

Reply to Hopkins and Cantalupo: Chimpanzee Right-Handedness Reconsidered—Sampling Issues and Data Presentation

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GENERAL ISSUES REGARDING PRIMATE LATERALITY STUDIES

Hopkins et al. (2001) deserve much credit for having raised the bar for laterality studies in nonhuman primates by routinely studying such a large number of individuals and by developing well-defined tasks, such as the TUBE task, to try to quantify individual laterality in a reliable way. They also deserve credit for repeating prior studies to assess the consistency of results, because true replications are so rarely conducted (Palmer, 2000). Nonetheless, the reply by Hopkins and Cantalupo raises several important issues regarding their and others' work on chimpanzee handedness.

First, Hopkins and Cantalupo are correct that the unexpected patterns revealed by funnel graphs of the 1994 handedness data (Hopkins, 1994; Palmer, 2002) only became apparent because sample size (number of handedness observations per individual) varied. They are also correct that standardizing the number of observations per individual totally eliminates any possible sample-size effects: a funnel graph is only useful after the fact, as a form of quality-check of the data. The real question, however, is not as Hopkins and Cantalupo suggest, "How many observations to take per individual chimpanzee?" but rather, "What aspects of the behavioral sampling protocol gave rise to the unexpected patterns in the first place?"

Eliminating variation in the number of observations per individual merely eliminates the symptoms, but not the underlying cause(s), of the unusual distributions reported in Palmer (2002): why was right-handedness of individual chimpanzees more pronounced among those individuals for which fewer observations were recorded? If the underlying causes were not eliminated in the present study as indicated by Hopkins and Cantalupo, then they may still contribute to an apparent population-level right-handedness. Some further reflections by Hopkins et al. on the possible underlying causes of the odd patterns in the 1994 data might provide valuable insights that would help improve the design of future primate handedness studies.

Second, my critique (Palmer, 2002) was also intended to illustrate how graphical presentation of data in as unreduced a form as possible (e.g., scatterplots, frequency distributions) is preferable to

statistical summaries. Tabulated statistical summaries, although economical in terms of journal space, invariably obscure details about the data that may affect confidence in the results or that might suggest alternative interpretations. If, as was done in the original 1994 study, Hopkins and Cantalupo were to publish the raw data behind the statistical summaries tabulated in their reply and also in the more extensive study of Hopkins et al. (2001), this would allow the evidence for population-level right-handedness (at least among chimpanzees at the Yerkes Primate Research Center (YRPRC)) to be judged more fully and fairly.

For example, Hopkins kindly provided to me raw data on the TUBE task for 109 chimpanzees at the YRPRC (from Hopkins et al., 2001), where the overall percent right-hand use was very similar to that reported in Hopkins (1994) for bimanual feeding (Table 1). Seventy-five of these individuals were also included in the 1994 study, and of these, handedness was based on more than 25 observations for 56 of them (for the justification to exclude individuals with 25 or fewer observations, see Palmer, 2002). The correlation between percent right-hand use during bimanual feeding (holding food in one hand while removing portions with the other) and percent right-hand use by the same individual in the TUBE task (holding a tube in one hand and scooping out peanut butter with a finger of the other) is not overly compelling (Fig. 1). Although these tasks are somewhat different, I am surprised to see so little consistency between tasks that require the simultaneous use of both hands in such a similar, coordinated fashion during feeding. If chimpanzees at the YRPRC exhibit population-level right-handedness for bimanual tasks, as the data in Table 1 suggest, rather little of this right-handedness appears to derive from consistent hand preferences by individual chimpanzees.

Finally, as someone outside the field of primate laterality, I have always been troubled by handedness data obtained from captive animals, as have other primatologists (McGrew and Marchant, 1997). No matter how much care is taken to avoid introducing handedness biases in the sampling protocol

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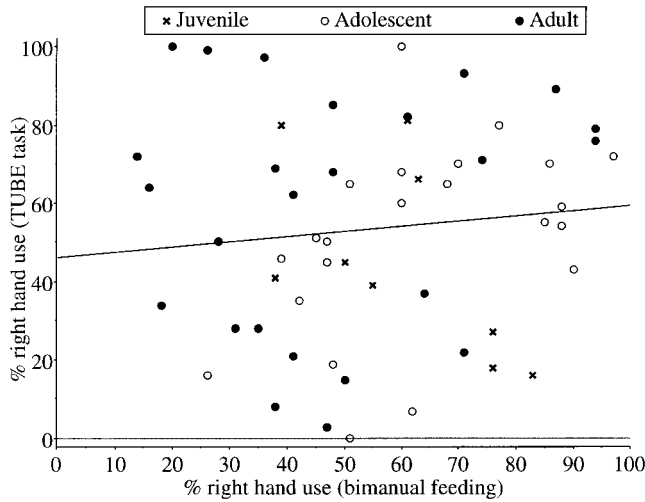


Figure 1. Consistency of handedness (raw percent right-hand use) for two related tasks among 56 individual chimpanzees at YRPRC: bimanual feeding (holding a food object in one hand while removing portions of it with the other, from Hopkins, 1994) and TUBE task (holding a tube in one hand and scooping out peanut butter with a finger of the other, from Hopkins et al., 2001). Line represents least-squares linear regression fit to the data. The association, although positive, is not significant statistically, either for all individuals ($r = 0.12, P = 0.36$, Spearman coefficient of rank correlation) or when restricted to individuals that were already adolescents and adults in the 1994 study ($N = 47, r = 0.21, P = 0.16$). For reasons outlined in Palmer (2002), only individuals with more than 25 hand-use observations in the 1994 data were included. Handedness for all individuals in the TUBE task was based on more than 25 observations, so none were excluded. Age groupings among chimps in the 1994 study were: juvenile (<7 years old), adolescent (7–15 years old), adult (>15 years old).

of a particular study, I wonder to what degree captive chimpanzees have been irreconcilably biased toward right-handedness simply by watching their strongly right-handed captors go about many other daily tasks unrelated to the study. Chimps may not only imitate human behaviors, or behaviors of other chimps; they may also imitate the overwhelming human tendency to use the right hand for most tasks. I'm afraid I see little solution to this problem but to encourage more studies of wild populations, like those of Marchant and McGrew (1996) and McGrew and Marchant (2001).

TECHNICAL ISSUES REGARDING HOPKINS AND CANTALUPO

To avoid confusion, I should note that Hopkins and Cantalupo misrepresent one expected pattern revealed by a funnel graph. No “basic statistical assumptions of increasing effects with increasing sample size” are made when interpreting a funnel graph. As outlined in my original paper (Fig. 1 of Palmer, 2002), the *variability* should actually decrease with increasing sample size, and the expected *mean effect size* should be independent of sample size.

Hopkins and Cantalupo are correct that the number of observations per individual chimpanzee in the 1994 study was confounded by age (i.e., more observations were obtained from younger individuals, and younger individuals tend to be less lateralized), and that this at least partly contributed to the decline in right-handedness with increasing number of observations per individual, as I too noted (Palmer, 2002). However, this pattern was even more pronounced among older chimpanzees (see Table 3 of Palmer, 2002), so the patterns revealed by the funnel graphs were not due solely to the confounding effects of age. The question therefore still remains: why was right-handedness more pronounced among individuals for which fewer observations were recorded?

Finally, as I understand their methods, the results reported by Hopkins and Cantalupo appear to be confounded by pseudoreplication (Hurlburt, 1984), and may therefore yield inflated estimates of individual hand preference. Equal sample sizes were obtained for each individual chimpanzee by recording “the first 20 hand-use responses” on four separate occasions when performing the TUBE task (Hopkins et al., 2001). However, if an individual chimp holds the tube in its left hand, and inserts its right finger into the tube 20 times in succession, is it appropriate to score this as 20 independent insertions of the right finger (as Hopkins and Cantalupo appear to have done), or should it simply be scored as one grasp of the tube with the left hand? If each finger insertion was scored as an independent observation, I am not surprised that “the majority (90%) of chimpanzees show a significant hand preference” according to this measure (note, however, that the actual data reported in Hopkins and Cantalupo (2002) show only 100 of 132 chimpanzees (or 76%)

TABLE 1. Frequencies of hand use by chimpanzees at YRPRC reported in different studies

Left	Number of individuals		% Right ²	Activity (source)
	Ambilateral ¹	Right		
28	58	54	65.9%	Bimanual feeding (Hopkins, 1994)
32	19	59	64.8%	TUBE task (Hopkins, 1995)
33	22	54	62.1%	TUBE task (Hopkins et al., 2001)
29	32	71	71.0%	TUBE task (Hopkins and Cantalupo, 2003)

¹ Ambilateral means difference in hand use between sides in an individual did not exceed that expected due to binomial sampling variation.

² Percent of those individuals exhibiting significant handedness.

exhibited significant handedness). Might this also account for the somewhat higher percent right-handedness reported in Hopkins and Cantalupo compared to Hopkins et al. (2001) (Table 1)? Perhaps Hopkins and Cantalupo could report the number of times a chimp picked the tube up, or rotated the tube to access the other end with the same hand, or switched hands used to extract the peanut butter with the other hand. These behaviors would seem to provide better independent measures of hand preference.

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