordinated actions. These initial reports were criticized for being  
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34 184 based upon single laboratory samples (McGrew and Marchant, 1997; Papademetriou, Sheu and Michel  
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36 185 2005 for reviews), methodological and theoretical grounds (McGrew and Marchant, 1997; Palmer, 2002,  
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38 186 2003; Crow, 2004) and the suggestion that apes' exposure to human culture might have induced a bias of  
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40 187 hand use in manual actions (e.g. McGrew and Marchant 1997). However skepticism over these findings  
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42 188 have largely been dispelled as newly obtained data in support of a right hand bias continues to mount from  
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44 189 an increasing number of great ape species for a range of manual actions (e.g. Hopkins, Wesley, Izard, Hook  
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46 190 and Schapiro 2004; Meguerditchian et al. 2010; Meguerditchian, Vauclair and Hopkins 2010; Llorente,  
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48 191 Mosquera and Fabre´ 2009; Llorente et al. 2011) across captive and wild settings (Llorente et al. 2011;  
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50 192 Lonsdorf and Hopkins, 2005).

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53 193 Along with object use, there has been a recent interest in great ape handedness for social  
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55 194 communication to evaluate theories of language origins linked to hemispheric specialization (Shafer 1993;  
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57 195 Hopkins and Leavens 1998; Hopkins et al. 2005; Meguerditchian, Vauclair, Hopkins, 2010; Hopkins and  
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59 196 Vauclair, in press). While great apes apparently do not possess human-like language skills, scientists argue

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4 197 that communicative gestures may represent a unique behavior, similar to humans, and may be important for  
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6 198 drawing a causal link between the evolution of communication and handedness (Falk 1987; Hewes 1973;  
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8 199 Kimura 1993). Evidence suggests that great apes communicate by gestures across a variety of different  
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10 200 social contexts (e.g., Call and Tomasello, 2007; Goodall, 1986; Pika, Leibal, Call and Tomasello 2005).  
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12 201 Group-level right-handedness for gestural communication has been reported in small samples of captive  
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14 202 bonobos and gorillas (Shafer 1993; Hopkins and de Waal, 1995). Although as with studies of object  
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16 203 manipulation, studies reporting a right hand bias (e.g. Hopkins et al. 2005) have been criticized for  
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18 204 exclusively coding chimpanzee gestures directed towards human experimenters (e.g. McGrew and  
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20 205 Marchant, 1997). However, a further study (Meguerditchiana, Vauclair Hopkins 2010) revealed significant  
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22 206 right hand dominance regardless of whether the receiver was a conspecific or human, diminishing concerns  
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24 207 that ape handedness is biased by enculturation.

26 208         Although the evidence is limited, it has recently been suggested that there may be an even higher  
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28 209 rate of right-handedness in great ape communicative gesture compared with actions directed upon  
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30 210 inanimate objects (Hopkins et al. 2011). The authors argue that communicative gestures may be the result  
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32 211 of different underlying neural generators from those employed during object manipulation. However, it  
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34 212 could also be argued that handedness tied to both object interaction and gestural communication are highly  
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36 213 right-lateralized behaviors because they both exploit the left hemisphere's functional capabilities to produce  
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38 214 hierarchical temporal sequences of events to reach a goal state. In great apes, communicative gestures may  
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40 215 represent an evolutionary step towards language skills, extending the left hemisphere's specialized  
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42 216 processing derived from tool use. This line of reasoning would suggest that this step occurred prior to our  
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44 217 evolutionary split from great apes and may be unique to humans and great apes. Based on the review above,  
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46 218 great ape handedness appears to be present for interactions with objects and during communicative  
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48 219 gestures, expressing a similar pattern of handedness with humans and reinforcing the ape model for the  
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50 220 evolution of language. This is consistent with recent characterizations of apes' gestures as a kind of social  
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52 221 tool use (Bard 1990, 1992; Gomez 2007; Leavens, Hopkins, and Bard 2005). Limited handedness data have  
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54 222 also been collected during observational studies of self-directed behaviors in great apes. Similar to the  
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56 223 limited human data, studies have not revealed a right-hand bias. In the handful of studies, a few have  
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58 224 revealed both equal frequency use of both hands for self-directed behaviors, (Aruguete, Ely and King 1992;



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4 225 Hopkins and de Waal, 1995; Marchant and McGrew, 1996; Forrester et al. 2011) while others observed a  
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6 226 left-hand bias for face-touching in orangutans (*Pongo pygmaeus*) (Rogers and Kaplan 1995) and gorillas  
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8 227 (*Gorilla gorilla*) (Dimond and Harries 1983).  
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10 228 Interestingly, all studies of self-directed behaviors report a larger contribution of the left hand,  
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12 229 compared with manual actions involving inanimate objects. Similar to the human research, scientists  
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14 230 propose a greater involvement of the left side of the body during social arousing situations compared with  
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16 231 non-emotive stimuli may be due to the right hemisphere's dominant role in perceiving emotion, with  
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18 232 differential effects on primary cutaneous afferents across the left and right hemispaces of the integument  
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20 233 (e.g. Hopkins, Russell, Freeman, Reynolds, Griffis, and Leavens, 2006). Behavioral asymmetries tied to  
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22 234 emotive stimuli have also been reported for perception and production of facial expressions in both apes  
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24 235 and humans. These studies are consistent with the right-hemisphere dominance for emotive stimuli and  
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26 236 report an earlier activation of the left side of the face (e.g. Fernandez-Carriba, Loches, and Hopkins, 2002;  
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28 237 Borod, Koff, Perlman Lorch, Nicholas, 1986).  
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30 238 It is clear from a review of the literature that there are large discrepancies in the way we collect  
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32 239 handedness data from human and nonhuman primate populations that cause confounds for direct  
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34 240 comparisons both within and between species. However, even with these methodological confounds, there  
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36 241 are striking similarities in the handedness patterns for humans and apes for interactions with inanimate  
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38 242 objects, communicative gestures and self-directed manual actions potentially highlighting the different  
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40 243 processing capabilities of the left and right hemispheres. While we are not the first authors to raise the issue  
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42 244 of inconsistencies in handedness measurements across species (e.g. Aurgete, Ely and King 1992), we  
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44 245 highlight the need for a consistent investigative framework under which to assess naturalistic handedness  
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46 246 across a range of behaviors in order to make valid comparisons both within and between species  
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48 247 Previous work with gorillas sought to investigate differences in hand preference to animate and  
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50 248 inanimate target stimuli for spontaneous behaviors in captive, semi-free-ranging lowland gorillas (Forrester  
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52 249 et al. 2011). That study took into account a comprehensive range of interactions with both social (animate)  
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54 250 and non-social (inanimate) targets employing a Multidimensional Method (MDM) that systematically  
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56 251 captures, codes and analyzes naturalistic behavior for the purpose of allowing valid comparisons across  
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58 252 human and nonhuman primate species (Forrester 2008). In that study, we did not categorize or code  
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253 actions towards conspecifics as communicative gestures and therefore did not test the right-hand social  
254 communication hypothesis. However, we hypothesized that the bilateral use of both arms for self-directed  
255 and conspecific-directed actions combined, may represent an increased participation of the right  
256 hemisphere for targets with social-emotional components (e.g. conspecific) compared with non-emotive  
257 targets (e.g. inanimate objects). The findings demonstrated that when we teased apart animate targets from  
258 inanimate tasks, a right-handed bias for inanimate target objects was revealed. We postulated that these  
259 data give credence to the theory that there is a causal relationship between left hemisphere language centers  
260 in humans and right-handedness that is inherited from the last common ancestor whose right-handed  
261 actions for tool-use was underpinned by left-hemisphere specialized areas for orchestrating hierarchical  
262 sequences of events to reach a goal state. We further speculated that sequences of actions to reach a goal  
263 could be described as a very basic syntax, and that these types of activities may have paved the way for the  
264 evolution of language skills. Therefore, it brings into question whether tests of complex bimanual action are  
265 required to observe individual and population-level right-handedness. Rather, we ask, can the animacy of  
266 the target object be enough to bias the hand of use? The anticipation of a manipulation may draw on the left  
267 hemisphere processing resources. If so, it can be argued that right-handedness may be the result of a long-  
268 standing left hemisphere neural bias whose processing abilities were molded from our ancient ancestors'  
269 interactions with tools. Since that time, we have extended the hierarchical sequencing abilities of the left  
270 hemisphere to evolve language like skills.

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

278  
279 **Material and methods**

280 *Subjects and housing*

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4 281 This study included a group of nine captive chimpanzees (*Pan troglodyte*) hosted at the Garda Zoological  
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6 282 Park Parco Natura Viva, in Verona (Italy). The group included: 2 males, 5 adult females and 2 juveniles.  
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8 283 The individuals were institutionalized animals with a variety of rearing histories. The enclosure (only  
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10 284 accessible by motor vehicle) was split into different segments comprised of a smaller round indoor room  
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12 285 linked to a large outdoor island (2113 m<sup>2</sup>) accessed through a mesh corridor. The island was furnished with  
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14 286 two vertical wood towers, linked by ropes, a small branch and two caves. The island was surrounded by  
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16 287 water (9 m wide). Chimpanzees slept and ate in the indoor enclosure. Daily nourishment consisted of  
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18 288 mainly fruits and vegetables. Enrichment activities were provided on a daily basis in order to increase the  
19  
20 289 manifestation of natural behaviors and maintain high standards of animal welfare.  
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#### 23 291 *Data capture*

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26 292 In order to ensure reliable chimpanzee identification, and allow for the subject groups to adapt to the  
27  
28 293 presence of the experimenter and experimental equipment, a familiarization period was necessary. This  
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30 294 process involved taking video samples for each subject and their daily natural behaviors and activities in  
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32 295 the outdoor enclosure using a focal animal sampling method. Once reliable identification was achieved, a  
33  
34 296 continuous focal sampling was initiated where each recording session lasted 10 minutes, counterbalanced  
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36 297 over day the time of the observation (e.g. Altman 1974). Data sets consisted of 9 sessions for each focal  
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38 298 sampling, equating to 90 minutes per subject. While we were unable to perform dual-synchronized video  
39  
40 299 recording as prescribed by the MDM method (Forrester et al 2011), the view of the video camera was wide  
41  
42 300 enough to include not only the focal subject but also the social context within which the focal individual  
43  
44 301 was behaving. Video footage was captured using a Sony digital video camera, which was subsequently  
45  
46 302 streamed and saved on a Macintosh computer for off-line coding and analysis.  
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#### 49 304 *Coding categorization*

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52 305 The Multidimensional Method (MDM) was employed for variable categorization, coding and analyses to  
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54 306 facilitate direct comparisons with previous our previous investigations (Forrester 2008; Forrester et al.  
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56 307 2011). Specifically, we identified the laterality of each unimanual action towards an external target as left  
57  
58 308 or right. This coding procedure referred to the hand used to conduct the action rather than the direction of  
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4 309 the action. In addition, we coded the animacy of the target object. The target was deemed animate when the  
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6 310 hand was directed towards and made contact with either the self or a conspecific. Targets were identified as  
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8 311 inanimate when the hand was directed towards, and made contact with, an object, the enclosure or the  
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10 312 environment (e.g. tapping the ground). Frequencies of inanimate targets excluded locomotion. In line with  
11  
12 313 Forrester et al. (2011), in order to avoid postural confounds, unimanual actions towards animate and  
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14 314 inanimate targets were considered only when both hands were equally available to perform the task  
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16 315 (Aruguete, Ely and King 1992; Westergaard, Kuhn and Suomi 1998; Braccini et al. 2010) (see Table 1).  
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18 316 Therefore, in cases where one hand reached towards a target object but the other hand was used for postural  
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20 317 support or a separate manual activity, the action was excluded from analyses.  
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23  
24 319 - **Insert Table 1** -

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28 321 *Analyses*

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30 322 Data were analyzed using a 2 (left hand, right hand) x 2 (animate target, inanimate target) repeated  
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32 323 measures analysis of variance (ANOVA), with paired-sample t-tests for post-hoc analyses. All subject data  
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34 324 were based on 90 minutes of observation time and analyses were all based on frequencies. Normalization  
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36 325 by rate (rate = number of frequency counts/ observation time in minutes) was not required because all  
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38 326 subjects were observed for the same amount of time. However, a second method of standardization was  
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40 327 established to equalize the effect of each subject on the data set. To equalize the weighting that each subject  
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42 328 contributed to the data set, we calculated proportions for each subject of each response type in relation to  
43  
44 329 the total number of actions for that subject. To facilitate direct comparisons between the present study and  
45  
46 330 our previously published data on gorillas (Forrester et al. 2011), we re-analyzed the gorilla data by  
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48 331 proportions, and exactly reproduced the statistical patterns originally reported on only 6 gorillas. In the  
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50 332 reanalysis, 11 of the 12 gorillas were included. One exclusion was made for a adult female (Kibi) who only  
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52 333 produced 1 animate response.  
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54 334

55 335 **Results**

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4 337 *Gorillas*

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6 338 A reanalysis of gorilla data from the previous study (Forrester et al. 2011) yielded the following results: a  
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8 339 non-significant trend for hand, ( $F_{1,10} = 4.13, P = 0.07$ ) (favoring the right hand), a main effect of target  
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10 340 animacy, ( $F_{1,10} = 606.61, P < 0.001$ ) (indicating a higher frequency of inanimate events), and a stronger  
11  
12 341 significant interaction than previously reported between hand and target animacy, ( $F_{1,10} = 6.309, P =$   
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14 342  $0.032$ ), such that the right hand was significantly more often directed towards inanimate targets, in  
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16 343 comparison to animate targets.  
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20 345 *Chimpanzees*

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22 346 The 2 (left hand, right hand) x 2 (animate target, inanimate target) ANOVA (proportion and frequency)  
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24 347 revealed significant interactions of lateralized unimanual action and target animacy (frequency:  $F_{1,8} =$   
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26 348  $8.813, P = 0.018$ ; proportions:  $F_{1,8} = 11.902, P = 0.009$ ) (see Figure 1). Main effects of target type  
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28 349 (animate, inanimate) demonstrated higher overall rates of actions towards inanimate targets versus actions  
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30 350 directed towards animate targets (frequency:  $F_{1,8} = 28.19, P < 0.001$ ; proportion:  $F_{1,8} = 46.60, P < 0.001$ ).  
31  
32 351 Main effects of hand (left, right) were also identified (frequency:  $F_{1,8} = 10.250, P = 0.013$ ; proportion:  $F_{1,8}$   
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34 352  $= 8.306, P = 0.020$ ) indicating a higher frequency of right-handed actions compared to left handed actions.  
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36 353 Post-hoc analyses were conducted using paired-sample t-tests to test the dominance of right-handed actions  
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38 354 (frequency:  $M = 37, SE = 4.19$ ; proportion:  $M = .444, SE = .015$ ) compared with left-handed actions  
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40 355 (frequency:  $M = 27.1, SE = 3.88$ ; proportion:  $M = .313, SE = .327$ ) for inanimate targets only, (frequency:  
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42 356  $t(8) = -4.080, P = .004$ ; proportion:  $t(8) = -3.817, P = 0.005$ ). We also compared right-handed actions  
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44 357 (frequency:  $M = 9.66, SE = 2.39$ ; proportion:  $M = .129, SE = .030$ ) with left-handed actions (frequency:  $M$   
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46 358  $= 9.66, SE = 1.51$ ; proportion:  $M = .1142, SE = .012$ ) for animate targets only, (frequency:  $t(8) = .000, P =$   
47  
48 359  $1.000$ ; proportion:  $t(8) = -.566, P = 0.587$ ) which demonstrated no such significant difference.  
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53 361 - **Insert Figure 1** -

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57 363 **Figure 1.** Hand by animacy interaction in chimpanzees

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6 366 **Discussion**

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8 367         Results demonstrated a significant interaction between handedness and target animacy, where the  
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10 368 right hand was more influenced by the animacy of the target than the left hand. Post-hoc t-tests revealed a  
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12 369 significant bias for the right hand for actions directed towards inanimate objects, whereas both hands were  
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14 370 used with equal frequency for actions directed towards animate targets. These findings are identical to the  
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16 371 unimanual handedness pattern that we reported for captive semi-free ranging western lowland gorillas  
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18 372 (Forrester et al. 2011). This pattern was also demonstrated by Aruguete and colleagues (1992), but was not  
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20 373 discussed in light of underlying neural generators.

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22 374         With respect to the previous literature, it is not surprising that we identified a right hand bias for  
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24 375 manual actions in a group of captive apes. What is interesting is that the right hand bias was only  
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26 376 significant for actions directed towards inanimate target objects regardless of task type, complexity or  
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28 377 social context. This implies a dominance for left hemisphere processing of external inanimate stimuli. This  
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30 378 finding is not in conflict with either the human or ape handedness data that we have reviewed, but our  
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32 379 interpretation of the results reflects a causal relationship between tool use and the evolution of language  
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34 380 like skills. We propose that interactions with inanimate objects require a sequence of hierarchical actions to  
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36 381 create a valid goal state. The hierarchical sequence of manual events leading up to a goal state could be  
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38 382 comparable to a simple or proto-syntax, similar to that which underpinned an early human proto-language.  
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40 383 Interactions with objects (and ultimately tool-use) may have extended the left hemisphere's temporal-  
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42 384 sequential processing abilities (originally selected for external stimuli) to a language-based syntax (internal  
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44 385 stimuli).

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46 386         We postulate that the left hemisphere has a preference for either manipulating and/or *predicting*  
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48 387 manipulations required by the engagement with the object. We also considered the scenario where the left  
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50 388 hemisphere *predicts* or *plans* for manipulation based on the inanimate characteristics afforded by the  
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52 389 external object, thus electing the right hand for action towards the object. At this time we cannot distinguish  
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54 390 if it is the animacy of the target object that biases the neural processing of external stimuli and thus the  
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56 391 hand that is employed or, if it is the predicted tasks afforded by the external stimuli. It may be more likely  
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58 392 that an inanimate object requires manipulation to reach a goal state compared with an animate object. For  
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4 393 example, tools require manipulation in order to achieve a goal. On the other hand, emotive interactions with  
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6 394 conspecifics (excluding communicative gestures) and the self may require perseverative actions to fulfill a  
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8 395 social requirement, but no immediate goal state (e.g. grooming).  
9

10 396 To address the equal use of the left and right hands to animate target objects, we argue that there  
11  
12 397 was also an evolutionary selection for hemispheric dominance in the control and processing of emotive  
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14 398 external stimuli. Our mixed-handed findings for self-directed behaviors and conspecific-directed manual  
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16 399 actions are not inconsistent with previous studies of great ape handedness (e.g. Aruguete, Ely and  
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18 400 King1992). These interactions demonstrate a greater involvement of right hemisphere/left hand compared  
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20 401 with actions to inanimate objects. However, if animate objects require an increase in right hemisphere  
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22 402 processing compared with inanimate objects, or if inanimate objects require an increase left hemisphere  
23  
24 403 processing compared with animate objects is yet to be determined.

26 404 We concede that it is difficult to draw a definitive causal relationship between hemispheric  
27  
28 405 specialization for language and handedness based on our simplistic coding of unimanual actions directed  
29  
30 406 towards animate and inanimate target objects. This investigation does not account for task complexity, goal  
31  
32 407 states, bimanual actions, sequences of actions or different types of grips and postures, all which have been  
33  
34 408 shown to influence great ape handedness. Nevertheless, we can debate claims that only particular tasks with  
35  
36 409 varying complexities, particularly bimanual tasks (e.g. Hopkins and Rabinowitz 1997), are necessary to  
37  
38 410 influence the manifestation of preferential hand use in non-human primates. We may also contest that  
39  
40 411 simple manual actions are a poor measure of handedness and will fail to elicit a bias (Meguerditchian et al.  
41  
42 412 2010), as our study will have certainly had a mix of all types of tasks with varying complexities. In fact, our  
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44 413 study brings into questions whether it is the task that influences handedness or the animacy of the object  
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46 414 that influences handedness.

48 415 Our findings indicate a right-hand dominance for actions towards inanimate objects, consistent  
49  
50 416 with theories that implicate tool-use as a critical precursor to language like skills. Further evidence that  
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52 417 great ape communicative gesture also demonstrates a right hand bias suggests that it dines on the same left  
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54 418 hemisphere neural resources as object manipulation. This is interesting because it supposes that  
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56 419 communicative gesture is underpinned by neural regions for hierarchical structured sequences (like human  
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58 420 language) rather than processing of emotion, creating a causal link between tool use and communication  
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4 421 skills in great apes (see Meguerditchian, Vauclair and Hopkins 2010, for evidence that laterality of  
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6 422 communicative gestures is not correlated with laterality of self-directed behaviors in chimpanzees). While  
7  
8 423 further research is required to distinguish between communicative gestures and other animate interactions  
9  
10 424 with conspecifics, our bottom-up approach using the MDM to investigate great ape handedness has now  
11  
12 425 revealed the same significant interaction of hand and animacy across two independent species of captive  
13  
14 426 great apes. We argue that this pattern of results is associated with the specialization of cerebral hemisphere  
15  
16 427 processing for the two external animate and inanimate target objects, and that a dissociation for processing  
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18 428 these stimuli existed prior to our evolutionary split from great apes.  
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22 429

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27  
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**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

