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Independence of Data Points in the Measurement of Hand Preferences in Primates: Statistical Problem or Urban Myth?

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Abstract

Lack of independence of data points or the pooling fallacy has been suggested as a potential problem in the study of handedness in nonhuman primates, particularly as it relates to whether hand use responses should be recorded as individual events or bouts of activity. Here, I argue that there is no evidence that the concept of statistical independence of data points or the pooling fallacy is a problem in the evaluation of population-level handedness in previous studies in nonhuman primates. I further argue these statistical concepts have been misapplied to the characterization of individual hand preferences. Finally, I argue that recording hand use responses as bouts rather than events has no significant effect on reports of hand use in nonhuman primates and, in fact, may unintentionally bias hand use toward the null hypothesis. Several suggestions for improvement in the measurement and statistical determination of individual handedness are offered in the paper.

Keywords

Handedness; Nonhuman primates; Methods; Statistics

One defining behavioral trait of humans is population-level handedness. That is to say, a statistical majority of individuals self-report themselves as being right-handed for a number of different tasks and actions (Annett, 2002; Perelle and Ehrman, 1994; Porac and Coren, 1981; Raymond and Pontier, 2004). Many historic and contemporary scholars believe that population-level handedness, and in particular right-handedness, reflects an inherent specialization of the left hemisphere for motor skill and is unique to hominin evolution (Cashmore, 2009; Cashmore et al., 2008; Crow, 2004; Crow, 2009; Ettlinger 1988; McGrew and Marchant 1997; McManus 2002; Schoenemann 2006; Warren 1980). In the past 25 years there has been a plethora of studies evaluating handedness in nonhuman primates with the aim of testing whether population-level handedness is unique to humans and to assess the evolutionary origins of this trait (Cashmore et al., 2008; Fagot and Vauclair, 1991; Hook-Costigan and Rogers, 1997; Hopkins, 2006; Marchant and McGrew, 1991; McGrew and Marchant, 1993; Papademetriou et al., 2005; Uomini, 2009). The purpose of this paper is not to review the myriad of studies on handedness in nonhuman primates. Rather, the aim is to address the continued claim by some authors that some handedness studies are flawed or biased because the investigators failed to account for independence of data in the

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collection of individual hand preference responses. For example, in the review of handedness findings in nonhuman primates by McGrew and Marchant (1997), they excluded any studies they viewed did not control for independence of data points and this resulted in only a partial presentation of the existing findings. More recently, Cashmore et al. (2008) devoted a section of their review paper on handedness in nonhuman primates to what they described as potential problems related to independence of data points. In this paper, I question whether the bases for concerns regarding independence of data points are legitimate from a statistical and methodological perspective.

At the heart of the matter is how to treat hand use responses when they occur as repeated or sequences of actions without intervening events. For example, a number of investigators have tested for handedness in primates using a measure called the TUBE task including among New World monkeys (Lilak and Phillips, 2007; Meguerditchian et al., 2012; Meunier and Vauclair, 2007; Spinozzi et al., 1998), Old World monkeys (Bennett et al., 2008; Schmitt et al., 2008; Schweitzer et al., 2007; Vauclair et al., 2005; Zhao et al., 2012) and great apes (Chapelain and Hogervorst, 2009; Chapelain et al., 2011; Hopkins et al., 2011; Llorente et al., 2010). With the TUBE task, a sticky food substrate is smeared on the inside edges of poly-vinyl-chloride (PVC) pipes (or a similar type object) and handed to the subject. The subjects typically pick up the TUBE, hold it in one hand and extract the food with a digit from the opposite hand. Often times, the subject repeats the extract and feed action without any intervening events. Some have approached quantifying handedness for the TUBE task in this circumstance by using focal subject sampling with continuous recording, thereby quantifying all instances (or events) of left and right hand use (Bennett et al., 2008; Hopkins et al., 2011; Lilak and Phillips, 2007; Llorente et al., 2010; Meguerditchian et al., 2012; Meunier and Vauclair, 2007; Vauclair et al., 2005). In contrast, others have suggested that each of the hand use responses presented above is not independent of the other and therefore represents a “lack of data independence” (Chapelain and Hogervorst, 2009; Chapelain et al., 2011; Hopkins et al., 2001; Schmitt et al., 2008; Schweitzer et al., 2007; Zhao et al., 2012). The argument is that because the first hand use event predicts or is correlated with subsequent responses, the data are not independent of each other. To resolve this issue, some believe that investigators must treat the recording of hand preference as bouts of activity rather than individual events (Byrne and Byrne, 1991; Corp and Byrne, 2004; Harrison and Byrne, 2000; Harrison and Nystrom, 2008; Harrison and Nystrom, 2010; McGrew and Marchant, 1997). For these reasons, many authors and reviewers continue to claim that studies that use continuous recording of hand use events are invalid and, in the absence of recording bouts, lead to biased findings. I believe that there are several problems with these arguments as they have been articulated in the literature and that continuous recording of hand use for each event is a perfectly valid and, indeed arguably, better method for assessing hand preference in primates.

What is independence of data points?

The book *Measuring behavior: An introductory guide* by Martin and Bateson (1986) is the most frequently cited primary reference for discussion of independence of data points in relation to the study of handedness in nonhuman primates and the problem is often framed as a statistical one. The problem with this framework is that the issue of independence of data, as it relates to the quantification of individual hand preference whether recording hand use as individual events or bouts, has absolutely nothing to do with statistical theory. When Martin and Bateson (1986) and others (Machlis et al., 1985) discussed independence of data points (or what Machlis et al. termed the “pooling fallacy” or “pseudoreplication” (Hurlbert, 1984; Lazic, 2010), they were referring to the necessity that each data point in any statistical analysis represent a single subject’s data. Whether scientists record bouts or events of hand use as the outcome measure in determining hand preferences, they are not violating the basic

concept of statistical independence of data points, at least when testing for population-level biases. In the case of recording either bouts or events in hand use, each subject has its own handedness score as a measure of their preference. Thus, each data point in the analysis performed to determine population-level handedness is independent of the other. What Martin and Bateson (1986) were concerned with when discussing independence of data points, in the context of statistics, are when raw frequency data are treated as independent observations. For example, if I tested 10 monkeys for handedness on the TUBE task and each made 3 left and 7 right hand responses, I would not have an $N = 100$ (70 right, 30 left) but rather $N = 10$. To determine whether the monkeys show population-level right or left-handedness, we would not compare the 30 versus 70 because the raw observations are not independent of each other. Instead, we would want to compare the number of individuals who are classified as right- or left-handed based on some type of individual determination of hand preference for each subject. Based on the findings from several meta-analyses of handedness in nonhuman primates, the “pooling fallacy” rarely, if ever, occurs in the literature when evaluating population-level handedness (Hook-Costigan and Rogers, 1997; Hopkins, 2006; Papademetriou et al., 2005).

In my view, the misapplication of the “independence of data points” concept occurs because some are trying to apply it to the measurement and statistical determination of individual hand preference for a given task (i.e., whether an individual animal is right- or left-handed). The problem is that the independence of data points position articulated by Martin and Bateson (1986) cannot be applied to the determination of individual hand preference because they pertain to different levels of analysis. Specifically, whether recording hand use as bouts or events, as long as the data are collected from the same individual, they are never independent of each other from a statistical standpoint. For instance, an experimenter could test a chimpanzee for handedness and present them with one trial each day for 30 days. At the end of the 30 day period, the experimenter could then sum the number of left and right hand responses to determine their hand preference. In comparison, the same chimpanzee could be given one test trial and the experimenter could record 30 hand use responses and, again sum the number of left and right hand responses to determine their individual hand preference. In both of these test scenarios, from a purely statistical standpoint, the data points are not independent of each other because they are derived from the same individual. Therefore, in my view, the term “lack of independence of data points” or the “pooling fallacy” concept is being misapplied in the discussion of determining individual hand preferences in nonhuman primates, at least as defined by Martin and Bateson (1986) and others (Machlis et al., 1985).

Independence of data points as a methodological problem

To be clear, one can certainly argue the merits or limitations of recording individual hand use as events or bouts but this issue is not a statistical problem. Rather, it is a methodological one. In the TUBE example provided above, the assumptions for those advocating the bouts level of analysis is that the hand used by the subject in removing the food predicts their subsequent hand use on the next response. Thus, it is argued that the individual hand use events are correlated (i.e., non-independent of each other or auto-correlated) and therefore need to be separated by some intervening event that presumably breaks up the sequence and allows, essentially, the hands to go back to some neutral state and thereby become equa-probable for the subjects use. Previous studies have defined intervening events as actions like a) rotating the tube b) dropping the current tube and selecting a new one or c) switching hand use (see Hopkins et al., 2001; McGrew and Marchant, 1997 for discussion).

This is certainly a valid perspective but it also has limitations. First, what defines an intervening event is purely up to the experimenter or observer. There is no law or rule that governs this decision and therefore what constitutes the onset and offset of a “bout” of hand use (or what defines an intervening event) is arbitrary. Second, and perhaps more importantly, I would argue that those who advocate the purely bout approach have failed to adequately apply appropriate observational methodology for capturing the complexity and variability in hand use. In short, they have failed to adequately adopt appropriate methods for measuring a “bout” of hand use activity. Martin and Bateson (1986) suggest that, when recoding bouts of behavior, it is critical to also record the duration or number of occurrences of behavior within a bout in order to capture the payoff between how often a behavior occurs contrasted to how long the subjects might engage in the behavior. Another example illustrates this point. Imagine a baboon foraging on a leafy substrate in which they hold the plant stem with the left hand and pluck off and eat 5 leaves in succession with the right hand. The baboon then stops, selects another plant, holds the stem with the right hand and then plucks off and eats one leaf with their left hand. This baboon repeats the same foraging sequence on 10 different occasions. At the end of the observation period, the baboon would have 50 right and 10 left hand event responses. In contrast, the same baboon would have 10 right and 10 left hand bout responses. The fundamental question is this: Which of these two levels of analysis best characterizes the baboon’s individual hand preference? Based on the behavior of the baboon, I think it is fair to say that recording bouts *alone* does not adequately capture the subject’s handedness because it ignores the simple fact that the hand use events are occurring in an asymmetrical sequential manner within a feeding bout. For this reason, I believe that the continued belief by some that bouts alone must be the level of analysis in determining individual hand preference is not justified.

More importantly, Martin and Bateson (1986) suggest that the best way to record event behavior (i.e., hand use) is the use of continuous recording because it provides a true and faithful record of the behavior, particularly for those that occur in sequences. Indeed, Martin and Bateson (1986) argue that biases in frequency data can occur if the measurement is terminated before the bout of the behavior actually ends. Thus, some scientists measuring handedness have limited their hand use observations to the first response when the behavioral events occur in bouts or sequences (Byrne and Byrne, 1991; McGrew and Marchant, 1992; Westergaard et al., 2001). This procedure allegedly controls for the problem of independence of data points but may in fact lead to biased results (as demonstrated in the above example). By not considering hand use as a sequence of events but rather as bouts, handedness researchers are potentially underestimating or biasing hand preferences toward the null hypothesis (i.e., no hand preference). Perhaps the easiest way to think about this perspective is the following: If the onset and offset of bouts in hand use were defined *solely* on the basis of a change in hand use, how would any subject ever show a significant hand preference? To demonstrate hand preferences, hand use responses *must be correlated* across observational periods whether separated by one sec, one minute, one hour, one day or one year.

Lastly, it has been suggested that by recording each hand use event instead of bouts, sample sizes are inflated and this potentially leads to biased findings with respect to hand preferences (McGrew and Marchant, 1997). This is an empirical question and can be tested based on data reported in the literature. Shown in Table 1 are hand preference data from 9 studies on handedness in nonhuman primates that were selected because hand use was recorded for both bouts and events. Included in Table 1 are the mean handedness index (HI) values as well as the distribution of hand preference for each method of recording. HI values were derived following the formula $[HI = (R - L) / (R + L)]$ with positive values reflecting right hand preferences and negative values indicating left hand preferences. As can be seen, the mean HI scores calculated on the basis of bouts and events are nearly identical and do

not differ significantly from each other in those studies where both values were reported. Additionally, the correlation coefficients between HI scores calculated on the basis of bouts and events are all positive and significant. This indicates that these two approaches are measuring the same degree of handedness at the individual level. Thus, at least with respect to HI scores, there is no empirical evidence that recording hand use as events compared to bouts biases the results.

Z-scores and the characterization of individual handedness

As noted above, when using HI scores, there is no difference in the degree of handedness exhibited by individual subjects when based on bouts or events in hand use. However, characterization of individual handedness on the basis of bouts compared to events can change when attempts are made to classify subjects as right-, left- or ambiguously-handed based on binomial *z*-scores. A standard practice in the nonhuman primate handedness literature is to compute individual *z*-scores based on the frequency in left and right hand, whether determined on the basis of bouts or events. Subjects with individual *z*-scores $\geq +1.96$ or ≤ -1.96 are classified as right- and left-handed while all other individuals are called ambiguously-handed or non-preferent. The critical values of -1.96 or $+1.96$ for classifying hand preference are chosen because *z*-scores at these values exceed a probability of less than .025 (i.e., $p < .05$ for two-tailed tests). Thus, if an individual subject has a *z*-score of ≤ -1.96 or $\geq +1.96$, then the experimenter can confidently declare that their hand preference is “significant” whereas all others are “non-significant”.

The use of *z*-scores to characterize individual hand preferences is problematic for several reasons. First, cut-off points of ± 1.96 are very conservative and increase the probability that Type II error can occur (that is, falsely accepting the null hypothesis). That is to say, it is very likely that subjects who show moderate hand preferences are being classified as non-preferent. Second, *z*-scores are seldom if ever used to characterize individual handedness in adult human subjects (even though they could be used even with questionnaire data). This by itself is not necessarily a problem, but it does create challenges when trying to compare the distribution of handedness between humans and other nonhuman primates. The exceptions are studies on handedness with developing children but often times, the *z*-score cut-off points used to classify handedness groups are more liberal (i.e., $z = \pm 1.50$ or $z = \pm 1.0$) (e.g., Fagard and Marks, 2000).

Third, because *z*-scores are sensitive to sample size, “significant” hand preference might be detected when based on event frequencies in hand use rather than bouts (because one typically has fewer numbers of right and left hand use for bouts). As an example, suppose I obtained hand use data from two chimpanzees. Chimpanzee one used its left hand 3 times and right hand 7 times to grasp a food item while chimpanzee two used its left hand 30 times and its right hand 70 times. These two apes would have the exact same percentage right hand use (*Mean* = 70%) or HI score (*Mean* = .40) but chimpanzee two would have a *z*-score of 1.26 and chimpanzee one would have a *z*-score of 4.00. Though quantitatively these two chimpanzees have the same hand preference, based on the standard practice of using *z*-scores to determine handedness, chimpanzee one would be classified as ambiguously-handed and chimpanzee two would be right-handed. The manifestation of how this problem creates confusion in the interpretation of handedness data is highlighted in Figures 1 and 2. Shown in Figure 1 is the percentage of subjects classified as right-handed on the basis of *z*-scores computed on the frequencies in hand use based on bouts and events for the 8 studies shown in Table 1. As can be seen, the percentage of subjects classified as right-handed are comparable between methods within each study. In contrast, shown in Figure 2 are the percentage of subjects classified as ambiguously-handed based on frequencies in hand use for bouts and events for each study. As can be seen, the percentage of ambiguously-handed

subjects is substantially higher when based on bouts compared to events for every single study. Thus, comparing the results based on these two approaches only influences the number of individuals classified as ambiguously-handed, a group that most scientists interested in handedness ignore. This effect is entirely attributable to the use of *z*-scores and adopting a critical value of ± 1.96 to classify subjects as right- or left-handed. Recall that the HI scores do not differ between the methods; thus, the basic differences in the interpretation of individual handedness lies entirely with whether the data are quantified on a continuous or categorical scale of measurement and whether *z*-scores of ± 1.96 are adopted to classify subjects as right- or left-handed.

CONCLUSIONS AND RECOMMENDATIONS

In summary, I do not believe that there is any statistical justification for claims that a lack of independence of data points is a potential problem in the measurement of handedness in nonhuman primates. Moreover, and perhaps more importantly, recording bouts *alone* as the level of analysis in hand use seems misguided and has the potential to remove important information on asymmetries in sequences of hand use. It should be emphasized that recording hand use as events or bouts have some strengths and weaknesses but, most importantly, the available data do not suggest that one approach is better than another nor leads to a different set of findings.

The most obvious solution to resolve this disagreement is to record and report both bouts and frequency in hand use as has been done by some investigators (see Table 1). This is quite reasonable and should satisfy everyone working on the question of handedness (or other forms of behavioral asymmetry) in primates. The problem is that some authors and reviewers continue to assert that recording bouts rather than frequency in hand use is a *better* and, indeed, the *only* legitimate method for assessing hand use because of the lack of independence of data points (Cashmore et al., 2008; McGrew and Marchant, 1997). Unfortunately this is not based on any empirical facts nor is it a justifiable argument based on statistical theory or standard observational methodological practices. In my view, if measuring hand use as bouts of activity is a better method of quantifying hand preferences or potentially leads to a different outcome in terms of handedness, then the onus of responsibility to prove this claim lies with those who advocate this position.

Analysis of the extant findings on handedness further showed that there is no evidence that recording individual hand use events instead of bouts biases the handedness results, at least when quantified on a continuous scale of measurement (see Table 1). Differences in hand preference distributions between methods do emerge when using *z*-scores to classify subjects as right-, left- or ambiguously-handed but this is largely attributable to the number of observations used in calculating the *z*-score. Going forward, in my view, there are several ways that scientists could potentially improve the characterization of individual hand preferences in nonhuman primates. First, within a study, if HI scores based on events and bouts of hand use are strongly positively correlated with each other (as is the case in all published studies, see Table 1), there is absolutely no reason for researchers to calculate *z*-scores and classify handedness based on the bout measures. Instead, *z*-scores should be computed on the basis of frequencies in hand use events. This would increase the statistical power for determining individual hand preference when using *z*-scores without compromising the validity of the measure. Second, rather than use *z*-scores at all, scientists could classify subjects as right-, left- or ambiguously-handed based on the consistency in the sign of the HI scores derived from bouts and events. If the signs are the same when computed on the basis of frequencies in bouts and events (either both positive or negative), then they would be classified as right- or left-handed. Subjects with inconsistent signs (one positive, one negative) for their HI values would be classified as ambiguously-handed.

Third, one could simply increase the number of bouts of hand use recorded at the individual level of analysis so that they might approximate event frequencies. This is certainly plausible but pragmatically could be challenging under conditions where one has little control over how much data can be collected on any given subject, such as in field settings.

A final suggestion might be to consider abandoning the use of *z*-scores all together and instead define handedness categories based on either a) arbitrary cut-off points applied to HI scores or b) based on consistency in hand use across multiple test sessions. In terms of assigning arbitrary cut-off points to HI scores, this is the predominant approach used in studies of handedness in human adults (Salmaso and Longoni, 1985). In many studies on human handedness, a laterality quotient (LQ) is derived using the same formula as that used for the HI score. Subjects are then classified as right, left- and non-preferent based on arbitrary cut-off points applied to the LQ scores. I emphasize arbitrary because there is no consistency in the cutoff -points used in many studies with human subjects; thus, to be useful for comparative studies in nonhuman primates, uniform cut-off points would be ideal. I would suggest that cut-off points of $-.20$ and $+.20$ be used to characterize left- and right-handed subjects whereas all other would be classified as ambiguously-handed. I have chosen $.20$ as the value because we have previously found that HI values of $-.20$ or $+.20$ roughly correspond to *z*-scores of ± 1.96 when a minimum of 30 responses are obtained in the measurement handedness. One advantage of adopting this approach is that it would remove the problem illustrated in Figure 2 because HI scores are not sensitive to variation in the sample size.

Another alternative approach to characterizing hand preferences would be to base it on consistency rather than total frequency in hand use across different tests, whether recoding bouts or events. Shown in Table 2 are hypothetical hand use data for 6 subjects. In this example, each subject was tested on 4 occasions and frequency in hand use was summed across all tests. As can be seen, all 6 subjects showed a significant right hand preference based on *z*-scores computed on the total frequencies in left and right hand use. However, examination of the individual HI scores for each test shows that subjects 2, 4 and 6 showed inconsistent preferences across the test. These subjects are classified as right-handed because frequency in right hand use is elevated in some tests compared others and the data from these tests are inflating the sample sizes so as to skew their individual hand preference.

Whether this is a problem in the existing nonhuman primate handedness literature is unclear because consistency in hand use across different test sessions or observation periods is seldom reported (Hopkins et al., in press). However, two recent studies on handedness for the TUBE task in chimpanzees collected hand use data in 4 separate test sessions (Hopkins et al., in press; Llorente et al., 2010). HI scores were calculated for each test session and the chimpanzees' handedness was classified based on their consistency in hand use across tests. Shown in Figure 3 is the distribution of hand preference based on consistency in hand use across test sessions in each study. As can be seen, a significant higher proportion of chimpanzees consistently preferred their right hand compared to all other possible combinations of hand use. I would argue that characterizing individual hand preferences based on consistency within or between tasks is more similar to the approaches used in studies in humans and this might facilitate comparisons between species. This approach may not always be possible, particularly in field studies where one has little control over how often data can be collected from a specific individual but it certainly can be accomplished in most laboratory settings.

In closing, a number of evolutionary models of handedness have postulated the importance of such traits as bimanual coordination, tool manufacture and use, bipedalism and language to the emergence of right-handedness in early and modern humans (Bradshaw and Rogers,

1993; Corballis, 1997; Corballis et al., 2012). Studies in nonhuman primates are vital for testing these different models and for potentially developing new theories on the evolution of handedness in primates. If scientists working on the question of handedness in nonhuman primates cannot come to some basic agreements on how best to measure and quantify individual handedness, then progress on this research field will remain stalled. It is hoped that the arguments and recommendations offered here provide a framework for advancing the field and will aid in bringing a more balanced and systematic approach to the study of handedness in primates, including humans.

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Figure 1.

Percentage of right-handed subjects when based on measuring the frequency in either bouts or events of hand use for each of the six studies in Table 1 for which both sets of data were available. 1 = Lambert (in press), 2 = Meguerditchian et al. (2010), 3 = Chapelain et al. (2011), 4 = Hopkins et al. (2001), 5 = Zhao et al. (2012), 6 = McGrew and Marchant (1992), 7 = Bogart et al. (2012). Handedness classification in each study was determined by *z*-scores using cut-off points of ± 1.96 .

Figure 2.

Percentage of ambiguously-handed subjects when based on measuring the frequency in either bouts or events of hand use for each of the six studies in Table 1 for which both sets of data were available. 1 = Lambert (in press), 2 = Meguerditchian et al. (2010), 3 = Chapelain et al. (2011), 4 = Hopkins et al. (2001), 5 = Zhao et al. (2012), 6 = McGrew and Marchant (1992), 7 = Bogart et al. (2012). Handedness classification in each study was determined by *z*-scores using cut-off points of ± 1.96 .

Figure 3.

Percent of chimpanzee samples that show consistent right hand use for four separate tests of the TUBE task. YNPRC = data from Yerkes National Primate Research Center and published by Hopkins et al. (in press). MONA = data from chimpanzees housed at the Mona Foundation Rescue Center in Spain and Chimfunshi Wildlife Orphanage published by Llorente et al. (2010).

Descriptive Handedness Data for 9 Studies on Handedness in Nonhuman Primates that Recorded Bouts and Frequency in Hand Use

Table 1

Authors	Species	Task	N	HI		Bout		HI		Bout		Event	
				Bout	Event	r	#R	#A	#L	#R	#A	#L	#A
Lambert (in press)	Gorilla	BF	14	-.03	-.03	.96	3	6	5	5	2	7	7
Meguerdichian et al. (2010)	Gorilla	BF	32	.35	.32	.94	18	12	2	21	7	4	4
Chapelain et al. (2011)	Bonobo	TUBE	77	.03	.04	.95	14	41	14	33	9	35	35
Hopkins et al. (2001)	Chimpanzee	TUBE	109	.13	.13	.92	24	70	15	54	22	33	33
Zhao et al. (2012)	Snub nose	TUBE	24	-.31	-.32	.99	4	7	13	7	0	16	16
McGrew & Marchant (1992)	Chimpanzee	TOOL	15	-.06	-.14	.98	5	5	5	6	1	8	8
Bogart et al. (2012)	Chimpanzee	TOOL	27	-.15	-.21	.93	5	19	3	9	2	16	16
Braccini et al. (2010)	Chimpanzee	TOOL	46	NP	.12	.71	NP	NP	NP	25	4	17	17
Humle & Matsuzawa (2009)	Chimpanzee	TOOL	24	NP	.15	.96	NP	NP	NP	17	1	10	10

BF = bimanual feeding, TUBE = the tube task, TOOL = tool use. NP = data not provided. For Braccini et al. (2010), I have provided only the results for bipedal tool use. For Humle & Matsuzawa. (2009), I grouped subjects as right, left- and ambiguously-handed based on the consistency in hand use across the 5 measures of hand use recorded in this study

Table 2

Hypothetical Handedness Data Showing Consistency in Hand Use across Tests

Subject	Test 1		Test 2		Test 3		Test 4		Total		z-score
	# R	# L	# R	# L	# R	# L	# R	# L	Left	Right	
1	12	5	31	12	13	4	22	9	78	30	4.61
2	22	4	3	7	18	2	12	19	55	32	2.47
3	34	2	12	1	31	16	19	11	96	30	5.88
4	1	12	3	9	34	3	16	1	54	25	3.26
5	43	3	23	8	17	4	13	1	96	16	7.55
6	23	2	52	20	20	30	15	24	110	76	2.49

#R = number of right hand response, #L = number of left hand responses. **Bolded** rows indicate those subjects that show inconsistent hand preferences across test sessions.