AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 118:191–199 (2002)

Chimpanzee Right-Handedness Reconsidered: Evaluating the Evidence With Funnel Plots

A. Richard Palmer*

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

KEY WORDS primates; apes, behavior; laterality; statistics; meta-analysis; sampling error

ABSTRACT Evidence for population-level right-handedness in nonhuman primates seems inconsistent and contradictory, and many hypotheses have been advanced to account for this volatility. Funnel plots (scatter plots of percent right-hand use vs. sample size) offer a straightforward graphical technique for assessing: 1) the strength and consistency of handedness, 2) whether variability is consistent with normal sampling variation, and 3) how likely reports of statistically significant handedness might have arisen due to chance (i.e., type I error). They are informative for both within- and among-population variation.

Reexamination of within-population variation from a detailed and widely cited study reporting significant population-level right-handedness in 140 individual captive chimpanzees (Hopkins [1994] Dev. Psychobiol. *27:*395–407) revealed several puzzling patterns: 1) funnel plots showed higher percent right-hand use among individuals for which fewer observations were recorded, 2) when individuals with fewer than 25 observations were excluded, statistical support for population-level right-handedness either became marginal ($P = 0.043$, when computed as average percent use of the right hand) or disappeared ($P = 0.62$, when computed as proportion of individuals using the right hand more than the left, whether they did so significantly or not), and 3) the proportion of statistically ambilateral chimpanzees actually increased with increasing number of observations per individual, rather than decreased as would be expected for true population-level right-handedness. In addition, funnel plots of among-population variation from an earlier meta-analysis (McGrew and Marchant [1997] Yrbk. Phys. Anthropol. *40:*201–232) suggested that the four reports of significant right-handedness, out of 37 estimates from 14 studies, were likely those that achieved statistical significance simply due to chance. Funnel plots, and the more refined statistical tests they suggest, confirm that the current evidence for population-level right-handedness in chimpanzees remains equivocal. Am J Phys Anthropol 118:191–199, 2002.

Does any nonhuman primate exhibit a population-level tendency to use the right hand in preference to the left? Decades of handedness research have yielded inconsistent and sometimes contradictory results for prosimians, New and Old World monkeys, and apes (reviewed in Marchant and McGrew, 1991; Hopkins and Morris, 1993; McGrew and Marchant, 1997; Hopkins, 1999).

Whether directional handedness exists in nonhuman primates remains central to discussions of the evolutionary origins of human handedness (MacNeilage et al., 1987; MacNeilage, 1991; Bradshaw and Rogers, 1993; Hellige, 1993; Hopkins and Morris, 1993; Corballis, 1997). If some nonhuman primates exhibit significant population-level handedness, however weak, or if some exhibit heritable variation for the direction of handedness, then further studies of these taxa may provide critical clues about the evolutionary history of human right-handedness. Otherwise, we have little hope of reconstructing the origins of this conspicuous yet enduringly enigmatic human characteristic.

Early studies of chimpanzee handedness suggested that individual chimps developed a preference to use one hand over the other, but right- and left-hand preferences were equally common at the population level (Finch, 1941). However, more recent studies reported significant right-handedness in captive chimpanzees when using one arm to initiate a tripedal walk/run (Heestand, 1986), when drinking from their hand and making waves in water (Colell et al., 1995), and when picking up food from an upright posture (Hopkins, 1993; Hopkins and Fernandez-Carriba, 2000). Most significantly, two detailed studies of captive animals suggested population-level right-handedness during bimanual feeding (Hopkins, 1994, 1995). These results have been cited often (Hopkins, 1996; Corballis, 1997;

Grant sponsor: Natural Sciences and Engineering Research Council of Canada; Grant number: A7245.

*Correspondence to: A. Richard Palmer, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. E-mail: rich.palmer@ualberta.ca

Received 22 January 2001; accepted 3 December 2001.

DOI 10.1002/ajpa.10063
Published online in Wiley InterScience (www.interscience.wiley.com).

McGrew and Marchant, 1997; Hopkins, 1999; Lacreuse et al., 1999; Harrison and Byrne, 2000) because of their large sample sizes (>100 individuals in each), even though the pattern has not been confirmed among wild chimpanzees (Marchant and McGrew, 1996). Thus the existence of directional handedness in chimpanzees remains controversial.

Studies of primate hand preference are plagued by many problems (Marchant and McGrew, 1991; McGrew and Marchant, 1997; Hopkins, 1999), including: 1) small sample sizes (both number of observations per individual and number of individuals), 2) inconsistent methods, both for quantifying handedness at the individual level and for testing for departures from random hand use at the population level, 3) conflicting results for different behaviors in the same species, and 4) lack of independence of data because many different observations are often taken on the same small sample of individuals. Furthermore, some of the published reports of statistically significant departures from 50:50 hand use have undoubtedly arisen simply due to sampling variation, since studies that yield statistically significant results are more likely to be published than those that do not, particularly if based on small sample sizes (Palmer, 2000).

EXPLORING HANDEDNESS VARIATION WITH FUNNEL PLOTS

Funnel plots (Light and Pillemer, 1984) offer an attractive approach for visualizing handedness variation. They were developed as part of the suite of tools used in meta-analysis (the quantitative synthesis of research results across multiple studies; Cooper and Hedges, 1994), and are used primarily to detect publication biases that arise due to selective reporting (e.g., absence of nonsignificant results at small sample sizes or dependence of effect size on sample size; Light and Pillemer, 1984). However, they are also valuable for visualizing how statistically well-behaved data are, and for visualizing how compelling the evidence is for an overall effect, or for differences among groups of interest (Palmer, 2000). On both of these grounds, they are a valuable addition to potentially misleading tables of summary statistics.

A funnel plot is nothing more than a scatter plot of some standardized statistical descriptor as a function of sample size. If a single true mean exists, and if variation in the descriptor arises solely from sampling error, statistical theory predicts four properties of such a scatter plot (Palmer, 1999): 1) variation about the mean should be approximately normal at all sample sizes, 2) variation about the mean should decrease with increasing sample size, 3) the mean should be independent of sample size, and 4) approximately 1 in 20 observations should be significant statistically at $P < 0.05$, regardless of sample size, as would be expected due to chance.

Examples of likely patterns of handedness variation are best illustrated via simulation. If no hand preference exists, average percent right-handedness should not differ from 50% (Fig. 1a), and the distribution should exhibit all four properties listed above due to sampling variation. Note that the expected patterns here, and for all simulations of Figure 1, are the same for both within-population variation (percent use of right hand per individual) and among-population variation (percent of individuals using right hand per sample).

If a true population-level hand preference exists, and if all variation in percent right-handedness is due only to sampling variation, then five predictions obtain (Fig. 1b): 1) percent right-handedness should be normally distributed about a mean that is greater than 50% regardless of sample size, 2) the variation in right-handedness should decline with increasing sample size and converge towards a mean that is greater than 50%, 3) the extent of right-handedness should be independent of sample size, 4) more than 1 out of 20 cases should reach statistical significance at the $P < 0.05$ level, and 5) more cases should exhibit statistically significant right- rather than left-handedness.

If, as is likely, the true level of handedness varies among individuals or among samples (due, e.g., to learning or to genetic differences), then handedness variation arises from two sources: 1) true heterogeneity in expected hand use, and 2) sampling variation. The exact form of handedness heterogeneity is probably complex, but a rough idea of its effect on funnel graphs may be obtained by assuming that the expected right-handedness varies randomly about some mean value. If the mean is close to 50%, many more individuals or samples will exhibit statistically significant handedness, either right or left (Fig. 1c), than if the scatter was due solely to sampling variation (Fig. 1a). However, statistically significant right- and left-handed cases should be equally frequent. In addition, depending on the level of heterogeneity, the scatter should decline with increasing sample size (Fig. 1c). Finally, if the mean right-handedness is truly greater than 50% (Fig. 1d), significant estimates of right-handedness should outnumber those for left-handedness, and if handedness heterogeneity is only modest, the scatter should decline with increasing sample size.

To assess the strength of the evidence for population-level hand preference in a chimpanzees, I used funnel plots, and some associated statistical tests, to reexamine results from two published studies: the extensive and detailed within-population study reported by Hopkins (1994) for 140 captive chimpanzees, and a detailed summary of among-population variation tabulated by McGrew and Marchant (1997).

METHODS

Handedness simulations

To illustrate some of the expected patterns that funnel graphs might exhibit, right-handedness vari-

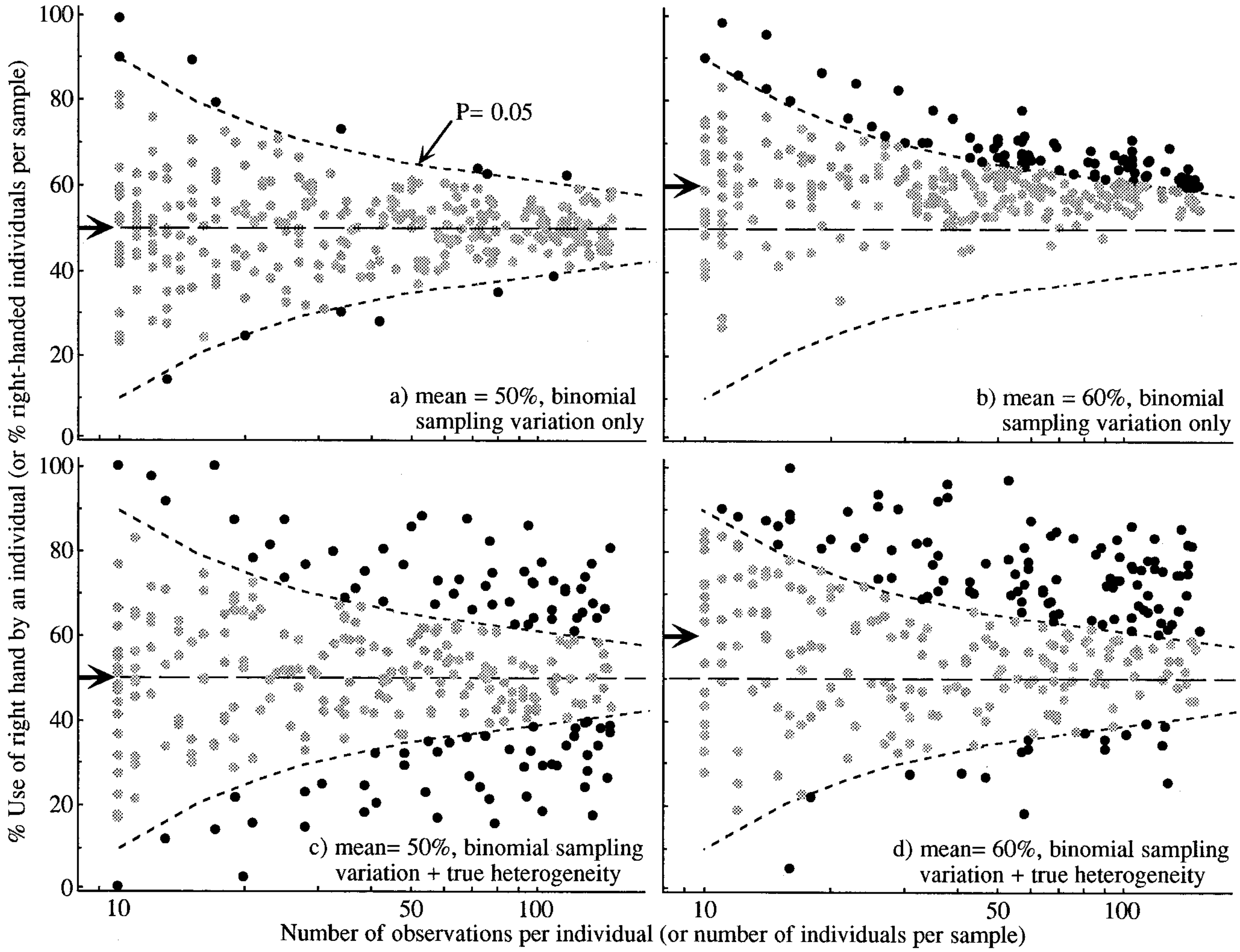

Fig. 1. Simulated variation in right-hand use as a function of number of observations per individual (or number of individuals per sample), for four alternative hypotheses: (**a**) *no laterality*: expected percent right-handedness is 50% for all individuals or all samples, scatter due only to binomial sampling variation; (**b**) *weak, invariant right-handedness*: expected percent right-handedness is 60% for all individuals or all samples, scatter due only to binomial sampling variation; (**c**) *no population-level handedness but true handedness heterogeneity among individuals or samples*: average percent right-handedness is 50%, scatter due both to binomial sampling variation and to random variation in expected right-handedness among individuals or among samples due to learning or genetic differences; and (**d**) *weak population-level right-handedness with true handedness heterogeneity among individuals or samples*: the average percent right-handedness is 60%, scatter arises as in c. Long-dashed line indicates 50% right-handedness. Arrowheads indicate expected mean right-handedness. Curved dashed lines indicate statistical significance levels for a binomial distribution ($\alpha = 0.05$), from Table Q of Rohlf and Sokal (1995). Grey points are those not significant at the $\alpha = 0.05$ level. Note that the x-axis is log scale. See Methods for simulation protocol.

ation, as a function of sample size, was simulated for four alternative hypotheses (Fig. 1): a) *no laterality*: expected proportion right-handed, p = 0.5, variability due only to binomial sampling variation; b) *weak, invariant right-handedness*: expected proportion right-handed, p = 0.6, variability due only to binomial sampling variation; c) *no population-level handedness, but true handedness heterogeneity*: the expected proportion right-handed was a random normal variate, p = random normal (mean = 0.5, SD = 0.15), so that variability was due both to binomial sampling variation and to random variation in expected right-handedness due to learning or genetic differences; and d) *weak population-level right-handedness with true handedness heterogeneity*: the expected proportion right-handed was a random normal variate centered on 0.6, p = random normal (mean = 0.6, SD = 0.15), variability due to the same sources as simulation c. Note that the simulations are identical for either within-population variation (x axis = number of observations per individual, y axis = percent right hand use per individual) or among-population variation (x axis = number of individuals per sample, y axis = percent of right-handed individuals per sample).

For all simulations, N (number of individuals or number of samples) = 300; n (number of observations per individual or individuals per sample) = ([random uniform (range, 0–1)]^2 * 141) + 10, which yields values of n that range from 10–150 and that are more numerous for smaller n; p (the proportion of times the right hand was used by an individual or the proportion of right-handed individuals in a sample) varied as indicated above for each simulation; $q = 1 - p$; binomial variation in percent right-handedness was computed using a normal approximation, $\%R = 100 * (p + ([(p * q)/n] * \text{random normal } (0, 1)))$. Simulations were conducted with StatView 5 (SAS Institute, Cary, NC).

Within-population patterns

Within-population variation was examined using data from Table 1 of Hopkins (1994), who reported individual handedness data for bimanual feeding (holding food in one hand and using the other hand to transfer portions of the food to the mouth) for 140 captive chimpanzees. These data included: sex (male, female), rearing category (mother-reared, nursery-reared), individual age, pecent right-hand use, number of feeding observations per individual, and a coding of each individual as "right-handed," "left-handed," or "ambilateral" that was based on the statistical significance of that individual's hand preference (i.e., to be scored as handed, an individual chimpanzee had to use one hand more frequently than expected due to binomial sampling variation). Individuals with fewer than 15 observations were excluded from the analysis in the original study. See Hopkins (1994) for further details about protocol and analysis.

Funnel plots (Light and Pillemer, 1984) were used to examine the dependence of right-handedness on the number of feeding observations per individual. Funnel plots were also used to judge whether different groups of chimpanzees (e.g., different sexes, rearing conditions, or ages) exhibited different patterns of variation.

Population-level handedness was tested statistically in several ways. First, departures of the frequencies of right- and left-handed individuals from 50:50 were tested twice using chi-square tests (Sokal and Rohlf, 1995): once for all individuals regardless of whether their individual hand preference was significant statistically, and once restricted to individuals that exhibited a statistically significant hand preference (as determined by Hopkins, 1994). Second, departures of mean hand use from 50% among all individuals were tested using a simple *t*-test. Third, the first two tests were repeated using only individuals for which more than 25 behavioral observations had been recorded.

The statistical dependence of individual handedness on the number of behavioral observations taken per individual was tested using two-way contingency tables (Sokal and Rohlf, 1995). The sample was divided into four groups, based on number of behavioral observations: = 26–31, 32–37, and >37 observations per individual. The thresholds were chosen solely to obtain four groups of as equal a sample size as possible, and yielded an average of 35 individuals per group (see Table 1). These analyses

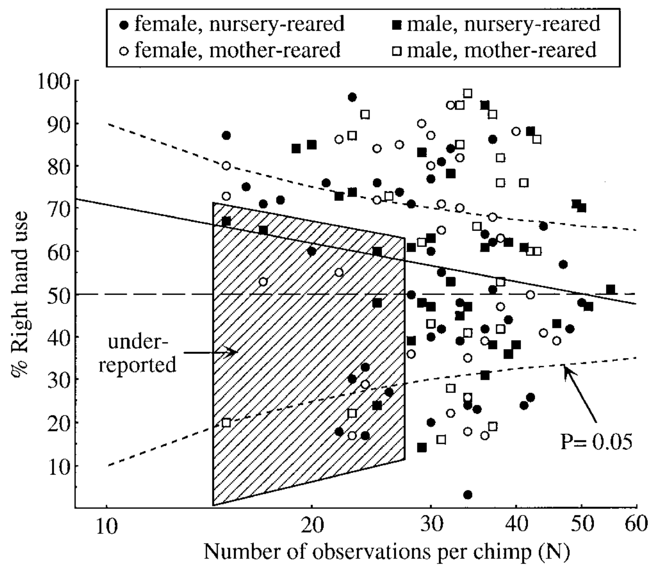

Fig. 2. Percent use of right hand as a function of sample size for individual male and female chimpanzees (*Pan troglodytes*), reared either by their mother or in a nursery; data from Hopkins (1994). All ages were included. Dashed lines as in Figure 1. Solid line indicates a least-squares, linear regression fit to all the data (N = 140, least-squares linear regression slope (SE) = −30.0 (15.42); Spearman's r = −0.15; $P = 0.074$). Shaded area indicates where fewer observations were reported than would have been expected in normal, within-sample variation (e.g., Fig. 1c).

were conducted once for all chimpanzees, regardless of whether their individual hand preference was significant statistically, and once for the restricted sample of chimpanzees that exhibited statistically significant individual hand preference. These contingency table analyses were also repeated, as above, using only individuals with more than 25 behavioral observations.

Among-population patterns

Among-population variation was examined using all of the data tabulated for a variety of behaviors, in both wild and captive chimpanzees, from Table 6 of McGrew and Marchant (1997). Funnel plots were used to examine the variation in right-handedness among the 37 separate population estimates from 14 published studies.

RESULTS

Within-population patterns

Funnel plots of data from Hopkins (1994) on percent right-hand use as a function of number of observations per individual chimpanzee revealed three unexpected patterns. First, right-handedness was more prevalent among chimps for which fewer behavioral observations had been obtained (Fig. 2, Table 1). Second, this pattern was apparent for both sexes and both rearing conditions (Fig. 2), as well as among different age groups (Fig. 3). Third, the proportion of "ambilateral" chimpanzees (i.e., individual chimps whose hand use did not depart significantly from 50:50) was higher if more behavioral observa-

TABLE 1. Percentage of individual chimpanzees scored as right-handed, left-handed, or ambilateral as a function of sample size[1]

a) Handedness determined statistically (four sample-size groups)[2]

Handedness category	Number of observations per chimp <26	26–31	32–37	>37	N	Overall % R	Statistical significance (P)[3] Independence of sample size	Directionality
All sample sizes								
Right	55.6%	34.4%	35.9%	27.3%	54	65.9%	0.003**	0.006**
Left	22.2%	12.5%	33.3%	9.1%	28			
Ambilateral	22.2%	53.1%	30.8%	63.6%	58			
Total individuals (N)	36	32	39	33	140			
Sample sizes >25 only								
Right		34.4%	35.9%	27.3%	34	63.0%	0.024*	0.077†
Left		12.5%	33.3%	9.1%	20			
Ambilateral		53.1%	30.8%	63.6%	50			
Total individuals (N)		32	39	33	104			

b) Handedness based on raw counts (four sample-size groups)

Handedness category	Number of observations per chimp <26	26–31	32–37	>37	N	Overall % R	Statistical significance (P)[3] Independence of sample size	Directionality
All sample sizes								
Right	72.2%	58.1%	46.2%	56.3%	80	58.0%	0.153	0.074†
Left	27.8%	41.9%	53.9%	43.8%	58			
Total individuals (N)	36	31[4]	39	32[4]	138			
Sample sizes >25 only								
Right		58.1%	46.2%	56.3%	54	52.9%	0.552	0.621
Left		41.9%	53.9%	43.8%	48			
Total individuals (N)		31[4]	39	32[4]	102			

c) Handedness determined statistically (three sample-size groups)[2]

Handedness category	Number of observations per chimp <29	29–35	>35	N	Statistical significance (P)[3] Independence of sample size
All sample sizes					
Right	52.2%	34.8%	29.2%	54	0.048*
Left	19.6%	26.1%	14.6%	28	
Ambilateral	28.3%	39.1%	56.3%	58	
Total individuals (N)	46	46	48	140	

[1] Data from Table 1 of Hopkins (1994) and as presented in Figures 2 and 3. N, number of chimps.
[2] Individuals were scored as right- or left-handed only if they used one hand significantly more frequently than would be expected by chance, based on a binomial test; remaining individuals were scored as ambilateral (coded as R, L, or A, respectively, in Table 1 of Hopkins, 1994).
[3] *P* values for "independence" indicate the probability that handedness state was independent of number of handedness observations per chimp (contingency table analysis); significant *P* values indicate lack of independence. *P* values for "directionality" were obtained from a chi-square test (corrected for continuity; Sokal and Rohlf, 1995) of total observed numbers of right- and left-handed individuals compared to null proportions of 50:50, and indicate level of statistical support for population-level right-handedness.
[4] One individual used both hands equally frequently and could not be included in these analyses.
† $0.1 > P > 0.05$.
* $0.05 > P > 0.01$.
** $0.01 > P > 0.001$.

tions were taken: among individuals with more than 35 observations, 56.3% were ambilateral, whereas among individuals with 29–35 observations, 39.1% were ambilateral and only 28.3% of chimps with <29 observations were statistically ambilateral (Fig. 2; see also Table 1c). This graphical evidence suggested that I undertake further statistical analyses.

Contingency table analyses confirmed a significant dependence of handedness on the number of observations taken per individual chimpanzee when hand preference was determined statistically (Table 1a). This dependence existed when all sample sizes were included ($P = 0.003$), when only individuals with more than 25 feeding observations were included ($P = 0.024$), and when the data were grouped into three sample-size categories rather than four ($P = 0.048$, Table 1c). This dependence was not apparent when all individuals were included, whether significantly handed or not (Table 1b).

The proportion of right-handed chimps was higher than expected due to chance among all the individual chimps showing a statistically significant hand preference ($P = 0.006$, Table 1a), as reported by Hopkins (1994) in the original study. However, when individuals with fewer than 26 observations were excluded, this rightward bias became nonsignificant, though only marginally so ($P = 0.077$; Table 1a). Furthermore, if all individuals were included in the analysis, whether their individual handedness was significant or not, the side bias was not significant ($P = 0.074$; Table 1b). Significantly, this weak tendency toward right-handedness disappeared entirely if individuals with fewer than 26 observations were excluded ($P = 0.621$; Table 1b).

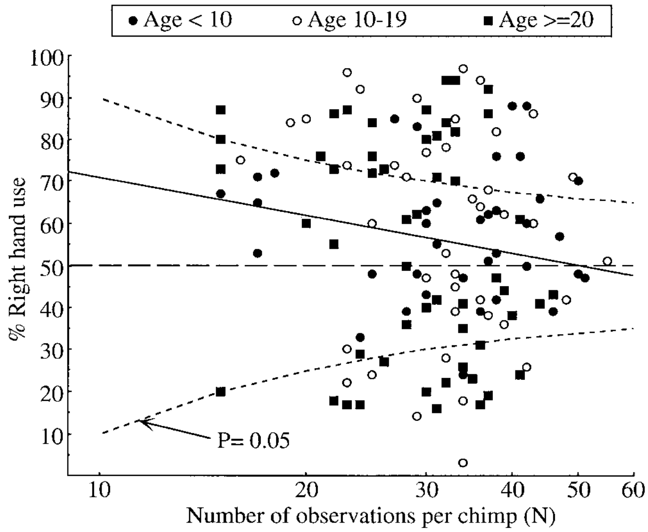

Fig. 3. Percent use of right hand as a function of sample size for individual chimpanzees (*Pan troglodytes*) of different ages; data from Hopkins (1994). Both sexes and rearing categories were pooled. Dashed lines as in Figure 1.

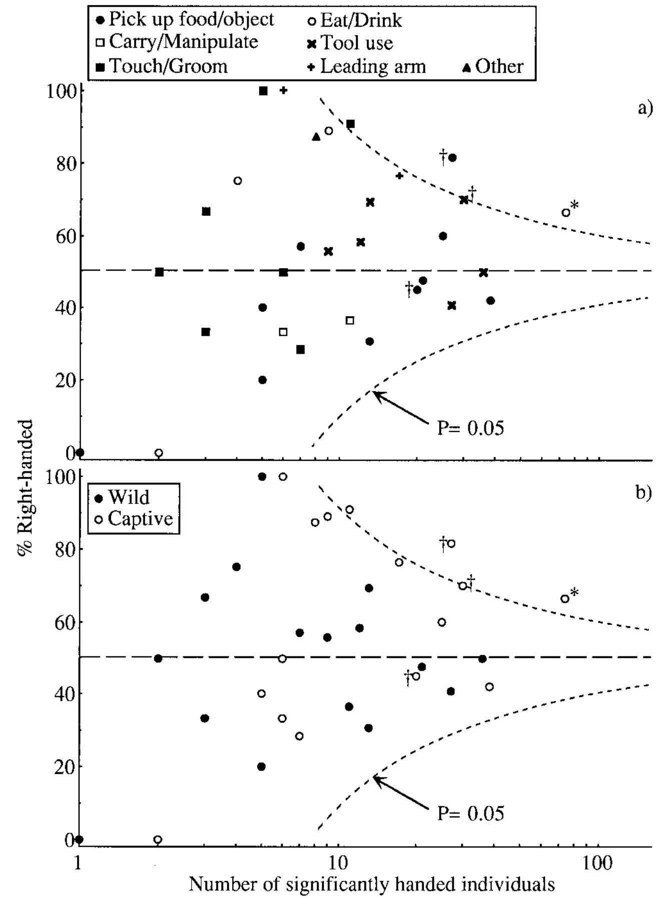

Fig. 4. Percent of right-handed individuals (*Pan troglodytes*) among those found to be significantly handed (to either right or left), as a function of sample size, from all published studies tabulated by McGrew and Marchant (1997, their Table 6). Dashed lines as in Figure 1. Asterisks indicate focal study by Hopkins (1994); daggers indicate other studies by Hopkins.

The same patterns were apparent when testing for population-level asymmetry (Table 2a). When all individuals were included, regardless of sample size, the average right hand-use of 56.4% was highly significant (N = 140, $P < 0.001$), as reported in Hopkins (1994). In addition, average percent right hand use was significant among male (but not female) chimpanzees and among the youngest individuals (<10 years of age). These departures from random hand use remained significant even after using a sequential Bonferroni correction for multiple tests (N = 10 tests; Rice, 1989).

However, when analyses were restricted to individual chimpanzees with more than 25 feeding observations, the patterns were considerably less pronounced (Table 2b). The average use of the right hand of 54.5% became only marginally significant (N = 104, $P = 0.043$), and the only remaining significant right-bias was among young individuals (< 10 years of age; $P = 0.015$). However, neither of these results remained significant after a sequential Bonferroni correction for multiple tests (N = 10 tests; Rice, 1989).

The statistical support for right-handedness therefore depended heavily on whether individuals for which few observations were taken were included (all individuals vs. individuals with more than 25 observations) and on the type of analysis conducted (comparison of mean % hand use vs. contingency table analysis of frequency data).

Among-population patterns

Among the 37 handedness estimates from 14 published studies tabulated by McGrew and Marchant (1997), only four revealed significantly more right-handed chimpanzees (among individuals found to exhibit a statistically significant hand preference). A funnel plot (Fig. 4) suggests that the few studies that reached statistical significance were those that did so due to chance, because only one fell substantially outside the 95% confidence intervals. In addition, although right-handed chimpanzees were significantly more common among individuals exhibiting a statistically significant handedness when all data were pooled (227 of 387; $P < 0.001$), significantly right-handed chimpanzees were no longer most common when the three studies by Hopkins (1994, 1995, 1996) were excluded from this analysis (135 of 250; $P = 0.23$).

DISCUSSION

Within-population patterns

The funnel plots of within-population variation in chimpanzee handedness were particularly informative (Fig. 2). They resembled the simulation results in Figure 1c more closely than those in Figure 1a, and therefore suggest that true handedness heterogeneity existed among individuals (i.e., hand use by many *individual* chimps departed significantly from 50%). However, the distribution was not as expected

TABLE 2. Mean percent right hand use by chimpanzees of different sexes, rearing conditions, and ages[1]

	a) All sample sizes			b) Sample size >25, only		
Group	N	% R-handed mean (SE)	P^2	N	% R-handed mean (SE)	P^2
All females pooled	81	54.9 (2.61)	0.067†	58	52.1 (2.94)	0.484
Females, nursery-reared	46	52.7 (3.31)	0.416	33	49.6 (3.51)	0.918
Females, mother-reared	35	57.7 (4.20)	0.077	25	55.3 (5.02)	0.303
All males pooled	59	58.4 (2.96)	0.006**	46	57.5 (3.25)	0.057†
Males, nursery-reared	34	57.3 (3.28)	0.033*	25	54.8 (3.78)	0.220
Males, mother-reared	25	59.9 (5.43)	0.080†	21	60.8 (5.53)	0.065†
Age <10 years	41	58.1 (2.51)	0.002**	33	57.2 (2.79)	0.015*
Age 10–19 years	45	56.9 (3.75)	0.071†	35	54.9 (4.07)	0.241
Age >20 years	54	54.6 (3.55)	0.205	36	51.7 (4.25)	0.697
All individuals pooled	140	56.4 (1.96)	<0.001***	104	54.5 (2.19)	0.043*

[1] Computed either for all data or for chimps that were scored for handedness more than 25 times. Data from Table 1 of Hopkins (1994), and as presented in Figures 2 and 3.
[2] *P*-values were all obtained from one-sample *t*-tests comparing the observed mean % right-handed to an expected mean of 50%. Virtually identical results were obtained when % right-handedness values were arcsine-transformed (Sokal and Rohlf, 1995) before computing means and SE (i.e., all significant *P* values were the same to at least two decimal places), so for simplicity only results for raw percentages are presented here. None of the results for sample sizes >25 remained statistically significant when *P* values were subject to a sequential Bonferroni correction for multiple tests (10 tests; Rice, 1989).
† $0.1 > P > 0.05$.
* $0.05 > P > 0.01$.
** $0.01 > P > 0.001$.
*** $P < 0.001$.

for well-behaved within-population variation (Fig. 1a,c), which summary statistics tended to obscure. The subsequent statistical analyses prompted by this odd distribution raise doubts about the strength of the evidence for population-level right-handedness in this large sample of chimpanzees. In all, three aspects of these data are puzzling.

First, percent right-handedness (Figs. 2, 3) did not vary as expected for simple within-population variation (Fig. 1c,d). The within-population chimpanzee handedness data of Hopkins (1994) departed from three of the expectations for well-behaved data (see Exploring Handedness Variation With Funnel Plots, above): 1) although variation increased as sample size decreased from 60 to 35 observations per chimp, it then declined among individuals with fewer than 35 observations (compare to Fig. 1c,d), 2) ambivalent or left-handed chimpanzees were conspicuously underrepresented among individuals for which fewer observations had been obtained (Fig. 2), so that variation was not normally distributed about the population mean at all sample sizes, and 3) mean right-handedness actually decreased with increasing sample size instead of remaining constant, although this effect was not quite significant statistically ($P = 0.074$, Fig. 2). Furthermore, the funnel plots (Figs. 2, 3) reveal that these peculiar patterns occurred within all groupings of the data (sex, rearing condition, and age).

Second, the statistical support for population-level right-handedness depended heavily on individuals for which few observations were recorded per chimp (25–30 observations). When the 25% of individuals with the smallest sample sizes (which are suspect for the reasons outlined above) were excluded from the analysis, the evidence for population-level handedness became marginal as average percent use of the right hand ($P = 0.043$, Table 2b), or disappeared entirely as proportion of individuals using the right hand more than the left whether they did so significantly or not ($P = 0.621$, Table 1b). In part, this reduced significance resulted from the lower statistical power of an analysis based on fewer individuals. However, the mean percent of individuals using their right hand also dropped, from 65.9% to 63.0% when only "significantly" handed individuals were included (Table 1a), and from 58.0% to 52.9% when all individuals were included (Table 1b). In addition, average percent hand use also dropped from from 56.4% to 54.5% when individuals with fewer observations were excluded (Table 2a,b). Although these declines of 2–5% might not seem large, they have a large impact on statistical significance because they are so close to the null hypothesis of 50%: the statistical significance of directionality either disappeared (Table 1a,b) or became marginal (Table 2b), depending on how handedness was computed, when individuals with fewer than 26 observations were excluded.

Finally, the sample-size dependence of statistically ambilateral hand use was the reverse of that expected due to normal within-population variation (Fig. 1d). On purely statistical grounds, as sample size increases, the likelihood of detecting departures from 50:50 hand use in an individual (the power of the statistical test for individual handedness) increases (Sokal and Rohlf, 1995). Therefore, if a true directional handedness existed within this population of chimpanzees, it should have been most apparent among individuals with the largest number of handedness observations (Fig. 1d). However, contrary to expectation, statistically ambilateral chimps were *most* common among individuals with the largest, rather than smallest, number of behavioral ob-

TABLE 3. Percent ambilateral hand use by chimpanzees of different ages[1]

Age	Sample size		
	<29	29–35	>35
<10 years	63.6%	77.8%	71.4%
10–19 years	8.3%	38.9%	40.0%
>19 years	21.7%	21.1%	50.0%

[1] Data from Table 1 of Hopkins (1994), and as presented in Figure 3.

servations (Fig. 2): 63.6% of chimps were statistically ambilateral among individuals with more than 37 observations, whereas only 22.2% were statistically ambilateral among individuals with fewer than 26 observations (Table 1a). Similarly, 56.3% of chimps were statistically ambilateral among individuals with more than 35 observations, whereas only 28.3% were statistically ambilateral among individuals with fewer than 29 observations (Table 1c). Therefore, the increase in proportion of ambilateral chimps was apparent regardless of whether the data were grouped into three or four categories based on sample size.

These increases in the percentage of ambilateral chimps as sample size increased were not confounded by sex, or rearing condition (Fig. 2), although they may have been partly influenced by age (W.D. Hopkins, personal communication). For the age groups of Figure 3, two-thirds of individuals with the greatest number of observations ($N > 37$) were <10 years old, whereas approximately two-thirds of individuals with the fewest number of observations ($N < 26$) were at least 20 years old ($P = 0.012$, χ^2 test of independence between the three age groups of Fig. 3 and four sample-size groups of Table 1a; proportions and significance were approximately the same when using the three sample-size groups of Table 1c, $P = 0.032$). Nonetheless, the increase in ambilaterality with increasing sample size (Fig. 3) was more pronounced among the older two age groups (Table 3), so the excess of young chimps with large sample sizes alone cannot account for this pattern.

How the excess of right-handedness at smaller sample sizes arose, remains a puzzle. Care appears to have been taken to avoid introducing unwanted biases due to the setting of the observations (McGrew and Marchant, 1997) or to imitation (Miklosi, 1999): caregivers apparently gave food to chimps with their right and left hand at random, and they placed the food in the right or left hand of the chimp at random (Hopkins, 1994). In addition, W.D. Hopkins (personal communication) said he could offer no plausible explanation for this pattern. Clearly, additional studies not confounded by such puzzling patterns are needed before conclusions can be drawn about the extent of population-level right-handedness in chimpanzees.

Among-population patterns

Funnel plots also yielded insights into causes of among-population variation in chimpanzee handedness and its dependence on activity and setting (McGrew and Marchant, 1997). First, funnel plots revealed little more than random sampling variation (see Fig. 4a vs. Fig. 1a). Of the 4 cases that reached statistical significance, 3 did so only barely. Furthermore, the statistical support for overall population-level right-handedness depended heavily on whether studies by Hopkins (1994, 1995, 1996) were included in the analysis or not. With these studies excluded, no statistical support remains for population-level right-handedness ($P = 0.23$). In view of uncertainties about the data in the detailed study by Hopkins (1994) (Figs. 2, 3; Table 1), exclusion of these studies from data summaries would seem prudent until the results of all of them have been reassessed via funnel plots.

Second, the funnel plot revealed that handedness was not more pronounced in different activities (Fig. 4a) or different settings (wild vs. captive, Fig. 4b). Clearly, additional data will be needed to make a compelling case for population-level right-handedness in chimpanzees.

Graphical approaches ensure explicit presentation of handedness data

As both the within-population and among-population examples illustrate, statistical summaries of results may obscure important features of handedness data. Funnel plots offer an attractive supplement (Light and Pillemer, 1984; Palmer, 2000). Readers can judge for themselves whether data are well-behaved and therefore whether the summary statistics reliably represent the underlying data. Funnel plots are particularly useful where a clear-cut null hypothesis exists, such as 50% right-hand use (no directional bias) in among-population studies of handedness. In addition, they provide a clear and easily interpreted picture of how compelling the differences are among groups of interest (e.g., Fig. 3a,b). Why such graphical approaches are not more widely used probably stems more from the culture of science than from anything else. As Magnusson (2000) observed, "[Scatter plots] are not very scientific. After all, anyone, even a nonscientist, could interpret them."

In view of the effort required to collect extensive sets of handedness observations, perhaps funnel plots should be incorporated in all reports where numbers of observations vary. By doing so, all data for individual animals, or for individual studies, may be presented in a clear and economical manner that will better allow readers (and those writing reviews) to judge the validity of the evidence. Summary statistics too often obscure critical aspects of the data (Palmer, 2000). An adequate presentation of the data would greatly accelerate our progress towards understanding handedness variation in nonhuman primates.

ACKNOWLEDGMENTS

I thank L. Hammond, W.D. Hopkins, W.C. McGrew, L.F. Marchant, and two anonymous reviewers for helpful comments on the manuscript. W.D. Hopkins generously shared other data files and offered many thoughtful observations on handedness patterns and their interpretation. C. Strobeck provided useful assistance with the handedness simulations.

LITERATURE CITED

Bradshaw JL, Rogers LJ. 1993. The evolution of lateral asymmetries, language, tool use, and intellect. San Diego: Academic Press.

Colell M, Segarra MD, Sabater PJ. 1995. Hand preferences in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and orangutans (*Pongo pygmaeus*) in food-reaching and other daily activities. Int J Primatol 16:413–434.

Cooper H, Hedges LV, editors. 1994. The handbook of research synthesis. New York: Russel Sage Foundation.

Corballis MC. 1997. The genetics and evolution of handedness. Psychol Rev 104:714–727.

Finch G. 1941. Chimpanzee handedness. Science 94:117–118.

Harrison KE, Byrne RW. 2000. Hand preferences in unimanual and bimanual feeding by wild vervet monkeys (*Cercopithecus aethiops*). J Comp Psychol 114:13–21.

Heestand JE. 1986. Behavioral lateralization in four species of apes? Ph.D. thesis, University of Washington, Seattle.

Hellige JB. 1993. Hemispheric asymmetry. Cambridge, MA: Harvard University Press.

Hopkins WD. 1993. Posture and reaching in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). J Comp Psychol 107:162–168.

Hopkins WD. 1994. Hand preferences for bimanual feeding in 140 captive chimpanzees (*Pan troglodytes*): rearing and ontogenetic determinants. Dev Psychobiol 27:395–407.

Hopkins WD. 1995. Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): cross-sectional analysis. J Comp Psychol 109:291–297.

Hopkins WD. 1996. Chimpanzee handedness revisited: 55 years since Finch (1941). Psychonom Bull Rev 3:449–457.

Hopkins WD. 1999. On the other hand: statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. Int J Primatol 20:851–866.

Hopkins WD, Fernandez-Carriba S. 2000. The effect of situational factors on hand preferences for feeding in 177 captive chimpanzees (*Pan troglodytes*). Neuropsychologia 38:403–409.

Hopkins WD, Morris RD. 1993. Handedness in great apes: a review of findings. Int J Primatol 14:1–25.

Lacreuse A, Parr LA, Smith HM, Hopkins WD. 1999. Hand preferences for a haptic task in chimpanzees (*Pan troglodytes*). Int J Primatol 20:867–881.

Light RJ, Pillemer DB. 1984. Summing up: the science of reviewing research. Cambridge, MA: Harvard University Press.

MacNeilage PF. 1991. The "postural origins" theory of primate neurobiological asymmetries. In: Krasnegor NA, Rumbaugh DM, Schiefelbusch RL, editors. Biological and behavioral determinants of language development. Hillsdale, NJ: Lawrence Erlbaum. p 165–188.

MacNeilage PF, Studdert-Kennedy MG, Lindblom B. 1987. Primate handedness reconsidered. Behav Brain Sci 10:247–303.

Magnusson WE. 2000. Error bars: are they the king's clothes? Bull Ecol Soc Am 81:147–150.

Marchant LF, McGrew WC. 1991. Laterality of function in apes: a meta-analysis of methods. J Hum Evol 21:425–438.

Marchant LF, McGrew WC. 1996. Laterality of function in wild chimpanzees of Gombe National Park: comprehensive study of spontaneous activities. J Hum Evol 30:427–443.

McGrew WC, Marchant LF. 1997. On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. Yrbk Phys Anthropol 40:201–232.

Miklosi A. 1999. The ethological analysis of imitation. Biol Rev 74:347–374.

Palmer AR. 1999. Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. Am Nat 154:220–233.

Palmer AR. 2000. Quasireplication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. Annu Rev Ecol Syst 31:441–480.

Rice WR. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Rohlf FJ, Sokal RR. 1995. Statistical tables. San Francisco: Freeman.

Sokal RR, Rohlf FJ. 1995. Biometry. New York: Freeman.