A Meta-Analysis of Primate Hand Preferences, Particularly for Reaching[*]

By: Eros Papademetriou, Ching-Fan Sheu, and George F. Michel

Made available courtesy of American Psychological Association:
http://www.apa.org/pubs/journals/com/index.aspx

Humans, as do most vertebrate species studied, exhibit a limb preference for unimanual activities. However, two characteristics of the human limb preference are thought to distinguish it from that of other vertebrates: (a) The preference is the same across a variety of manual tasks that have few task demands or motor skills in common (handedness consistency); and (b) the handedness consistency is unevenly distributed in the population with a distinct right-handed skew. Thus, depending on the criteria used to define a preference, 70%–90% of humans exhibit a consistent right-hand preference for manual activities (Annett, 1985). This sharp population bias in the distribution of hand preference has been prevalent for much of the natural history of humans (Corballis, 1991) and is present in all cultures (Annett, 1985). Anthropological evidence suggests a population bias toward right-handedness in the hominid ancestors of humans that dates back at least 1.8 million years (McManus, 2002; Toth, 1985). The evidence shows both a right-hand dominance in the construction of tools and an asymmetry in form of tools such that their use would be much more manageable with the right hand. Thus, the right bias in human handedness seems to be an evolutionary extension of a right bias in hominid handedness.

Several theorists have proposed that the human hand, brain, upright posture, and pattern of locomotion coevolved (cf. McManus, 2002). There is no evidence from human or hominid anatomy that the right and left hands evolved differently (McManus, 2002). Therefore, the population bias in handedness must involve evolutionary changes in brain and posture. Indeed, given the cross-lateral pattern of innervation of the hands, the right bias in human handedness is another aspect of the human pattern of cerebral lateralized asymmetry of function and is most closely associated with the hemisphere specialization for language functions. Although handedness and other forms of lateralized brain functions (e.g., control of speech) are only mildly associated, patterns of atypical individual handedness, particularly left-handedness, seem to be associated with many types of human pathological (e.g., dyslexia, autism, schizophrenia) and nonpathological conditions (e.g., artistic skills, athletic prowess). Such associations have led many to seek among primates a nonhuman model for human handedness (e.g., Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002; Westergaard, Kuhn, & Suomi, 1998a).

Many different species of vertebrates show evidence of handedness (i.e., individuals show a preference to use one limb more than the other for particular tasks involving the use of one limb), which may reduce cognitive load (Flowers, 1975). Each time a single limb action is to be initiated and there is no bias in the situation (an asymmetry of the individual's posture or an asymmetry in the spatial coordinates of the goal of the action), there is a time delay and information-processing cost associated with the decision of which limb to use. A

"preference" (typical use of one limb) greatly reduces such cost across a large number of mundane unilimb tasks (e.g., initiation of locomotion, "pawing" an object). However, for many species, although a preference is exhibited for many different tasks, it is not consistent across tasks within an individual. Moreover, unlike humans, the handedness for most species is evenly distributed in the population (Annett, 1985; McManus, 2002).

Some species do demonstrate a population skew or bias in handedness (e.g., some toad species prefer to use the right leg to scratch the snout, chickens prefer to use the right foot to scratch the ground, some parrot species prefer to use the left foot to hold food, and 75% of humpback whales prefer to use their right flipper to slap the surface of the water). However, the bias in human hand-use preference exhibits individual consistency across a variety of rather distinctive manual skills. Moreover, either the phylogenetic distinctiveness among these different species with a bias in limb-use preference points to a general vertebrate characteristic, or such evidence does not reflect a gradual evolutionary sequence leading to the right bias in human handedness (cf. Crow, 2004; Rogers & Andrew, 2002).

In 1987, MacNeilage, Studdert-Kennedy, and Lindblom proposed that because right-handedness and language seem uniquely human, investigation of the evolution of handedness (via the comparison of handedness among different species of primate) might reveal something about the evolution of language. Their review of the evidence from 75 studies of primate handedness led them to propose that the ancestral, arboreal primate necessarily used one hand (the right) to cling to trees. Consequently, the left hand was used for visually guided reaching for and grasping of food. If it is presumed that the right hemisphere (controlling the left hand) is adapted to function more effectively than the left hemisphere for visuospatial skills, then the left-hand preference for the manual acquisition of food in a visuospatial field may be expected. Unfortunately, there is no evidence of which we are aware that the right hemisphere of prosimians is more efficient at visuospatial processing.

MacNeilage et al. (1987) proposed further that as terrestriality evolved, opportunities for bimanual manipulation occurred and the left hand continued to be used for reaching. Because the reaching hand typically is the hand that first obtains the object, the reaching left hand is preadapted to provide support for the right-hand manipulations during bimanual manipulation. Similarly, MacNeilage et al. proposed that right-hand gripping skills preadapted it for manipulation. Thus, the right hand came to dominate in bimanual manipulation. Eventually this evolved into a generalized right bias for all hand use, including reaching. Thus, according to the proposal of MacNeilage et al., the evolution of handedness may be identified by comparing various suborders of primates for their hand use when reaching for food.

One peculiarity of the MacNeilage et al. (1987) proposal is that the generalized right bias results in reaching shifting from a left preference to a right preference. This creates the more cumbersome action pattern of obtaining an object with the right hand and then transferring it to the left hand so that right hand dominance in role-differentiated bimanual manipulation can occur. Such a pattern is not typical of humans or other apes. However, this cumbersome pattern is exhibited by human infants during the latter part of their first year. It is then replaced at 13–14 months of age with the more efficient pattern of reaching for and obtaining an object with the nonpreferred hand (typically the left hand) so that role differentiated bimanual manipulation occurs more immediately, with the preferred hand (typically the right) dominating that action (Michel, 1998).

The MacNeilage et al. (1987) postural origins theory (POT) for the evolution of the right bias in human handedness proposed that in prosimian primates, the left hand became preferred for reaching while the right hand was used mainly for postural support (holding onto trees). Because some New World and Old World monkey species do not feed in the trees, they spend more time on the ground and subsequently, the right hand was freed from its postural support duties and was able to accomplish manipulation activities while the left hand remained dominant for reaching. Because there was little data on handedness in apes in 1987, the POT was not as specific as to how the more generalized bias to right-handedness occurred in the transition from monkeys to apes and from apes to humans. MacNeilage et al. did suggest that the handedness of apes was an "intermediate

between monkey and man" (p. 248); that is, the left hand reaching preference disappears and the right hand becomes dominant for all tasks, as is the case for humans.

MacNeilage et al. (1987) proposed that the right hand manipulation skills and postural control provided the left hemisphere with the structures needed for the sensorimotor control of the speech apparatus and that this led to the left hemisphere specialization for language. Although intended to be a theory of the evolution of hemispheric specialization for language, a major effect of the POT was to stimulate research on primate handedness.

One criticism of the MacNeilage et al. (1987) review is that it interpreted nonsignificant results as demonstrating a leftward bias in prosimians and New World primates. Another criticism of the theory is that it is simply a restatement of what the researchers' interpretation of the data seemed to show. It does not really give a testable model of why the earlier primates would prefer the left hand over the right hand for visually guided reaching or why the right hand would then be better suited for manipulative actions than would the left hand (McGrew & Marchant, 1997). Indeed, the "gripping" support actions of the left hand become essential for effective and efficient role-differentiated bimanual manipulation in humans for which the right hand typically is preferred for manipulating the object (Michel, 1998)—that is, the left hand grasps and grips the objects while the right hand manipulates it.

Of course, POT is not the only theory of primate handedness. In 1977, Warren proposed that hand-use preference in primates was a consequence of specific experiences and would be both task and situation specific (cf. Warren, 1987). Thus, there should be no population-level lateral bias in handedness for any species of primate that was not a result of some bias in the experience of the members of that population. In contrast, Fagot and Vauclair (1991) proposed that low-level manual tasks (familiar, well-practiced, simple actions with undemanding cognitive aspects—e.g., reaching) would not manifest a hand-use preference, whereas high-level manual tasks demanding more neural activity (novel, finely coordinated actions involving complex cognitive abilities) would exhibit not only handedness but also a population bias in handedness distribution reflecting underlying cerebral hemisphere specialization. Papademetriou (2003) reviewed the evidence both in support of and against the Fagot and Vauclair proposal. One problem with the theory is a lack of an a priori definition of what constitutes a cognitively demanding manual task (cf. McGrew & Marchant, 1997).

Since the publication of the POT, reports of a population bias in primate handedness have been mixed (McGrew & Marchant, 1997). In part, this ambiguity derives from the interpretation of studies that do not precisely define how handedness is assessed or specify how a population-level bias is determined. Therefore, one purpose of the current study is to reevaluate the evidence of primate handedness by using meta-analytic statistical techniques for the individual data collected by studies of primate handedness, especially for those conducted since 1987. In 1997, McGrew and Marchant published a meta-analysis of primate handedness that did not analyze data from the articles statistically. Rather, they reviewed articles that met their criteria for evaluation and presented the results from those studies in order to form a conclusion about primate handedness and its relation to human handedness. Of the 241 published studies that they identified, only 48 met the seven criteria for evaluation (i.e., independence of data points, data from adults, sufficient data points per subject for binomial analysis of lateralization, well-defined manual task, raw data, identification of species, and data from more than 6 subjects). They concluded that the 12 acceptable studies of prosimian handedness provided evidence for individual handedness but no evidence of any asymmetry of handedness within any species or for the group as a whole. They argued that the 19 acceptable studies of New World monkeys also failed to show anything more than individual handedness. Only 11 studies of Old World monkeys were acceptable for evaluation, and again there did not appear to be any evidence of a population bias in handedness. Eighteen studies of apes met the criteria with nearly half reporting only about chimpanzees. Although there was some evidence, especially from chimpanzees, of a population bias in ape handedness, this only occurred with captive animals. Wild-living apes seemed not to manifest a population bias in handedness, even for such tasks as "termite fishing" and "nut cracking." McGrew and Marchant (1997) concluded that their meta-analysis did not reveal evidence in support

of the POT or of any "human-like laterality of hand function" (p. 227) and that laterality of hand preferences in Homo sapiens may be uniquely associated with our specific evolution and self-domestication.

Although useful as a thorough review of the literature, the McGrew and Marchant (1997) version of the meta-analytic technique does not provide the same information as a statistical meta-analysis. Thus, the current study will examine the empirical data statistically. Similar to McGrew and Marchant, we searched the literature for data sets with individual data. Papademetriou (2003) provided a detailed review of 142 studies of nonhuman handedness published since 1987. Of these 142 studies, 62 met our criteria for statistical analysis.

In his review, Papademetriou (2003) noted that many studies use a handedness index (HI) as a measure of laterality. This index is calculated by the formula $(R - L)/(R + L)$, where R = number of right-hand responses and L = number of left-hand responses. This index ranges from −1 to 1 and is taken to measure strength of hand preference along a continuum, with positive values indicating a right bias and negative values indicating a left bias. However, it is unclear whether this index actually captures significant hand-use preference as opposed to a simple difference in proportion of hand use. That is, with the HI index it is difficult to classify individuals according to their handedness because an individual could be classified as right-handed whether the HI is 0.1 or 1.0. Despite the continuous nature of handedness, most researchers and others are generally interested in the number of right- and left-handed individuals. Consequently, some other technique must be used if individuals are to be classified as right- or left-handed, and this technique must permit identification of whether an individual's proportion of left- or right-hand use differs significantly from 50%. Thus, many researchers use HI only as a measure of the continuum of lateralization, with the absolute value of the HI interpreted to reflect strength or degree of lateralization. Unfortunately, it is unlikely that this index, or any measure, can validly quantify strength of lateralization. The frequency data on which it is based essentially translate into an ordinal number series in which relative difference in score reflects relative position (first, second, third, etc.) rather than degree of difference between positions. 1

Moreover, there is no theory or even consensus about what constitutes stronger lateralization or even what stronger lateralization might mean. Does lateralization mean that one hand (or hemisphere) exclusively performs certain tasks and the other does not; that one hand (hemisphere) performs certain tasks more efficiently than the other; that one hand (hemisphere) typically performs certain tasks and the other does not and hence, they differ in skill; or that one hand (hemisphere) is more prepared to perform certain tasks for which the other is not? Might individuals differ on some or all of these lateralization distinctions and hence show greater or lesser lateralization? Using a numerical difference that is the consequence of a simple relative frequency of use is not a substitute for an evaluation of the meaning of strength of lateralization. Hence, as yet the validity of the absolute value of HI as a measure of strength of lateralization cannot be determined. However, a higher index number can make one more confident in the classification of the individual as left- or right-handed (see Footnote 1).

In past research (cf. Michel, 1998), Michel, Sheu, and Brumley (2002) proposed that a more appropriate way to classify individuals might be with a z-score equivalent of a binomial test of the relative frequency of left- and right-hand use. If the frequency of observations for each individual is sufficient (~25), this score provides an estimate of the likelihood of misclassification of an individual's hand-use preference based on a Fisher's normal approximation of a binomial distribution. The z score has been used in many studies of this type in both human and primate research (cf. Michel et al., 2002). Unlike HI, the size of the z score provides a conventional means of specifying the confidence with which one can classify individuals into three categories: ambiguous preference, right preference, and left preference (i.e., conventional levels of significance, such as .05, may be used to create these categories). Thus, the z score is one of the few classification techniques that permit specification of the probability of misclassification. This use of the z score has been shown to be very illuminating about the hand-use preferences of human infants (Michel et al., 2002). There is no evidence that the z score indicates degree or strength of laterality.

For the current study, neither z scores nor HI scores were used as the unit of analysis for the meta-analyses. We used the z scores to classify subject's handedness for presentation in tables, and we derived the scores from the raw data available from the articles. Thus, the classification of subjects in the tables as left-, right-, or ambiguously handed was based on a z test (with an alpha level of.05) calculated from each individual's number of left- and right-hand reaches. For the meta-analyses, in contrast, all data were analyzed by using the proportion of left-hand use for each subject. Because instances of use of both hands were removed from the analysis, the proportion of left-hand use is the complement of the proportion of right-hand use. Thus, we conducted a meta-analysis of the reaching data (proportion of left-hand reaches) for all four nonhuman primate suborders to determine whether any group exhibited a population bias in handedness and, if so, whether the direction of bias was consistent with the predictions of the POT.

Method

Three different methods were used to obtain articles concerning primate hand-use preferences for reaching. The computer-based literature search (PsycINFO, PrimateLit, Medline, Anthropological Index Online, and EBSCOhost) used the following search terms: primate handedness, primate laterality, primate hand preference, primate hand use, and nonhuman primate. The second method was to examine the references of relevant articles and to attempt to obtain those references. A third method involved contacting researchers to request their raw data and any other sources they might recommend.

Criteria for Inclusion

From the body of articles obtained, articles that met three inclusion criteria were chosen for meta-analysis. First, some form of reaching task had to have been used (e.g., reaching for food on the ground, from a box, or from a string), but no distinctions were made among these tasks. Reaching typically is not assessed in studies of handedness in adult humans; rather, their handedness is assessed by questionnaires that query hand use for role-differentiated bimanual manipulation tasks. When adult handedness is assessed by actual action, the skills examined usually involve accuracy and speed of picking up and placing pegs in holes or marking dots in the center of circles. However, reaching is a very reliable task for identifying handedness in human infants and young children.

Because it has been shown that different manual tasks can elicit differences in hand preference (Ward & Cantalupo, 1997), manual tasks were separated into reaching (food and nonfood reaching) and nonreaching (holding, probing, stone striking, carrying, performing joystick tasks, nut cracking, etc.) tasks in two different analyses. Our criterion for reaching did not include tasks that required bipedal reaches or multicomponents to the task (e.g., haptic searching—that is, tactually discriminating which item to retrieve). Most studies included a simple reaching task, but some studies had additional tasks that required the individual to adopt an unusual bipedal posture in order to reach or that did not permit the individual to see the object to be obtained by the reach. These tasks occasionally yielded results different from those involving a simple reach. Because most studies were not consistent in the type of more complicated reaching tasks used, we decided not to analyze data collected by unusual reaching tasks. We do not believe that our choice of simple reaching as a dependent measure weakens the evaluation of the POT because that theory relates more directly to simple reaching.

A second criterion used for including data from a study was that species type must have been provided with enough specificity that the subjects could be classified according to their taxonomic group. Third, individual data must have been reported in the study or obtained by contacting the author. The individual data that were relevant were the number of left- or right-hand reaches and the total number of reaches for each individual. If it was possible to derive this information from what was reported, then the study was included. Although sex differences have been reported in some studies of primate handedness (Dodson, Stafford, Forsythe, Seltzer, & Ward, 1992; Milliken, Forsythe, & Ward, 1989), this has not been observed consistently (McGrew & Marchant, 1997). A preliminary analysis of the data revealed no sex difference for any dependent variable; therefore, those studies that failed to report on the sex of their subjects were included in the analysis.

Authors occasionally reported using some of the same subjects in separate studies. Therefore, if repeated subjects were identified by name or ID number, then only data from the subject's earliest publication were used in the present analysis. This increased the likelihood of independence of the data. Because the literature review revealed many studies that reported on several different types of handedness tasks, a separate meta-analysis was conducted on the data from all of the nonreaching tasks (most involved tool use such as termite fishing or nut cracking), including bimanual manipulation tasks (e.g., extracting paste from a tube or sliding panels horizontally or vertically in order to extract food). Again, the individual hand-use data from all of these different tasks was combined into a single score of proportion of left-hand use.

Data Analysis

In contrast to conventional meta-analyses, which code effect sizes from different studies and compare them by using various statistical methods (Lipsey & Wilson, 2001), this study analyzed individual data. This change permitted modeling the variability among the individuals across studies by treating them as a random sample. The scope of inference then encompasses the population from which these individual primates were drawn. The basic observation and unit of analysis is the frequency of left-hand use in a total number of trials for an individual primate. It was assumed that the relative frequency (or proportion) of left-hand use follows a binomial distribution with an unknown probability of a primate making a right-hand use. A logistic link was used to relate the unknown probability to the known taxonomic characteristic of the primates—in this case, a fixed effect. Thus, a mixed-effect logistic regression model was used to analyze the data (Agresti, 2002; Sheu, 2002). The fixed effect in this analysis is a taxonomic type (e.g., suborder), and the random effect is the between-subjects variation, which is assumed to follow a normal distribution.

A mixed-effect analysis provides information on both the variability between individual primates sampled and the trial-to-trial variability within the same individual. That is, instead of estimates of individual variability being incorporated into the error term of a traditional fixed-effects analysis, the mixed model approach allows this variability to be modeled and a more reliable estimate to be attained. For a review of this method of meta-analysis involving normal data, see Sheu and Suzuki (2001). The data were analyzed with the SAS statistical package (Version 8.2). The NLMIXED procedure was used to fit the models to data (Wolfinger, 2001).
Results

The Literature Review

The literature search identified 142 articles that investigated handedness in nonhuman primates. Of these, 24 were review articles or abstracts for which raw data were not obtainable. Of the 118 remaining articles, 62 (53%) met the inclusion criteria (marked with an asterisk in the reference list), with 42 of these articles (35%) providing data on reaching actions and 20 articles (17%) providing data on some other aspect of manual behavior. (One article provided data for both reaching and nonreaching behaviors.) The primary reason for the relatively small proportion of articles meeting criteria was a failure to obtain the individual data needed for the meta-analysis.

We classified the 56 articles that did not have individual data by using the direction of bias that each article reported in its results section separately for each of the tasks measured (see Table 1). Fifty articles reported evidence for no population-level bias in handedness, whereas 15 reported evidence for a population-level right-hand bias and 15 reported evidence for a population-level left-hand bias (see Table 2). Some articles reported evidence for different combinations (right, left, and/or no bias) of population biases depending on the task (Hopkins, 1993; Hopkins, Bennett, Bales, Lee, & Ward, 1993; Spinozzi & Cacchiarelli, 2000; Spinozzi, Castorina, & Truppa, 1998; Spinozzi & Truppa, 1999; Westergaard, Kuhn, & Suomi, 1998b), the species (Hopkins, Stoinski, Lukas, Ross, & Wesley, 2003; Olson, Ellis, & Nadler, 1990; Westergaard & Suomi, 1996a, 1996b), and the age of subjects (Westergaard & Lussier, 1999). Because the same article can be counted as reporting evidence for no, right, and left bias, no statistical analyses were performed.

Table 1
Handedness Bias Reported in the 56 Articles That Did Not Provide Individual Data

Source	Species	Task	N	Reported bias
		Prosimians		
Dodson et al. (1992)	*Galago moholi*	Food reaching	16	No bias
Sanford et al. (1984)	*Galago senegalensis*	Bipedal reaching	25	Left
Sanford et al. (1984)	*Galago senegalensis*	Quadrupedal reaching	12	No bias
Ward et al. (1990)	*Lemur* spp.	Food reaching	194	No bias
Ward & Cantalupo (1997)	*Otolemur garnettii*	Bipedal reaching	27	No bias
Ward & Cantalupo (1997)	*Otolemur garnettii*	Quadrupedal reaching	27	No bias
Cantalupo & Ward (2000)	*Otolemur garnettii*	Food reaching	20	No bias
Dodson et al. (1992)	*Microcebus murinus*	Food reaching	8	No bias
		New World monkeys		
Hook & Rogers (2000)	*Callithrix jacchus*	Food holding	15	No bias
Cameron & Rogers (1999)	*Callithrix jacchus*	Food reaching	20	No bias
Hook-Costigan & Rogers (1998)	*Callithrix jacchus*	Food holding	15	No bias
Bicca-Marques et al. (1998)	*Saguinus fuscicollis*	Food reaching	11	No bias
Bicca-Marques et al. (1998)	*Saguinus imperator*	Food reaching	11	Right
King (1995)	*Saguinus oedipus*	Multiple grasping measures	30	Right
Roney & King (1993)	*Saguinus oedipus*	Food reaching	14	No bias
Spinozzi & Truppa (1999)	*Cebus apella*	Food reaching	25	Right
Spinozzi & Truppa (1999)	*Cebus apella*	Horizontal panel task	25	Right
Spinozzi & Truppa (1999)	*Cebus apella*	Vertical panel task	25	No bias
Anderson et al. (1996)	*Cebus apella*	Multiple hand-use measures	10	No bias
Westergaard & Suomi (1993b)	*Cebus apella*	Food reaching	21	Right
Westergaard & Suomi (1993a)	*Cebus apella*	Sponging task	14	No bias
Lacreuse & Fragaszy (1999)	*Cebus apella*	Haptic reaching task	16	Left
Lacreuse & Fragaszy (1999)	*Cebus apella*	Reaching task	16	No bias
Westergaard et al. (2000)	*Cebus apella*	Aimed throwing	25	No bias
Parr et al. (1996)	*Cebus apella*	Haptic reaching task	22	Left
Parr et al. (1996)	*Cebus apella*	Food reaching	22	No bias
Westergaard & Suomi (1994)	*Cebus apella*	Tool use	13	No bias
Westergaard & Suomi (1996a)	*Cebus apella*	Bimanual feeding	45	No bias
Spinozzi & Cacchiarelli (2000)	*Cebus apella*	Haptic reaching task	26	Left
Spinozzi & Cacchiarelli (2000)	*Cebus apella*	Food reaching	26	Right
Christel & Fragaszy (2000)	*Cebus apella*	Food reaching	5	No bias
Westergaard et al. (1998a)	*Cebus apella*	Bipedal reaching	16	Right
Westergaard et al. (1998a)	*Cebus apella*	Quadrupedal reaching	16	No bias
Westergaard et al. (1998a)	*Cebus apella*	Tool use	16	No bias
Panger (1998)	*Cebus capucinus*	Reaching task	48	No bias
Laska (1996a)	*Ateles geoffroyi*	Multiple hand-use measures	13	Left
Bicca-Marques et al. (1998)	*Callicebus cupreus*	Food reaching	Unknown	No bias
Roney & King (1993)	*Saimiri sciureus*	Food reaching	30	No bias
Laska (1996b)	*Saimiri sciureus*	Multiple hand-use measures	12	No bias
		Old World monkeys		
Harigel (1991)	*Macaca fuscata*	Food reaching	14	No bias
Kubota (1990)	*Macaca fuscata*	Food reaching	44	No bias
Deuel & Dunlop (1980)	*Macaca mulatta*	Multiple hand-use measures	60	No bias
Drea et al. (1995)	*Macaca mulatta*	Food reaching	16	Left
Fagot et al. (1991)	*Macaca mulatta*	Haptic reaching task	29	Left
Harigel (1991)	*Macaca mulatta*	Food reaching	12	No bias
Hopkins et al. (1992)	*Macaca mulatta*	Joystick task	35	No bias
Westergaard (1999)	*Macaca mulatta*	Quadrupedal reaching	27	Left
Westergaard & Suomi (1996a)	*Macaca mulatta*	Bimanual feeding	55	Right
Westergaard et al. (1997)	*Macaca mulatta*	Food reaching	19	Left
Westergaard et al. (1997)	*Macaca mulatta*	Bimanual feeding	19	Left
Westergaard & Lussier (1999)	*Macaca mulatta*	Quadrupedal reaching	34	Left
Westergaard & Lussier (1999)	*Macaca mulatta*	Quadrupedal reaching	30	Right
Westergaard, Lussier, & Higley (2001)	*Macaca mulatta*	Quadrupedal reaching	70	No bias
Brooker et al. (1981)	*Macaca radiata*	Food reaching	69	No bias
Brinkman (2001)	*Macaca fascicularis*	Food reaching	200	No bias
Westergaard, Lussier, & Higley (2001)	*Macaca fascicularis*	Quadrupedal reaching	65	No bias
Martinoli et al. (1995)	*Macaca nemestrina*	Multiple hand-use measures	13	No bias
Rigamonti et al. (1998)	*Macaca nemestrina*	Food reaching	10	No bias

Table 1 (*continued*)

Source	Species	Task	N	Reported bias
		Old World monkeys (*continued*)		
Westergaard, Lussier, & Higley (2001)	*Macaca nemestrina*	Quadrupedal reaching	70	No bias
Beck & Barton (1972)	*Macaca speciosa*	Multiple hand-use measures	10	No bias
Aruguete et al. (1992)	*Papio* spp.	Face touching	18	No bias
Vauclair & Fagot (1987)	*Papio* spp.	Food reaching	18	No bias
Teichroeb (1999)	*Erythrocebus patas*	Food reaching	5	No bias
		Apes		
Rogers & Kaplan (1996)	*Pongo pygmaeus*	Self-touching	43	Left
Rogers & Kaplan (1996)	*Pongo pygmaeus*	Food reaching	43	No bias
Byrne & Byrne (1993)	*Gorilla gorilla*	Food reaching	44	No bias
Byrne & Byrne (1991)	*Gorilla gorilla*	Food reaching	44	No bias
Hopkins & Pearson (2000)	*Pan troglodyte*	Multiple hand-use measures	187	Right
Hopkins (1995b)	*Pan troglodyte*	Bimanual feeding	110	Right
Colell et al. (1995b)	*Pan troglodyte*	Food reaching	24	No bias
Tonooka & Matsuzawa (1995)	*Pan troglodyte*	Food reaching	80	No bias
Hopkins et al. (1994)	*Pan troglodyte*	Bipedal reaching	76	Right
Hopkins et al. (1994)	*Pan troglodyte*	Quadrupedal reaching	76	No bias
Kirby (1992)	*Pan troglodyte*	Food reaching	4	No bias
Hopkins et al. (2000)	*Pan troglodyte*	Bimanual feeding	165	Right
Hopkins (1999)	*Pan troglodyte*	Bimanual feeding	188	Right
Lacreuse et al. (1999)	*Pan troglodyte*	Haptic reaching task	20	Right
Lacreuse et al. (1999)	*Pan troglodyte*	Food reaching	16	No bias
Lacreuse et al. (1999)	*Pan troglodyte*	Bimanual feeding	19	No bias
De Vleeschouwer et al. (1995)	*Pan paniscus*	Food reaching	5	Left

Table 2
Distribution of Handedness Bias Reported in Articles

Primate group	Right bias	Left bias	No bias
	Individual data not provided (*n* = 56)		
Ape	6	2	10
New World monkey	7	4	18
Old World monkey	2	8	15
Prosimian	0	1	7
Total	15	15	50
	All articles (*N* = 118)		
Prosimian	3	8	7
New World monkey	15	9	19
Old World monkey	4	10	12
Ape	17	6	27
Total	39	33	65

Of the 56 articles, the number that reported a bias in handedness distribution, regardless of direction, is lower than the number that did not report a bias (Table 2). With the exception of Old World monkeys and apes, the difference in the direction of bias also appears rather similar. A left-hand bias was reported for 80% of those articles reporting a hand-use bias in Old World monkeys. In contrast, a right-hand bias was reported for 75% of those articles reporting a hand-use bias for apes. However, as Table 2 shows, in each case there were more reports of no bias in hand use than of a left or right bias, respectively.

Table 2 also shows the direction of bias reported in the results section of all 118 articles on primate handedness. Again, the number reporting a bias does not appear to be strikingly different from the number that did not report a bias. The number reporting a right bias is lower than the number reporting no bias, but the number of articles reporting a right bias is not much different from those reporting a left bias. However, the number of articles reporting a left bias appears to be much smaller than those reporting no bias. Of the four primate suborders,

only the articles on apes showed more reporting of a right bias than of a left bias and more reporting of no bias than of a left bias. However, the number of articles reporting no bias was not strikingly different from those reporting a right bias. More articles on Old World monkeys reported a left bias than a right bias. It should be noted that these differences could not be assessed statistically because some articles were counted for two or more of the population-level bias categories (right, left, or no), depending on species or task differences (e.g., bipedal vs. quadrupedal reaching).

Mixed-Model Analysis—General Handedness Data

We used the mixed-model method to analyze the proportion of left-hand reaches for each individual from the 62 articles that met the criteria. Tables 3 through 7 show the distribution of hand preferences as reported in each article (i.e., not from our analysis) of different primate infraorders and representative taxonomic subgroups within those suborders. (Chimpanzees are reported separately from other apes because of their high representation in the sample.) We used the z score estimate of the binomial to compute an individual's hand preference for articles in which preference was not categorized. Note that although this estimate was calculated as a way of classifying individual handedness for representation on these tables, the data used for our meta-analyses were coded as individual binomial proportions of left-hand use.

Table 3

Prosimians: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Ward (1998)	*Galago moholi*	Food reaching	3	.00	.00	720	.63	.37
Larson et al. (1989)	*Galago senegalensis*	Food reaching	10	.30	.70	4,563	.40	.60
Mason et al. (1995)	*Propithecus verreauxi*	Food reaching	15	.27	.46	1,500	.46	.54
Milliken et al. (1991)	*Otolemur garnetti*	Food reaching	23	.57	.30	4,182	.53	.47
Forsythe & Ward (1988)	*Lemur macaco*	Food reaching	33	.36	.61	3,924	.39	.61
Stafford et al. (1993)[a]	*Hapalemur griseus*	Food reaching	13	.38	.62	1,020	.33	.67
Milliken et al. (1989)	*Lemur catta*	Food reaching	13	.23	.54	520	.37	.63
Forsythe et al. (1988)	*Varecia variegate*	Food reaching	5	.00	.20	517	.46	.54
Feistner et al. (1994)[b]	*Daubentonia madagascariensis*	Hold	11	.00	.27	1,023	.50	.50

[a] Used simple food-reaching task.   [b] Article was used in the nonreaching task analysis.

Table 4
New World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Singer & Schwibbe (1999)	*Callithrix jacchus*	Novel simple reaching	14	.29	.71	444	.33	.67
Box (1977)	*Callithrix jacchus*	Combined 3 reaching tasks	8	.13	.50	2,363	.46	.54
Matoba et al. (1991)	*Callithrix jacchus*	Food reaching	69	.28	.41	3,450	.47	.53
Hook-Costigan & Rogers (1995)	*Callithrix jacchus*	Simple visuospatial reaching	8	.25	.13	1,468	.34	.66
de Sousa et al. (2001)	*Callithrix jacchus*	Food reaching	46	.43	.54	4,600	.48	.52
Singer & Schwibbe (1999)	*Saguinus*	Novel simple reaching	10	.60	.30	352	.60	.40
Diamond & McGrew (1994)	*Saguinus oedipus*	Reaching	20	.95	.00	3,121	.70	.30
Singer & Schwibbe (1999)	*Leontopithecus*	Novel simple reaching	15	.60	.33	585	.64	.36
Westergaard & Suomi (1996b)[a]	*Cebus apella*	Stone striking	10	.70	.10	648	.84	.16
Westergaard et al. (1998b)	*Cebus apella*	Food reaching	35	.29	.11	1,319	.53	.47
Lacreuse & Fragaszy (1996)	*Cebus apella*	Food reaching	17	.24	.24	1,360	.52	.48
Spinozzi & Truppa (2002)[a]	*Cebus apella*	Multicomponent food reaching	2	1.00	.00	200	.85	.15
Spinozzi et al. (1998)	*Cebus apella*	Quadrupedal food reaching	26	.42	.31	2,636	.55	.45
Masataka (1990)	*Cebus apella*	Food reaching	31	.81	.13	3,100	.67	.33
Fragaszy & Mitchell (1990)[b]	*Cebus apella*	Food reaching	7	.14	.43	1,808	.45	.55
Westergaard (1991)[a]	*Cebus apella*	Probing	5	.20	.80	614	.20	.80
Westergaard, Haynie, & Lundquist (1999)[a]	*Cebus apella*	Carry	38	.55	.37	1,601	.56	.44
Westergaard & Suomi (1993b)[a]	*Cebus apella*	Stone striking	8	.50	.38	495	.71	.29
Westergaard, Wagner, & Suomi (1999)	*Cebus albifrons*	Quadrupedal food reaching	8	.38	.75	400	.53	.47
Panger & Wolfe (2000)[a]	*Cebus capucinus*	Carry	25	.08	.04	213	.56	.44

[a] Article was used in the nonreaching task analysis.   [b] Feeding condition used.

Table 5
Old World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions
Holder (1999)[a]	*Colobus badius*	Multiple hand-use measures	30	.47	.40	1,973
Mittra et al. (1997)	*Presbytis entellus*	Retrieve objects	10	.20	.00	1,242
Watanabe & Kawai (1993)[b]	*Macaca fuscata*	Food reaching	80	.20	.48	16,939
Itakura (1992)	*Macaca fuscata*	Food reaching	2	.00	1.00	600
Westergaard et al. (1998c)	*Macaca mulatta*	Quadrupedal food reaching	28	.25	.71	1,400
Westergaard, Lussier, Suomi, & Higley (2001)[c]	*Macaca mulatta*	Quadrupedal food reaching	27	.33	.67	1,350
Andrews & Rosenblum (1994)[a]	*Macaca radiate*	Joystick task	8	.75	.25	23,444
Fragaszy & Adams-Curtis (1993)[a]	*Macaca fascicularis*	Bimanual actions	4	.00	.25	6,986
Fragaszy & Adams-Curtis (1993)	*Macaca fascicularis*	Pick up objects	4	.75	.00	400
Westergaard (1991)[a]	*Macaca silenus*	Probing	4	.25	.50	227
Holder (1999)[a]	*Cercocebus albigena*	Multiple hand-use measures	13	.38	.31	1,424
Holder (1999)[a]	*Cercopithecus ascanius*	Multiple hand-use measures	16	.38	.44	1,557
Harrison & Byrne (2000)[a]	*Cercopithecus aethiops*	Bimanual actions	24	.00	.00	546

[a] Article was used in the nonreaching task analysis.   [b] Wheat-reaching condition used.   [c] Because there was no table of raw data in this article, data were extra

Table 6

Great and Lesser Apes (Except for Chimpanzees): Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Olson et al. (1990)[a]	*Hylobates lar*	Food reaching	8	.25	.75	2,000	.32	.68
Stafford et al. (1990)	*Hylobate lar*	Food reaching	4	.75	.25	511	.60	.40
Stafford et al. (1990)	*Hylobate syndactylus*	Food reaching	8	.38	.35	1,255	.51	.49
Stafford et al. (1990)	*Hylobate concolor*	Food reaching	7	.43	.14	709	.71	.29
Olson et al. (1990)[a]	*Pongo pygmaeus*	Food reaching	12	.33	.25	1,500	.51	.49
Cunningham et al. (1989)	*Pongo pygmaeus*	Nonfood and food reaching	1			902	.62	.38
Colell et al. (1995a)	*Pongo pygmaeus*	Food reaching	3	.67	.00	315	.63	.37
Hopkins et al. (2003)	*Pongo pygmaeus*	Food reaching	12	.08	.92	1,361	.30	.70
Hopkins (1993)	*Pongo pygmaeus*	Quadrupedal reaching	9	.22	.44	573	.46	.54
Byrne et al. (2001)	*Gorilla gorilla*	Thistle leaf procurement	31	.19	.13	1,418	.53	.47
Olson et al. (1990)[a]	*Gorilla gorilla*	Food reaching	12	.42	.17	1,500	.54	.46
Hopkins et al. (2003)	*Gorilla gorilla*	Food reaching	31	.45	.42	3,055	.52	.48
Fagot & Vauclair (1988)	*Gorilla gorilla*	Food reaching	10	.30	.30	1,203	.50	.50
Holder (1999)[b]	*Gorilla gorilla*	Multiple hand-use measures	6	.50	.5	466	.42	.58
Parnell (2001)[b]	*Gorilla gorilla*	Plant processing	33	.10	.24	1,213	.49	.51

[a] Used floor-retrieval task.   [b] Article was used in the nonreaching task analysis.

Table 7

Chimpanzees: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Jones-Engel & Bard (1996)	*Pan trog.*	Food reaching	13	.08	.23	470	.43	.57
Hopkins et al. (2002)	*Pan trog.*	Food reaching	94	.46	.17	5,003	.56	.44
Hopkins (1995b)	*Pan trog.*	Food reaching	39	.54	.33	1,505	.60	.40
Hopkins (1994)[a]	*Pan trog.*	Bimanual feeding	108	.40	.19	3,368	.56	.44
Hopkins (1993)	*Pan trog.*	Quadrupedal reaching	40	.28	.30	2,721	.49	.51
Boesch (1991)	*Pan trog.*	Food reaching	20	.25	.20	1,133	.46	.54
Finch (1941)[a,b]	*Pan trog.*	Manipulative reaching	30	.37	.47	24,000	.47	.53
Colell et al. (1995a)	*Pan trog.*	Food reaching	31	.48	.32	3,196	.53	.47
Sugiyama et al. (1993)[a]	*Pan trog.*	Nut cracking	11	.55	.37	756	.36	.64
Marchant (1983; from McGrew & Marchant, 1996)	*Pan trog.*	Reaching	26	.38	.42	16,390	.49	.51
Morris et al. (1993)	*Pan trog.*	Reaching	2	.50	.50	379	.53	.47
Fernandez-Carriba & Loeches (2001)[a]	*Pan trog.*	Fruit smearing	10	.57	.00	109	.80	.20
McGrew & Marchant (2001)[a]	*Pan trog.*	Multiple hand-use measures	44	.05	.18	12,838	.49	.51
McGrew & Marchant (1999)[a]	*Pan trog.*	Nut cracking	14	.50	.36	553	.60	.40
McGrew & Marchant (1992)[a]	*Pan trog.*	Termite fishing	15	.33	.40	442	.45	.55
Marchant & McGrew (1996)[a]	*Pan trog.*	Multiple hand-use measures	38	.13	.11	8,345	.51	.49
Holder (1999)[a]	*Pan trog.*	Multiple hand-use measures	20	.40	.45	2,868	.53	.47
Colell et al. (1995a)	*Pan pan.*	Food reaching	2	1.00	.00	134	.75	.25
Hopkins et al. (1993)	*Pan pan.*	Food reaching	11	.27	.10	1,804	.51	.49
Shafer (1997)	*Pan pan.*	Food reaching	14	.57	.21	13,840	.58	.42

Note. trog. = troglodyte; pan. = paniscus.
[a] Article was used in the nonreaching task analysis.   [b] Proportion of right and left subjects based on 80% one-hand use in the article.

Table 3

Prosimians: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Ward (1998)	*Galago moholi*	Food reaching	3	.00	.00	720	.63	.37
Larson et al. (1989)	*Galago senegalensis*	Food reaching	10	.30	.70	4,563	.40	.60
Mason et al. (1995)	*Propithecus verreauxi*	Food reaching	15	.27	.46	1,500	.46	.54
Milliken et al. (1991)	*Otolemur garnetti*	Food reaching	23	.57	.30	4,182	.53	.47
Forsythe & Ward (1988)	*Lemur macaco*	Food reaching	33	.36	.61	3,924	.39	.61
Stafford et al. (1993)[a]	*Hapalemur griseus*	Food reaching	13	.38	.62	1,020	.33	.67
Milliken et al. (1989)	*Lemur catta*	Food reaching	13	.23	.54	520	.37	.63
Forsythe et al. (1988)	*Varecia variegate*	Food reaching	5	.00	.20	517	.46	.54
Feistner et al. (1994)[b]	*Daubentonia madagascariensis*	Hold	11	.00	.27	1,023	.50	.50

[a] Used simple food-reaching task.   [b] Article was used in the nonreaching task analysis.

Table 4
New World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Singer & Schwibbe (1999)	*Callithrix jacchus*	Novel simple reaching	14	.29	.71	444	.33	.67
Box (1977)	*Callithrix jacchus*	Combined 3 reaching tasks	8	.13	.50	2,363	.46	.54
Matoba et al. (1991)	*Callithrix jacchus*	Food reaching	69	.28	.41	3,450	.47	.53
Hook-Costigan & Rogers (1995)	*Callithrix jacchus*	Simple visuospatial reaching	8	.25	.13	1,468	.34	.66
de Sousa et al. (2001)	*Callithrix jacchus*	Food reaching	46	.43	.54	4,600	.48	.52
Singer & Schwibbe (1999)	*Saguinus*	Novel simple reaching	10	.60	.30	352	.60	.40
Diamond & McGrew (1994)	*Saguinus oedipus*	Reaching	20	.95	.00	3,121	.70	.30
Singer & Schwibbe (1999)	*Leontopithecus*	Novel simple reaching	15	.60	.33	585	.64	.36
Westergaard & Suomi (1996b)[a]	*Cebus apella*	Stone striking	10	.70	.10	648	.84	.16
Westergaard et al. (1998b)	*Cebus apella*	Food reaching	35	.29	.11	1,319	.53	.47
Lacreuse & Fragaszy (1996)	*Cebus apella*	Food reaching	17	.24	.24	1,360	.52	.48
Spinozzi & Truppa (2002)[a]	*Cebus apella*	Multicomponent food reaching	2	1.00	.00	200	.85	.15
Spinozzi et al. (1998)	*Cebus apella*	Quadrupedal food reaching	26	.42	.31	2,636	.55	.45
Masataka (1990)	*Cebus apella*	Food reaching	31	.81	.13	3,100	.67	.33
Fragaszy & Mitchell (1990)[b]	*Cebus apella*	Food reaching	7	.14	.43	1,808	.45	.55
Westergaard (1991)[a]	*Cebus apella*	Probing	5	.20	.80	614	.20	.80
Westergaard, Haynie, & Lundquist (1999)[a]	*Cebus apella*	Carry	38	.55	.37	1,601	.56	.44
Westergaard & Suomi (1993b)[a]	*Cebus apella*	Stone striking	8	.50	.38	495	.71	.29
Westergaard, Wagner, & Suomi (1999)	*Cebus albifrons*	Quadrupedal food reaching	8	.38	.75	400	.53	.47
Panger & Wolfe (2000)[a]	*Cebus capucinus*	Carry	25	.08	.04	213	.56	.44

[a] Article was used in the nonreaching task analysis. [b] Feeding condition used.

Table 5
Old World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Holder (1999)[a]	*Colobus badius*	Multiple hand-use measures	30	.47	.40	1,973	.50	.50
Mittra et al. (1997)	*Presbytis entellus*	Retrieve objects	10	.20	.00	1,242	.45	.55
Watanabe & Kawai (1993)[b]	*Macaca fuscata*	Food reaching	80	.20	.48	16,939	.43	.57
Itakura (1992)	*Macaca fuscata*	Food reaching	2	.00	1.00	600	.04	.96
Westergaard et al. (1998c)	*Macaca mulatta*	Quadrupedal food reaching	28	.25	.71	1,400	.35	.65
Westergaard, Lussier, Suomi, & Higley (2001)[c]	*Macaca mulatta*	Quadrupedal food reaching	27	.33	.67	1,350	.38	.62
Andrews & Rosenblum (1994)[a]	*Macaca radiate*	Joystick task	8	.75	.25	23,444	.63	.37
Fragaszy & Adams-Curtis (1993)[a]	*Macaca fascicularis*	Bimanual actions	4	.00	.25	6,986	.47	.53
Fragaszy & Adams-Curtis (1993)	*Macaca fascicularis*	Pick up objects	4	.75	.00	400	.62	.38
Westergaard (1991)[a]	*Macaca silenus*	Probing	4	.25	.50	227	.33	.67
Holder (1999)[a]	*Cercocebus albigena*	Multiple hand-use measures	13	.38	.31	1,424	.53	.47
Holder (1999)[a]	*Cercopithecus ascanius*	Multiple hand-use measures	16	.38	.44	1,557	.47	.53
Harrison & Byrne (2000)[a]	*Cercopithecus aethiops*	Bimanual actions	24	.00	.00	546	.46	.54

[a] Article was used in the nonreaching task analysis. [b] Wheat-reaching condition used. [c] Because there was no table of raw data in this article, data were extrapolated from a graph in the article.

Table 6

Great and Lesser Apes (Except for Chimpanzees): Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Olson et al. (1990)[a]	*Hylobates lar*	Food reaching	8	.25	.75	2,000	.32	.68
Stafford et al. (1990)	*Hylobate lar*	Food reaching	4	.75	.25	511	.60	.40
Stafford et al. (1990)	*Hylobate syndactylus*	Food reaching	8	.38	.35	1,255	.51	.49
Stafford et al. (1990)	*Hylobate concolor*	Food reaching	7	.43	.14	709	.71	.29
Olson et al. (1990)[a]	*Pongo pygmaeus*	Food reaching	12	.33	.25	1,500	.51	.49
Cunningham et al. (1989)	*Pongo pygmaeus*	Nonfood and food reaching	1			902	.62	.38
Colell et al. (1995a)	*Pongo pygmaeus*	Food reaching	3	.67	.00	315	.63	.37
Hopkins et al. (2003)	*Pongo pygmaeus*	Food reaching	12	.08	.92	1,361	.30	.70
Hopkins (1993)	*Pongo pygmaeus*	Quadrupedal reaching	9	.22	.44	573	.46	.54
Byrne et al. (2001)	*Gorilla gorilla*	Thistle leaf procurement	31	.19	.13	1,418	.53	.47
Olson et al. (1990)[a]	*Gorilla gorilla*	Food reaching	12	.42	.17	1,500	.54	.46
Hopkins et al. (2003)	*Gorilla gorilla*	Food reaching	31	.45	.42	3,055	.52	.48
Fagot & Vauclair (1988)	*Gorilla gorilla*	Food reaching	10	.30	.30	1,203	.50	.50
Holder (1999)[b]	*Gorilla gorilla*	Multiple hand-use measures	6	.50	.5	466	.42	.58
Parnell (2001)[b]	*Gorilla gorilla*	Plant processing	33	.10	.24	1,213	.49	.51

[a] Used floor-retrieval task.   [b] Article was used in the nonreaching task analysis.

Table 7

Chimpanzees: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Jones-Engel & Bard (1996)	*Pan trog.*	Food reaching	13	.08	.23	470	.43	.57
Hopkins et al. (2002)	*Pan trog.*	Food reaching	94	.46	.17	5,003	.56	.44
Hopkins (1995b)	*Pan trog.*	Food reaching	39	.54	.33	1,505	.60	.40
Hopkins (1994)[a]	*Pan trog.*	Bimanual feeding	108	.40	.19	3,368	.56	.44
Hopkins (1993)	*Pan trog.*	Quadrupedal reaching	40	.28	.30	2,721	.49	.51
Boesch (1991)	*Pan trog.*	Food reaching	20	.25	.20	1,133	.46	.54
Finch (1941)[a,b]	*Pan trog.*	Manipulative reaching	30	.37	.47	24,000	.47	.53
Colell et al. (1995a)	*Pan trog.*	Food reaching	31	.48	.32	3,196	.53	.47
Sugiyama et al. (1993)[a]	*Pan trog.*	Nut cracking	11	.55	.37	756	.36	.64
Marchant (1983; from McGrew & Marchant, 1996)	*Pan trog.*	Reaching	26	.38	.42	16,390	.49	.51
Morris et al. (1993)	*Pan trog.*	Reaching	2	.50	.50	379	.53	.47
Fernandez-Carriba & Loeches (2001)[a]	*Pan trog.*	Fruit smearing	10	.57	.00	109	.80	.20
McGrew & Marchant (2001)[a]	*Pan trog.*	Multiple hand-use measures	44	.05	.18	12,838	.49	.51
McGrew & Marchant (1999)[a]	*Pan trog.*	Nut cracking	14	.50	.36	553	.60	.40
McGrew & Marchant (1992)[a]	*Pan trog.*	Termite fishing	15	.33	.40	442	.45	.55
Marchant & McGrew (1996)[a]	*Pan trog.*	Multiple hand-use measures	38	.13	.11	8,345	.51	.49
Holder (1999)[a]	*Pan trog.*	Multiple hand-use measures	20	.40	.45	2,868	.53	.47
Colell et al. (1995a)	*Pan pan.*	Food reaching	2	1.00	.00	134	.75	.25
Hopkins et al. (1993)	*Pan pan.*	Food reaching	11	.27	.10	1,804	.51	.49
Shafer (1997)	*Pan pan.*	Food reaching	14	.57	.21	13,840	.58	.42

Note. trog. = troglodyte; pan. = paniscus.
[a] Article was used in the nonreaching task analysis.   [b] Proportion of right and left subjects based on 80% one-hand use in the article.

Table 8 shows the results of the mixed-model analysis when handedness was assessed by any hand-use measure (i.e., reaching, tool use, haptic searching, as reported in 62 articles). The prosimian species showed a significant population bias toward the preferred use of the left hand (.60, p =.01). However, Table 8 shows that the proportion of individuals (.48) with statistically significant left-hand use preferences (defined as $z < -1.65$) was not that much different from the proportion (.40) with significant right-hand use preferences (defined as $z > 1.65$). It should be noted that the last two columns (proportion left- and right-hand subjects) in Tables 8–11 are simply an aggregate of the number of left- and right-handed subjects as defined by the z score and as reported in each of the articles used. These z scores were not used in the mixed-model analysis. The Old World monkeys also showed a significant left-hand bias with an average of.61 with a left-hand use (p <.0001). However, the

proportion of individuals (.44) with significant left-hand use preference (as defined by z) was nearly twice as large as the proportion (.23) with significant right-hand use preference. New World monkeys (p =.07), lesser apes (p =.99), and greater apes (p =.06) did not show a significant population bias for the preferred use of one hand. In addition, subject variability, as tested by the mixed-model approach, was also significant (p <.0001), suggesting a great deal of individual variability of handedness for all primate species (see Table 8).

Table 8
Proportion of Preferred Left-Hand Use

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
			Complete handedness			
Fixed effects						
Prosimian	**0.39**	**.16**	**.01**	**.60**	.48	.40
New World monkey	−0.17	.09	.07	.46	.35	.46
Old World monkey	**0.43**	**.11**	**< .0001**	**.61**	.44	.23
Lesser ape	−0.02	.34	.96	.50	.44	.44
Greater ape	−0.12	.07	.06	.47	.28	.37
Random effect						
Subject variability	**1.72**	**.04**	**< .0001**			
			Reach handedness			
Fixed effects						
Prosimian	**0.43**	**.16**	**.01**	**.61**	.50	.42
New World monkey	−0.12	.10	.22	.47	.36	.44
Old World monkey	**0.66**	**.14**	**< .0001**	**.66**	.52	.17
Lesser ape	−0.02	.33	.96	.50	.44	.44
Greater ape	−0.12	.09	.16	.47	.28	.40
Random effect						
Subject variability	**1.70**	**.05**	**< .0001**			
			Nonreaching			
Fixed effects						
Prosimian	−0.08	.55	.89	.48	.50	.42
New World monkey	−0.37	.22	.09	.41	.32	.54
Old World monkey	0.08	.18	.65	.52	.32	.32
Greater ape	−0.13	.10	.19	.47	.27	.33
Random effect						
Subject variability	**1.76**	**.07**	**< .0001**			

Note. Boldface indicates that results are significant at *p* < .05.

Table 9
Reach Handedness Data

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
			Prosimian			
Fixed effects						
Galago	0.05	.39	.89	.51	.39	.61
Lemur	**0.76**	**.30**	**.01**	**.68**	.58	.31
Sifaka	0.30	.61	.62	.58	.47	.40
Random effect						
Subject variability	**2.34**	**.19**	**< .0001**			
			Old World monkey			
Fixed effects						
Japanese macaque	**0.68**	**.16**	**< .0001**	**.66**	.52	.21
Rhesus macaque	**0.74**	**.20**	**< .01**	**.68**	.58	.11
C. Macaque	−0.53	.73	.47	.37	.00	.75
Langur	0.23	.46	.62	.56	.30	.00
Random effect						
Subject variability	**1.44**	**.10**	**< .0001**			
			New World monkey			
Fixed effects						
Capuchin	−0.33	.18	.07	.42	.23	.44
Tamarin	**−0.90**	**.31**	**< .01**	**.29**	.18	.76
Marmoset	0.30	.17	.08	.58	.52	.34
Random effect						
Subject variability	**1.99**	**.10**	**< .0001**			

Note. Boldface indicates that results are significant at $p < .05$.

Table 10
Great Apes Reach Handedness Data

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
Fixed effects						
Orangutan	0.36	.21	.08	.59	.46	.27
Gorilla	−0.12	.14	.38	.47	.30	.42
Chimpanzee	**−0.16**	**.08**	**.04**	**.46**	.27	.41
Bonobo	−0.31	.24	.19	.42	.11	.48
Random effect						
Subject variability	**1.22**	**.05**	**< .0001**			

Note. Boldface indicates that results are significant at $p < .05$.

Table 11
Nonreaching Handedness Data

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
			Old World monkeys			
Fixed effects						
Vervet monkey	0.12	.25	.63	.53	.04	.00
Red-tailed monkey	0.09	.27	.74	.52	.44	.38
Red colobus monkey	−0.01	.20	.96	.50	.40	.47
Lion-tailed macaque	**2.11**	**.65**	**< .01**	**.89**	.50	.25
Crab-eating macaque	0.13	.53	.81	.53	.75	.00
Bonnet macaque	−0.47	.38	.22	.39	.25	.75
Grey-cheeked mangabey	−0.08	.30	.78	.48	.38	.38
Random effect						
Subject variability	**1.06**	**.08**	**< .0001**			
			Great apes			
Fixed effects						
Gorilla	0.19	.28	.49	.55	.33	.21
Chimpanzee	−0.17	.10	.09	.46	.26	.34
Random effect						
Subject variability	**1.68**	**.08**	**< .0001**			

Note. Boldface indicates that results are significant at *p* < .05.

Mixed-Model Analysis—Reaching Data

Because the POT hypothesizes specifically about hand preferences for reaching, we conducted an analysis of hand preference on the individuals that performed reaching tasks as reported in 42 articles. Again, the different primate species used for the analysis of reaching data are presented in Tables 3 through 7. Table 8 shows the results of the analysis of reaching. Prosimians showed a significant population bias toward left-hand preference with an average left-hand use of .61 (p <.01). However, the proportion of individuals who exhibited significant left-hand use preference (.50) was not that strikingly different from the proportion that exhibited a significant right-hand use preference (.42).

Table 3
Prosimians: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Ward (1998)	*Galago moholi*	Food reaching	3	.00	.00	720	.63	.37
Larson et al. (1989)	*Galago senegalensis*	Food reaching	10	.30	.70	4,563	.40	.60
Mason et al. (1995)	*Propithecus verreauxi*	Food reaching	15	.27	.46	1,500	.46	.54
Milliken et al. (1991)	*Otolemur garnetti*	Food reaching	23	.57	.30	4,182	.53	.47
Forsythe & Ward (1988)	*Lemur macaco*	Food reaching	33	.36	.61	3,924	.39	.61
Stafford et al. (1993)[a]	*Hapalemur griseus*	Food reaching	13	.38	.62	1,020	.33	.67
Milliken et al. (1989)	*Lemur catta*	Food reaching	13	.23	.54	520	.37	.63
Forsythe et al. (1988)	*Varecia variegate*	Food reaching	5	.00	.20	517	.46	.54
Feistner et al. (1994)[b]	*Daubentonia madagascariensis*	Hold	11	.00	.27	1,023	.50	.50

[a] Used simple food-reaching task. [b] Article was used in the nonreaching task analysis.

Table 4
New World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Singer & Schwibbe (1999)	*Callithrix jacchus*	Novel simple reaching	14	.29	.71	444	.33	.67
Box (1977)	*Callithrix jacchus*	Combined 3 reaching tasks	8	.13	.50	2,363	.46	.54
Matoba et al. (1991)	*Callithrix jacchus*	Food reaching	69	.28	.41	3,450	.47	.53
Hook-Costigan & Rogers (1995)	*Callithrix jacchus*	Simple visuospatial reaching	8	.25	.13	1,468	.34	.66
de Sousa et al. (2001)	*Callithrix jacchus*	Food reaching	46	.43	.54	4,600	.48	.52
Singer & Schwibbe (1999)	*Saguinus*	Novel simple reaching	10	.60	.30	352	.60	.40
Diamond & McGrew (1994)	*Saguinus oedipus*	Reaching	20	.95	.00	3,121	.70	.30
Singer & Schwibbe (1999)	*Leontopithecus*	Novel simple reaching	15	.60	.33	585	.64	.36
Westergaard & Suomi (1996b)[a]	*Cebus apella*	Stone striking	10	.70	.10	648	.84	.16
Westergaard et al. (1998b)	*Cebus apella*	Food reaching	35	.29	.11	1,319	.53	.47
Lacreuse & Fragaszy (1996)	*Cebus apella*	Food reaching	17	.24	.24	1,360	.52	.48
Spinozzi & Truppa (2002)[a]	*Cebus apella*	Multicomponent food reaching	2	1.00	.00	200	.85	.15
Spinozzi et al. (1998)	*Cebus apella*	Quadrupedal food reaching	26	.42	.31	2,636	.55	.45
Masataka (1990)	*Cebus apella*	Food reaching	31	.81	.13	3,100	.67	.33
Fragaszy & Mitchell (1990)[b]	*Cebus apella*	Food reaching	7	.14	.43	1,808	.45	.55
Westergaard (1991)[a]	*Cebus apella*	Probing	5	.20	.80	614	.20	.80
Westergaard, Haynie, & Lundquist (1999)[a]	*Cebus apella*	Carry	38	.55	.37	1,601	.56	.44
Westergaard & Suomi (1993b)[a]	*Cebus apella*	Stone striking	8	.50	.38	495	.71	.29
Westergaard, Wagner, & Suomi (1999)	*Cebus albifrons*	Quadrupedal food reaching	8	.38	.75	400	.53	.47
Panger & Wolfe (2000)[a]	*Cebus capucinus*	Carry	25	.08	.04	213	.56	.44

[a] Article was used in the nonreaching task analysis.　　[b] Feeding condition used.

Table 5
Old World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Holder (1999)[a]	*Colobus badius*	Multiple hand-use measures	30	.47	.40	1,973	.50	.50
Mittra et al. (1997)	*Presbytis entellus*	Retrieve objects	10	.20	.00	1,242	.45	.55
Watanabe & Kawai (1993)[b]	*Macaca fuscata*	Food reaching	80	.20	.48	16,939	.43	.57
Itakura (1992)	*Macaca fuscata*	Food reaching	2	.00	1.00	600	.04	.96
Westergaard et al. (1998c)	*Macaca mulatta*	Quadrupedal food reaching	28	.25	.71	1,400	.35	.65
Westergaard, Lussier, Suomi, & Higley (2001)[c]	*Macaca mulatta*	Quadrupedal food reaching	27	.33	.67	1,350	.38	.62
Andrews & Rosenblum (1994)[a]	*Macaca radiate*	Joystick task	8	.75	.25	23,444	.63	.37
Fragaszy & Adams-Curtis (1993)[a]	*Macaca fascicularis*	Bimanual actions	4	.00	.25	6,986	.47	.53
Fragaszy & Adams-Curtis (1993)	*Macaca fascicularis*	Pick up objects	4	.75	.00	400	.62	.38
Westergaard (1991)[a]	*Macaca silenus*	Probing	4	.25	.50	227	.33	.67
Holder (1999)[a]	*Cercocebus albigena*	Multiple hand-use measures	13	.38	.31	1,424	.53	.47
Holder (1999)[a]	*Cercopithecus ascanius*	Multiple hand-use measures	16	.38	.44	1,557	.47	.53
Harrison & Byrne (2000)[a]	*Cercopithecus aethiops*	Bimanual actions	24	.00	.00	546	.46	.54

[a] Article was used in the nonreaching task analysis.　　[b] Wheat-reaching condition used.　　[c] Because there was no table of raw data in this article, data were extrapolated from a graph in the article.

Table 6

Great and Lesser Apes (Except for Chimpanzees): Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Olson et al. (1990)[a]	*Hylobates lar*	Food reaching	8	.25	.75	2,000	.32	.68
Stafford et al. (1990)	*Hylobate lar*	Food reaching	4	.75	.25	511	.60	.40
Stafford et al. (1990)	*Hylobate syndactylus*	Food reaching	8	.38	.35	1,255	.51	.49
Stafford et al. (1990)	*Hylobate concolor*	Food reaching	7	.43	.14	709	.71	.29
Olson et al. (1990)[a]	*Pongo pygmaeus*	Food reaching	12	.33	.25	1,500	.51	.49
Cunningham et al. (1989)	*Pongo pygmaeus*	Nonfood and food reaching	1			902	.62	.38
Colell et al. (1995a)	*Pongo pygmaeus*	Food reaching	3	.67	.00	315	.63	.37
Hopkins et al. (2003)	*Pongo pygmaeus*	Food reaching	12	.08	.92	1,361	.30	.70
Hopkins (1993)	*Pongo pygmaeus*	Quadrupedal reaching	9	.22	.44	573	.46	.54
Byrne et al. (2001)	*Gorilla gorilla*	Thistle leaf procurement	31	.19	.13	1,418	.53	.47
Olson et al. (1990)[a]	*Gorilla gorilla*	Food reaching	12	.42	.17	1,500	.54	.46
Hopkins et al. (2003)	*Gorilla gorilla*	Food reaching	31	.45	.42	3,055	.52	.48
Fagot & Vauclair (1988)	*Gorilla gorilla*	Food reaching	10	.30	.30	1,203	.50	.50
Holder (1999)[b]	*Gorilla gorilla*	Multiple hand-use measures	6	.50	.5	466	.42	.58
Parnell (2001)[b]	*Gorilla gorilla*	Plant processing	33	.10	.24	1,213	.49	.51

[a] Used floor-retrieval task.   [b] Article was used in the nonreaching task analysis.

Table 7

Chimpanzees: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Jones-Engel & Bard (1996)	*Pan trog.*	Food reaching	13	.08	.23	470	.43	.57
Hopkins et al. (2002)	*Pan trog.*	Food reaching	94	.46	.17	5,003	.56	.44
Hopkins (1995b)	*Pan trog.*	Food reaching	39	.54	.33	1,505	.60	.40
Hopkins (1994)[a]	*Pan trog.*	Bimanual feeding	108	.40	.19	3,368	.56	.44
Hopkins (1993)	*Pan trog.*	Quadrupedal reaching	40	.28	.30	2,721	.49	.51
Boesch (1991)	*Pan trog.*	Food reaching	20	.25	.20	1,133	.46	.54
Finch (1941)[a,b]	*Pan trog.*	Manipulative reaching	30	.37	.47	24,000	.47	.53
Colell et al. (1995a)	*Pan trog.*	Food reaching	31	.48	.32	3,196	.53	.47
Sugiyama et al. (1993)[a]	*Pan trog.*	Nut cracking	11	.55	.37	756	.36	.64
Marchant (1983; from McGrew & Marchant, 1996)	*Pan trog.*	Reaching	26	.38	.42	16,390	.49	.51
Morris et al. (1993)	*Pan trog.*	Reaching	2	.50	.50	379	.53	.47
Fernandez-Carriba & Loeches (2001)[a]	*Pan trog.*	Fruit smearing	10	.57	.00	109	.80	.20
McGrew & Marchant (2001)[a]	*Pan trog.*	Multiple hand-use measures	44	.05	.18	12,838	.49	.51
McGrew & Marchant (1999)[a]	*Pan trog.*	Nut cracking	14	.50	.36	553	.60	.40
McGrew & Marchant (1992)[a]	*Pan trog.*	Termite fishing	15	.33	.40	442	.45	.55
Marchant & McGrew (1996)[a]	*Pan trog.*	Multiple hand-use measures	38	.13	.11	8,345	.51	.49
Holder (1999)[a]	*Pan trog.*	Multiple hand-use measures	20	.40	.45	2,868	.53	.47
Colell et al. (1995a)	*Pan pan.*	Food reaching	2	1.00	.00	134	.75	.25
Hopkins et al. (1993)	*Pan pan.*	Food reaching	11	.27	.10	1,804	.51	.49
Shafer (1997)	*Pan pan.*	Food reaching	14	.57	.21	13,840	.58	.42

Note. trog. = troglodyte; pan. = paniscus.
[a] Article was used in the nonreaching task analysis.   [b] Proportion of right and left subjects based on 80% one-hand use in the article.

Old World monkeys also were skewed significantly toward left-hand use with an average of .66 using their left hand more than their right (p <.0001). In contrast to the prosimians, the proportion of Old World monkeys with significant left-hand use (.52) was three times larger than the proportion with significant right-hand use (.17). New World monkeys, lesser apes, and greater apes did not show a significant bias in hand use for reaching. As in the analysis of general handedness, subject variability was significant (p <.0001). Given the relatively small sample sizes and the relatively large variety of tasks used to assess simple reaching, it is not possible to model the amount of individual variability that is due to differences in task, age, and species. Nevertheless, the highly significant amount of variability associated with individuals indicates that these and other factors contribute more to differential hand use than does gross taxonomic grouping.

Because the POT assumes an evolutionary gradation of reaching hand preference over time, we tested the regression coefficients of prosimians, New World monkeys, and Old World monkeys for differences. A significant difference between prosimians and New World monkeys was found, (p =.004), as well as between New World monkeys and Old World monkeys (p <.001). No difference was found between the regression coefficients of prosimians and Old World monkeys. Also, the differences observed do not reflect the type of gradation predicted by POT or any other notion about the relation between primate evolution and suborder taxonomic groupings.

We conducted another analysis to discern whether any particular taxonomic group was responsible for the results for that primate suborder. Of the three taxonomic groups of prosimian data (see Table 9), only lemurs showed a significant bias toward the left-hand preference (p =.01), with an average of.68 preferring to use the left hand and nearly twice as many exhibiting a statistically significant classification (as defined by z) of left-hand preferring (.58) as compared with a classification of significant right-hand preferring (.31). Of the four taxonomic groups of Old World monkeys, both Japanese (p =.0001) and rhesus macaques (p <.0003) were responsible for the left-hand bias in hand-use preference, with an average of.68 and.66 respectively preferring to use the left hand. More than twice as many Japanese macaques exhibited a significant classification as left-hand preferring (.52) compared with a significant classification as right-hand preferring (.21). For rhesus macaques, the proportion with a significant left-hand preference classification (.58) was more than five times greater than the proportion with a significant right-hand preference classification (.11).

Table 9
Reach Handedness Data

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
			Prosimian			
Fixed effects						
Galago	0.05	.39	.89	.51	.39	.61
Lemur	**0.76**	**.30**	**.01**	**.68**	**.58**	**.31**
Sifaka	0.30	.61	.62	.58	.47	.40
Random effect						
Subject variability	**2.34**	**.19**	**< .0001**			
			Old World monkey			
Fixed effects						
Japanese macaque	**0.68**	**.16**	**< .0001**	**.66**	**.52**	**.21**
Rhesus macaque	**0.74**	**.20**	**< .01**	**.68**	**.58**	**.11**
C. Macaque	−0.53	.73	.47	.37	.00	.75
Langur	0.23	.46	.62	.56	.30	.00
Random effect						
Subject variability	**1.44**	**.10**	**< .0001**			
			New World monkey			
Fixed effects						
Capuchin	−0.33	.18	.07	.42	.23	.44
Tamarin	**−0.90**	**.31**	**< .01**	**.29**	**.18**	**.76**
Marmoset	0.30	.17	.08	.58	.52	.34
Random effect						
Subject variability	**1.99**	**.10**	**< .0001**			

Note. Boldface indicates that results are significant at p < .05.

These more specific analyses of smaller taxonomic groups were applied also to those primate suborders that did not exhibit an overall significant bias. Of the New World monkey species, only tamarins exhibited a significant reaching bias (.71, p =.004) for right-hand preference. The proportion that exhibited a significant right-hand

preference (.76) was more than four times greater than the proportion that exhibited a significant left-hand preference (.18). Of the great ape species (see Table 10), only chimpanzees exhibited a significant population bias (.54, p =.04) for right-hand preference. However, unlike humans, the proportion with a statistically significant right-hand preference for reaching (.41) was not greater than.50 of the population. Of the lesser apes, all were gibbons and the sample size was too small for further evaluation. Note, however, that subject variability was significant beyond the p =.0001 level for each of these more specific analyses.

Table 10
Great Apes Reach Handedness Data

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
Fixed effects						
Orangutan	0.36	.21	.08	.59	.46	.27
Gorilla	−0.12	.14	.38	.47	.30	.42
Chimpanzee	**−0.16**	**.08**	**.04**	**.46**	.27	.41
Bonobo	−0.31	.24	.19	.42	.11	.48
Random effect						
Subject variability	**1.22**	**.05**	**< .0001**			

Note. Boldface indicates that results are significant at *p* < .05.

Mixed-Model Analysis—Nonreaching Handedness Data

The distribution of different primate types within the suborders that provided data for the analysis of the hand-use preference for nonreaching actions are presented in bold in Tables 3 through 7. Table 8 shows the results of the analysis of hand preference for nonreaching actions. None of the primate suborders showed a significant bias toward either the left or the right hand. Only individual variability was significant (p <.0001). Of course, the sample sizes are much smaller for this analysis. For example, only one taxonomic group of prosimian provided data, and for New World monkeys, the sample size imbalance between two types of capuchin monkey prevented further analysis.

Table 3
Prosimians: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Ward (1998)	*Galago moholi*	Food reaching	3	.00	.00	720	.63	.37
Larson et al. (1989)	*Galago senegalensis*	Food reaching	10	.30	.70	4,563	.40	.60
Mason et al. (1995)	*Propithecus verreauxi*	Food reaching	15	.27	.46	1,500	.46	.54
Milliken et al. (1991)	*Otolemur garnetti*	Food reaching	23	.57	.30	4,182	.53	.47
Forsythe & Ward (1988)	*Lemur macaco*	Food reaching	33	.36	.61	3,924	.39	.61
Stafford et al. (1993)[a]	*Hapalemur griseus*	Food reaching	13	.38	.62	1,020	.33	.67
Milliken et al. (1989)	*Lemur catta*	Food reaching	13	.23	.54	520	.37	.63
Forsythe et al. (1988)	*Varecia variegate*	Food reaching	5	.00	.20	517	.46	.54
Feistner et al. (1994)[b]	*Daubentonia madagascariensis*	Hold	11	.00	.27	1,023	.50	.50

[a] Used simple food-reaching task.   [b] Article was used in the nonreaching task analysis.

Table 4

New World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Singer & Schwibbe (1999)	*Callithrix jacchus*	Novel simple reaching	14	.29	.71	444	.33	.67
Box (1977)	*Callithrix jacchus*	Combined 3 reaching tasks	8	.13	.50	2,363	.46	.54
Matoba et al. (1991)	*Callithrix jacchus*	Food reaching	69	.28	.41	3,450	.47	.53
Hook-Costigan & Rogers (1995)	*Callithrix jacchus*	Simple visuospatial reaching	8	.25	.13	1,468	.34	.66
de Sousa et al. (2001)	*Callithrix jacchus*	Food reaching	46	.43	.54	4,600	.48	.52
Singer & Schwibbe (1999)	*Saguinus*	Novel simple reaching	10	.60	.30	352	.60	.40
Diamond & McGrew (1994)	*Saguinus oedipus*	Reaching	20	.95	.00	3,121	.70	.30
Singer & Schwibbe (1999)	*Leontopithecus*	Novel simple reaching	15	.60	.33	585	.64	.36
Westergaard & Suomi (1996b)[a]	*Cebus apella*	Stone striking	10	.70	.10	648	.84	.16
Westergaard et al. (1998b)	*Cebus apella*	Food reaching	35	.29	.11	1,319	.53	.47
Lacreuse & Fragaszy (1996)	*Cebus apella*	Food reaching	17	.24	.24	1,360	.52	.48
Spinozzi & Truppa (2002)[a]	*Cebus apella*	Multicomponent food reaching	2	1.00	.00	200	.85	.15
Spinozzi et al. (1998)	*Cebus apella*	Quadrupedal food reaching	26	.42	.31	2,636	.55	.45
Masataka (1990)	*Cebus apella*	Food reaching	31	.81	.13	3,100	.67	.33
Fragaszy & Mitchell (1990)[b]	*Cebus apella*	Food reaching	7	.14	.43	1,808	.45	.55
Westergaard (1991)[a]	*Cebus apella*	Probing	5	.20	.80	614	.20	.80
Westergaard, Haynie, & Lundquist (1999)[a]	*Cebus apella*	Carry	38	.55	.37	1,601	.56	.44
Westergaard & Suomi (1993b)[a]	*Cebus apella*	Stone striking	8	.50	.38	495	.71	.29
Westergaard, Wagner, & Suomi (1999)	*Cebus albifrons*	Quadrupedal food reaching	8	.38	.75	400	.53	.47
Panger & Wolfe (2000)[a]	*Cebus capucinus*	Carry	25	.08	.04	213	.56	.44

[a] Article was used in the nonreaching task analysis.   [b] Feeding condition used.

Table 5

Old World Monkeys: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Holder (1999)[a]	*Colobus badius*	Multiple hand-use measures	30	.47	.40	1,973	.50	.50
Mittra et al. (1997)	*Presbytis entellus*	Retrieve objects	10	.20	.00	1,242	.45	.55
Watanabe & Kawai (1993)[b]	*Macaca fuscata*	Food reaching	80	.20	.48	16,939	.43	.57
Itakura (1992)	*Macaca fuscata*	Food reaching	2	.00	1.00	600	.04	.96
Westergaard et al. (1998c)	*Macaca mulatta*	Quadrupedal food reaching	28	.25	.71	1,400	.35	.65
Westergaard, Lussier, Suomi, & Higley (2001)[c]	*Macaca mulatta*	Quadrupedal food reaching	27	.33	.67	1,350	.38	.62
Andrews & Rosenblum (1994)[a]	*Macaca radiate*	Joystick task	8	.75	.25	23,444	.63	.37
Fragaszy & Adams-Curtis (1993)[a]	*Macaca fascicularis*	Bimanual actions	4	.00	.25	6,986	.47	.53
Fragaszy & Adams-Curtis (1993)	*Macaca fascicularis*	Pick up objects	4	.75	.00	400	.62	.38
Westergaard (1991)[a]	*Macaca silenus*	Probing	4	.25	.50	227	.33	.67
Holder (1999)[a]	*Cercocebus albigena*	Multiple hand-use measures	13	.38	.31	1,424	.53	.47
Holder (1999)[a]	*Cercopithecus ascanius*	Multiple hand-use measures	16	.38	.44	1,557	.47	.53
Harrison & Byrne (2000)[a]	*Cercopithecus aethiops*	Bimanual actions	24	.00	.00	546	.46	.54

[a] Article was used in the nonreaching task analysis.   [b] Wheat-reaching condition used.   [c] Because there was no table of raw data in this article, data were extrapolated from a graph in the article.

Table 6

Great and Lesser Apes (Except for Chimpanzees): Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Olson et al. (1990)[a]	*Hylobates lar*	Food reaching	8	.25	.75	2,000	.32	.68
Stafford et al. (1990)	*Hylobate lar*	Food reaching	4	.75	.25	511	.60	.40
Stafford et al. (1990)	*Hylobate syndactylus*	Food reaching	8	.38	.35	1,255	.51	.49
Stafford et al. (1990)	*Hylobate concolor*	Food reaching	7	.43	.14	709	.71	.29
Olson et al. (1990)[a]	*Pongo pygmaeus*	Food reaching	12	.33	.25	1,500	.51	.49
Cunningham et al. (1989)	*Pongo pygmaeus*	Nonfood and food reaching	1			902	.62	.38
Colell et al. (1995a)	*Pongo pygmaeus*	Food reaching	3	.67	.00	315	.63	.37
Hopkins et al. (2003)	*Pongo pygmaeus*	Food reaching	12	.08	.92	1,361	.30	.70
Hopkins (1993)	*Pongo pygmaeus*	Quadrupedal reaching	9	.22	.44	573	.46	.54
Byrne et al. (2001)	*Gorilla gorilla*	Thistle leaf procurement	31	.19	.13	1,418	.53	.47
Olson et al. (1990)[a]	*Gorilla gorilla*	Food reaching	12	.42	.17	1,500	.54	.46
Hopkins et al. (2003)	*Gorilla gorilla*	Food reaching	31	.45	.42	3,055	.52	.48
Fagot & Vauclair (1988)	*Gorilla gorilla*	Food reaching	10	.30	.30	1,203	.50	.50
Holder (1999)[b]	*Gorilla gorilla*	Multiple hand-use measures	6	.50	.5	466	.42	.58
Parnell (2001)[b]	*Gorilla gorilla*	Plant processing	33	.10	.24	1,213	.49	.51

[a] Used floor-retrieval task.   [b] Article was used in the nonreaching task analysis.

Table 7

Chimpanzees: Distribution of Hand Preference and Task Used in Meta-Analysis

Source	Species	Task	N	Proportion right-handed subjects	Proportion left-handed subjects	Total actions	Proportion right reaches	Proportion left reaches
Jones-Engel & Bard (1996)	*Pan trog.*	Food reaching	13	.08	.23	470	.43	.57
Hopkins et al. (2002)	*Pan trog.*	Food reaching	94	.46	.17	5,003	.56	.44
Hopkins (1995b)	*Pan trog.*	Food reaching	39	.54	.33	1,505	.60	.40
Hopkins (1994)[a]	*Pan trog.*	Bimanual feeding	108	.40	.19	3,368	.56	.44
Hopkins (1993)	*Pan trog.*	Quadrupedal reaching	40	.28	.30	2,721	.49	.51
Boesch (1991)	*Pan trog.*	Food reaching	20	.25	.20	1,133	.46	.54
Finch (1941)[a,b]	*Pan trog.*	Manipulative reaching	30	.37	.47	24,000	.47	.53
Colell et al. (1995a)	*Pan trog.*	Food reaching	31	.48	.32	3,196	.53	.47
Sugiyama et al. (1993)[a]	*Pan trog.*	Nut cracking	11	.55	.37	756	.36	.64
Marchant (1983; from McGrew & Marchant, 1996)	*Pan trog.*	Reaching	26	.38	.42	16,390	.49	.51
Morris et al. (1993)	*Pan trog.*	Reaching	2	.50	.50	379	.53	.47
Fernandez-Carriba & Loeches (2001)[a]	*Pan trog.*	Fruit smearing	10	.57	.00	109	.80	.20
McGrew & Marchant (2001)[a]	*Pan trog.*	Multiple hand-use measures	44	.05	.18	12,838	.49	.51
McGrew & Marchant (1999)[a]	*Pan trog.*	Nut cracking	14	.50	.36	553	.60	.40
McGrew & Marchant (1992)[a]	*Pan trog.*	Termite fishing	15	.33	.40	442	.45	.55
Marchant & McGrew (1996)[a]	*Pan trog.*	Multiple hand-use measures	38	.13	.11	8,345	.51	.49
Holder (1999)[a]	*Pan trog.*	Multiple hand-use measures	20	.40	.45	2,868	.53	.47
Colell et al. (1995a)	*Pan pan.*	Food reaching	2	1.00	.00	134	.75	.25
Hopkins et al. (1993)	*Pan pan.*	Food reaching	11	.27	.10	1,804	.51	.49
Shafer (1997)	*Pan pan.*	Food reaching	14	.57	.21	13,840	.58	.42

Note. trog. = troglodyte; pan. = paniscus.
[a] Article was used in the nonreaching task analysis.   [b] Proportion of right and left subjects based on 80% one-hand use in the article.

The analysis of specific taxonomic groups of Old World monkeys (see Table 11) indicated that only lion-tailed macaques showed a significant left-hand population bias (.89, p =.002) for nonreaching tasks. However, population-level generalizations cannot be made confidently because there were only 4 lion-tailed macaques included in the analysis. Analysis of the greater apes did not show any significant population bias for either of the two taxonomic groups of ape. Again, subject variability was significant for all of these analyses (p <.0001).

Table 11
Nonreaching Handedness Data

Test and parameter	Estimate	SE	p	Proportion left-hand use	Proportion left-handed subjects	Proportion right-handed subjects
			Old World monkeys			
Fixed effects						
Vervet monkey	0.12	.25	.63	.53	.04	.00
Red-tailed monkey	0.09	.27	.74	.52	.44	.38
Red colobus monkey	−0.01	.20	.96	.50	.40	.47
Lion-tailed macaque	**2.11**	**.65**	**< .01**	**.89**	.50	.25
Crab-eating macaque	0.13	.53	.81	.53	.75	.00
Bonnet macaque	−0.47	.38	.22	.39	.25	.75
Grey-cheeked mangabey	−0.08	.30	.78	.48	.38	.38
Random effect						
Subject variability	**1.06**	**.08**	**< .0001**			
			Great apes			
Fixed effects						
Gorilla	0.19	.28	.49	.55	.33	.21
Chimpanzee	−0.17	.10	.09	.46	.26	.34
Random effect						
Subject variability	**1.68**	**.08**	**< .0001**			

Note. Boldface indicates that results are significant at $p < .05$.

Discussion

The nonstatistical review of the literature found, at best, conflicting support for a population bias in handedness for any of the suborders of primates. For all handedness tasks, more articles reported no population-level bias than either a left- or a right-hand bias in hand preference. Moreover, the number of studies that reported a left-versus a right-hand bias was not different. Therefore, as reported in McGrew and Marchant (1997) and in contrast to the MacNeilage et al. (1987) conclusion, reviewing the published research does not reveal any evidence that different primate suborders show a population bias toward either right- or left-handedness. However, by using a systematic meta-analysis that incorporated individual variability into the model rather than in the error term of the calculations, our research revealed a population bias in two suborders of primates (prosimians and Old World monkeys). This bias emerged whether the task measured any aspect of handedness or when it measured only handedness for simple reaching. Thus, the meta-analysis provides some support for the assertion that primates other than humans exhibit a population bias for handedness. As postulated by the POT, prosimians have a predominantly left-hand preference for reaching. Also, as postulated (although this postulation is not as clearly articulated as that for prosimians and New World monkeys), Old World monkeys have a left-hand preference for reaching. Consistent with the McGrew and Marchant (1997) review, neither the New World monkeys nor the lesser apes showed a significant population preference for any of the analyses. Because reaching tasks are relatively simple manual skills, the emergence of a population-level bias in preference for any group of primates directly contradicts the predictions of Fagot and Vauclair (1991). Of course, we cannot be sure that some relatively common bias in experience or task demands did not contribute to the bias in handedness (cf. Warren, 1977).

When analyses are conducted on species or genera within the suborder groups, the evidence in support of the POT weakens. Of the three types of prosimian analyzed in the reaching task analysis, only lemurs showed a significant population bias for a left-hand preference for reaching. Thus, this group was likely responsible for the left-hand shift seen for the entire suborder. This result is particularly troublesome for POT because MacNeilage et al. (1987) argued that bush babies (more direct descendants of ancient prosimian species) and not lemurs (who evolved several million years later) ought to exhibit a strong left-hand bias. Also, because the other groups that did not exhibit a population bias in handedness are just as arboreal as lemurs, these results do

not support the POT. A similar pattern occurs in Old World monkeys. Two of the four groups analyzed (rhesus and Japanese macaques) showed a significant population bias for a left-hand preference for reaching tasks. However, it could be argued that these two groups are relatively more terrestrial than those that did not exhibit a hand bias for reaching.

Although neither the New World monkeys nor the great apes showed a significant population preference in the reaching task analysis, certain taxonomic groups within these orders did show a population bias (some toward right-handedness, some toward left-handedness). These findings indicate that the variability between the groups of a suborder is such that not all groups show a population bias that is similar to that identified for the suborder. For apes, chimpanzees demonstrated a distinct right-hand bias in the population for reaching tasks. However, as McGrew and Marchant (1997) argued, this result may be confounded by the large amount of data that were obtained from the studies conducted by a single research group (headed by Hopkins) on a rather large captive population. Nevertheless, it does provide some evidence in support of the notion that chimpanzees might be used to model some aspects of human handedness.

For each meta-analysis, individual variability was highly significant. In addition to potential variability among species, this individual variability may be due to the variability of the tasks used to assess handedness (even for simple reaching) and the experience-based skills that each primate brings to the execution of the task, as well as the developmental status of the primates. Although individual variability was significant even when only data for reaching were used, our criteria still permitted some variety in task demands and skills required for the reaching tasks. That is, reaching could be for near or more distant foods, to the midline or to one side or the other of the primate, and so forth. These tasks vary not just in the pattern of reaching assessed but also in the posture of the primate (e.g., sitting or locomoting).

McGrew and Marchant (1997) noted that tasks testing primate handedness often involve reaching from an upright posture (a highly unusual posture for nonhuman primates). We tried to reduce some of that variability by selecting data from specific types of reaching tasks (i.e., visually guided reaching as opposed to haptic searching, etc., and from a sitting or quadrupedal posture rather than from a bipedal posture). However, much more data needs to be collected before the influence of task variability on hand-use preference can be estimated. Indeed, one major conclusion of this study is that some repository ought to be constructed for data collected on primate handedness and that repository should include a precise description of the task and the individual data on right- and left-hand use. Not only would such a repository permit more extensive future meta-analyses, but it would also enable researchers to identify more readily what types of data are needed from exactly which species.

As McGrew and Marchant (1997) noted, it is misleading to generalize to the suborder level from findings at the species level unless all species in the suborder provide data for the analysis. In their original review, MacNeilage et al. (1987) drew broad generalizations from a relatively small amount of data on only a few species. As large as our sample was, this bias still applies. If the largest sample of great apes—chimpanzees— was the focus of the analysis, then there would be evidence of a population bias in hand preference toward the right (albeit small and only 41% exhibiting a significant use of their right hand). However, this was observed only in the analysis of the simple reaching task; analysis of all manual tasks did not reveal a significant population bias for chimpanzees nor did analysis of the nonreaching tasks. Therefore, the evidence that chimpanzees exhibit a small population bias toward right-handedness only for reaching tasks does not provide strong support for the notion that human handedness shares an evolutionary history with chimpanzee handedness.

The postulated sequence for the evolution of human handedness as outlined by the POT (MacNeilage et al., 1987) was not supported by the meta-analysis. Our findings did reveal a left-hand population bias for reaching in prosimians and Old World monkeys. However, New World monkeys did not show a population bias for reaching preference, and a right-hand preference was not found for nonreaching tasks in New World monkeys,

Old World monkeys, or great apes. Therefore, the predicted shift from a right-hand postural support role to a right-hand manipulative role is not supported by the evidence.

Although there is some support that different species of primate have a population-level bias in their reaching preference, the evidence is not enough to conclude that any evolutionary progression has been demonstrated. The results demonstrate clearly that more handedness data must be collected with a variety of tasks presented to relatively large samples of all species in the field and in captivity. Only then may empirically based theories generate valuable predictions about the evolution of human brain-behavior relations.
The statistical method of analysis used in this study extracts more information from the data than traditional meta-analyses. The explicit modeling of individual variability (as opposed to simply allowing it to be collected in the residual variance) allowed more powerful interpretations of the results, including the recognition that the highly significant individual variability must be hiding important contributors to the manifestation of handedness in primates. And our results appear to indicate that these contributors may be more influential than taxonomic status.

Although this study may have collected the largest single data set of individual handedness in primates, a major limiting factor in the present study was the failure to obtain individual data from nearly half of the published studies. Therefore, more data might have changed our results. 2 Nevertheless, the current analysis does not support the POT or, as also concluded by McGrew and Marchant (1997), any other account of primate handedness.

In the 16 years since its publication, the MacNeilage et al. (1987) POT has stimulated the collection of handedness data on many more types of primates than had been collected before 1987. Yet we seem no closer to identifying an evolutionary basis for the population-level right bias in human handedness. In their original criticism of POT, Michel and Harkins (1987) noted that evolved structural characteristics do not necessarily follow the same form as their evolutionary precursors (e.g., reptilian jawbones are the precursors to ear bones in mammals). Therefore, functional characteristics like right-handedness in humans may not be derived from handedness in other primates, but from other factors (e.g., evolution of bipedal locomotion affecting gestational period and prenatal development of postnatal postural asymmetries; cf. Michel, 2002; Previc, 1991). Because the underlying cause of an asymmetry in hand preference has to do with structural changes in the brain that cause behavioral differences, it would not violate evolutionary principles, or degrade the evolutionary relation of humans to other primates, if the evolutionary precursors of human handedness were not the same factors determining primate handedness.

Footnotes
1 In order to illustrate the problems with the HI score, consider the reaching data from 3 hypothetical subjects (John, George, and Ringo). John has an HI score of 0.53, George has an HI score of 0.3, and Ringo has an HI of 0.5. However, because the character of the HI fluctuates with the frequency of reaches, we cannot conclude that John and Ringo are 50% more lateralized than George. Ringo may have reached 60 times with his right hand and 20 times with his left for a total of 80 reaches. George may have reached 13 times with his right hand and 7 with his left for a total of 20 reaches. In contrast, John reached 23 times with his right hand and 7 with his left for a total of 30 reaches. Using Fisher's z formula as an approximate of the binomial distribution, we find that George's reaching score yields a z of 1.34 or an alpha value of .09. By conventional decision criteria, we would not consider George's reaching bias to be significantly different from no bias. Ringo's reaching score yields a z of 4.47 with an alpha level of .00005. We can be much more confident that Ringo's frequency of reaching with his right hand represents a bias in reaching, and we know exactly the probability that such a classification would be incorrect by chance. John's pattern and frequency of reaching yields a z of 2.92 with an alpha of less than .002. Again, we can be confident that John's bias is unlikely to have occurred by chance. However, his slightly greater HI score than Ringo's does not indicate a greater degree of lateralization any more than it indicates a greater degree of lateralization than George's. We can be confident only in concluding that George may not be biased in hand use and that John and Ringo are biased in their hand use.

2 For example, an anonymous reviewer identified seven studies of great ape handedness and one on Old World monkeys that were not in our collection. Three were unpublished doctoral dissertations, two from more than two decades ago. Unfortunately, these could not be included in our analyses. However, we will make the information about these references available to anyone requesting it.

References

References marked with an asterisk indicate studies included in the meta-analysis.

Agresti, A. (2002). Categorical data analysis (2nd ed.). New York: Wiley.

Anderson, J. R., Degiorgio, C., Lamarque, C., & Fagot, J. (1996). A multi-task assessment of hand lateralization in capuchin monkeys (Cebus apella). Primates, 37, 97–103.

*Andrews, M. W., & Rosenblum, L. A. (1994). Automated recording of individual performance and hand preference during joystick-task acquisition in group-living bonnet macaques (Macaca radiata). Journal of Comparative Psychology, 4, 358–362.

Annett, M. (1985). Left, right, hand, and brain: The right shift theory. London: Erlbaum.

Aruguete, M. S., Ely, E. A., & King, J. E. (1992). Laterality in spontaneous motor activity of chimpanzees and squirrel monkeys. American Journal of Primatology, 27, 177–188.

Beck, C. H., & Barton, R. L. (1972). Deviation and laterality of hand preference in monkeys. Cortex, 8, 339–363.

Bicca-Marques, J. C., Nunes, C. A., & Schacht, K. (1998). Preliminary observation on handedness in wild tamarins (Saguinus spp.) and titi monkeys (Callicebus cupreus). Neotropical Primates, 6, 88–90.

*Boesch, C. (1991). Handedness in wild chimpanzees. International Journal of Primatology, 12, 541–558.

*Box, H. O. (1977). Observations on spontaneous hand use in the common marmoset (Callithrix jacchus). Primates, 18, 395–400.

Brinkman, C. (2001). Determinants of hand preference in individual Macaca fascicularis: A longitudinal study. Australasian Primatology, 14(4), 12.

Brooker, R. J., Lehman, R. W., Heimbuch, R. C., & Kidd, K. K. (1981). Hand usage in a colony of bonnet monkeys (Macaca radiata). Behavior Genetics, 11, 49–56.

Byrne, R. W., & Byrne, J. E. (1991). Hand preferences in the skilled gathering tasks of mountain gorillas (Gorillag. beringei). Cortex, 27, 521–546.

Byrne, R. W., & Byrne, J. E. (1993). Complex leaf-gathering skills of mountain gorillas (Gorillag. beringei). American Journal of Primatology, 31, 241–261.

*Byrne, R. W., Corp, N., & Byrne, J. E. (2001). Estimating the complexity of animal behaviour: How mountain gorillas eat thistles. Behaviour, 138, 525–557.

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (Callithrix jacchus): Problem solving and responses in a novel setting. Journal of Comparative Psychology, 113, 149–157.

Cantalupo, C., & Ward, J. P. (2000). Interaction between lateralized systems: Exploring the complexity of laterality. Brain and Cognition, 43, 73–78.

Christel, M. I., & Fragaszy, D. (2000). Manual function in Cebus apella: Digital mobility, preshaping, and endurance in repetitive grasping. International Journal of Primatology, 21, 697–719.

*Colell, M., Segarra, M. D., & Sabater-Pi, J. (1995a). Hand preferences in chimpanzees (Pan troglodytes), bonobos (Pan paniscus), and orangutans (Pongo pygmaeus) in food-reaching and other daily activities. International Journal of Primatology, 16, 413–434.

Colell, M., Segarra, M. D., & Sabater-Pi, J. (1995b). Manual laterality in chimpanzees (Pan troglodytes) in complex tasks. Journal of Comparative Psychology, 109, 298–307.

Corballis, M. C. (1991). The lopsided ape: Evolution of the generative mind. New York: Oxford University Press.

Crow, T. J. (2004). Directional asymmetry is the key to the origin of modern Homo sapiens (the Broca-Annett axiom). Laterality, 9, 233–242.

*Cunningham, D., Forsythe, C., & Ward, J. P. (1989). A report of behavioral lateralization in an infant orangutan (Pongo pygmaeus). Primates, 30, 249–253.

*de Sousa, M. C., Xavier, N. S., da Silva, H. A., & de Oliveira, M. S. (2001). Hand preference study in marmosets (Callithrix jacchus) using food reaching tests. Primates, 42, 57–66.

Deuel, R. K., & Dunlop, N. L. (1980). Hand preferences in the rhesus monkey: Implications for the study of cerebral dominance. Archives of Neurology, 37, 217–221.

De Vleeschouwer, K., Van Elsacker, L., & Verheyen, R. F. (1995). Effect of posture on hand preference during experimental food reaching in bonobos (Pan paniscus). Journal of Comparative Psychology, 109, 203–207.

*Diamond, A. C., & McGrew, W. C. (1994). True handedness in the cotton-top tamarin (Saguinus oedipus)?Primates, 35, 69–77.

Dodson, D. L., Stafford, D., Forsythe, C., Seltzer, C. P., & Ward, J. P. (1992). Laterality in quadrupedal and bipedal prosimians: Reach and whole-body turn in the mouse lemur (Microcebus murinus) and the galago (Galago moholi). American Journal of Primatology, 23, 191–202.

Drea, C. M., Wallen, K., Akinbami, M. A., & Mann, D. R. (1995). Neonatal testosterone and handedness in yearling rhesus monkeys (Macaca mulatta). Physiology & Behavior, 58, 1257–1262.

Fagot, J., Drea, C. M., & Wallen, K. (1991). Asymmetrical hand use in rhesus monkeys (Macaca mulatta) in tactually and visually regulated tasks. Journal of Comparative Psychology, 105, 260–268.

*Fagot, J., & Vauclair, J. (1988). Handedness and bimanual coordination in the lowland gorilla. Brain, Behavior & Evolution, 32, 89–95.

Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: A distinction between handedness and manual specialization. Psychological Bulletin, 109, 76–89.

*Feistner, A. C., Price, E. C., & Milliken, G. W. (1994). Preliminary observations on hand preference for tapping, digit-feeding and food-holding in captive aye-ayes (Daubentonia madagas). Folia Primatologica, 62, 136–141.

*Fernandez-Carriba, S., & Loeches, A. (2001). Fruit smearing by captive chimpanzees: A newly observed food-processing behavior. Current Anthropology, 42, 143–147.

*Finch, G. (1941, August1). Chimpanzee handedness. Science, 94, 117–118.

Flowers, K. (1975). Handedness and controlled movement. British Journal of Psychology, 66, 39–52.

*Forsythe, C., Milliken, G. W., Stafford, D. K., & Ward, J. P. (1988). Posturally related variations in the hand preferences of the ruffed lemur (Varecia variegata variegata). Journal of Comparative Psychology, 102, 248–250.

*Forsythe, C., & Ward, J. P. (1988). Black lemur (Lemur macaco) hand preference in food reaching. Primates, 29, 369–374.

*Fragaszy, D. M., & Adams-Curtis, L. E. (1993). An exploration of manual preference and performance in crab-eating macaques. In W. D.Hopkins & J. P.Ward (Eds.), Primate laterality: Current behavioral evidence of primate asymmetries (pp. 75–105). New York: Springer-Verlag.

*Fragaszy, D. M., & Mitchell, S. R. (1990). Hand preference and performance on unimanual and bimanual tasks in capuchin monkeys (Cebus apella). Journal of Comparative Psychology, 104, 275–282.

Harigel, E. (1991). Hand preference in juvenile Japanese and rhesus monkeys. Primate Report, 31, 16.

*Harrison, K. E., & Byrne, R. W. (2000). Hand preferences in unimanual and bimanual feeding by wild vervet monkeys (Cercopithecus aethiops). Journal of Comparative Psychology, 114, 13–21.

*Holder, M. K. (1999). Influences and constraints on manual asymmetry in wild African primates: Reassessing implications for the evolution of human handedness and brain lateralization (Doctoral dissertation, Rutgers University, 1999). Dissertation Abstracts International, 60(02), 0470A.

Hook, M. A., & Rogers, L. J. (2000). Development of hand preferences in marmosets (Callithrix jacchus) and effects of aging. Journal of Comparative Psychology, 114, 263–271.

*Hook-Costigan, M. A., & Rogers, L. J. (1995). Hand, mouth, and eye preferences in the common marmoset (Callithrix jacchus). Folia Primatologica, 64, 190–191.

Hook-Costigan, M. A., & Rogers, L. J. (1998). Eye preferences in common marmosets (Callithrix jacchus): Influence of age, stimulus, and hand preference. Laterality, 3, 109–130.

*Hopkins, W. D. (1993). Posture and reaching in chimpanzees (Pan troglodytes) and orangutans (Pongo pygmaeus). Journal of Comparative Psychology, 107, 162–168.

*Hopkins, W. D. (1994). Hand preferences for bimanual feeding in 140 captive chimpanzees (Pan troglodytes): Rearing and ontogenetic determinants. Developmental Psychobiology, 27, 395–407.

Hopkins, W. D. (1995a). Hand preferences for a coordinated bimanual task in 110 chimpanzees (Pan troglodytes): Cross-sectional analysis. Journal of Comparative Psychology, 109, 291–297.

*Hopkins, W. D. (1995b). Hand preferences for simple reaching in juvenile chimpanzees (Pan troglodytes): Continuity in development. Developmental Psychology, 31, 619–625.

Hopkins, W. D. (1999). Heritability of hand preference in chimpanzees (Pan troglodytes): Evidence from a partial interspecies cross-fostering study. Journal of Comparative Psychology, 113, 307–313.

Hopkins, W. D., Bales, S. A., & Bennett, A. J. (1994). Heritability of hand preference in chimpanzees (Pan troglodyte). International Journal of Neuroscience, 74, 17–26.

*Hopkins, W. D., Bennett, A., Bales, S., Lee, J., & Ward, J. P. (1993). Behavioral laterality in captive bonobos (Pan paniscus). Journal of Comparative Psychology, 107, 403–410.

*Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees (Pan troglodytes): Evidence of a left hemisphere specialization in motor skill. Journal of Experimental Psychology: General, 131, 412–423.

Hopkins, W. D., Dahl, J. F., & Pilcher, D. (2000). Birth order and left-handedness revisited: Some recent findings in chimpanzees (Pan troglodytes) and their implications for developmental and evolutionary models of human handedness. Neuropsychologia, 38, 1626–1633.

Hopkins, W. D., & Pearson, K. (2000). Chimpanzee (Pan troglodytes) handedness: Variability across multiple measures of hand use. Journal of Comparative Psychology, 114, 126–135.

*Hopkins, W. D., Stoinski, T. S., Lukas, K. E., Ross, S. R., & Wesley, M. J. (2003). Comparative assessment of handedness for a coordinated bimanual task in chimpanzees (Pan troglodytes), gorillas (Gorilla gorilla), and orangutans (Pongo pygmaeus). Journal of Comparative Psychology, 117, 302–308.

Hopkins, W. D., Washburn, D. A., Berke, L., & Williams, M. (1992). Behavioral asymmetries of psychomotor performance in rhesus monkeys (Macaca mulatta): A dissociation between hand preference and skill. Journal of Comparative Psychoogy, 106, 392–397.

*Itakura, S. (1992). Task-specific hand preferences of two Japanese macaques on mirror-guided reaching. Psychological Record, 42, 173–178.

*Jones-Engel, L. E., & Bard, K. A. (1996). Precision grips in young chimpanzees. American Journal of Primatology, 39, 1–15.

King, J. E. (1995). Laterality in hand preferences and reaching accuracy of cotton-top tamarins (Saguinus oedipus). Journal of Comparative Psychology, 109, 34–41.

Kirby, C. J. (1992). Hand preference in a reaching task in young captive chimpanzees (Pan troglodytes). American Journal of Primatology, 27, 39.

Kubota, K. (1990). Preferred hand use in the Japanese macaque troop, Arashiyama-R, during visually guided reaching for food pellets. Primates, 31, 393–406.

*Lacreuse, A., & Fragaszy, D. M. (1996). Hand preferences for a haptic searching task by tufted capuchins (Cebus apella). International Journal of Primatology, 17, 613–632.

Lacreuse, A., & Fragaszy, D. M. (1999). Left-hand preferences in capuchins (Cebus apella): Role of spatial demands in manual activity. Laterality, 4, 65–78.

Lacreuse, A., Parr, L. A., Smith, H. M., & Hopkins, W. D. (1999). Hand preferences for a haptic task in chimpanzees (Pan troglodytes). International Journal of Primatology, 20, 867–881.

*Larson, C. F., Dodson, D. L., & Ward, J. P. (1989). Hand preferences and whole-body turning biases of lesser bushbabies (Galago senegalensis). Brain, Behavior & Evolution, 33, 261–267.

Laska, M. (1996a). Manual laterality in spider monkeys (Ateles geoffroyi) solving visually and tactually guided food-reaching tasks. Cortex, 32, 717–726.

Laska, M. (1996b). A study of correlates of hand preferences in squirrel monkeys (Saimiri sciureus). Primates, 37, 457–465.

Lipsey, M. W., & Wilson, D. B. (2001). Practical meta-analysis. London: Sage.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. Behavioral and Brain Sciences, 10, 247–303.

*Marchant, L. F., & McGrew, W. C. (1996). Laterality of limb function in wild chimpanzees of Gombe National Park: Comprehensive study of spontaneous activities. Journal of Human Evolution, 30, 427–443.

Martinoli, L. C., Camperio Ciani, A. S., Rigamonti, M. M., Turrio, I., Castiglioni, R., Poli, M. D., & Fazio, F. (1995). Natural and induced hand preference in a captive Macaca nemestrina colony. Primate Report, 42, 13.

*Masataka, N. (1990). Handedness of capuchin monkeys. Folia Primatologica, 55, 189–192.

*Mason, A. M., Wolfe, L. D., & Johnson, J. C. (1995). Hand preference in the sifaka (Propithecus verreauxi coquereli) during feeding in captivity. Primates, 36, 275–280.

*Matoba, M., Mastaka, N., & Tanioka, Y. (1991). Cross-generational continuity of hand use preferences in marmosets. Behaviour, 117, 280–286.

*McGrew, W. C., & Marchant, L. F. (1992). Chimpanzees, tools, and termites: Hand preference or handedness?Current Anthropology, 33, 1992.

*McGrew, W. C., & Marchant, L. F. (1996). On which side of the apes? Ethological study of laterality of hand use. In W. C.McGrew, L. F.Marchant, & T.Nishida (Eds.), Great ape societies (pp. 255–272). New York: Cambridge University Press.

McGrew, W. C., & Marchant, L. F. (1997). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. Yearbook of Physical Anthropology, 40, 201–232.

*McGrew, W. C., & Marchant, L. F. (1999). Manual laterality in anvil use: Wild chimpanzees cracking Strychnos fruits. Laterality, 4, 79–87.

*McGrew, W. C., & Marchant, L. F. (2001). Ethological study of manual laterality in the chimpanzees of the Mahale mountains, Tanzania. Behaviour, 138, 329–358.

McManus, C. (2002). Right hand, left hand: The origins of asymmetry in brains, bodies, atoms, and cultures. Cambridge, MA: Harvard University Press.

Michel, G. F. (1998). A lateral bias in the neuropsychological functioning of human infants. Developmental Neuropsychology, 14, 445–469.

Michel, G. F. (2002). Development of infant handedness. In D. J.Lewkowicz & R.Lickliter (Eds.), Conceptions of development: Lessons from the laboratory (pp. 165–185). New York: Psychology Press.

Michel, G. F., & Harkins, D. A. (1987). Ontogenetic considerations in the phylogenetic history and adaptive significance of the bias in human handedness. Behavioral and Brain Sciences, 10, 283–284.

Michel, G. F., Sheu, C.-F., & Brumley, M. R. (2002). Evidence of a right-shift factor affecting infant hand-use preferences from 7 to 11 months of age as revealed by latent class analysis. Developmental Psychobiology, 40, 1–13.

*Milliken, G. W., Forsythe, C., & Ward, J. P. (1989). Multiple measures of hand-use lateralzation in the ring-tailed lemur (Lemur catta). Journal of Comparative Psychology, 103, 262–268.

*Milliken, G. W., Stafford, D. K., Dodson, D. L., Pinger, C. D., & Ward, J. P. (1991). Analyses of feeding lateralization in the small-eared bushbaby (Otolemur garnettii): A comparison with the ring-tailed lemur (Lemur catta). Journal of Comparative Psychology, 105, 274–285.

*Mittra, E. S., Fuentes, A., & McGrew, W. C. (1997). Lack of hand preference in wild hanuman langurs (Presbytis entellus). American Journal of Physical Anthropology, 103, 455–461.

*Morris, R. D., Hopkins, W. D., & Bolser, G. L. (1993). Assessment of hand preference in two language-trained chimpanzees (Pan troglodytes): A multimethod analysis. Journal of Clinical and Experimental Neuropsychology, 15, 487–502.

*Olson, D. A., Ellis, J. E., & Nadler, R. D. (1990). Hand preferences in captive gorillas, orang-utans and gibbons. American Journal of Primatology, 20, 83–94.

Panger, M. A. (1998). Hand preference in free-ranging white throated capuchins (Cebus capucinus) in Costa Rica. International Journal of Primatology, 19, 133–163.

*Panger, M. A., & Wolfe, L. D. (2000). Carrying and hand-use patterns in Panamanian white-faced capuchins (Cebus capucinus). Primates, 41, 407–411.

Papademetriou, E. (2003). A meta-analysis of primate hand preference for reaching and other hand-use measures.Unpublished master's thesis, DePaul University, Chicago.

*Parnell, R. J. (2001). Hand preference for food processing in wild western lowland gorillas (Gorilla gorilla gorilla). Journal of Comparative Psychology, 115, 365–375.

Parr, L. A., Hopkins, W. D., & DeWall, F. M. (1996). Haptic discrimination in capuchin monkeys (Cebus apella): Evidence of manual specialization. Neuropsychology, 35, 143–152.

Previc, F. H. (1991). A general theory concerning the prenatal origins of cerebral lateralization in humans. Psychological Review, 98, 299–334.

Rigamonti, M. M., Previde, E. P., Poli, M. D., Marchant, L. F., & McGrew, W. C. (1998). Methodology of motor skill and laterality: New test of hand preference in Macaca nemestrina. Cortex, 34, 693–705.

Rogers, L. J., & Andrew, R. J. (2002). Comparative vertebrate lateralization. Hove, UK: Psychology Press.

Rogers, L. J., & Kaplan, G. (1996). Hand preferences and other lateral biases in rehabilitated orang-utans, Pongo pygmaeus pygmaeus. Animal Behaviour, 51, 13–25.

Roney, L. S., & King, J. E. (1993). Postural effects on manual reaching laterality in squirrel monkeys (Saimiri sciureus) and cotton-top tamarins (Saguinus oedipus). Journal of Comparative Psychology, 107, 380–385.

Sanford, C., Guin, K., & Ward, J. P. (1984). Posture and laterality in the bushbaby (Galago senegalensis). Brain, Behavior & Evolution, 25, 217–224.

*Shafer, D. D. (1997). Hand preference behaviors shared by two groups of captive bonobos. Primates, 38, 303–313.

Sheu, C.-F. (2002). Fitting mixed-effects models for repeated ordinal outcomes with the NLMIXED procedure. Behavioral Research Methods, Instruments, and Computers, 34, 151–157.

Sheu, C.-F., & Suzuki, S. (2001). Meta-analysis using linear mixed models. Behavioral Research, Methods, Instruments, and Computers, 33, 102–107.

*Singer, S. S., & Schwibbe, M. H. (1999). Right or left, hand or mouth: Genera-specific preferences in marmosets and tamarins. Behaviour, 136, 119–145.

Spinozzi, G., & Cacchiarelli, B. (2000). Manual laterality in haptic and visual reaching tasks by tufted capuchin monkeys (Cebus apella). An association between hand preference and hand accuracy for food discrimination. Neuropsychologia, 38, 1685–1692.

*Spinozzi, G., Castorina, M. G., & Truppa, V. (1998). Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (Cebus apella). Journal of Comparative Psychology, 112, 183–191.

Spinozzi, G., & Truppa, V. (1999). Hand preferences in different tasks by tufted capuchins (Cebus apella). International Journal of Primatology, 20, 827–849.

*Spinozzi, G., & Truppa, V. (2002). Problem-solving strategies and hand preferences for a multicomponent task by tufted capuchins (Cebus apella). International Journal of Primatology, 23, 621–638.

*Stafford, D. K., Milliken, G. W., & Ward, J. P. (1990). Lateral bias in feeding and brachiation in Hylobates. Primates, 31, 407–414.

*Stafford, D. K., Milliken, G. W., & Ward, J. P. (1993). Patterns of hand and mouth lateral biases in bamboo leaf shoot feeding and simple food reaching in the gentle lemur (Hapalemur griseus). American Journal of Primatology, 23, 195–207.

*Sugiyama, Y., Fushimi, T., Sakura, O., & Matsuzawa, T. (1993). Hand preference and tool use in wild chimpanzees. Primates, 34, 151–159.

Teichroeb, J. A. (1999, January). A review of hand preferences in nonhuman primates: Some data from patas monkeys. Laboratory Primate Newsletter, 38, 10–13.

Tonooka, R., & Matsuzawa, T. (1995). Hand preferences of captive chimpanzees (Pan troglodytes) in simple reaching for food. International Journal of Primatology, 16, 17–35.

Toth, N. (1985). Archeological evidence for preferential right-handedness in lower and middle Pleistocene and its possible implications. Journal of Human Evolution, 14, 35–40.

Vauclair, J., & Fagot, J. (1987). Spontaneous hand usage and handedness in a troop of baboons. Cortex, 23, 265–274.

*Ward, J. P. (1998). Left-hand advantage for prey capture in the galago (Galago Moholi). International Journal of Comparative Psychology, 11, 173–184.

Ward, J. P., & Cantalupo, C. (1997). Origins and functions of laterality: Interactions of motoric systems. Laterality, 2, 279–303.

Ward, J. P., Milliken, G. W., Dodson, D. L., Stafford, D. K., & Wallace, M. (1990). Handedness as a function of sex and age in a large population of Lemur. Journal of Comparative Psychology, 104, 167–173.

Warren, J. M. (1977). Handedness and cerebral dominance in monkeys. In S.Harnad, R. W.Tody, L.Goldstein, J.Jaynes, & G.Krauthamer (Eds.), Lateralization in the nervous system (pp. 151–172). New York: Academic Press.

Warren, J. M. (1987). Primate handedness: Inadequate analysis, invalid conclusions. Behavioral and Brain Sciences, 10, 288–289.

*Watanabe, K., & Kawai, M. (1993). Lateralized hand use in the precultural behavior of the koshimi monkeys (Macaca fuscata). In W. D.Hopkins & J. P.Ward (Eds.), Primate laterality: Current behavioral evidence of primate asymmetries (pp. 183–192). New York: Springer-Verlag.

*Westergaard, G. C. (1991). Hand preference in the use and manufacture of tools by tufted capuchin (Cebus apella) and lion-tailed macaque (Macaca silenus) monkeys. Journal of Comparative Psychology, 105, 172–176.

Westergaard, G. C. (1999). Immune functioning and reactivity predict hand preference in rhesus macaques. American Journal of Primatology, 49, 114.

Westergaard, G. C., Champoux, M., & Suomi, S. J. (1997). Hand preference in infant rhesus macaques (Macaca mulatta). Child Development, 68, 387–393.

*Westergaard, G. C., Haynie, M. K., & Lundquist, A. L. (1999). Carrying, sharing, and hand preference in tufted capuchins (Cebus apella). International Journal of Primatology, 20, 153–162.

*Westergaard, G. C., Kuhn, H. E., & Suomi, S. J. (1998a). Bipedal posture and hand preference in humans and other primates. Journal of Comparative Psychology, 112, 55–64.

Westergaard, G. C., Kuhn, H. E., & Suomi, S. J. (1998b). Effects of upright posture on hand preference for reaching vs. the use of probing tools by tufted capuchins (Cebus apella). American Journal of Primatology, 44, 147–153.

*Westergaard, G. C., Kuhn, H. E., & Suomi, S. J. (1998c). Laterality of hand function in tufted capuchin monkeys (Cebus apella): Comparison between tool use actions and sponataneous non-tool actions. Ethology, 104, 119–125.

Westergaard, G. C., Liv, C., Haynie, M. K., & Suomi, S. J. (2000). A comparative study of aimed throwing by monkeys and humans. Neuropsychologia, 38, 1511–1517.

Westergaard, G. C., & Lussier, I. D. (1999). Left-handedness and longevity in primates. International Journal of Neuroscience, 99, 79–87.

Westergaard, G. C., Lussier, I. D., & Higley, J. D. (2001). Between-species variation in the development of hand preference among macaques. Neuropsychologia, 39, 1373–1378.

*Westergaard, G. C., Lussier, I. D., Suomi, S. J., & Higley, J. D. (2001). Stress correlates of hand preference in rhesus macaques. Developmental Psychobiology, 38, 110–115.

Westergaard, G. C., & Suomi, S. J. (1993a). Hand preference in capuchin monkeys varies with age. Primates, 34, 295–299.

*Westergaard, G. C., & Suomi, S. J. (1993b). Hand preference in the use of nut-cracking tools by tufted capuchin monkeys (Cebus apella). Folia Primatologica, 61, 38–42.

Westergaard, G. C., & Suomi, S. J. (1994). The use of probing tools by tufted capuchins (Cebus apella): Evidence for increased right-hand preference with age. International Journal of Primatology, 15, 521–529.

Westergaard, G. C., & Suomi, S. J. (1996a). Hand preference for a bimanual task in tufted capuchins (Cebus apella) and rhesus macaques (Macaca mulatta). Journal of Comparative Psychology, 110, 406–411.

*Westergaard, G. C., & Suomi, S. J. (1996b). Hand preference for stone artefact production and tool-use by monkeys: Possible implications for the evolution of right-handedness in hominids. Journal of Human Evolution, 30, 291–298.

*Westergaard, G. C., Wagner, J. L., & Suomi, S. J. (1999). Manipulative tendencies of captive Cebus albifrons. International Journal of Primatology, 20, 751–759.

Wolfinger, R. D. (2001). Fitting nonlinear mixed models with the new NLMIXED procedure. [Computer software and manual]. Retrieved December 2002, from http://www2.sas.com/proceedings/sugi24/Stats/p287-24.pdf