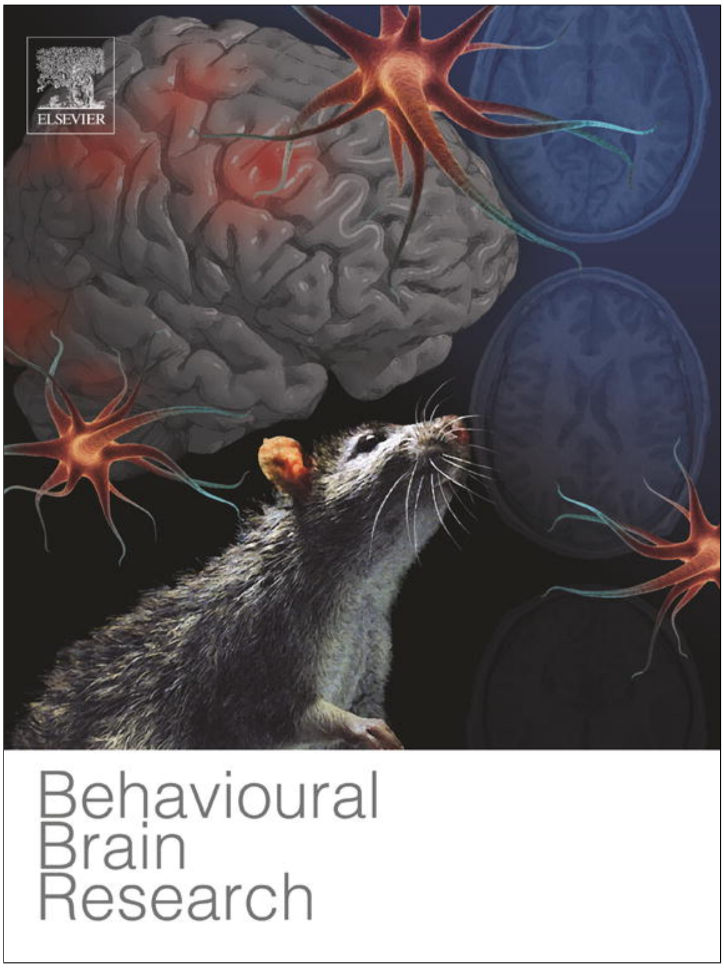

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Research report

Human handedness: An inherited evolutionary trait

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HIGHLIGHTS

- We investigated child handedness during naturalistic behavior.
- Using focal video sampling, we coded for actions to animate and inanimate targets.
- Children were right hand biased only for manual actions toward inanimate targets.
- We compared child and great ape handedness under a unified method.
- We suggest human right-handedness derives from early cerebral lateralization.

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ABSTRACT

Our objective was to demonstrate that human population-level, right-handedness, is not species specific, precipitated from language areas in the brain, but rather is *context* specific and inherited from a behavior common to both humans and great apes. In general, previous methods of assessing human handedness have neglected to consider the context of action, or employ methods suitable for direct comparison across species. We employed a bottom-up, context-sensitive method to quantitatively assess manual actions in right-handed, typically developing children during naturalistic behavior. By classifying the target to which participants directed a manual action, as *animate* (social partner, self) or *inanimate* (non-living functional objects), we found that children demonstrated a significant right-hand bias for manual actions directed toward inanimate targets, but not for manual actions directed toward animate targets. This pattern was revealed at both the group and individual levels. We used a focal video sampling, corpus data-mining approach to allow for direct comparisons with captive gorillas (Forrester et al. Animal Cognition 2011;14(6):903–7) and chimpanzees (Forrester et al. Animal Cognition, in press). Comparisons of handedness patters support the view that population-level, human handedness, and its origin in cerebral lateralization is not a new or human-unique characteristic. These data are consistent with the theory that human right-handedness is a trait developed through tool use that was inherited from an ancestor common to both humans and great apes.

1. Introduction

The human brain is not symmetrical, neither functionally nor anatomically. There are different functional specializations of the left and right hemispheres for processing sensory information [for a review, see 1]. Furthermore, the organization of the brain is such that the innervations of the musculature that come from the motor cortices extend contralaterally. The left hemisphere controls the right side of the body and the right hemisphere controls the left side of the body. The result of such organization means that cerebral lateralization can manifest in contralateral physical actions [e.g. 2]. Thus, in some cases, physical actions can be used as indirect markers of underlying neural generators [for a review, see 3].

While behavioral lateralization, driven by dominant contralateral neural regions, was historically considered to be unique to humans, it is now widely accepted that lateralized motor action underpinned by contralateral neural regions is present in both vertebrates [4,5] and invertebrates [e.g. 6]. This division of labor

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between the two hemispheres is proposed to be an advantageous evolutionary adaptation that provides the brain with increased neural efficiency. Lateralized brains allow for disparate functions to operate in parallel within the left and right hemispheres. Additionally, by avoiding the duplication of functioning across hemispheres, there is no concern regarding the simultaneous initiation of incompatible responses [4,7,8]. Recent research suggests that cerebral lateralization for specific capabilities emerged before the rise of vertebrates such that the left hemisphere evolved to control well-established patterns of behavior and the right hemisphere became adapted for detecting and responding to unexpected stimuli [for a review, see 9].

The most notable example of human lateralized motor action underpinned by cerebral lateralization for cognitive function is handedness and the neural regions associated with speech production (e.g. inferior frontal gyrus [10]), and comprehension (superior temporal gyrus [11]). For the vast majority of the population, brain processes controlling language function and handedness are located within the left hemisphere [e.g. 12]. It is commonly reported that the human population exhibits approximately 90% right-handedness [e.g. 13] and within this population approximately 95% of individuals have language-processing regions situated in the left hemisphere of the brain [14]. Human population-level right-handedness has been theorized to have evolutionary links with gesture [15,16], speech [17], tool use [e.g. 18,19], coordinated bimanual actions [20,21], posture [22] and bipedalism [23,24]. Scientists have been drawn to the unique coupling of manual action and brain organization for skilled communication in the hopes that it may shed light on the origins of human language. However, to date, a causal relationship between human handedness and language function remains a hotly debated topic [25].

Evolutionary psychologists contend that the most comprehensive method to study the origin of handedness and hemispheric specialization for language may be to observe the spontaneous behaviors of our closest living 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 [26], the ability to occasionally locomote bipedally [27] and the capacity to exhibit intentionally communicative gestures [e.g. 28–32]. Great apes do not only share physical characteristics with humans, the neural organization of the great ape brain shares many structural and processing capabilities with the human brain. Recent neuroimaging studies have indicated that all four species of great apes display homologous human Broca's [33,34] and Wernicke's [34,35] areas that are asymmetrically larger in the left hemisphere of all species of great apes. In humans, perceiving language and using tools are theorized to be related to the origin and evolution of human language in so much as studies report an overlap of brain activity between language and praxis in Broca's area [36,37]. It has been suggested that the neural processes for the computation of complex structured sequences exist in great apes without language, making tool-use an attractive candidate as a cognitive skill that could have been exapted to support the evolution of human grammar capabilities [38].

Handedness has been extensively explored from a plethora of different methods in both captive and wild apes. While a range of studies find no clear evidence of species-level manual lateralization [e.g. 39–44], others have reported group-level right-hand biases in chimpanzees (*Pan troglodytes*) for: bimanual feeding, coordinated bimanual actions, bipedal reaching and throwing [for reviews, see 45,46], in captive gorillas for bimanual feeding [47] and for communicative gesture in chimpanzees [e.g. 16,48,49]. Alternatively, it has been noted that rehabilitated orangutans exhibited a significant group-level left-handed preference for scratching and for the fine manipulation of parts of the face [50]. Contrarily, chimpanzees exhibited a significant group-level increase in right-handed, self-directed behaviors with increased task complexity [51], which were interpreted by the authors as evidence that self-directed behaviors may be influenced by motivational factors underpinned by a right hemisphere dominance within both social and nonsocial contexts (due to the descending neuromodulatory influences, which are primarily ipsilateral). To date, there is no consensus in findings across laboratories using different behavioral methods to indicate a population-level lateral manual bias in great apes with a significance level to rival that of humans. Furthermore, some results, particularly related to chimpanzees, have been challenged on methodological grounds [e.g. 52] and sampling factors [53,54].

More recently, large, systematic investigations of ape handedness have attempted to clarify confounds in earlier studies. Hopkins et al. investigated the influences of rearing histories on handedness [55], while Llorente et al. tested the influence of bimanual and unimanual tasks on handedness [56,57]. Although these multiple colony-level ape manual biases still do not compare to the strength of lateralization found in humans, they have nevertheless demonstrated significant colony-wide, right-hand biases, supporting the possibility of population-wide ape handedness, consistent with the hypothesis for an early adaptation of a left hemisphere specialization for behaviors requiring structured sequences of actions [e.g. 9].

Human handedness measures are not without their own methodological concerns. Despite strong neuropsychological correlates for handedness, methods of assessment are not uniform or consistent across development. Human handedness is typically assessed through self-report, questionnaires and observations. For adults, questionnaires, such as the Edinburgh Handedness Inventory [58] and the Waterloo Handedness Questionnaire [59], focus exclusively on literate populations, querying with which hand subjects pick up or manipulate a functional object (e.g. pencil and scissors). While human population-level right-handedness appears to be an extremely robust and universal finding [60], questionnaires focus exclusively on precision tool use, and therefore represent a specific subset of individuals on a specific subset of tasks. The few studies that explore spontaneous naturalistic handedness demonstrate patterns that are more complex and may give clues to the neural generators driving the behaviors. For example, during observations of naturalistic conversation, manual actions, which did not otherwise touch anything and occurred during speaking but not silent verbal tasks or nonverbal communication, were significantly biased to the right hand in left hemisphere language dominant individuals [61]. In another study of naturalistic behavior, handedness was tracked across three different preliterate populations and demonstrated that although there was a general population trend for right-handedness, individuals were mixed-handed for all actions with the exception of tool use, which was distinctly right-handed [62]. Alternatively, reports of human left-handed preferences were found for the self-directed behavior of face touching, in individuals who were otherwise right-handed [63], suggesting that social or emotive hand action might activate the right hemisphere's dominance for emotional processing [64].

For children, individual-level handedness has been demonstrated to be a potential determinant of cognitive development. Left- or mixed-handedness has been associated with atypical cognitive abilities [65,66] and mental health [67]. Observing the writing hand of children is often the easiest approach for children aged 6–10 years of age [68], although this approach can be criticized based on cultural bias [69]. Other tests attempt to distinguish between lateral dominance (based on whether a task is easier to perform with the left or right hand) [e.g. 70] or the preference of hand (focusing on the quality of the performance and spontaneous hand preference) [e.g. 71]. Few studies have opted for an ethological approach to assessing handedness through observations of videoed naturalistic handedness behavior [72,73]. Researchers have recently established a standardized hand assessment for preschool children, aged 4–6 years old [74]. While the method establishes a very high correlation between parent estimates of child handedness and observations of writing hand, it focuses exclusively on the manipulation of functional objects. One large-scale investigation has taken a comparative, task dependent approach employing consistent observational methods across humans and apes. This break-through study investigated children (3–5 years old) and gorillas, noted that small object manipulation was the only activity in which children elicited the greatest number of right hand responses and all gorillas used one hand more than the other. The authors concluded that handedness in both gorillas and human children is a continuum of bias from left to right with individual variations in the strength of the bias, but generally skewed to the right [75].

A review of the literature suggests that handedness may well give clues to the evolution and neural organization underlying lateralized behavior. However, disparate methods for testing group-level handedness across laboratories and between species inhibit the ability to assess handedness from an evolutionary perspective. Therefore, it is difficult to discern if apes truly lack population-level handedness, or if the pattern is masked by discordant methods. Based on the current body of literature, the general perception remains that while other animals may demonstrate some lateralized behaviors, no other animal shows this trait to an equal level of significance as population-level right-handedness in humans. Therefore, humans retain a *special* evolutionary status, primarily resting on the *lack* of evidence for population-level handedness in nonhuman primates.

To date, we have not explored human and ape handedness systematically under a unified methodological framework that supports direct comparisons. Consequently, the current study employed a naturalistic behavior observation technique to investigate if handedness is influenced by context. We designed the study to methodologically match two previous studies on handedness conducted on two species of great apes: gorillas [76] and chimpanzees [77]. We simply questioned whether the target of a manual action can influence the hand with which a child chooses to interact with that target. Based on these pervious studies of great apes, we hypothesized that right-handed children would vary their choice of hand, depending on the functional (inanimate) or social (animate) aspects of the target of their manual reach, indicating that right-handedness is specifically tied to functional objects and underpinned by left hemisphere brain regions, while manual actions toward social targets involve more distributed influences from the left and right hemispheres.

2. Methods

2.1. Subjects

Ten typically developing children (mean age = 47.7 months, range: 40.5–53.2 months) participated in the study: four native English-speaking participants (males) and six native Italian-speaking participants (5 males, 1 female). Based on parent reports and overall percentage of lateralized hand actions (Table 1) all children were classified as right-handed. Children within this age range were chosen because evidence suggests that stable handedness has already emerged [78,79], while exposure for social conditioning for right-handed dominant individuals is minimized.

The Multidimensional Method (MDM) [80] was employed for data capture, coding and analyses to facilitate direct comparisons with previous investigations on great apes [76,77]. The bottom-up collection method was designed to reveal patterns in behavior comprising fine-grained physical actions.

2.2. Data handling

2.2.1. Data capture

To allow for the focal individuals to habituate to the experimenter and camera equipment, a two-day familiarization period was conducted. Video samples for each participant were taken during natural, spontaneous activities within their school classroom and playground. Subsequent experimental data collection involved 5-min continuous focal sampling sessions, counterbalanced such that each participant's data represented behaviors throughout a typical day [e.g. 81]. The final data set consisted of 90 min per participant. Dual-synchronized video recording was, as prescribed by the MDM was utilized for the capture of fine motor actions (e.g. eye gaze) as well as gross manual motor actions, within context. Digital video cameras (Panasonic NVGS11B: UK; Sony DCR – TRV900E, IT) were tripod mounted, but mobile, and followed child activity using zoom, tilt and swivel to optimize view. Synchronization of the two video streams was established using a flash bulb. Video footage was collected at 24 frames/s, and saved off-line for subsequent statistical analysis. Synchronized video streams were compressed into a single file (15 frames/s) viewed in a top/bottom format for subsequent coding, such that the focal view was placed above the wide-angle view.

2.2.2. Data coding

OBSERVATRON software designed to run on the Mac OS X platform was used to code and store action records [see 81]. Unimanual actions were classified as single-handed lateralized (left, right) actions that acted upon (made physical contact) with an animate (conspecific, self) or inanimate target (objects, ground, and enclosure), while the other hand remained at rest. Rest was a state of physical inactivity. Any action where one hand was already engaged or was performing an act of posture support or locomotion was excluded from the dataset. Animate targets were classified as those involving the self or a social partner. Inanimate targets were classified as those involving both loose and fixed non-living objects. The subsequent task performed by the hand was not considered, only the nature of the target itself.

There is some discussion in the literature about whether bouts or frequencies (events) of hand actions constitute the most accurate measure of manual bias for statistical analysis [16,52,82]. Frequencies have raised concerns for experiments investigating bimanual actions, (e.g. bimanual feeding) because these actions tend to develop into sequences, thus violating an independent choice of two hands for actions subsequent to the initial dominant hand choice. Because both hands were required to be ‘at rest’ for the coding of unimanual actions, we preserved independence of the two hands. Therefore, we effectively employed the more conservative measures of bouts rather than events. This methodological approach also allowed us to circumvent the possibility of perseverative unimanual activities (e.g. drumming) that, like sequences of events, have the potential to skew a dataset.

Two different environments were used to establish generality. Environment 1 (soft play) was a padded room with fixed climbing equipment and no loose objects to elicit social interactions. Environment 2 was within the main classroom where children engaged in an instructed object manipulation task, food consumption (e.g. snack and lunch) or free play. Neither of the two environments elicited interactions with exclusively animate or inanimate targets, and all unimanual actions were coded across both environments. A unimanual hand frequency count was attributed to an action where the child reached and made contact with the target (see Table 1). All subjects were sampled for 45 min in each environment (90 min per child), counterbalanced by time and day using 5-min sampling sessions.

2.2.3. Data analysis

Group data were analyzed using a 2(left hand, right hand) × 2(animate target, inanimate target) repeated measures analysis of variance (ANOVA). Paired-sample t tests were used to test simple effects. Because all participants were observed for equal durations, statistical calculations were performed on raw frequencies of manual actions. However, proportions were also calculated for each participant in parallel analyses to equalize the weighting that each participant contributed to the data set. Proportions were calculated by dividing the frequency of left or right hand actions by the total frequency of actions. Binomial approximations to the z-scores and handedness index (HI) scores were calculated to highlight individual participant patterns. Individuals were categorized as being left-handed or right-handed based on their HI scores (left handed HI scores were negative, right handed HI scores were positive). Sign tests were conducted on the signs of individual z-scores to assess the contribution of individuals contributing to the overall group patterns. Alpha was set at 0.05 and all tests were two-tailed.

3. Results

Raw frequencies, binomial approximations of z-scores for each participant (P) by lateralized target condition (animate, inanimate) and HI scores are presented in Table 1. Participants with frequencies of less than 10 for either target condition (animate, inanimate) were excluded from binomial and sign test calculations (e.g. n/a in Table 1).

A 2 × 2 ANOVA revealed a significant interaction of handedness and animacy when assessing both frequencies ($F_{1,9} = 10.79$, $P = 0.009$) and proportions ($F_{1,9} = 19.35$, $P = 0.002$) (Fig. 1).

Main effects of target type (animate, inanimate) demonstrated significantly increased frequencies ($F_{1,9} = 34.22$, $P < 0.001$) and

Table 1
Frequencies, binomial approximations of *z*-scores and HI scores of unimanual lateralized hand actions.

P	Animate left	Animate right	Animate HI	*z*-Score animate	*P*-value animate	Inanimate left	Inanimate right	Inanimate HI	*z*-Score inanimate	*P*-value inanimate
1	36	25	−0.18	−1.28	0.200	56	180	0.53	8.01	<0.001*
2	24	62	0.44	3.99	<0.001*	53	89	0.25	2.94	0.003*
3	11	19	0.27	1.28	0.200	27	49	0.29	2.41	0.016*
4	5	4	−0.11	n/a	n/a	11	39	0.56	3.81	<0.001*
5	11	6	−0.29	−0.97	0.332	54	151	0.47	6.70	<0.001*
6	10	9	−0.05	0.00	1.000	80	119	0.20	2.70	0.007*
7	8	12	0.20	0.67	0.503	101	100	0.00	0.00	1.000
8	7	9	0.13	0.25	0.803	45	177	0.59	8.79	<0.001*
9	14	24	0.26	1.46	0.144	52	292	0.70	12.89	<0.001*
10	18	17	−0.03	0.00	1.000	43	221	0.67	10.90	<0.001*

* Signifies that $p < 0.05$.

proportions ($F_{1,9} = 111.82$, $P < 0.001$) of inanimate compared with animate targets. A main effect of hand (left, right) illustrated a significantly higher frequencies ($F_{1,9} = 14.78$, $P = 0.004$) and proportions ($F_{1,9} = 32.30$, $P < 0.001$) of right-handed compared with left-handed actions.

Planned comparisons were conducted using paired-sample *t*-tests to assess the dominance of handedness within the animate and inanimate conditions. Participants demonstrated a significant preference for right hand actions (frequencies: $M = 141.7$, $SE = 24.91$; proportions: $M = 0.605$, $SE = 0.043$) versus left hand actions (frequencies: $M = 52.2$, $SE = 7.92$; proportions: $M = 0.240$, $SE = 0.032$;) only within the inanimate target condition (frequencies: $t(9) = -3.605$, $P = 0.006$; proportions: $t(9) = -5.357$, $P < 0.001$). No such difference was found comparing right hand actions (frequencies: $M = 18.7$, $SE = 5.33$; proportions: $M = 0.088$, $SE = 0.024$) with left hand actions (frequencies: $M = 14.4$, $SE = 2.98$; proportions: $M = 0.067$, $SE = 0.011$) within the animate target condition (frequencies: $t(9) = -1.02$, $P = 0.333$; proportions: $t(9) = -1.110$, $P < 0.296$).

We further confirmed the overall pattern of the parametric tests with very conservative non-parametric sign tests to assess group patterns. Sign tests were conducted to compare the number of individuals within each target condition who demonstrated a significant lateralization of handedness with those who did not. Significant lateralization was based upon the *P*-values for the binomial approximations of the *z*-scores. These tests revealed that nine of the ten children demonstrated a right-hand dominance within the inanimate target condition (sign test, $n = 10$, $P = 0.021$), whereas only one of the nine children (one child with <10 animate counts was excluded from this analysis) demonstrated a significant right hand dominance within the animate target condition (sign test, $n = 9$, $P = 0.039$). One child demonstrated no lateral bias in both the animate or inanimate target condition (see Table 1 for binomial approximations of *z*-scores).

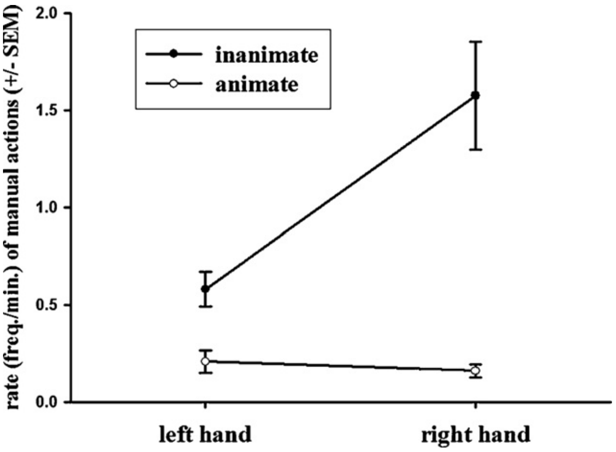

Fig. 1. The figure demonstrates a significant interaction between the lateralization of manual actions directed by children and the animacy of the target with which they interact. The inanimate target condition demonstrated a greater degree of variation in handedness compared with the animate target condition. The figure depicts the interaction using rates per minute to foster direct comparisons between these human children and previous findings in great apes.

4. Discussion

Results indicated a significant interaction between handedness and target condition where the right hand was more influenced by the animacy of the target than the left hand. Planned comparisons revealed a significant group right hand bias for actions toward inanimate objects, but no significant difference between left and right hand actions for interactions with animate targets. Although there was a clear difference in the frequencies of animate and inanimate unimanual actions, over 330 unimanual actions contributed to the animate condition, extinguishing concerns that a lack of right-handedness in this condition was generated by a "floor effect". At the individual-level, binomial approximations for *z*-scores confirmed the group pattern held true in the vast majority of participants. Nine of the ten children demonstrated a significant right-hand bias for manual actions directed toward inanimate targets. Additionally, eight of the ten children demonstrated no significant difference in hand use for manual actions directed toward animate targets. One child possessed insufficient counts within the animate condition to warrant an inferential test.

Although the group demonstrated a significant general right-hand bias, should we have ignored the context of action, we would simply have replicated the standard view that humans are right-handed dominant for manual actions. The patterns of handedness reported here are consistent with those recently uncovered in two populations of great apes [76,77] (Fig. 2).

The clear implication is that human right-handedness is *not* species-specific, but *is* context dependent. Our findings are consistent with claims that cerebral lateralization resulting in lateralized behaviors is an extremely old evolutionary adaptation and that more recent cognitive capabilities embedded in behavior are likely to be extensions to previously existing neural architecture [9]. While this perspective may stand in contrast to the perception that humans have a *special* evolutionary status, it fits well with our understanding of natural selection which dictates that it is more likely that new behavioral and cognitive capabilities emerge from existing skills, rather than from scratch. From an evolutionary perspective, one interpretation of our results is that both humans and great apes possess an early, neural division that distinguishes between objects that require functional manipulation in an ordered sequence of actions to reach a goal state, and those that do not. In support of this hypothesis, recent archeological

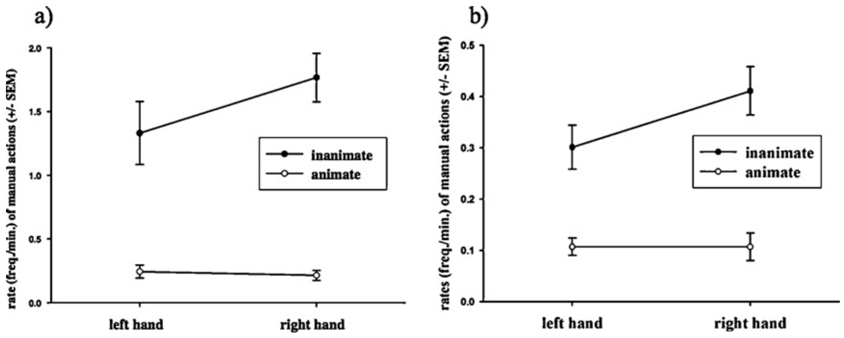

Fig. 2. The figure demonstrates a significant interaction between the lateralization of unimanual actions and the animacy of the target for: (a) gorillas (reproduced from Forrester et al. [76]) and (b) chimpanzees (reproduced from Forrester et al. [77]). Both species demonstrated a significant right hand bias in the inanimate target condition, but not in the animate target condition. The figure depicts the interaction using rates per minute. Figures reproduced with permission from Springer.

evidence reports that humans have been right-handed tool users for over 2.5 million years [83,84] while the current view is that language emerged less than one hundred thousand years ago [85], a finding that directly challenges the historical perspective that human population-level, right-handedness is the result of language capabilities that emerged specifically within hominid evolution.

Our findings are consistent with '*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 implicate tool-use as a likely precursor and catalyst for the emergence of language-like skills [15,18]. The tool theory, put forward over three decades ago, argues that speech, produced by the movements of the tongue, lips, and vocal chords, requires precisely timed and sequenced actions to manifest communication [86]. This process, likened to that of the construction of tools, involves skilled serial motor activities, such as the movements of arms, hands and fingers, hierarchically employed to reach a goal.

Many researchers support the theory that right-handed actions are underpinned by left-hemisphere specialized areas for orchestrating hierarchical sequences of events [e.g. 87–89], and postulate that language could have evolved as an extension of right hand and left hemisphere ability to produce temporal sequences of motor activities derived from tool use [90–93]. This interpretation would also explain why studies of both apes and humans indicate that communicative gestures are often found to be right-hand dominant [e.g. 44,74]. This theory is gaining support from imaging studies that have demonstrated 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 [33–35], yet do not possess human-like language capabilities. Additionally, reports have indicated a high correlation between brain areas responsible for tool use in apes in and those that process language in humans [e.g. 38].

To generalize our findings, further investigations are required to determine if this handedness pattern is visible across larger and more varied samples of human and ape subjects, particularly comparing species that are known to be tool users and those that are not. Further investigations are also required to explore handedness within varied social contexts, as the frequency of left-handed actions may prove to be a useful indirect marker of cerebral lateralization for processing social-emotional content [e.g. 64] and aid to gauge stressors related to increased task complexity [51]. Furthermore, in order to verify the manipulative intent of the unimanual action, it would be beneficial to explore the manual behaviors that occur subsequent to physical contact with the target object (e.g. type of grip and type and complexity of manipulation).

The finding resulting from our methodological approach is just one example of new corpus techniques that have the capability to reveal context-specific, latent behavioral patterns across species. The technological developments that have led to the results revealed by this particular corpus collection system (MDM) [80] have allowed for dense data analyses akin to those that have been so informative in recent human language studies [e.g. 94]. The MDM demonstrates the strength of a forward movement of quantifiable context-dependent behavior, which will lead to the unveiling of potentially richly structured behavioral patterns unfolding across space and time, thus generating a better understanding of the evolution and development of humans and other animal species.

In conclusion, our findings demonstrate matching handedness patterns between typically developing preschool children and great apes, facilitating explanations of findings from across disparate fields and providing the first quantitative, comparative behavioral dataset, supporting the theory that right-handedness is a behavioral manifestation of context-specific brain regions for processing external physical syntax inherent in the manipulation of functional objects. Taken together with our recent studies on gorilla and chimpanzee handedness, our findings support the view that human handedness, and its origin in hemispheric brain organization, is not a new or human-unique characteristic, but rather a property developed through tool use, and a trait that was inherited from an ancestor common to both humans and great apes.

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