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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.

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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

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