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Chimpanzees are right-handed when recording bouts of hand use

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Whether nonhuman primates exhibit population-level handedness remains a topic of considerable debate. Previous research has shown that chimpanzees are right-handed when frequencies of hand use are recorded but some have questioned the validity of this approach. In this study, we evaluated handedness in 180 captive chimpanzees for a task measuring bimanual actions. Bouts rather than frequency of hand use were recorded in each subject. Population-level right-handedness was found using both continuous and nominal scales of measurement. Neither sex nor rearing history had a significant effect on hand use. These results indicate that chimpanzees are right-handed, even when using a more conservative measure of handedness. Limitations in the use of bouts in handedness assessment are also discussed.

Historically, population-level handedness has been considered a hallmark of human evolution and related to the evolution of complex human behaviour such as tool-use and language (Annett, 1985; Bradshaw & Rogers, 1993; Corballis, 1992; Warren, 1980); however, recent studies in a host of vertebrates have called into question the uniqueness of population-level asymmetries for limb preferences and the assumption that language is a necessary condition for the expression of functional asymmetries (see MacNeilage, Studdert-

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Kennedy, & Lindblom, 1987; Rogers & Andrews, 2002; Ward & Hopkins, 1993). In primates, despite considerable evidence of population-level neuroanatomical asymmetries (see Hopkins, Cantalupo, & Pilcher, 2004, for a review), there remains considerable debate over the presence or absence of population-level functional asymmetries, notably handedness (see Hopkins & Cantalupo, in press; McGrew & Marchant, 1997; Palmer, 2002, for recent discussions).

One of the main issues surrounding the debate over whether nonhuman primates exhibit population-level handedness is the measurement of hand use. In their review article on handedness in nonhuman primates, McGrew and Marchant (1997) excluded any studies in which independence in data points was not controlled for when recording hand use. Specifically, McGrew and Marchant (1997) and others (Boesch, 1991; Byrne & Byrne, 1991; Lehman, 1993; Palmer, 2003) have argued that recording frequency of hand use for repeated motor actions that are not independent of each other inflates the sample size and increases the probability of classifying subjects as right-or left-handed. For example, when primates repeatedly reach to pick up foods, according to McGrew and Marchant (1997), right or left hand use should not be recorded for each reaching response but rather bouts of hand use should be recorded. McGrew and Marchant (1997) argue that each reaching response is not independent of each other unless they are separated by some behavioural event that would return the hands to a neutral state for eventual use. Because McGrew and Marchant (1997) adopted this criterion in their review paper, many articles reporting evidence of population-level handedness were excluded in their analyses. For example, evidence of population-level right-handedness for a coordinated bimanual task, referred to as the tube task, in chimpanzees (Hopkins, 1995), rhesus monkeys (Westergaard & Suomi, 1996; Westergaard, Champoux, & Suomi, 1997), and capuchin monkeys (Spinozzi, Castornina, & Truppa, 1998) were omitted from their analyses because frequency of hand use was recorded rather than bouts.

Despite recent empirical evidence suggesting that bouts and frequencies measure the same degree of laterality in nonhuman primates (see Damerose & Hopkins, 2002; Hopkins, Fernandez-Carriba, Wesley, Hostetter, Pilcher, & Poss, 2001), some continue to argue that the lack of independence of data points is a significant confound in the assessment of handedness in nonhuman primates, and specifically for the tube task (Palmer, 2003). The purpose of the current study was to evaluate individual hand preferences for the tube task based on bouts of hand use rather than frequencies. If previous studies in chimpanzees and other apes are confounded by measuring frequency rather than bouts of hand use then no evidence of population-level right handedness should be found using this level of analysis. In addition, the degree of asymmetry in hand use should differ significantly for estimates based on bouts as opposed to frequencies in hand use.

METHOD

Subjects

There were 180 chimpanzees in this study including 101 females and 79 males. Within the female sample, there were 34 mother-reared, 56 human-reared, and 11 wild-caught subjects. Within the male sample, there were 36 mother-reared, 33 human-reared, and 10 wild-caught individuals. Human-reared chimpanzees were subjects that were born in captivity and had been removed due to inadequate maternal care prior to 30 days of life and subsequently raised by humans. Mother-reared chimpanzees were subjects that were born in captivity but raised by their mother. Wild-caught chimpanzees were individuals captured in Africa prior to 1973 and raised in captivity since that time.

Procedure

Hand preference was assessed using a task designed to elicit coordinated bimanual actions, referred to as the tube task (see Figure 1). The procedure for this task has been described in detail elsewhere (Hopkins, 1995; Hopkins et al., 2001). Briefly, peanut butter is smeared on the inside edge of poly-vinyl-chloride (PVC) tubes approximately 15 cm in length and 2.5 cm in diameter. Peanut butter is smeared on both ends of the PVC pipe and is placed far enough down the tube that the chimpanzees cannot lick the contents completely off with their mouths but rather must use their fingers to remove the substrate.

The PVC tubes were handed to the subjects in their home cages to collect individual data from each subject. The hand and finger used to extract the peanut butter was recorded as either right or left by the experimenter. Data were collected until the subject either dropped the tube, stopped extracting peanut butter for a period of 10 seconds, or returned the PVC pipe to the experimenter. The 10-second limit did not include instances in which the subjects were locomoting with the PVC pipe. Rather this time limit was specific to instances in which they had the PVC in hand, were stationary in positional behaviour, and were not attempting to feed (usually due to the absence of any remaining peanut butter). All subjects were tested in their home cages and focal animal sampling was used to collect individual data for subjects living in larger social groups.

All of the subjects were tested on eight occasions. Most of the subjects received four test sessions per day and were tested on two different days. A 5–10-minute interval separated each test session, during which time the PVC pipes were retrieved from the chimpanzees, cleaned, and refilled with peanut butter. Bouts of right and left hand use were recorded. Bouts of hand use were separated by any event that would result in the potential change in the use of one hand or the other. In this study, bouts were separated by either the chimpanzees' movement to a different area to resume feeding or when the subjects rotated the tube in order to access the peanut butter in the opposite end. With respect to

Figure 1. Chimpanzee doing the tube task.

rotation of the tube, a change in bout was only recorded when the tube was physically rotated and not when the subject simply rotated their wrist in order to access the peanut butter in the tube. At the end of testing, the total number of left-and right-handed bouts was summed across the eight test sessions.

Data analysis

Hand preferences were characterised in two ways. First, a handedness index (HI) was calculated by subtracting the total number of left-hand bouts from the total number of right-hand bouts and dividing by the total number of bouts. Second, based on the total left-and right-hand bouts, *z*-scores were used to evaluate whether the hand preferences of individual subjects deviated significantly from chance. This is the procedure most frequently used in the nonhuman primate literature (see Hopkins, 1999). As has been done previously (Hopkins, 1995),

subjects with *z*-scores greater than 1.64 or less than –1.64 were classified as right-and left-handed, respectively. All other subjects were classified as ambiguously handed.

RESULTS

Population effects

A one-sample *t*-test based on the HI scores revealed significant population-level right-handedness, $t(179) = 4.31$, $p < .001$ with a mean HI score of .137. Using *z*-scores as the criterion for hand preference classification, there were 67 right-handed, 83 ambiguously handed, and 30 left-handed chimpanzees. The number of right-handed, $\chi^2(1, 97) = 14.11$, $p < .01$, and ambiguously handed, $\chi^2(1, 113) = 24.86$, $p < .01$, chimpanzees was significantly higher than the number of left-handed individuals. No significant difference was found in the number of right- and ambiguously handed chimpanzees.

Sex and rearing effects

A two-factor analysis of variance on the HI scores with sex and rearing history serving as independent variables failed to reveal any significant main effects or interactions. Similarly, chi-square tests of independence failed to reveal significant associations between either rearing history or sex and handedness classification.

Consistency in hand use within subjects and between samples

Of the chimpanzees in this study, 95 were subjects in the Hopkins et al. (2001) paper in which bouts and frequency of hand use was recorded for four test sessions. To evaluate consistency in hand use over time, the overall handedness index for the bout and frequency data presented in the Hopkins et al. (2001) paper were correlated with the HI values for the bouts data collected in this study. Significant positive correlations were found between the bout HI data and the bout ($r = .54$, $df = 93$, $p < .001$) and frequency ($r = .63$, $df = 93$, $p < .001$) data reported by Hopkins et al. (2001). We also compared the mean HI scores for the original sample of chimpanzees tested on the tube task ($n = 109$) to the HI scores from the chimpanzees not previously tested ($n = 71$) using an independent samples *t*-tests. No significant difference in HI scores was found between the two groups.

DISCUSSION

The results of this study indicate that chimpanzees are right-handed for the tube task when bouts rather than frequencies in hand use are used as the level of analysis. These results are consistent with previous findings in chimpanzees

using a variety of different methods of assessment. Shown in Figure 2 are the mean handedness index scores for the tube task in six different studies. Right-handedness for the tube task in chimpanzees is evident when (a) the hand used by the experimenter to provide the tube is controlled for (Hopkins, 1995), (b) the hand used by the chimpanzees to take the tube is controlled for (Hopkins et al., 2001), (c) only the first 20 responses are recorded on four separate tests (Hopkins & Cantalupo, 2003), and (d) recording bouts rather than frequency of hand use (this study). These collective findings suggest strong internal validity in the assessment of handedness for the tube task in chimpanzees. From the standpoint of external validity, evidence of population-level right-handedness in two other populations of captive chimpanzees suggests that the findings are not restricted to the Yerkes chimpanzees (Hopkins, Hook, Braccini, & Schapiro, 2003; Hopkins, Wesley, Izard, Hook, & Schapiro, in press) and likely reflects a species-specific trait, although this awaits additional studies in wild chimpanzees that assess hand use for tasks with similar motor demands to the tube task (see Hopkins & Cantalupo, in press, for discussion).

One significant difference between the findings reported here and previous findings is in the number of ambiguously handed subjects. In previous studies on hand use for the tube task, there were significantly more right-handed compared to ambiguously and left-handed chimpanzees in the samples, a finding that differs from the patterns of results reported here using bouts. Based on this observation, it could be argued that measuring bouts of hand use yields different results compared to using frequencies of hand use. One problem with this interpretation is that hand preference classifications based on *z*-

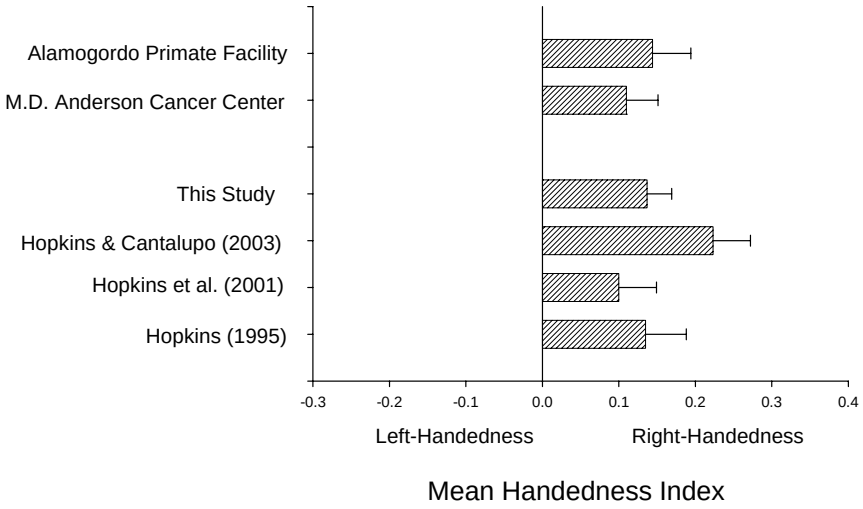

Figure 2. Mean handedness index scores for the tube task in six studies with chimpanzees.

scores will be influenced by the total number of observations, with statistical significance being more difficult to detect with smaller sample sizes. The mean number of bouts produced by the chimpanzees in this study was 49.34, whereas the mean number of responses based on frequencies reported in the Hopkins et al. (2001) paper was 118.52. Thus, in order to fairly compare the distributions in hand preferences based on *z*-scores, the mean number of bouts would need to approximate the mean number of responses based on frequencies. This observation reflects one of the central problems of using *z*-scores with an alpha of $p < .05$ to classify the subjects' hand preferences. This is a very conservative approach and it increases the likelihood of classifying as ambiguously handed subjects that are probably not truly ambidextrous but weakly right-or left-handed, particularly when sample sizes are small. Moreover, as has been argued elsewhere (Hopkins, 1999), using *z*-scores to classify subjects into different handedness groups reduces the sensitivity of the measurement of handedness from a continuous to a nominal scale. Arguably, there is no need to adopt this approach if one assumes that handedness lies on a continuous (strongly left-to strongly right-handed) rather than on a discrete scale of measurement (right-, ambiguously, or left-handed). Lastly, the ability to compare handedness distributions between species, particularly between human and nonhuman primates, is compromised by using *z*-scores because hardly anyone studying handedness in humans uses *z*-scores to classify subjects into different handedness groups.

As an alternative to using *z*-scores with alpha set to $p < .05$ to classify subjects into different handedness groups, we have argued elsewhere that other approaches can be used (Hopkins & Pearson, 2000). Specifically, we have adopted a procedure in which subjects that have handedness index values that are greater or less than three standard errors from a hypothetical mean of zero (which would be predicted if the sample were normally distributed) are classified as right-or left-handed. Subjects with handedness index values falling within three standard errors are classified as ambiguously handed. This approach allows for classification of subjects into handedness groups, but it is not as conservative as the use of *z*-scores. In addition, because the standard error values would be influenced by the number of subjects in the study, it is sensitive to variability in sample sizes between studies. The distribution of handedness when applying this analysis to the four tube task studies discussed previously is shown in Table 1. As can be seen, the relative distribution of handedness is comparable and more consistent with the handedness index data than the distributions based on *z*-scores.

Despite the evidence of population-level right-handedness found in this study using bouts, we are not convinced that using bouts alone is the best or the most sensitive measure of laterality in nonhuman primates. For example, Hopkins (1999) has argued that one limitation of only assessing hand use using bouts is that subjects can exhibit asymmetries in bout length that are

TABLE 1
Distribution of handedness based on handedness classifications derived from standard error scores

	Hand preference		
Study	*L*	*A*	*R*
Hopkins, 1995	35	15	60
Hopkins et al., 2001	32	21	56
Hopkins & Cantalupo, 2003	36	20	76
This study	52	27	101

L = left-handed, A = ambiguously handed, R = right-handed.

not accounted for by measuring bouts alone. For example, a subject could make 10 single responses with the left hand and 10 bouts of 9 responses with the right hand, for a total of 90 responses. If bouts were the only level of analysis then the example above would yield an ambiguously handed subject (10 left-and 10 right-hand bouts). Using the frequency measure, the subject would be classified as right-handed. Clearly using bouts as the sole measure of laterality would not fully capture the expression of asymmetries in hand use by this subject.

Finally, on theoretical grounds, we believe the argument that the lack of independence of data points has confounded the expression of population-level asymmetries in previously reported studies in nonhuman primates is not warranted (McGrew & Marchant, 1997; Palmer, 2003). The argument is that the lack of independence of data points when recording frequencies in hand use increases the sample size of individual observations and increases the likelihood of being classified as right-or left-handed. However, there is no reason to assume that the increased observations would necessarily bias the sample towards increased representation of right-or left-handed individuals at the population level. In other words, the bias should be randomly distributed and therefore should not skew the population in one direction or another.

In conclusion, using bouts as the level of analysis in evaluating individual hand preference, chimpanzees showed population-level right-handedness for a task requiring coordinated bimanual actions. These results are consistent with previous studies using frequency of hand use as the level of analysis, and the cumulative results on handedness for the tube task suggest that chimpanzees are right-handed independent of the manner in which hand use is characterised or the method of assessment. Under certain experimental circumstances or observational conditions, or for certain behaviours, measuring bouts of hand use may be appropriate, but using bouts as the sole criterion for assessment of handedness seems unwarranted and potentially limiting. Investigations of handedness in

nonhuman primates should use as many levels of analysis as possible so that multiple approaches to data analysis can be utilised for comparison to findings between species, including humans.

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REFERENCES

Annett, M. (1985). *Left, right, hand, and brain: The right-shift theory*. Hove, UK: Lawrence Erlbaum Associates Ltd.

Boesch, C. (1991). Handedness in wild chimpanzees. *International Journal of Primatology*, *6*, 541–558.

Bradshaw, J., & Rogers, L. J. (1993). *The evolution of lateral asymmetries, language, tool use and intellect.* San Diego, CA: Academic Press.

Byrne, R. W., & Byrne, J. M. (1991). Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla gorilla berengei*). *Cortex*, *27*, 521–536.

Corballis, M. C. (1992). *The lopsided brain: Evolution of the generative mind.* New York: Oxford University Press.

Damerose, E., & Hopkins, W. D. (2002). A comparison of scan and focal sampling procedures in the assessment of laterality for maternal cradling and infant nipple preferences in olive baboons (*Papio anubis*). *Animal Behaviour*, *63*, 511–518.

Hopkins, W. D. (1995). Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *Journal of Comparative Psychology*, *105*, 178–190.

Hopkins, W. D. (1999). On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, *20*, 851–866.

Hopkins, W. D., & Cantalupo, C. (2003). Does variation in sample size explain individual differences in hand preferences of chimpanzees (*Pan troglodytes*)? An empirical study and reply to Palmer (2002). *American Journal of Physical Anthropology*, *121*, 378–381.

Hopkins, W. D., & Cantalupo, C. (in press). Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): A critical analysis and some alternative explanations. *Laterality.*

Hopkins, W. D., Fernandez-Carriba, S., Wesley, M. J., Hostetter, A., Pilcher, D., & Poss, S. (2001). The use of bouts and frequencies in the evaluation of hand preferences for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): An empirical study comparing two different indices of laterality. *Journal of Comparative Psychology*, *115*, 294–299.

Hopkins, W. D., Hook, M., Braccini, S., & Schapiro, S. J. (2003). Population-level right handedness for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): Replication and extension in a second colony of apes. *International Journal of Primatology*, *24*, 677–689.

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., Pilcher, D., & Cantalupo, C. (2004). Neural basis of cognition, communication and handedness in nonhuman primates. In D. Maiestripieri (Ed.), *Primate psychology* (pp. 424–450). Cambridge, MA: Harvard University Press.

Hopkins, W. D., Wesley, M. J., Izard, K., Hook, M., & Schapiro, S. J. (in press). Chimpanzees are right-handed predominantly: Replication and extension in a third colony of apes. *Behavioral Neuroscience*.

Lehman, R. A. W. (1993). Manual preference in prosimians, monkeys, and apes. In J. P. Ward & W. D. Hopkins, (Eds.), *Primate laterality: Current behavioral evidence of primate asymmetries* (pp. 107–124). New York: Springer-Verlag.

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

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.

Palmer, A. R. (2002). Chimpanzee right-handedness reconsidered: Evaluating the evidence with funnel plots. *American Journal of Physical Anthropology*, *118*, 191–199.

Palmer, A. R. (2003). Reply to Hopkins and Cantalupo: Chimpanzees' right-handedness reconsidered: Sampling issues and data presentation. *American Journal of Physical Anthropology*, *121*, 382–384.

Rogers, L. J., & Andrews, R. J. (2002). *Comparative vertebrate lateralization.* Oxford: Oxford University Press.

Spinozzi, G., Castornina, 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.

Ward, J. P., & Hopkins, W. D. (1993). *Primate laterality: Current behavioral evidence of primate asymmetries.* New York: Springer-Verlag.

Warren, J. M. (1980). Handedness and laterality in humans and other animals. *Physiological Psychology*, *8*, 351–359.

Westergaard, G. C., & Suomi, S. J. (1996). 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., Champoux, M., & Suomi, S. J. (1997). Hand preference in infant rhesus macaques (*Macaca mulatta*). *Child Development*, *68*, 387–393.