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# Bipedal tool use strengthens chimpanzee hand preferences

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ABSTRACT

The degree to which non-human primate behavior is lateralized, at either individual or population levels, remains controversial. We investigated the relationship between hand preference and posture during tool use in chimpanzees (*Pan troglodytes*) during bipedal tool use. We experimentally induced tool use in a supported bipedal posture, an unsupported bipedal posture, and a seated posture. Neither bipedal tool use nor these supported conditions have been previously evaluated in apes. The hypotheses tested were 1) bipedal posture will increase the strength of hand preference, and 2) a bipedal stance, without the use of one hand for support, will elicit a right hand preference. Results supported the first, but not the second hypothesis: bipedalism induced the subjects to become more lateralized, but not in any particular direction. Instead, it appears that subtle pre-existing lateral biases, to either the right or left, were emphasized with increasing postural demands. This result has interesting implications for theories of the evolution of tool use and bipedalism, as the combination of bipedalism and tool use may have helped drive extreme lateralization in modern humans, but cannot alone account for the preponderance of right-handedness.



## Introduction

One characteristic that distinguishes humans from other primates is that a majority of humans, close to 90%, are right-handed (Gilbert and Wysocki, 1992; Perelle and Ehrman, 1994). A bias of this magnitude has not been found in any other primate species. Despite considerable disagreement as to how handedness should be defined or measured, the handedness of multiple primate species has been evaluated in a variety of tasks. Handedness is one component of the concept of laterality (having a behaviorally dominant side or limb), often presumed to be indicative of asymmetry of the brain (Heestand, 1986; Hopkins and Morris, 1993; Hopkins, 2007). Laterality can be evaluated by determining which side of the body has more control relative to the other, or by determining which side of the brain is more responsible for specific actions or behaviors. Individual laterality and side preferences have been shown in many species, including rats, chickens, elephants, whales, and even snakes for slithering direction (Walker, 1980; Rogers, 1989; Rogers and Workman, 1993; Clapham et al., 1995; Bisazza et al., 1998; Martin and Niemitz, 2003).

Primates and other vertebrate species show laterality of function, but no other primate species shows such a marked or extensive cerebral asymmetry at a population level as humans (Vallortigara and Rogers, 2005). Therefore, laterality is often thought to have played an important role in the evolution of human cognition. Speech is typically lateralized to the left hemisphere of the human brain, but can occasionally be expressed in the right hemisphere (Knecht et al., 2000a,b). Apes do not exhibit spoken language, but if they do display laterality, it probably reflects a trait present in the last common ancestor of humans and other great apes, and this trait may have acted as a pre-adaptation in the evolution of language (Hopkins and Cantero, 2003; Vallortigara and Rogers, 2005; Steele and Uomini, 2009). Other lateralized behaviors hypothesized to have influenced the evolution of cognition include tool use (Gibson and Ingold, 1993; Preston, 1998), manual gestures (Hopkins and Leavens, 1998; Rizzolatti and Arbib, 1998; Corballis, 2003; Pollick and de Waal, 2007), and throwing (Hopkins et al., 1993, 2005a,b). Furthermore, posture has been shown in some previous studies to influence handedness (Roney and King, 1993, Hopkins and Morris, 1993), with upright or bipedal postures increasing right-handedness, suggesting a need to evaluate the effects of tool use and bipedal posture concurrently.

The aim of the present study is to examine the relationship between hand preference and posture during a tool use task in captive chimpanzees. We manipulated the task demands so that

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the tool-use could be accomplished 1) while seated, 2) while bipedal but with one hand against a wall, and 3) while fully bipedal. The main goals were to test the prediction that assumption of bipedal posture would increase the strength of right-hand hand preference during tool use. Based on the existing literature, we tested two specific hypotheses: H1) bipedal posture increases the **strength** of hand preference, without respect to side, and H2) more specifically, a bipedal stance, without the use of one hand for support, elicits a **right hand** preference.

These two hypotheses need to be distinguished because previous work in nonhuman animals show that a group of animals may differ in laterality overall (that is, some animals in a group may be ambidextrous, while others are strongly lateralized, but with equal numbers of left- and right-lateralized individuals). Such lateralized species might still lack any group- or population-level directional bias to use the *right* hand. Humans, of course, are both lateralized (ambidextrous individuals are rare) and directionally lateralized to the right side (left-handed individuals are equally rare), but these two characteristics need not go together. We distinguish between these two logical possibilities by calculating, for each subject, both a handedness index (HI; ranging from 1.0 to −1.0, and whose sign reveals the directional bias to the right or left respectively) and an *absolute* handedness index (ranging from 0.0 for ambidextrous, to 1.0 for strongly lateralized animals which use either the left or right hand exclusively).

## Methods

### Subjects

For this experiment, 46 chimpanzees (28 males and 18 females) ranging in age from 12 to 47 years (mean age of 28.15 years) of various subspecies (mostly *Pan troglodytes verus*) were used. The chimpanzees are housed at the Michale E. Keeling Center for Comparative Medicine and Research at The University of Texas M.D. Anderson Cancer Center in Bastrop, Texas (MDACC), and research was conducted with relevant IACUC approvals. The facility has eight open top corrals, each providing both indoor and outdoor housing to 7–14 animals per group. All chimpanzees remained in their home corrals for testing. Subjects were chosen from all corrals to be included in all experimental conditions. Subjects were selected based on their handedness in previous studies and included 15 right-handed, 16 left-handed, and 15 ambidextrous individuals (Hopkins et al., 2003). These animals all have considerable experience extracting food from tubes, due to both frequent enrichment (pipe feeders are provided on a weekly basis which require tools to be inserted into fixed pipes to extract various food substances) and previous exposure to a similar task (Hopkins et al., unpublished data).

### Materials

A poly-vinyl-chloride (PVC) tube (135 cm in length, 4 cm in diameter) with peanut butter in the center was suspended in an outdoor enclosure using 80 lb test fishing line connected to an eyelet in the cap of the tube. Fishing line was used so that the line broke each time a chimpanzee grabbed hold of the food tube and pulled downwards, ensuring that the animals could not climb up the line and escape their enclosure. In the event that a chimpanzee jumped and grabbed the tube, the researcher returned to ground level and recovered the tube, cap, and broken line. In order to better maintain a consistent distance, the fishing line was strung through a 1.35 m PVC tube and secured (Fig. 1). The food tube was lowered into the enclosure until it was approximately 2.8 m off the ground, which is the total of the average height of an adult chimpanzee (150 cm), the average length of a chimpanzee arm (83 cm), and the length of the tool (45 cm). The distance of the food tube from the interior walls of the corral differed based on experimental condition.

**Fig. 1.** Peanut butter tube suspension apparatus viewed from the side. The tube about to be put into the corral is in front of the suspension system and the fishing line is run through the larger PVC and wrapped around the top extension to secure it.

### Procedures

All subjects participated in all three of the experimental conditions, first in the seated condition (data collected in 2002), then the supported bipedal conditional, the bipedal condition, and finally in a retest of the seated condition. The initial seated data were used to allocate individuals to three groups of equal size (of left- handed, right-handed, and ambidextrous individuals). For all conditions, trials were run daily, with a minimum of 36 hours between trials for any particular group. All trials took place in the outdoor section of the subject's home corral and subjects from each corral were tested. Research in a particular corral lasted at least 2 hours in order for all focal animals to have the opportunity to gain access.

Each trial, regardless of condition, began with the researcher placing cut bamboo sticks (45 cm long) within reach of every member of the test group. These tools were then gathered by the subjects, without any restriction on the hand used to take the stick. PVC tubes with peanut butter smeared in the center (near the midpoint of the tube's axis) were provided to the chimpanzees along with tools in the form of the cut bamboo sticks. Peanut butter was placed only in the center of the tube to encourage tool use and prevent subjects from using their hands to extract the peanut butter.

We recorded data for all sessions on a dictaphone via spoken commentary. We use the term 'event' to designate one instance of feeding (e.g., inserting the tool into the tube, pulling out the tool, inserting the tool into the mouth, and repeating) and trials continued until the focal subjects in each group had displayed at least 50 events, over a minimum of three testing trials. "Bouts" were groups of events, which either occurred on different days, or in which the subject put down the tool, left the test apparatus, and later returned during a single test session. "Bout-wise" data were scored using only the first event of each bout as independent data points, while "event-wise" analyses incorporated all events as data points. In order to meet the designated minimum of 50 events, between 3 and 11 data collection trials were completed by the