Human handedness: An inherited evolutionary trait

Gillian S. Forrester[a*], Caterina Quaresmini[b], David A. Leavens[c], Denis Mareschal[d], Michael S. Thomas[d]

[a]Department of Psychology, University of Westminster, 309 Regent Street, London, England, W1B 2UW

[b]Center for Mind/Brain Sciences, University of Trento, Palazzo Fedrigotti, corso Bettini 31, 38068 Rovereto, Italy (TN)

[c]School of Psychology, University of Sussex, Falmer, England, BN1 9HQ

[d]Centre for Brain and Cognitive Development & Department of Psychological Sciences, Birkbeck, University of London, Malet Steet, London, England, WC1E 7HX

**Authors**:

*Gillian S. Forrester: email: g.forrester@westminster.ac.uk; tel: +44 208 911 5000 x6960

Caterina Quaresmini: email: caterina.quaresmini@gmail.com; tel +39 340 273 4865

David A. Leavens. email: davidl@sussex.ac.uk; tel: +44 127 367 8526

Denis Mareschal: email: d.mareschal@bbk.ac.uk;  tel: +44 207 631 6582

Michael S. Thomas: email: m.thomas@bbk.ac.uk; tel: +44 207 631 6386

*Correspondence concerning this article should be addressed to Gillian Forrester, Department of Psychology, 309 Regent Street, University of Westminster, London, W1B 2UW

Contact:  g.forrester@westminster.ac.uk

**Abstract**

Our objective was to demonstrate that human 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 employed 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 their manual action, as *animate* (social partner, self) and *inanimate* (non-living functional objects), we found that children demonstrated a significant right-hand bias for manual actions directed towards inanimate targets, but not for manual actions directed towards animate targets. This pattern was revealed at both the group and individual levels. Using a focal video sampling corpus data mining approach allowed for direct comparisons with captive gorillas (Forrester et al. in Anim Cogn 14(6):903–907, 2011) and chimpanzees (Forrester et al. in Anim Cogn in press, 2012). Comparisons of handedness patters support the view that human handedness, and its origin in cerebral lateralization is not a new or human-unique characteristic. Additionally these data are consistent with the theory that human population-level right-handedness is a trait developed through tool use that was inherited from an ancestor common to both humans and great apes.


*Keywords*: human, handedness, cerebral lateralization, evolution

**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 action can be used as indirect markers of underlying neural generators [for a review, see 3].

The most notable example of lateralized motor action underpinned by cerebral lateralization for cognitive function in humans is handedness and neural regions associated with speech production (e.g. inferior frontal gyrus [4]), and comprehension (superior temporal gyrus [5]). For the vast majority of the population, language function and handedness are both hosted by the left hemisphere [e.g. 6]. Additionally, it is commonly reported that the human population exhibits approximately 90% right-handedness [e.g. 7] and within this population approximately 95% of individuals have language-processing regions situated in the left hemisphere of the brain [8]. Human population-level right-handedness has been theorized to have evolutionary links with gesture [9, 10], speech [11], tool use [e.g. 12], coordinated bimanual actions [13, 14], posture [15] and bipedalism [16, 17]. 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 [18].

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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 [19, 20] and invertebrates [e.g. 21]. This division of labor 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 hemisphere. Additionally, by avoiding the duplication of functioning across hemispheres, there is no concern regarding the simultaneous initiation of incompatible responses [19, 22, 23]. 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 24].

The studies above suggest 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. 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. This position is also consistent with evidence from disparate fields (e.g. archeology and neuroscience discussed in more detail below), suggesting that language and tool use share cognitive characteristics supported by the same left hemisphere neural architecture, which provides support for right-handedness emerging from a skill that preceded and potentially gave rise to language capabilities.

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Recent archeological evidence reports that humans have been right-handed tool users for over 2.5 million years [25, 26] while modern human language is thought to have emerged less than one hundred thousand years ago [27]. Additionally, new functional magnetic resonance imaging (fMRI) results have demonstrated an overlap of activity between tasks related to language and tool use in Broca's Area (Broadmann's Area 44) in a group of healthy humans [28]. Broca's area has historically been categorized as the brain region responsible for speech production. The overlap of location for language and tools in Broca's Area suggests that these two behaviors share similar computational principles for processing hierarchical sequences of events. These findings directly challenge the historical perspective that human right-handedness is the result of language capabilities that emerged specifically within hominid evolution.

All of these findings together are consistent with the 'tool-use' theory put forward over three decades ago which argued that speech, produced by the movements of the tongue, lips, and vocal chords, requires precisely timed and sequenced actions to manifest communication [29]. This process was likened to that of the construction of tools, which involves skilled serial motor activities, such as the movements of arms, hands and fingers, hierarchically employed to reach a goal. Others posited that the ability to build and use tools is linked to language, as both activities can generate infinite complex hierarchical structures [30]. For example, during tool use, humans can combine together different constructive elements (action grammar) in the same way that language requires grammar, which is based on rules for combining words in a meaningful order [31]. Many researchers support the theory that right-handed actions are underpinned by left-hemisphere specialized areas for orchestrating hierarchical sequences of events to reach a goal state [9, 32-35], 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

[36-39]. Until recently, were missing convincing behavioral data from our closest living relatives to support archeological and neuroscientific findings in favor of the tool use theory.

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 [40], the ability to occasionally locomote bipedally [41] and the capacity to exhibit intentionally communicative gestures [e.g. 42-46]. 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 also display homologous human Broca's [47] and Wernicke's [48] areas that are asymmetrically larger in the left hemisphere of all species of great apes. Further neuroimaging studies corroborate a left hemisphere specialization for tool use in apes demonstrating an overlap with brain regions associated with language-like skills in humans [49-51].

While all four species of great apes have been shown to be tool users both in captivity and in the wild, interestingly, to date, there are no consistent population-level behavioral findings that indicate a lateral manual bias in great apes. Great ape handedness has been extensively explored from a plethora of different methods. While a range of studies find no clear evidence of species-level manual lateralization [e.g. 52-57], others have reported right-hand biases in chimpanzees (*Pan troglodytes*) for: bimanual feeding, coordinated bimanual actions, bipedal reaching and throwing [for reviews, see 58, 59], in captive gorillas for bimanual feeding [60] and

for communicative gesture in chimpanzees [e.g. 10, 61, 62]. Alternatively, it has been noted that orangutans a exhibited a significant left-hand preference for scratching and for fine manipulation of parts of the face in rehabilitated orangutans [63], while chimpanzees exhibited a significant increase in left-handed self-directed behaviors with increased in task complexity [64] contending that self-directed behaviors may be influenced by motivational factors underpinned by a right hemisphere dominance within both social and nonsocial contexts. Along with inconsistent finding across laboratories, some results, particularly related to chimpanzees, have been challenged on methodological grounds [e.g. 65] and sampling factors [66, 67].

More recently, systematic investigations of ape handedness, employing larger sample sizes have attempted to clarify confounds in earlier studies. Hopkins et al. investigated the influences of rearing histories on handedness [68], while Llorente et al. tested the influence of bimanual and unimanual tasks on handedness [69, 70]. Although no ape study has revealed a manual bias with a similar degree of lateralization compared with the human population, each of the above investigations demonstrated significant right-hand biases using their own methodological assessment, consistent with the hypothesis of an early adaptation for a left hemisphere specialization for behaviors requiring structured sequences of actions [e.g. 13].

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 [71] and the Waterloo Handedness Questionnaire [72], focus exclusively on literate populations, querying with which hand subjects pick up or manipulate a functional object (e.g. pencil, scissors). While human right-handedness appears to be an extremely robust and universal

finding [73], 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 [74]. 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 [75]. Additionally, others reported a human left hand preference for the self-directed behavior of face touching, in individuals who were otherwise right-handed [76], suggesting that social or emotive hand action might activate the right hemisphere's dominance for emotional processing [77].

For children, handedness has been demonstrated to be a potential determinant of cognitive development. Left- or mixed-handedness has been associated with atypical cognitive abilities [78, 79] and mental health [80]. Observing the writing hand of children is often the easiest approach for children aged 6 to 10 years of age [81], although this approach can be criticized based on cultural bias [82]. Other tests attempt to either distinguish between lateral dominance (based on whether a task is easier to perform with the left or right hand) [e.g. 83], or hand preference, focusing on the quality of the performance and spontaneous hand preference [e.g. 84]. Others still have opted for an ethological approach to assessing handedness through observations of videoed naturalistic handedness behavior [85, 86]. More recently a standardized

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hand assessment for preschool children has been established for aged 4-6 years old [87]. While the method establishes a very high correlation with parent's estimates of child handedness and observations of writing hand, it focuses exclusively on the manipulation of functional objects. One remarkable large-scale study that did investigate children (3-5 years old) and gorillas within similar experimental parameters 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 conclude that handedness in both gorillas and human children is a continuum of bias from left to right with individual variations in in the strength of the bias, but generally skewed to the right [88].

A review of the literature suggests that human handedness may well give clues to the evolution and neural organization underlying lateralized behavior. However, it is necessary to construct a methodological approach that can accommodate a range of human and primate populations to identify common patterns of behavior across species. 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. Diverse methods for testing handedness exist across laboratories, within human populations and between species, inhibiting 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.

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 [89] and chimpanzees [90]. We

simply questioned if the target of a manual action can influence the hand with which a child

choses 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 towards social targets involve an increase in

right hemisphere resources demanding an increase in left-handed actions.

## 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 [91, 92], while exposure for social conditioning for right-handed dominant individuals

is minimized.

      The Multidimensional Method (MDM) [93] was employed for data capture, coding and

analyses to facilitate direct comparisons with previous investigations on great apes [83, 84]. The

bottom-up collection method was designed to reveal patterns in behavior comprised of 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-minute continuous focal sampling sessions, counterbalanced such that each participant's data represented behaviors throughout a typical day [e.g. 94]. The final data set consisted of 90 minutes 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 per second, and saved off-line for subsequent statistical analysis. Synchronized video streams were compressed into a single file (15 frames per second) 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.

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, 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 minutes in each environment (90 minutes per child), counterbalanced by time and day using 5-minute sampling sessions.

*2.2.3 Data Analysis*

Group data were analyzed using a 2(left hand, right hand) x 2(animate target, inanimate target) repeated measures analysis of variance (ANOVA). Paired-sample *t* tests were used to test simple effects. Binomial tests and z-scores were calculated to highlight individual participant patterns. Because all participants were observed for equal durations, statistical calculations were performed on raw frequencies of manual actions. However, proportions were 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. Alpha was set at 0.05 and all tests were two-tailed.


**3. Results**

Raw frequency counts, z-scores and binomial statistics for each participant (P) by lateralized

target condition (animate, inanimate) are illustrated in Table 1. Participants with frequency

counts of less than 10 for either target condition (animate, inanimate) were excluded from

binomial calculations (e.g., n/a in Table 1).


**Table 1.**

(Frequencies, z-scores and binomial results of unimanual lateralized hand actions)


A 2x2 ANOVA revealed a significant interaction of handedness and animacy when

assessing both raw frequency ($F_{1,9} = 10.79$, $P = 0.009$) and proportions ($F_{1,9} = 19.35$, $P = 0.002$)

(Figure 1).


Figure 1. 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.

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Main effects of target type (animate, inanimate) demonstrated significantly increased frequency ($F_{1,9} = 34.22$, $P < 0.001$) and proportion ($F_{1,9} = 111.82$, $P < 0.001$) of inanimate compared with animate targets. A main effect of hand (left, right) illustrated a significantly higher frequency ($F_{1,9} = 14.78$, $P = 0.004$) and proportion ($F_{1,9} = 32.30$, $P < 0.001$) 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 (frequency: $M = 141.7$, SE = 24.91; proportion: $M = 0.088$, SE = 0.024) versus left hand actions (frequency: $M = 52.2$, SE = 7.92; proportion: $M = 0.067$, SE = 0.011) only within the inanimate target condition (frequency: $t(9) = -3.605$, $P = 0.006$; proportion: $t(9) = -1.11$, $P < 0.001$). No such difference was found comparing right hand actions (frequency: $M = 18.7$, SE = 5.33; proportion: $M = 0.605$, SE = 0.043) with left hand actions (frequency: $M = 14.4$, SE = 2.98; proportion: $M = 0.240$, SE = 0.032) within the animate target condition (frequency: $t(9) = -1.02$, $P = 0.333$; proportion: $t(9) = -5.357$, $P = 0.296$).

We further investigated individual patterns of handedness using binomial tests. These tests revealed that nine of the ten children indicated a right-hand dominance within the inanimate target condition, ($Z(9) = 2.21$, $P = 0.022$) and only one of the ten children revealed a significant right hand dominance within the animate target condition ($Z(9) = -2.21$, $P = 0.021$). One child demonstrated no lateral bias in either the animate or inanimate conditions (see Table 1 for z-scores and binomial results).

**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. Post-hoc t-tests revealed a significant group right hand bias for actions towards 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 raw frequencies of animate and inanimate unimanual actions, over 330 unimanual actions contributed to the animate condition, extinguishing concerns that the pattern revealed was generated by a "floor effect". At the individual participant level, binomial tests confirmed the pattern held true in the vast majority of participants. Nine of the ten children demonstrated a significant right-hand bias for manual actions directed towards inanimate targets. Additionally, eight of the ten children demonstrated no significant difference in hand use for manual actions directed towards 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 [89, 90]. The clear implication is that human right-handedness is *not* species-specific, but *is* context dependent. From an evolutionary perspective, one interpretation of these results is that both humans and great apes possessed 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.

These findings are consistent with '*tool theory*', which argue 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 [1, 9, 29]. The left hemisphere's dominance for interacting with objects that require the processing of hierarchical sequences of manual actions (e.g., tool use, tool manufacture, food preparation) could be described as a proto-syntax and may have provided the necessary scaffolding for the evolution of a human protolanguage. This interpretation would also explain why both ape and human studies indicate that communicative gestures are often found to be right-hand dominant [e.g. 44, 74]. We provide the first quantitative comparative behavioral results that are consistent with this theory, demonstrating that right-handedness is a behavioral manifestation of context-specific brain regions for processing external physical syntax inherent in the manipulation of functional objects.

Technological advancements allow for corpus data analyses akin to those that have been so informative in recent human language studies [e.g. 95]. The MDM [93] is just one example of a new corpus technique that has successfully revealed context-specific, latent behavioral patterns across disparate species, demonstrating the strength of data-rich methods and forging a path towards a consistent, comparative experimental framework. Techniques such as this, will lead to the unveiling of potentially richly structured behavioral patterns unfolding across space and time, generating a better understanding of both the evolution and development of humans and other animal species.

To generalize our findings to the general human population and all great ape species, further investigations are required to see if this handedness pattern is visible across larger samples human participants and other populations of primates, particularly investigating the

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context of handedness in species that are known to be tool users and those that are not. Further investigations are also required to explore handedness within a social or stressful context, as a rise in the proportion of left-handed actions within a social context may prove to be a useful indirect marker of cerebral lateralization for processing social-emotional content [e.g. 77] and increasing task complexity [64]. Finally, in order to verify the manipulative intent of the unimanual action, it would be beneficial to also explore the different aspects of the behaviors that occur once unimanual action makes contact with the target object (e.g. type of grip/grasp, type and complexity of manipulation).

Our behavioral data, demonstrating matching handedness patterns between typically developing preschool children and great apes, facilitates explanations of findings from archeology and the neurosciences. For example, a right-handed preference for unimanual actions directed towards inanimate objects, but not animate objects goes some distance to explain why archeological evidence indicates that humans have been right-handed tool users for more than two million years [25, 26], while the current view is that language emerged less than one hundred thousand years ago [27]. Moreover, these data help to clarify why recent neuroimaging studies reveal that all four species of great apes (all known to be tool users in both captivity and in the wild) possess neuroanatomical left hemisphere asymmetries consistent with language areas in humans [47, 48], yet do not possess human-like language capabilities. Finally, these data are consistent with recent brain-imaging studies that indicate a high correlation between brain areas responsible for tool use in great apes and those that process language in humans [49-51]. These findings taken together with our recent studies on gorilla and chimpanzee handedness 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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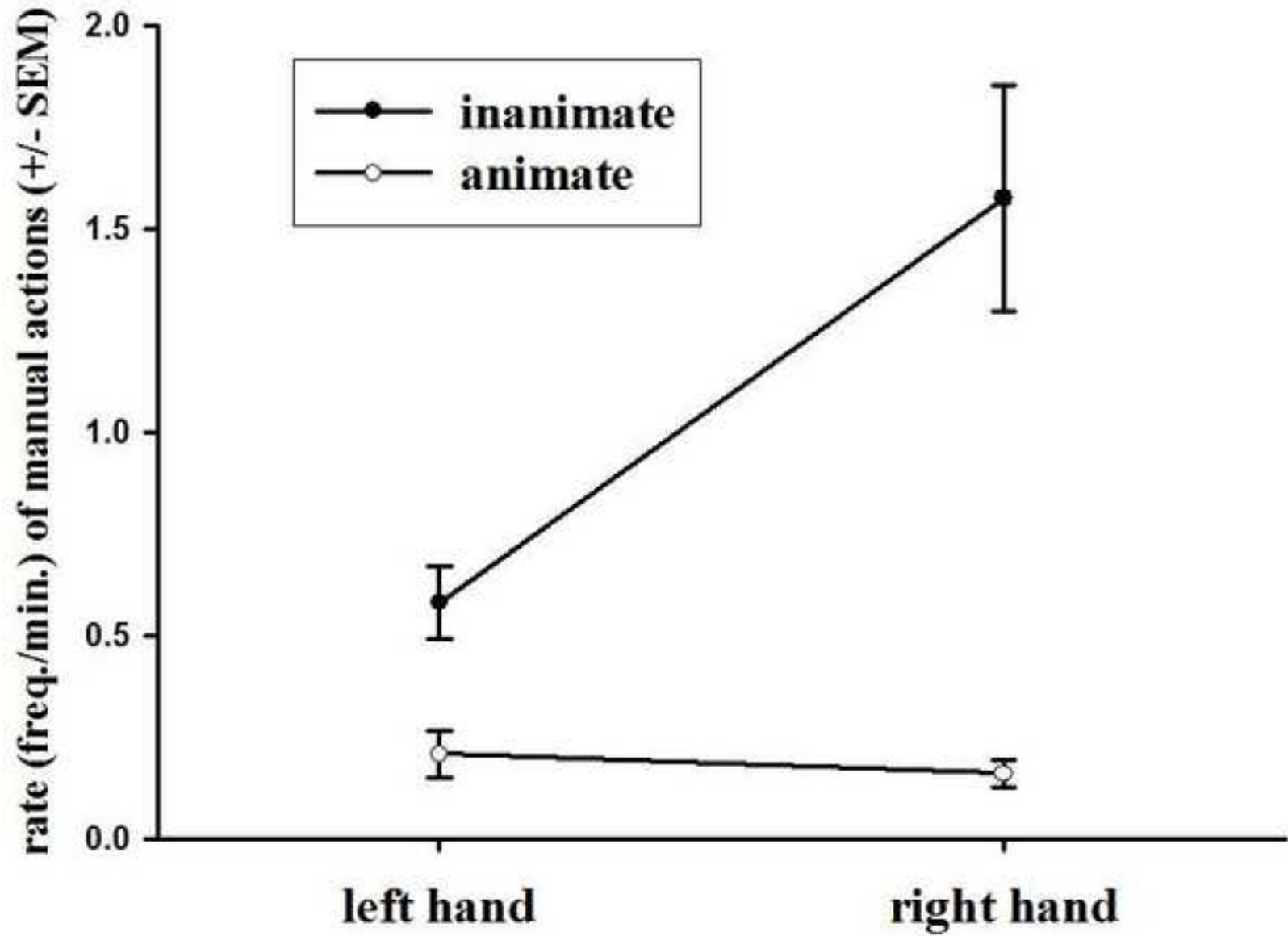
Table 1.

| P | animate left | animate right | inanimate left | inanimate right | total freq. | *z-score* animate | *p-value* animate | *z-score* inanimate | *p-value* inanimate |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 36 | 25 | 56 | 180 | 297 | -1.28 | 0.200 | 8.01 | <.001* |
| 2 | 24 | 62 | 53 | 89 | 228 | 3.99 | <.001* | 2.94 | 0.003* |
| 3 | 11 | 19 | 27 | 49 | 106 | 1.28 | 0.200 | 2.41 | 0.016* |
| 4 | 5 | 4 | 11 | 39 | 59 | n/a | n/a | 3.81 | <.001* |
| 5 | 11 | 6 | 54 | 151 | 222 | -0.97 | 0.332 | 6.70 | <.001* |
| 6 | 10 | 9 | 80 | 119 | 218 | 0.00 | 1.000 | 2.70 | 0.007* |
| 7 | 8 | 12 | 101 | 100 | 221 | 0.67 | 0.503 | 0.00 | 1.000 |
| 8 | 7 | 9 | 45 | 177 | 238 | 0.25 | 0.803 | 8.79 | <.001* |
| 9 | 14 | 24 | 52 | 292 | 382 | 1.46 | 0.144 | 12.89 | <.001* |
| 10 | 18 | 17 | 43 | 221 | 299 | 0.00 | 1.000 | 10.90 | <.001* |