

of human handedness, it would be best to look at skill or dexterity differences between the hands and to concentrate the search on the nearest relatives of humans.

MacNeilage et al. place considerable stress on the Japanese studies of manual preferences of macaques for catching food thrown by the experimenters (see Table 1 of the target article). Across 435 animals, they note a statistically significant "left-hand preference." Yet most of the animals do not show a left-hand preference — 38.2% show a left preference, 29.0% a right preference, and 32.9% no preference. These minuscule differences are statistically significant, but do not constitute strong evidence of left-hand preference.

When one looks at Table 7 of the target article, which provides a summary of hand preferences in nonhuman primates, one sees only a single left preference and two right preferences listed for the great apes. The left preference is for "face touching" (Dimond & Harries 1984). MacNeilage et al. note in the text that this has also been found for English-speaking, but not for Japanese-speaking, humans. Would it make any sense, evolutionary or otherwise, to conclude that the great apes and English-speakers manifest more evidence of "handedness" than do Japanese-speakers? Should we be puzzled by the *de novo* disappearance of left face-touching dominance in Japanese-speakers? The right-hand preferences listed for the great apes are for (1) the hand used to initiate chest-beating and (2) reaching "and other use." A footnote to Table 7, however, notes that the latter preference was not replicated by Preilowski and Leder (1984). Thus, the three manual preferences of our closest nonhuman relatives, as reported by the authors, are hardly sufficient for ascribing handedness to them.

The most interesting results reported are Preilowski's (1979) finding that all eight rhesus monkeys tested showed greater ability to produce specific pressures between the fingertips of the right hand than of the left hand at the most difficult levels of the task, and the finding of Trevarthen (1978) regarding the dominance of one hand (the left in one animal and the right in the other) for performing a previously learned bimanual task within a few days after commissurotomy and chiasm-section. Although these findings do not suggest the existence of right- or left-handedness as a species characteristic, they do show cerebral dominance for the learning and execution of a complex task. MacNeilage et al. remark, as a limitation on the generalizability of the Trevarthen finding, that such dominance of one hand has not been reported in human commissurotomy patients, but this is clearly incorrect. Bogen (1969) has observed that left-hand apraxia is commonly seen in split-brain patients in the immediate postoperative period, and Trevarthen noted this in his own paper. My own experience with collosotomy patients is also consistent with this observation.

MacNeilage et al. have provided an interesting and useful review of what seems to me a remarkably unconvincing literature with respect to the proposition that nonhuman primates manifest handedness. That is not to say that the nonhuman primates do not possess handedness. For handedness to be judged to exist in nonhuman primates, it would not be necessary that a great majority of them have the same lateral preference. There may be more "left-handers" among nonhuman primates than among humans. What is required is consistency of preferences, within individual animals, across some universe of coherent, skilled, discrete, sequenced, manual acts, and ultimately some evidence of structural correlates and the hereditary transmission of them. If it should be found that a great majority of nonhuman primates do indeed manifest a right-hand superiority in such manual acts, and that they show evidence of hereditary transmission of manual preferences, then the hypothesis of a continuity of handedness between subhuman primates and humans would be powerfully supported. It would obviously be useful to have many more studies dealing with possible manual differences in tasks requiring skilled finger movements of each hand separately. It is to be hoped that

MacNeilage et al.'s target article will stimulate greater interest in such studies. For the present, the weight of the evidence seems generally negative with respect to the hypothesis of subhuman primate handedness, and MacNeilage et al.'s review does not justify a reconsideration of that conclusion.

On the one hand, on the other hand: Statistical fallacies in laterality research

I. C. McManus

Department of Psychology, University College London, London WC1E 6BT, England

The interesting theoretical speculation in MacNeilage et al.'s target article are heavily dependent for their validity on statistical analysis. Laterality research is unfortunately prone to misapplying complex statistics and producing wrong or uninterpretable findings. A recent example (and one that is pertinent to the present study) is the already influential paper by Healey, Liederman, and Geschwind (1986). Although Healey et al. purport to show that human handedness has a multidimensional structure, they in fact use a criterion for factorial significance which most statisticians would consider inappropriate (e.g., Zwick & Velicer 1986); as a result, in all probability their data might best be construed as containing only a single underlying factor.

The statistical analysis of laterality data has special problems that make it particularly vulnerable to error and confusion, and conventional statistics often cannot be applied with any ease (see McManus 1983). The target article presents a number of statistical difficulties, one of which is specific to laterality and will be considered in some detail. Other more general statistical difficulties could have been commented on, and two will be mentioned in passing: (1) The "file-drawer problem" consists of the preferential publication of statistically significant results (Rosenthal 1979). Any meta-analysis must consider whether or not it is concatenating a truly random sample of studies. In the present case, it is conceivable that researchers may only have published data when they found a population asymmetry. (2) Much emphasis is placed on the detailed data of Beck and Barton (1972), who analysed the preferences of 10 monkeys on 17 tasks. Beck and Barton's a priori hypothesis of left-hand preference for visual tasks and right-hand preference for tactual tasks was not supported by the data. Instead, a posteriori scrutiny suggested that the left hand was used for reaching tasks and the right hand for manipulative tasks. However, given the large number of tasks relative to individuals, it is inevitable that some combination of tasks must distinguish right- from left-hand usage, even with truly random use of the hands. The statistical significance of the differentiation of right- and left-hand tasks is therefore dubious.

Inappropriate use of the t-test for assessing population lateralisation. Fischer, Meunier, and White (1982) studied four lowland gorillas in some detail, a total of 619 assessments of handedness being made. The precise proportions of right-hand usage in each animal are not known, but conservative estimates of 100%, 100%, 100%, and 84% right-hand usage in the animals are reasonably made. Fischer et al. then carry out a conventional *t*-test to determine whether these four values are significantly different from a population estimate of 50%, and because the mean percentage for right-hand usage is 96% (with a standard error of 4%), they conclude that "this result is significantly beyond chance [$t(3) = 11.50, p < .01$]" (actual probability = .0012) (MacNeilage et al., sect. 5, para. 3). The method is used an additional four times in the present review, and twice in an analysis of the results of Beck and Barton (1972). In the case of the gorillas of Fischer et al., the conclusion is particularly disturbing, because if we had known only that the four animals

had each predominantly used their right hands, and if we had applied a binomial test, then we would have said that there was a 1 in 8 probability of obtaining four animals of the same handedness from a racemic population of right- and left-handers, providing no statistical evidence at the conventional .05 level for being "significantly beyond chance." It is a general maxim that when two statistical tests are asking apparently similar questions and they produce qualitatively different results, then either one test is violating its theoretical assumptions or the tests are actually asking different questions.

The problem can be made more acute by considering some variations on these data. If there had been only two animals, and if one had used the right hand on 94% of occasions and the other on 98% of occasions, a *t*-test would tell us that this was significantly beyond chance [$t(1) = 23, p = .027$]. If our two monkeys had been those that scored 100% right-hand usage on the tests, we would likewise have come to a similar conclusion, because the standard error would be zero, the *t*-statistic would be infinite, and hence the probability would be infinitely small and accordingly highly significant. More surprising still, because the calculations as carried out take no notice of the number of trials on which each animal has been assessed, even though the animals actually carried out 100 or more trials, nothing would have changed statistically if each had carried out just *one* trial and had attained 100% right-hand usage on that single trial: The *t*-statistic would still be infinite. Hence, we would apparently be forced to conclude, on the basis of a mere two individuals, each using its right hand once, that this was not a racemic population. Or, to put it as a more conventional statistical example, if we had tossed a coin twice, and on each occasion seen that it produced 100% heads (i.e., one head out of one), we would be forced to conclude that the coin was biased – a result surely at variance with our conventional notions of reasonableness, and also in conflict with the binomial theorem, which in each case (of four monkeys, two monkeys, or two coin tosses) correctly assures us that the results are compatible with chance probabilities.

The error here is an interesting one, and it arises because one of the assumptions of the *t*-test has been violated. Calculation of *t* requires a valid measure of the population variance of the observations, and in most applications it can be assumed that the sample variance is an adequate estimate of the population variance. That is *not* the case with laterality data, unless we expect that *all* individuals (in the population, not the sample) are lateralised in the same way (i.e., individuals differ only in *degree* of handedness and not *direction*). Let us imagine that in reality only 80% of these gorillas are right-handed and that on testing a fifth monkey we find it is left-handed, using its right hand on $(100 - 96) = 4\%$ of trials. The estimate of the standard deviation now rises from the value of 8% found in the four gorillas to a value of 41.7%, which is a far better approximation to the population variance. A *t*-test now gives a result of $t(4) = 1.479, p = .212$, which is nonsignificant. A single additional case has completely reversed our conclusions, and the method of testing has been shown to be nonrobust, a marginal change in the data producing a nonmarginal change in the conclusions. An appropriate analysis of these data applies the binomial theorem, either in the form of a chi-square test, or as a likelihood analysis [and a 2-support unit cutoff (Edwards 1972) then suggests that the proportion of right-handers in the population lies somewhere in the interval 32% to 100% – a result consonant with common sense]. Table 7 of the target article is therefore in error, for there is no evidence of a population asymmetry, and the failure of replication by Preilowski and Leder (1984) is not unexpected.

The removal of this particular statistical brick from the meta-analytic building does not cause the entire edifice to come tumbling down. It does suggest, however, that the architects' skills should not inspire total confidence, and that before moving all our possessions into the building, we should commission a careful structural survey to determine the extent of its defects.

Ontogenetic considerations in the phylogenetic history and adaptive significance of the bias in human handedness

George F. Michel^a and Debra A. Harkins^b

^aDevelopmental Psychobiology Unit, Children's Hospital Medical Center, Boston, Mass. 02115 and ^bPsychology Department, Clark University, Worcester, Mass. 01610

Previous accounts of nonhuman primate handedness have failed to find any population bias in the distribution of preference. Hence, it is generally believed that a bias in the distribution of handedness is restricted to humans. MacNeilage et al. contend that a reexamination of the nonhuman primate literature, with age of the animal, task demands, practice effects, and handedness criteria carefully assessed, demonstrates a left-hand population bias for reaching and a right-hand population bias for manipulating. Each of these biases in the distribution of handedness mirrors the functional specialization of primate right and left cerebral hemispheres, respectively. Indeed, MacNeilage et al. suggest that the nonhuman primate handedness biases may have contributed to increasing the functional differences between the hemispheres in the evolution of human brain asymmetries.

Most functional explanations for the evolution of the bias in human handedness have focused on the importance of hand preferences for tool use and certain unimanual activities (e.g., throwing). We agree with MacNeilage et al. that advantages in tool use and unimanual activities are inadequate explanations for the evolution of the right-handedness. Tool using and object throwing might have been factors in the evolution of individual hand preference because they would probably reduce decision time and help in skill acquisition. However, these are not compelling reasons why the majority of the population would need to share the same hand preference.

Recently, we (Michel & Harkins 1985a) proposed that the bias in the distribution of handedness might have evolved to facilitate the learning of manual activities through imitation – that is, manual skills are learned faster when there is concordance (as opposed to discordance) of handedness between "teacher" and "student." An individual would therefore have a greater advantage in acquiring socially relevant tool-making and food-gathering manual skills if he shared the hand use of the majority of the population. This advantage would result in a population dominated by a single hand preference. Although this explanation can account for the bias in handedness distribution, it leaves unexplained the right-handedness of the bias (perhaps this was simply a consequence of chance) and the maintenance in human populations of a minority of left-handers. MacNeilage et al. account for the right-hand bias by invoking notions of hemispheric specialization, a weak argument at best, and they leave unexplained the maintenance of left-handedness in the population.

MacNeilage et al. contend that an evolutionary approach requires that primate handedness include precursors for human handedness. They accordingly reexamine the research literature to identify biases in handedness of nonhuman primate species to construct phylogenetic lineage ending with humans. In building this lineage, however, they sometimes emphasize nonsignificant "trends" in the distribution of handedness when these support their argument (e.g., Beck & Barton 1972) and de-emphasize significant preferences (e.g., Rothe 1973) that fail to support it. Also, they sometimes argue inconsistently that more difficult tasks would (sect. 7.1, para. 3) or would not (sect. 2.3.2, para. 4) elicit hand preference.

In the excitement of reexamining the literature on nonhuman primate handedness, MacNeilage et al. sometimes forget that there are two separable aspects of human handedness: individual preference and the right bias in the distribution of the