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Insights Into Human and Nonhuman Primate Handedness From Measuring Both Hands

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Abstract

Handedness is part of our everyday lives, but where does it come from? Researchers studying nonhuman primates and young children have approached this question from different perspectives—evolutionary and developmental, respectively. Their work converges on the conclusion that measurement matters in the science of handedness. Coming to a consensus on assessment will guide future research into the origins of handedness. A candidate behavior for promoting multidisciplinary comparison is role-differentiated bimanual manipulation.

Keywords

handedness, bimanual manipulation, comparative, nonhuman primate, children

Handedness has captured the interest of laypeople and scientists alike. Having one hand that is “better” or used more frequently than the other hand is a shared experience for adults. Handedness is the most widely studied example of *laterality*, a bias for using one side of the body over the other (Ocklenburg & Güntürkün, 2017). These biases observed in behavior represent *hemispheric specialization* in the brain: The left hemisphere is largely responsible for controlling the right side of the body, and vice versa. Laterality had long been thought to be unique to humans, but compelling evidence from the animal literature has overturned this belief (Rogers et al., 2013).

Handedness garners significant attention in laterality research because of a population-level bias seen in humans: Most adults are indisputably right-handed (Fig. 1).[1] Right-handers make up approximately 90% of any population, whereas left-handers constitute approximately 10% (Papadatou-Pastou et al., 2020). Attributing this well-known 9:1 ratio to genetics, however, offers a false sense of security in thinking that the puzzle of where handedness comes from has been solved. The answer to this provocative question remains elusive. Genetic explanations, including those arising from genomewide association studies, although traditionally popular in handedness research, have not revealed any compelling answer to this question (Cuellar-Partida et al., 2021; de Kovel & Francks, 2019; Paracchini, 2021).

Researchers have turned to populations such as nonhuman primates and young children to study the origins of handedness.[2] These two lines of investigation face similar measurement challenges but operate from different theoretical backgrounds. Self-report questionnaires—the norm in assessing adult handedness—are not practical for use with monkeys or toddlers, and decades of research have led to important measurement insights from each discipline. Efforts to bridge the gap between the human and nonhuman literatures are expected to shape laterality research over the next decade (Ocklenburg et al., 2021). As a first step, this review synthesizes knowledge gained from an evolutionary lens with knowledge gained from a developmental lens to highlight the value of measuring the same behavior across species to answer outstanding questions about handedness.

Evolutionary Insights Into Handedness

Scientific reports on handedness in nonhuman primates date back more than 100 years, but it was the publication

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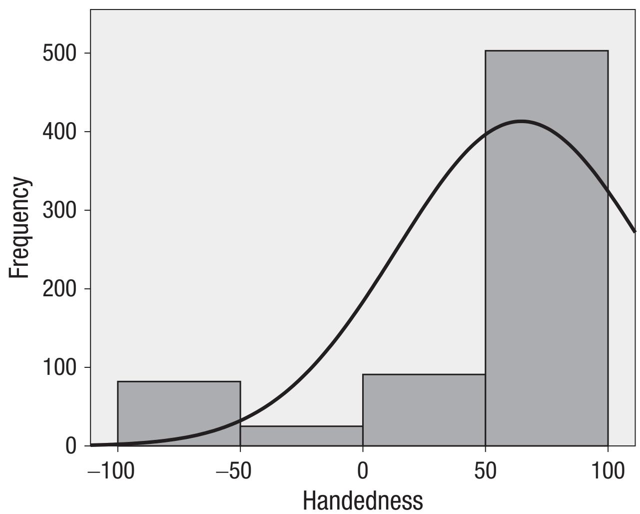

Fig. 1. The distribution of handedness in human adults in a representative study of 1,081 adults attending a 4-year public university (data from Gonzalez & Nelson, 2021). Handedness was measured using the Edinburgh Handedness Inventory (Oldfield, 1971), a 10-item self-report questionnaire. Participants respond by indicating which hand they prefer to use for each listed action; "+" indicates preferred use of the indicated hand, and "++" indicates that the participant would never use the other hand unless forced to do so. Scores can range from –100 (exclusive use of the left hand) to 100 (exclusive use of the right hand). The typical pattern of handedness was observed in this study: an overall strong preference for using the right hand (see note 1).

of an article by MacNeilage et al. (1987) that revitalized the field and launched a sharp rise in studies of handedness in nonhuman primates. In their review, MacNeilage et al. proposed a theory on the evolution of handedness that became known as the *postural-origins theory* (Fig. 2, left panel). This theory placed hand use in an ecological context to conceptualize a shift in hand-use patterns across primate evolution. The roles for the two hands were centered on where the species lived (in the trees or on the ground) and what they ate. The earliest primates were arboreal and had a diet that included insects. The left hand (right hemisphere) specialized in reaching for food, and the right hand (left hemisphere) was used in stabilizing posture. As later monkey and ape species shifted to a terrestrial lifestyle, the right hand became freed from posture and began to specialize in food processing, which required greater fine motor skill and coordination between the hands (e.g., to open fruit and nuts). Eventually, in humans, a right-hand preference became the general pattern across manual activities. The postural-origins theory separated hand preferences for different manual skills, which is an important distinction that is not always matched by human studies. Researchers raced to confirm or refute the directional predictions (left or right preference) made for particular species given their taxonomic position.

Thinking about how the hands are used in nonhuman primates was further shaped by Fagot and Vauclair (1991). Their *task-complexity hypothesis* introduced a way to categorize different types of tasks as low or high level. *Low-level tasks* were defined as actions that were familiar or highly regulated, whereas *high-level tasks* were defined as actions that were novel or complex (e.g., actions requiring precision, both hands, or a sequence). Low-level tasks were predicted to elicit *symmetry*, that is, no hand-use preference. An example of a low-level task for most nonhuman primates is reaching to pick up food from a flat surface, such as the ground. Reaching is a low-level task because it develops early in life, becomes practiced, and is therefore easy. Reaching demands are minimal when posture is stable and increase when posture is unstable.

By comparison, a high-level task should elicit *asymmetry*, or a bias in hand use. High-level tasks can involve both hands, but not all tasks involving both hands are high level. Some bimanual actions are *undifferentiated*, which means that the two hands are doing the same thing. An example is using both hands to carry a watermelon. Objects that induce bimanual grasping or holding tend to be poor measures of handedness. In contrast, when one hand stabilizes an object for the other hand's manipulation, the roles of the hands are clearly *differentiated*. An example is stabilizing a watermelon with one hand and cutting slices with the other (preferred) hand. In the literature on human handedness, this skill is described as *role-differentiated bimanual manipulation* (RDBM; also referred to as *functional asymmetry*, *complementary bimanual action*, and *collaborative hand use*). These contrasting examples of how two hands can be used differently to act on the same object highlight the importance of operationally defining the roles of each of the hands in measuring handedness and exercising caution in interpreting data obtained using ambiguous constructs.

To address the problem of poorly defined bimanual tasks in research on nonhuman primates, Hopkins (1995) introduced the *coordinated bimanual tube task* (Fig. 3a). It soon became clear that this task reliably elicited individual and sometimes even population-level hand preferences across a range of monkey and ape species tested (for a review, see Meguerditchian et al., 2013). It is a species-fair test (i.e., all primate species can perform it without any training). It has been used in wild populations and in species that are not considered dexterous, such as the spider monkey, whose hand has four fingers and no thumb (Nelson & Boeving, 2015). Moreover, it is adaptable for children (Figs. 3b and 3c), and there is a rich developmental literature using similar RDBM tasks that could be included in multidisciplinary comparisons (see Developmental Insights Into Handedness).[3]

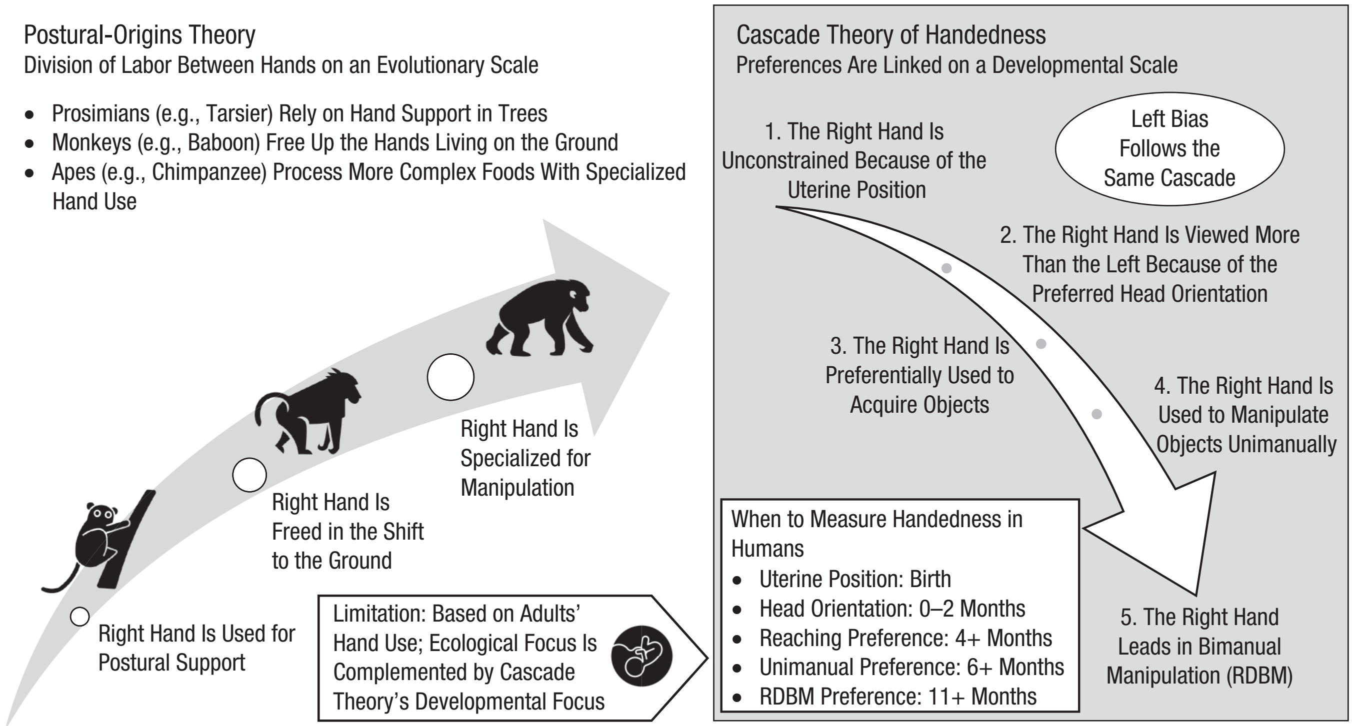

Fig. 2. Different theoretical perspectives on the development of handedness. The left panel depicts the postural-origins theory (MacNeilage et al., 1987), which explains the right bias observed in human adults within an evolutionary framework concerning the role of the right hand across primate taxonomy. However, this theory is based largely on observations of hand use among adult nonhuman primates and does not consider the individual's experiences across development. The right panel depicts the cascade theory of handedness (Michel, 2021; Michel et al., 2013), which frames the development of handedness as a series of cascading experiences that start prenatally. Each asymmetrical experience influences the next observed bias. Although a right bias is the pattern observed for most infants, a left bias follows the same cascade. A limitation in the literature on children's handedness is that researchers tend to collect data at one time point or focus on one behavior in the cascade. Researchers can benefit from integrating the two frameworks to understand the origins of handedness. The cascade theory and postural-origins theory complement each other in that the cascade theory focuses on how experience may shape hand use, whereas the postural-origins theory focuses on how environmental demands may shape hand use. RDBM = role-differentiated bimanual manipulation.

The failure to find population-level hand preferences, particularly for reaching, led some handedness researchers away from the postural-origins theory (Papademetriou et al., 2005). However, there is now general agreement that the tube task is a more reliable handedness measure than simple reaching is. Reaching is sensitive to situational factors such as the individual's posture and the position of objects relative to the individual, but these variables do not affect performance on the tube task. An aspect of the postural-origins theory that still holds merit is that it considers ecological demands that might confer an advantage for a division of labor between the hemispheres of the brain and ultimately between the hands. Hand preference measured by the tube task has been observed to correspond with whether the species is mostly arboreal (left trend) or mostly terrestrial (right trend; Meguerditchian et al., 2013). Moreover, MRI studies of the brain have shown that there are anatomical correlates of handedness as measured via the tube task in baboons (Margiotoudi et al., 2019), capuchins (Phillips & Sherwood, 2005), and chimpanzees (e.g., Hopkins & Cantalupo, 2004). Brain-behavior links are not observed when reaching is the handedness measure.

Where the postural-origins theory fell short is that it did not consider development across time in individuals. The omission is not surprising as most handedness data come from adult nonhuman primates. But trying to explain how handedness evolved and using human right-handedness as its endpoint is a "development to" perspective rather than a "development from" perspective (Michel & Tyler, 2007). Ecological conditions may differentially shape *developmental cascades*, in which developmental changes within and across domains have cumulative and interactive effects over time (Iverson, 2021). Portions of a hypothesized developmental cascade for handedness have been tested in nonhuman primates (e.g., Nelson et al., 2011), but this work has been limited in scope and conducted with small sample sizes. Thus, understanding developmental cascades in handedness requires turning to the literature on children.

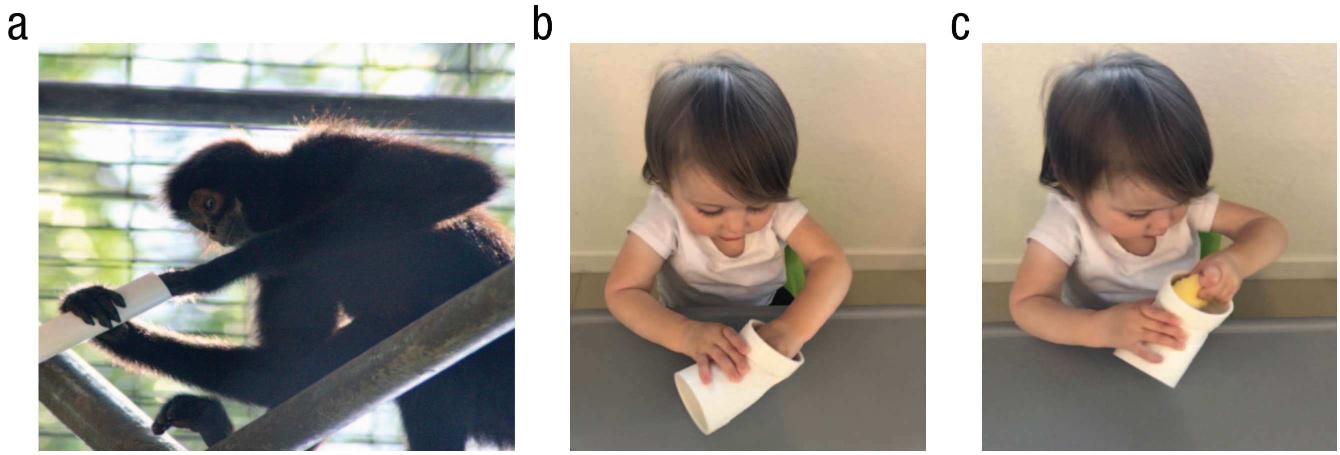

Fig. 3. Measuring handedness in two species on the basis of role-differentiated bimanual manipulation. The photograph in (a) shows a Colombian spider monkey (*Ateles fusciceps rufiventris*) using the right hand to hold a tube and the left hand to extract a mixture of peanut butter and jelly smeared on the inside of the tube. The left hand is recorded as the preferred hand in this trial. This coordinated bimanual tube task was first developed for chimpanzees (Hopkins, 1995). It has been widely used in studies of nonhuman primates because it does not require training, does not require animals to be separated for data collection, and reliably elicits hand preferences. The photographs in (b) and (c) show an 18-month-old human child using the right hand to stabilize a tube and the left hand to extract a soft ball that has been affixed to the inside of the tube with Velcro. The left hand is recorded as the preferred hand in this trial. The child version of the tube task shown here is part of a larger battery of tasks that was developed for toddlers ages 18 to 24 months to test hand use when a role-differentiated strategy is required (Nelson et al., 2013).

Developmental Insights Into Handedness

As in the prevailing theoretical framework in the literature on nonhuman primates, posture is the centerpiece in thinking about the emergence of handedness in the first years of life. The *cascade theory of handedness* suggests that handedness emerges in infancy from a series of cascades arising from continuous individual-environment interactions (Fig. 2, right panel; Michel et al., 2013). The cascade starts prenatally, but not with the hands. Instead, there is a postural asymmetry induced by the intrauterine environment. As the fetus grows, its position and movement become restricted. In the most common uterine position, the fetus is turned in a way that constrains turning the head to the left and moving the left arm. Research has shown that fetal position at birth predicts neonates' preferred head orientation (head turned to the left or right) when they are placed on the back. Infants spend a significant amount of time in this position in the first months of life, and the cascade continues to be shaped by postnatal postural experience: Infants look at one hand more than the other because of their head-turn bias. The hand that is viewed more is then moved more, and the early head-turn bias predicts which hand the infant prefers to use for acquiring objects after the onset of successful reaching. This prediction is not limited to infants with a right-turn head bias and later right-hand preference, who are the majority. Infants with a left-turn bias exhibit a later preference for reaching with the left hand. As infants gain trunk control, they can support themselves in a sitting posture, which frees up the hands for more complex object manipulation. The hand preference for reaching (measured when reaching is novel and difficult for the infant) predicts the hand preference observed for unimanual manipulation, which in turn predicts the hand preference for RDBM (for a detailed account of the cascade theory of handedness, see Michel, 2021).

The onset of reaching is a well-known benchmark in developmental science and pop culture: Most infants first exhibit this manual skill around 4 months of age. The onset of RDBM is more variable because this manual skill is highly task dependent (Fagard & Marks, 2000; Kimmerle et al., 1995, 2010). In other words, the objects chosen to measure RDBM hand preference must be carefully selected. Some objects are more likely than others to elicit RDBM, and these objects will afford a clear role for each hand, in contrast to objects that can be easily manipulated by just one hand or by the hands performing partly differentiated actions. In addition, role differentiation (and thus RDBM skill) increases with age. By the age of 1 year, children can perform simple RDBM tasks, such as removing one object from inside of another object, and about half of their bimanual actions are fully differentiated (i.e., there is a clear role for each hand). By 2 years of age, children can perform more complex RDBM tasks, such as unzipping a zipper, and nearly 100% of their bimanual manipulation is fully differentiated (for a review, see Gonzalez & Nelson, 2015). Finally, there is converging evidence that the difficulty of an RDBM skill is tied to lateralization; the greater the motor skill demanded, the more likely it is to be lateralized (Babik & Michel, 2016; Fagard & Marks, 2000; Potier et al., 2013). Although children may exhibit RDBM earlier, a hand preference for RDBM emerges only between 11 and 13 months of age, depending on task type; this preference may be well established by 18 months (Babik & Michel, 2016; Nelson et al., 2013). Reaching and unimanual manipulation are not robust measures of handedness once a child is capable of performing RDBM (Fagard & Marks, 2000).

Heldstab et al. (2020) examined feeding behavior of 36 species over a 7-year period in a mixed longitudinal/cross-sectional design to document the development of manipulation complexity in nonhuman primates. As in human infants, unimanual actions preceded bimanual actions, and symmetrical bimanual actions preceded asymmetrical bimanual actions (i.e., RDBM). There was variability between individuals and across species in the timing and frequency of manipulation skills; however, the order of the manual skills was consistent in all but one of the species examined, which suggests that the development of manipulation complexity in nonhuman primates is cumulative, not modular. Although data on the frequency of left- and right-hand use were not recorded, this study can serve as a guidepost for what to measure and when in future developmental research on handedness in nonhuman primates, and particularly in research on how the hands are used together.

The cascade theory of handedness was synthesized from a large corpus of longitudinal work with humans. However, this literature also includes cross-sectional and single-age designs. As in studies of nonhuman primates' handedness, small sample sizes are common in this research, which creates a problem for interpreting data. Also as in work with nonhuman primates, reaching has historically been the predominant measure of handedness (for a review, see Nelson & Gonzalez, 2020). But developmental researchers chase a moving target: They must challenge the child, taking into consideration that the child's manual repertoire is changing (Nelson et al., 2013). There is "noise" in the literature created from the variability in how handedness is measured and from the variability among the children themselves. It is not uncommon to see researchers interpreting fluctuations in an infant's or toddler's hand use within or across visits as evidence that handedness is unstable or cannot be measured in young children, with or without considering task differences. Some researchers have extrapolated even further to conclude that this variability means that handedness does not stabilize until later in childhood (for a discussion, see Jacobsohn et al., 2014). An important caution is that there is a distinction between using one lateralized bias to predict another (cascading preferences) and sampling the same behavior at different times to examine the stability of a specific lateralized preference. Although these two approaches are useful for answering different questions, they both require careful consideration of the task constraints and the individual's skill level in order for appropriate conclusions to be drawn.

Variability in sampling, including variability in how many time points, how many children, and what skills to measure, may have masked the fact that there are actually multiple trajectories in the development of handedness in humans (Michel et al., 2013). Early differences can lead to later similarities, and conversely, early similarities can lead to later differences. Trajectories in handedness, measured using early reaching between 6 and 14 months, are not linear; some infants have an identifiable right preference, some have an identifiable left preference, and some show no identifiable preference but a trend toward a right preference (Michel et al., 2014). Thus, some children exhibit consistent hand-use preferences from infancy, whereas others are variable. Consistency in the trajectory of hand-use preference matters because handedness trajectories for later-emerging RDBM skill predict language outcomes when children are 2, 3, and 5 years old (Gonzalez et al., 2020). Moreover, this link to language outcomes extends the cascade theory further in developmental time, past the emergence of a hand-use preference in RDBM tasks. These effects cannot be observed using a traditional "snapshot" approach examining handedness at one time point and language at one time point. Expanding a cascade perspective to other domains has the potential to unlock new knowledge about how the hands work together to shape development.

Conclusions

The goal of this review has been to reframe the question "where does handedness come from?" by shifting away from the traditional thinking about genes and "development to" the adult pattern and instead taking a "development from" approach resting on a comparative synthesis of different theoretical perspectives on handedness from the literatures on nonhuman primates and children. Such an approach requires taking into consideration how individuals continuously interact with their environment and how the ecological context may shift developmental cascades across the life span. This reframing should fundamentally change how researchers think about handedness, starting with how studies are designed. I have discussed several measurement challenges, and I offer here a starter recipe that can be applied to any primate population: use a task that measures how both hands are used. When the hands must work together in RDBM, the likelihood of observing a hand preference increases substantially. Skill is the not-so-secret ingredient. Coordinating the hands demands skill. If a task induces symmetrical hand use, it does not mean there is no handedness; rather, handedness has not been measured. RDBM, not reaching, is the candidate behavior that can bridge the measurement gap between studies of handedness in humans and studies of handedness in nonhuman primates.

How can these recommendations be applied to address knowledge gaps? First, very little is known about the development of handedness across time in nonhumans. Large-scale collaborations such as ManyPrimates (https://manyprimates.github.io/) may be a solution to generate the sample size needed to characterize different handedness trajectories in nonhuman primates' development. Second, much of what we know about handedness trajectories in children comes from carefully controlled lab settings. Future work could incorporate ecological settings. Third, studies of both children and nonhuman primates are likely to be shaped by advancements in technology that will allow researchers to connect behavioral data with structural and functional differences in the brain. The success of this approach will be determined by the way handedness is assessed. In the science of handedness, measurement matters.

Recommended Reading

Gonzalez, S. L., & Nelson, E. L. (2015). (See References). A review of hand preference for role-differentiated bimanual manipulation in infants and guidance for future research.

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Transparency

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Notes

1. According to citation counts, handedness in adults is most often measured using the Edinburgh Handedness Inventory (EHI; Oldfield, 1971). A criticism of the EHI and measures like it is that tasks performed with one hand (i.e., unimanually) are conflated with those performed with two hands (i.e., bimanually). For example, the EHI asks participants to report which hand they use to brush their teeth and which hand they use to write, but the hands are not used the same way in these two activities of daily living even though both tasks require skilled hand use. Brushing teeth can be done with a single hand, but writing requires two: one hand to stabilize the writing surface and the other hand to manipulate the writing instrument. An exercise to illustrate how the hands work together in many tasks that are often perceived as performed with only the preferred hand is to try to sign your name on a piece of paper with one hand behind your back. Unimanual and bimanual tasks tap into separate dimensions of handedness, but this distinction is not captured by traditional questionnaires used with adults (Gonzalez & Nelson, 2021). It is important for measuring handedness in nonhuman primates and children as well. (For a discussion on the use of the EHI and variations of it, see Edlin et al., 2015.)

2. Although this article focuses on investigating the origins of handedness in nonhuman primates and young children, limb preferences have been studied in all vertebrate classes (Ströckens et al., 2013).

3. Closing the measurement gap can be an easy problem to solve because the tube task is widely used. However, lingering in the literature are disagreements regarding how tube-task data should be collected, reported, and interpreted (for a discussion, see Hopkins, 2013). Establishing best practices by a consensus of handedness researchers working with different species would reconcile these outstanding methodological and statistical issues and thus facilitate comparisons across studies. My recommendation is to collect at least 25 responses from each tested individual to calculate a handedness index or a z score for statistical analyses. Whenever possible, researchers should provide individual-level and population-level interpretations of their data. Raw data on the frequency of left- and right-hand use should also be provided in publications or accompanying electronic supplements (for large samples) to facilitate comparisons between studies (i.e., meta-analysis).

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