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Commentary on Peter F. MacNeilage, Michael G. Studdert-Kennedy, and Bjorn Lindblom (1987) Primate handedness reconsidered. BBS 10:247-303.

Abstract of the original article: Most investigators believe that nonhuman primates do not have population-level asymmetries of hand preference. This conclusion, if correct, would imply *de novo* evolution in man of the left-hemisphere motor specialization typically considered to have played a key role in human evolution. Our review reveals numerous statistically significant instances of hand use asymmetries at the level of population samples. All but one of the left-hand preferences were for reaching. Right-hand preferences were for manipulation and practiced performance in stereotyped situations, among other things. We interpret earlier negative conclusions as arising primarily from tasks that did not call on the above preferences, involved young monkeys, failed to emphasize serial trends, or demanded uniform hand use across all acts. We suggest that primate handedness patterns evolved with structural and functional adaptations to feeding, that they are precursors to aspects of human left- and right-hemisphere specialization patterns, and that they evolved in the following order: (1) A left-hand (right-hemisphere) specialization for visually guided movement, accompanied by a specialization for postural support involving the right upper limb, may have evolved with the prehensile hand in prosimians (the left-hand preference remains in monkeys but not in humans); (2) a right-hand (left-hemisphere) specialization for manipulation and bimanual coordination may have evolved from the postural specialization, with the development of the opposable thumb, and decreasing demands on the right limb to support vertical posture in monkeys.

Handedness hangups and species snobbery

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MacNeilage et al.'s (1987) basic premise "that primate handedness patterns . . . are precursors to aspects of human left- and right-hemisphere specialization patterns" (p. 247) is fundamentally wrong. Their argument rests upon the assumption that handedness preceded brain laterality in phylogeny and, indeed, was the cause of hemispheric specialization. Thus, they state in their conclusions, "The necessity for a division of labor between the hands for arboreal reaching seems to be a plausible motivation for the development of specializations in both hemispheres . . ." (p. 263, italics added).

In restricting their review to nonhuman primates, they are guilty of species snobbery. Rats, mice, chicks, and songbirds have told us a lot about brain laterality, certainly as much as, and arguably more than, we have learned from studies of nonhuman primates to date. One very important generality that can be derived from research with these species is that the brain had already evolved into specialized hemispheres long before the appearance of primates, and long before the occurrence of handedness. I reviewed these studies in my own *BBS* target article several years ago (Denenberg 1981). They can be briefly summarized as follows:

The first documentation of population hemispheric asymmetry with animals was the finding of left-hemisphere dominance for song control in several songbirds (Nottebohm 1970; 1977; 1979). Later, studies with newborn chicks revealed that the left hemisphere is preferentially involved in visual discrimination learning, auditory, habituation, and attentional alteration, whereas the right hemisphere is dominant for attack and copulation, and is highly reactive to novel or threatening stimuli (Andrew et al. 1980; Rogers 1980; Rogers & Anson 1978; 1979).

Turning now to a mammal, in a two-lever situation rats favored the right bar over the left (Glick & Ross 1981), and in a Y maze more animals chose the right arm than the left (Cowey & Zek 1974). Lesions made by ligating the right or left middle cerebral artery of the rat have differential effects: Those with the right infarct increased their running wheel activity by 50% while shams and those with a left infarct slowly returned to their baseline levels (Robinson 1979). Rogers and Chen (personal communication) found that rats with only a functional right hemisphere made less errors on the Hebb-Williams maze than did those with only a functional left hemisphere.

Denenberg has found that giving rats handling stimulation in infancy induces or enhances laterality effects, including right-hemisphere dominance for right-left directionality, taste aversion, and mouse killing (Denenberg et al. 1980; Garbanati et al. 1983; Sherman et al. 1980). Hemispheric dominance for open-field activity was also obtained, but shifted sides as a function of whether the animals received handling stimulation with or without subsequent enriched environment experience (Denenberg et al. 1978). These researchers also found that standard laboratory rats had right hemispheric population asymmetry for right-left directionality choice and for taste aversion (Denenberg et al. 1980; Sherman et al. 1980).

Consistent with the behavioral asymmetry are findings that the rat's hemispheres are lateralized with respect to metabolic activity, levels of norepinephrine and dopamine, and cortical thickness (Diamond et al. 1980; Glick et al. 1979; Robinson 1979).

These data clearly establish that population-level hemispheric specialization of the brain can be found in species that evolved much earlier than did primates. Though these findings are sufficient to negate the thesis of MacNeilage et al., the nonhuman primate data will complete the argument. At the time of my *BBS* target article there were only a few experiments

demonstrating brain laterality in primates. Dewson (1977; 1978; 1979) used an operant nonspatial auditory discrimination task and measured short-term memory by introducing a delay between termination of the auditory signal and lighting of two panels which were the manipulanda. Four Iru macaques with lesions in the left superior temporal cortex performed very poorly on this task, whereas monkeys with lesions in the right superior temporal cortex ($N = 2$) or in the left primary auditory area ($N = 1$) performed well.

The left side of the Japanese monkey brain was also found to be the locus for processing species-specific communicative sounds (Peterson et al. 1978). All five subjects studied showed a significant right-ear advantage in discriminating between two classes of "coo" sounds. In contrast, when the animals were given communicatively irrelevant information they never exhibited a right-ear advantage (Beecher et al. 1979).

Petersen et al. suggested "that the specialized mechanisms used by the Japanese macaques in the perception of species-specific communication sounds may be analogous to those used by humans in the analysis of speech" (p. 326). In concluding my review of these studies I wrote that combining the Petersen et al. hypothesis "with Dewson's findings leads to the prediction that ablating the left superior temporal gyrus should abolish the Japanese monkeys' ability to make communicatively relevant discriminations" (Denenberg 1981, p. 9). That important study was done several years later by Heffner and Heffner (1984), and the prediction was confirmed. Japanese macaques were trained to discriminate between two species-specific coo vocalizations in a conditioned avoidance task. Then five monkeys received unilateral temporal lobe ablations that included all of the left primary and secondary auditory cortex; five others received unilateral lesions that included all of the right primary and secondary auditory cortex; and one monkey received a unilateral lesion of the left superior temporal gyrus that spared part of the auditory cortex. They were retested in the conditioned avoidance task. Following this, the animals received similar lesions in the other hemisphere, and were again retested.

Ablating the left, but not the right, superior temporal gyrus resulted in an initial deficit in the conditioning task. Removal of the homologous area in the other hemisphere totally abolished the conditioned discrimination. Neither unilateral nor bilateral lesions of cortex dorsal to and sparing the auditory cortex had any effect on the conditioned discrimination. Heffner and Heffner concluded that "the perception of species-specific vocalizations by Japanese macaques is mediated in the superior temporal gyrus. Furthermore, the left temporal lobe seems to play a predominant role in this perception" (p. 76). Interestingly, MacNeilage et al. cite the Heffner and Heffner study but do not appear to appreciate its importance.

This strong evidence for brain laterality in primates is to be contrasted with the weak evidence for handedness. Even the most generous reading of the MacNeilage et al. target article leads to the conclusion that only a modest percentage of animals show evidence of handedness. Thus, in their Table 1, between 32% and 44% showed neither a left nor a right preference, whereas in Table 2 (early testing) these values ranged from 48% to 59%. At best, handedness, even if found to be significantly different, is a relatively weak variable.

There is more, but this is enough to establish two generalities: (1) There is lateralization for brain-behavior processes in several vertebrate species that evolved earlier in phylogeny than the nonhuman primate, and (2) the evidence for the presence of hemispheric laterality in primates is much stronger than is the evidence for the presence of handedness. From the above it follows that hemispheric specialization preceded handedness.

Therefore, MacNeilage et al.'s conclusion that handedness patterns "are precursors to aspects of human left- and right-hemisphere specialization" is clearly wrong. If there is a causal association (and that is certainly debatable), then it is the hemispheres that specify the handedness. Thus, the lack of

definitive evidence of handedness in nonhuman primates is not an important theoretical issue. It simply means that it was not adaptive for the already specialized nonhuman primate brain to create differences in the use of the two hands. This position is in contradistinction to that of MacNeilage et al. who state that "manual specialization . . . is generally considered central to an understanding of left-hemisphere specialization in humans" (p. 247).

What next for handedness research?

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MacNeilage et al. (1987) have done an admirable job of bringing together the diverse literature on primate handedness in one review. The consequence is that it becomes painfully apparent how messy and incomplete the existing data on primate handedness actually are. Despite the fact that the data are generally inadequate for the task, MacNeilage et al. use them to develop a theoretical framework predicting populationwide hand preferences in nonhuman primates. The framework suggests a number of testable hypotheses concerning the nature of hand preferences. Their theory relates the evolution of hand biases to ecological and biomechanical constraints, and predicts phylogenetic differences in this domain. Although we think that the data supporting the theory are less than compelling, MacNeilage et al.'s effort is useful in many respects. It focuses on many of the right issues, it is sweeping in scope, and it is quite testable. One of the more compelling arguments is that primate handedness is a nonunitary phenomenon. A better way to view handedness is as a within-task rather than an across-task phenomenon, where "task" is defined functionally.

The most important claim made by MacNeilage et al. is that a population bias in nonhuman primates exists for reaching with the left hand when visual guidance of the hand is required (section 6.1). The data that support this contention consist mainly of simple "reach for food" tasks presented to the midline of the subjects. The first point in need of research is the status of this claim. It is quite possible that simply reaching for food in a fixed location does not require visual guidance in any rigorous sense, especially if the food is repeatedly presented to midline. A stronger test of a bias for the use of one hand in visually guided reaching would be an operant task requiring contact with a variably (unpredictably) positioned target. After all, a left-hand preference for reaching when an object is presented to the left side only is not much of a preference.

If a populationwide preference for reaching with one hand is indeed supported, then we must consider whether this preference would necessarily predict a bias toward the other hand for manipulation. There are two aspects to this prediction. One is a direct consequence of bimanual coordination. Why transfer an object from one hand to the other when it's more efficient for the nonreaching hand to manipulate what the reaching hand has grasped? Thus, one would predict that a species showing a populationwide left-hand preference for reaching would, as a consequence, show a right-hand bias for manipulation. The more interesting prediction is that an opposite preference for manipulation should be present even when it does not follow as a consequence of reaching with one hand. If a preference for one hand as a manipulator is a robust phenomenon, when an object requiring holding and manipulation must be grasped initially by the hand preferred for manipulation, the animal should switch the object to the other hand after grasping. This would result in the preferred hand performing the manipulation. Again, a hand preference for manipulation only when the other hand was

avored to grasp the object in the first place is not much of a preference.

Finally, MacNeilage et al.'s theory leads to the prediction that there should be detectable and testable benefits of lateralization for reaching and for manipulation. For example, an animal should reach more accurately or more quickly with the preferred reaching hand when the use of each hand is tested. Furthermore, it should be possible to demonstrate a hand preference when it is not to the subject's immediate advantage to use that hand. For example, a left-hand preference for visually guided reaching should be evident, even if diminished, when objects are presented to the right of the subject's midline. Hand preference should vary in an orderly fashion as a function of the costs of using one hand over the other, and the switch from preferred to nonpreferred hand should occur at some point beyond a neutral position.

The studies outlined above would test a few of the predictions following from MacNeilage et al.'s theory. Others could be presented, but we wish to devote the rest of our limited space to pointing out two general lines of inquiry that MacNeilage et al. did not develop. The first topic only hinted at by MacNeilage et al. is the relation between the use of precision grips and the occurrence of a hand preference. The use of a precision grip indicates a high degree of manipulative control. MacNeilage et al. state on p. 248 that there may be qualitative differences in "structure" (structure of what is left unsaid) contributing to the development of left- and right-hand preferences, with the right-hand preference for manipulation evolving coincidentally with the opposable thumb (see also p. 259). This relation can be examined phylogenetically. One phylogenetic comparison that comes to mind involves New World monkeys that do not display a precision grip (e.g., *Saimiri*) and those that do (*Cebus*). Is there a difference in the extent to which these two genera display a populationwide hand bias for reaching and manipulation? Available data do not suggest that there is, but the available data are not necessarily adequate to the task (Costello & Fragaszy, in press). A second interesting comparison is between Old World monkeys that retain a vestigial thumb (e.g., *Colobus*) and Old World monkeys that use opposable thumbs. For this comparison no data are available as yet.

Probably the most significant oversight of MacNeilage et al. concerns the development of hand preferences. There is a substantial literature on the ontogeny of hand preferences in humans (cf. Young et al. 1983). As MacNeilage et al. would predict, the human literature shows that the relationships among the development of postural control, hand preference, and task demands are complex. However, there is virtually no literature on the development of hand preferences in nonhuman primates. Perhaps one reason that MacNeilage et al. mention the human ontogenetic literature only in passing (on p. 260) is that it is not yet clear how to integrate the ontogenetic and evolutionary arguments for the appearance of handedness. Yet this integration needs to be achieved before any theory of handedness can be complete. The study of the development of hand preferences in nonhuman primates and its comparison with the development of hand preferences in humans must be given high priority.

As a final comment, we wish to emphasize that other tests of handedness are needed in addition to simple frequency counts of hand-use. These other measures include consistency of preference in the face of variable placements of the target, accuracy, response latency, and amount of practice needed to acquire new skills. Some human studies have relied on performance measures (e.g., Guiard et al. 1983), but we know of only one with nonhuman primates (Fragaszy 1986). In this study a few subjects of two different Neotropical genera (*Saimiri* and *Callicebus*) exhibited persistent biases for one hand even when it was disadvantageous to do so. A weak species-general bias for reaching with the left hand was evident in both species.

In conclusion, MacNeilage et al. have provided a fertile starting point for the continued investigation of nonhuman primate handedness. We expect their work to renew interest in the topic and to stimulate new lines of inquiry.

Cognition, not handedness, is lateralized in monkeys

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We commend MacNeilage et al. (1987) for reevaluating the state of handedness in nonhuman primates and for ferreting out some evidence for its existence. However, we are still unconvinced of the extent and importance of hand preferences in nonhuman primates because of the overall weakness of the preferences, the large amount of negative evidence, and the number of special arguments MacNeilage et al. must invoke to account for the existing data. This opinion appears to represent the feelings of most commentators, many of whom also noted the paucity of critical data on which to evaluate the suggestions of MacNeilage et al. From our "file drawer," therefore, we retrieved and reexamined our relevant data on simian hand preferences to see whether they support the proposed preferences for visually guided reaching with the left hand and manipulation with the right hand. We then related these various estimates of hand preference to our findings of lateralization for cognitive processing.

Hand preferences. We have tested over 50 rhesus monkeys (*Macaca mulatta*) for hand preferences on three tests that vary in complexity. The monkeys were juveniles (1.7–4.7 kg) of both sexes, wild-caught, and experimentally naive when tested for handedness. They reached between the bars of a small testing cage for food, usually while sitting but sometimes while standing or holding onto one of the bars. The tests took three or more days to complete. The first test (90 trials) measured preferences in reaching for food placed in one of three wells in a tray. This corresponds to the "simple reaching" of MacNeilage et al.; according to them there should be little or no hand preference in this laboratory environment. The second test (30 trials) involved reaching into a bottle held by the experimenter for a piece of food. MacNeilage et al. call this "complex reaching" and suggest that it should reveal a left-hand preference. The third test (30 trials) required the monkey to open a matchbox by pulling a small tab attached to the box and then retrieving a piece of food from within. Because two hands may be used for the actions involved, two separate handedness scores were calculated, one for opening the box and one for retrieving the food. In their Table 4 MacNeilage et al. classify this test as "manipulate and reach." For this type of test they predict a right-hand preference for manipulation (opening the matchbox) and a left-hand preference for reaching for food (retrieving the reward). We express hand preferences (based on the number of reaches with each arm) as an index, $HI = 100(R-L)/(R+L)$, which ranges from completely left-handed (-100) through equality (0) to completely right-handed (+100). This measure, which is analogous to the one we use for estimating laterality for cognitive tasks, is linearly related to the more common measure, percentage of right-handed reaches by the relationship: $\%RH = (HI+100)/2$.

Hand preferences of individual monkeys were distributed almost equally across the entire range of handedness indices, producing a flat or slightly U-shaped distribution for all four measures. These distributions may be visualized by projecting the points in Figures 1 and 2 onto the corresponding axes. The average handedness index for each of the tests was small and not significant on *t* tests (tray, -8.4 ± 60.6 ; bottle, -2.0 ± 71.5 ;

matchbox-open, 3.2 ± 73.8 ; matchbox-retrieve, -2.7 ± 62.4). If handedness is defined as making more than $\frac{1}{3}$ of the reaches with one hand then none of the distributions differed from chance according to χ^2 tests. Thus, the more complex tasks did not elicit the preferences predicted by MacNeilage et al., and, in fact, they echo the results typically found for simple reaching.

The correlations between hand preferences on the four measures were informative. As shown in Figure 1, the hand used for reaching to the tray correlated with the one used for reaching into the bottle ($r = .70, p < .001$), and the proportion of animals using the same hand on both tasks was more than expected by chance (37/54, $\chi^2 = 7.41, p < .01$). This indicates that the hand preferences of individuals were rather consistent for these two tasks, and therefore not just randomly chosen. More surprisingly, each of these preferences in reaching correlated with the manipulative component of the matchbox test (tray vs. matchbox-open, $r = .46, p < .01$; bottle vs. matchbox-open, $r = .64, p < .001$) and not with food retrieval (tray vs. matchbox-retrieve, $r = -.17, ns$; bottle vs. matchbox-retrieve, $r = -.14, ns$). This is contrary to the claim of MacNeilage et al. that reaching for food in complex tasks is predominantly left-handed (their Table 3). These correlations suggest instead that, for each monkey, the manipulative component of opening the matchbox is the equivalent of reaching for food on the tray or in the bottle. Perhaps this is because each of these movements is the first one the monkey makes. Finally, as shown in Figure 2, the two components of the matchbox task are inversely correlated ($r = -.46, p < .01$), consistent with a tendency for monkeys to use opposite hands to open the box and retrieve food. Inspection of the data for individual reaches confirms that this was largely the case for all but a few monkeys with very strong hand preferences who often used the same hand for both components. Because of the lack of an overall species-specific handedness, however, we interpret this bimanual coordination as reflecting a simple solution to the task requirements rather than as an example of complementary hemispheric specialization for two manual components as implied by MacNeilage et al.

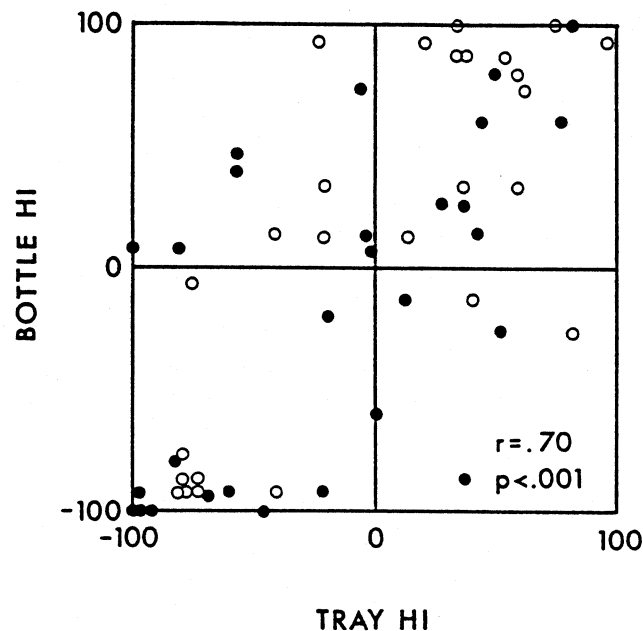


Figure 1 (Hamilton and Vermeire). The handedness index (HI, see text) for reaching for food placed on a tray is plotted against the HI for reaching into a bottle for each monkey. Filled circles represent male monkeys and open circles represent female monkeys. Overall, these measures were significantly correlated.

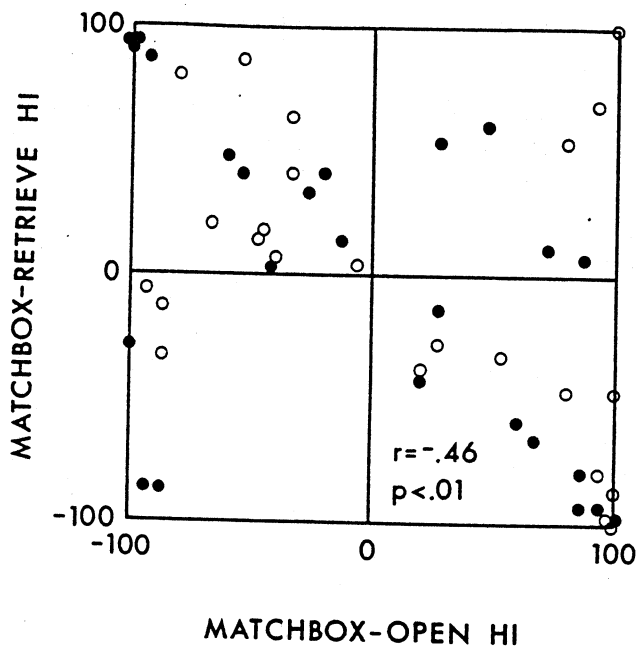


Figure 2 (Hamilton and Vermeire). The HI for opening the matchbox is plotted against the HI for retrieving the enclosed food. A significant inverse correlation is present.

How convincing are our results indicating that no species-specific handedness exists for rhesus monkeys? MacNeilage et al. might object that our monkeys are too young to have developed consistent handedness. However, judged from their weights, they are no younger than the 10 monkeys of Beck and Barton (1972) on whose data MacNeilage et al. base many of their speculations. Furthermore, most of the negative findings cited in MacNeilage et al.'s Table 4 also pertain to monkeys at least as old as those of Beck and Barton. (Note that this is contrary to the statements of MacNeilage et al. (p. 254), which appear to be based on a misreading of Tanner's (1962) graphs which show *rate* of change of weight with age; for example, a newborn monkey does not weigh 1.9 kg. Another objection might be that the one year of laboratory testing experienced by Beck and Barton's monkeys was necessary for their hand preferences to develop. Although plausible, it would be very difficult to ascertain whether those manual preferences developed on their own or resulted from inadvertent asymmetries that might have been present during training. A third objection might be that our tests are not complex enough to reveal consistent hand preferences even though they fit the guidelines set forth by MacNeilage et al. In particular, the matchbox test might involve less manipulation than required to reveal right-handed preferences, although it should still have been complex enough to elicit left-handed reaching. Finally, one could claim that the significant intertask correlations may have been inflated because of the temporal proximity of our three tests, or because of fortuitous similarities in the tasks, as Warren (1977) has critically discussed. Even if the correlations were spurious, however, our main finding of no laterality at the population level would remain.

Clearly, our results do not support the proposal of MacNeilage et al. that species-specific handedness is demonstrable for complex tasks if visually guided and manipulative components are analyzed separately. They are, however, in accord with the guidelines suggested by Lehman in his commentary [see the first round of commentary for all undated references mentioned here]. Furthermore, other large-scale studies also have found no population bias in macaques for reaching in complex (Deuel & Schaffer) or simple (Lehman) tasks. Similar

conclusions have resulted from studies with baboons (Vauclair & Fagot 1987) and chimpanzees (Steklis & Marchant). (The mention by Brésard & Bresson of right-handed preferences in gorillas but not chimpanzees is too incomplete to be evaluated.) Even the earlier large-scale studies that suggested some degree of handedness to MacNeilage et al. seem less convincing in view of the critical remarks of many commentators. Thus, we feel there is still no compelling reason to challenge the widespread opinion that neither monkeys nor apes possess species-specific handedness, either for visually guided reaching or for manipulation.

Any conclusion about handedness based on accepting the null hypothesis must face the possibility that new experiments may provide positive examples. In fact, two plausible candidates have been discussed in the commentaries and the authors' response. First, both prosimians (Sanford et al. 1984) and apes (Heestand 1987) have shown significant manual asymmetries under conditions that seem to favor postural biases, and postural asymmetries have been viewed as precursors of human laterality (MacNeilage et al.; Michel & Harkins; Turkewitz 1977). Second, monkeys have sometimes demonstrated manual preferences in complex tasks that conceivably require hemispherically specialized cognitive processing. Several commentators considered that the hand contralateral to the specialized hemisphere may be preferred for such tasks (Bradshaw; Ettlinger; Heuer; Kolb & Fantie; Fagot & Vauclair, in press). In these cases the preferred hand should vary according to the task, which would be unlike most manual preferences in human beings. In any event, it seems certain that the points raised by MacNeilage et al. will precipitate a flood of studies of primate handedness under a much wider variety of experimental conditions. Which, if any, of these manual preferences deserve further attention should then become clear.

Cognitive lateralization. In contrast to the lack of laterality we found for hand preferences, we have strong evidence in favor of lateralization for cognitive processing. About half of our monkeys subsequently had their cerebral hemispheres disconnected by midline division of the corpus callosum, anterior and hippocampal commissures, and optic chiasm. They then learned and performed with each hemisphere a variety of visual discriminations between stimuli of types that often reveal lateralized processing in human subjects (Hamilton, in press). A dominance index, $DI = 100(R-L)/(R+L)$, based on the errors-through-criterion made by the two sides was calculated for each discrimination learned by each monkey and the average DI was tested for significance. In these experiments responses were restricted to the hand contralateral to the viewing hemisphere to facilitate learning; therefore, hand preferences could not be assessed during learning of these problems.

When discriminating between photographs of monkey faces differing in expression or identity, there was a significant advantage ($DI = -7.18$, $t_{(26)} = 2.22$, $p < .05$) for the right hemisphere (Vermeire et al. 1983; Hamilton & Vermeire 1985), as is often reported with human subjects. When discriminating between differences of 15° in orientation of lines, there was a significant advantage ($DI = 23.97$, $t_{(25)} = 4.91$, $p < .001$) for the left hemisphere (Hamilton 1983; Hamilton & Vermeire 1985). This left-hemispheric superiority for discriminating spatial cues, although its direction is opposite to that usually found with human subjects, has been confirmed in related studies (Hamilton, in press; Jason et al. 1984). For the monkeys that learned both series of problems, the relative difference in lateralization was significant ($\Delta DI = 32.71$, $t_{(24)} = 5.40$, $p < .001$), as was the proportion of monkeys preferring the left hemisphere for lines and the right hemisphere for faces ($16/25$, $\chi^2 = 20.28$, $p < .005$). This complementary lateralization shows that uncontrolled asymmetries related to surgery or testing were not the cause of the lateralized behavior we measured (Hamilton & Vermeire 1985). Thus, there is a reliable difference in cognitive

processing by the two hemispheres of rhesus monkeys at the population level, which appears similar to hemispheric specialization in human beings.

Although these asymmetries in cognitive processing did not correlate with hand preferences based on our usual combined measure of reaching for food on a tray and in a bottle (Hamilton, in press), the review of MacNeilage et al. prompted us to examine these correlations separately for each of the four measures of handedness discussed above. However, dominance for discriminating faces or lines did not correlate significantly with any of these handedness measures (range, $-.18$ to $.25$). Therefore, we find no evidence for a relationship between preoperatively determined hand preferences and the superior hemisphere for cognitive processing in these experiments.

Remark. Although we have been unable to find evidence in monkeys for hand preferences at the population level, we have found evidence for lateralization of cognitive processing in the same subjects. A simple interpretation of this result would suggest that during evolution lateralization for cognitive processing preceded lateralization for manual preferences. Although this sequence of evolution is opposite to that most frequently championed by others, it seems quite natural to us, and may be viewed as returning the horse to the front of the cart.

This suggestion might imply that a "metafunctional capacity" (Calvin; Jerison) has been selected for during evolution. However, we doubt that the selection was for lateralization as general as, say, analytic or holistic processing. More likely, some basic biological property diverged qualitatively or quantitatively in the two hemispheres. This modified property would presumably find immediate utility in some important function that would maintain it as a base for developing other lateralized processes. Eventually, enough related lateralized functions would accrue that observant scientists would note their similarities and label them as the dichotomies that are popular today. For example, if the effective dendritic spread of sensory neurons became somewhat larger on the right or smaller on the left, this might immediately enhance a particular function such as differential analysis of spatial frequencies by the two hemispheres. Other functions such as detailed scrutiny of stimuli by the left side or global perception of facial features by the right might be similarly facilitated. Once a set of such related processes became specialized to each hemisphere it would be convenient to label them with terms such as analytic and holistic, although the common element would really be the more basic but less obvious biological change that had occurred. Which basic properties might have been so altered during the evolution of hemispheric specialization remains an exciting question to answer.

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Giving the primates a hand: Is the applause really justified?

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In reviewing the evidence for and against the presence of handedness in primates, MacNeilage et al. (1987) have performed a signal service. I know of no other analysis even remotely comparable in its thoroughness and comprehensiveness. Clearly, there is a good deal of evidence that deserves reevaluation and MacNeilage et al. are to be commended both for reviewing an area that has been somewhat ignored and for taking a strong position. Although I wish to be critical of some

aspects of their presentation, I would like to emphasize again that they have performed an impressive analysis in what has been a neglected area of study.

I focus on two aspects of the target article; one area concerns a statistical consideration and the other concerns the presentation of evidence that seems to me contradictory.

The statistical consideration relates to MacNeilage et al.'s reanalyses of reaching data from rhesus monkeys and other macaques (Tables 1 and 2). When I first read them I was quite skeptical about the data analysis. To do the kinds of analysis given in Table 1, the authors have to make some questionable assumptions. They must assume that the null hypothesis is given by the following kind of expected counts:

	Left Hand	Neutral	Right Hand	Total
Observed	Nl	Nn	Nr	N
Expected	.5(Nl + Nr)	Nn	.5(Nl + Nr)	N

The Chi-square statistic is then calculated with 2 degrees of freedom, because Observed Neutral Handedness and Expected Neutral Handedness are part of their assumption. For study A, this leads to:

Left	Neutral	Right	N
30	36	16	82

This is significant at the .05 level of significance. However, if the data had been of the observed frequencies:

Left	Neutral	Right	N
30	1,000	16	1,046

Then the Chi-square calculation would produce exactly the same result and the same significance level. However, it is questionable whether readers would be as comfortable accepting this as evidence for a hand preference as they would the data of study A.

One difficulty is that the authors have not specified that two questions are being asked:

1. Is there handedness in the population?
2. Are there more left-handed individuals than right-handed individuals?

Question 1 above, put more explicitly, states that if random handedness were present, no difference would be found when individuals were presented with a choice of using the left or the right hand. The data of studies A and B in Table 1 do not provide appropriate information to answer this question. However, study C of Table 1 provides a decision rule: 8 choices out of 10 with the (left) (right) hand is taken as evidence that the animal is (left) (right) handed. Then, if the choice of hands is random:

$$P(8 \text{ or more left-hand choices}) = P(8 \text{ or more right-hand choices}) =$$

$$\frac{10}{8} \times \frac{10}{9} \times \frac{10}{10} \times \frac{10}{10} \times (0.5) = 0.0547 = P_o$$

Then the question of testing whether the observed counts are from a random population reduces to testing for

$$P_l = P_o \text{ or } P_r = P_o$$

or, as an alternative,

$$P_l + P_r = 2P_o$$

If we do this calculation for the data of Study A, we have

	Left	Neutral	Right	N
Observed	17	16	8	41
Expected	2.24	36.51	2.24	

or, as the alternative,

	Neutral	Left + Right
Observed	16	25
Expected	36.51	4.48

producing a Chi-square of 105.35, rather more significant than the statistic produced by the authors.

The above analysis, produced by my colleague Mark Wilson, was sufficient to overcome my skepticism about the data for this group of primates. (Professor Wilson has extended his analyses to other aspects of this data and I have suggested that he prepare a commentary for a following issue of *BBS*.)

My remaining concern is with the data presented for the great apes. The data (and interpretations) for the great apes are extremely puzzling. The evidence cited for handedness in apes is so equivocal that MacNeilage et al. concede there is little basis for making any generalizations. What then, are we to do with the data of Table 9, offering comparisons in hemispheric asymmetries of humans with the asymmetries of great apes? The asymmetries found in humans have definite links to handedness, as is clearly demonstrated in Table 9. However, the asymmetries in the apes cannot be linked to handedness and the conceptual leap to possible language-based asymmetries is difficult to follow and lacks justification.

Despite these concerns, I think MacNeilage et al. have made a useful contribution. There are some points of comparison that they have overlooked, such as Semmes (1968) paper showing that fine motor coordination is focally represented in the left hemisphere and diffusely represented in the right hemisphere – a possible link to the fine motor activity of the right hand that they report for primates. I am not sure what to make of the reaching with the left hand and fine motor activity with the right, in relation to human handedness, because I know of no data relevant to this question. However, any right-handed person needing to perform any kind of skilled activity with the right hand on some object to be held will probably pick it up with the left hand. This may mean no more than the ability to plan ahead on often repeated tasks. Regardless of possible omissions, the authors are to be commended for the reanalysis and integration of primate handedness into a more meaningful framework.

Hand preference for visually guided reaching in human infants and adults

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MacNeilage et al. (1987) have argued that handedness, instead of being a uniquely human trait, as conventional wisdom goes, may be an attribute of other primate species. They have also proposed a provocative model for the sequence of evolutionary events culminating in primate handedness – first, bipedal posture, releasing the forelimbs from locomotor requirements; next, the emergence of the prehensile hand and the opposable thumb; and finally, the evolution of two different forms of lateral specialization that capitalize on these morphological developments: left-hand specialization for visually guided reaching followed by right-hand specialization for fine-motor manipulation.

In suggesting that the patterns of hand preference shown by nonhuman primates are evolutionary precursors to human handedness, MacNeilage et al. also suggest that the actual pattern found in nonhuman primates (monkeys) – left-hand visually guided reaching in coexistence with right-hand manipulation – is *not* found in human beings. This leads them to propose that monkeys and humans are “separated by an evolu-

tionary progression in which the importance of the ability to operate on the environment (including the use of bimanual coordination and the consequent right-hand preference) has so increased that the right hand [in human beings] now normally preempts the left, even for visually guided movement” (p. 260).

If this characterization of hand use in humans is correct, and if this indeed marks a “separation in the evolutionary progression,” what is the evidence? One sign would seem to be that, in studies of hand dominance in human infants where visually guided reaching is the dependent measure (e.g., Baldwin 1890; Carlson & Harris 1985; Gesell & Ames 1947; Michel 1983; Michel & Harkins 1985; Voelckel 1913), most infants by about 9 to 12 months reach preferentially with the right hand (e.g., 33 of 35 infants in Voelckel’s 1913 study). The “preemption” of the left hand by the right for visually guided movements would therefore seem to occur very early in development.

As MacNeilage et al. also point out, because monkeys normally favor reaches that do not cross the body midline, a test in which target objects are laterally positioned may obscure genuine hand preference (e.g., Cronholm et al. 1963; Lehman 1970). Human infants show a similar bias, but some evidence suggests that the midline is far from an absolute topographic obstacle (e.g., Carlson & Harris 1985; Provine & Westerman 1979). Reaches across the midline might therefore be particularly revealing of preemption by the dominant hand. They seem to have been in Baldwin’s (1890) case. When his daughter was 8 months old, he placed target objects, one at a time, to her left and right and found that she crossed the midline far more often with her right hand than with her left. As he later said, “The right hand intruded regularly upon the domain of the left” (Baldwin 1900; see Harris 1986).

We found a similar effect for a small sample ($N = 8$) of familial right-handed infant girls (Carlson & Harris 1985). We placed objects, one at a time, in three different positions: at midline and four inches to the left or right. We also varied the object’s distance from the infant, from 4 inches to 8 inches to 12 inches. (Baldwin also found that his daughter’s right-hand preference was strongest for objects placed at a distance, which he attributed to the greater effort required.) The subjects were given 54 trials at three-week intervals from 24 to 39 weeks of age and once again at 52 weeks. Finally, we pushed the pace by presenting a new object as soon as the infant grasped the target object.

The infants showed an overall right-hand preference at every age, peaking at 52 weeks, by which time over 60% of all midline reaches were with the right hand. As for objects placed to the left or right, the same-side hand predominated, but not equally so: The infants made right-hand reaches across midline to the left side on 50% of the left-side trials, but reached with the left hand to the right side on only 11% of the right-side trials. Right-hand preference, however, did not prove to be stronger for the far than for the near distance, even though the infants showed unmistakably greater effort and postural adjustment when reaching for the farthest placed objects.

The reliable use of one hand for visually guided reaching in a one-year-old child does not mean that handedness is firmly established in any way comparable to what we know to be the case in the older child or adult. Other evidence also suggests that at this age reliable hand use may vary according to the task used (Michel et al. 1986). We therefore were curious to see what right-handed adults (i.e., individuals presumed to have established hand dominance) would do under similar circumstances. To find out, we recently gave 40 right-handed and 40 left-handed college students (20 men and 20 women in each group) the same test that we used with the infants but now with all test dimensions scaled to adult proportions. In order to prevent the subjects from reflecting on the task, we pushed the pace as we had for the infants by presenting a new test object immediately after the previous object was picked up. We again used three different test objects (a pellet, a 2.25-inch cube, and a 5-inch ball) in order to see whether hand preference for reaching would

Table 1 (Harris and Carlson). *Percentage of reaches crossing the midline by sex and handedness*

		Preferred hand	Nonpreferred hand
Right-hand females	(n = 20)	41%	7%
Left-hand females	(n = 20)	40%	7%
Right-hand males	(n = 20)	26%	9%
Left-hand males	(n = 20)	29%	7%

be affected by the kind of grasp required. We expected that, for the pellet, which could be picked up only with a pincerlike grasp, adults would favor their dominant hands more than they would for either the ball, which was invariably picked up with a palmer grasp, or the cube, which could be picked up with either kind of grasp.

The results were very similar in all four sex-by-handedness groups. For the midline position, the dominant hand was used from 66% to 72% of the time, percentages only slightly higher than that shown by the infants. As was true for the infants, lateral position of target objects influenced hand choice, such that the adults reached more often with the same-side hand regardless of whether it was the dominant or nondominant hand. Table 1 shows that, like the infants, adults crossed the midline more often with their dominant hand than with their nondominant hand, the difference (for the women) being by about the same margin as shown by the infants. Thus, right-handed women crossed right hand to left side (R to L) on 41% of the left-side trials, but left hand to right side (L to R) on only 7% of the left-side trials. For right-handed men, the figures were 26% and 9%. Left-handed women crossed L to R on 40% of the right-side trials, but R to L on only 7% of the left-side trials. For left-handed men, the figures were 29% and 7%. Women, in other words, showed stronger hand-dominance effects than men. Object distance, once again, did not affect hand use. In summary, even on the lateral-position trials, the dominant hand substantially "preempted" the nondominant hand, notwithstanding the greater effort required by crossing the midline.

We also found that object size affected hand use, but only for objects placed in the midline, and then only for the ball (the largest object) versus the pellet and cube, which did not differ. The effect was also reversed for right- and left-handers. For both handedness groups, the percentage of dominant-hand midline reaches ranged from 76% to 82% for the pellet and cube. For the ball, the percentage decreased to 58% for the right-handers, but increased to 88% for the left-handers. We found no sex differences here. Object size therefore influenced the extent to which the dominant hand was used for reaching, but in different ways for right- and left-handers.

The evidence from human infants and adults would thus seem to support the proposal by MacNeilage et al. that there is a "separation in the evolutionary progression" between monkey and man, such that in man the right hand preempts the left for visually guided reaching. Or does it? A possible objection is that our test of visually guided reaching is like what MacNeilage et al. call a "simple reach" test in which the subject merely picks up a single item placed on a flat surface. In such a test, as Beck and Barton's (1972) study suggests, monkeys likewise made more right-hand than left-hand reaches, the reason being, according to MacNeilage et al., that with only a small number of food locations along with the small range of required movements, the animal can plan and execute its reaching with minimal visual information. In our test, demands for visual guidance may likewise appear to have been relatively reduced, except that on each trial, the location of the test object varied

unpredictably across nine different positions in two dimensions. Our impression was that for the infants, the task elicited strong visual engagement and sustained effort. Although this was much less true for the adults, even for them the pace of the task and the unpredictability of the target location and the type of grasp required at least meant that no reach could be initiated and completed without visual inspection. So perhaps our test was not a "simple reach" test after all. Because reaching tasks have never been part of the standard assessment of adult handedness, we cannot resolve this matter at this time. What does seem clear is that task analysis of the kind applied to handedness (e.g., Annett 1985; Provins 1956; Provins et al. 1982) could be profitably applied to the analysis of visually guided reaching, with appropriate controls for sex and handedness. Until then, any conclusions about the nature of the evolutionary progression between man and other primates may be premature.

On handedness in primates and human infants

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Two observations from my own experiments bear on the MacNeilage et al. (1987) hypothesis on the evolution of primate handedness. One involves handedness in Old World monkeys; the other postural asymmetries in the human infant.

First, some background on the experiments from which these observations are derived: We do not study handedness, but for the past ten years we have been testing primates' and human infants' ability to perform in auditory discrimination experiments involving speech. The research program focuses on the biology and evolution of the brain mechanisms subserving language and speech. Of particular interest is the phonetic level of language and the brain mechanisms involved in the perceptual processing of speech. Our tests are aimed at finding out whether monkeys demonstrate perceptual phenomena that are hallmarks of infants' perception of speech, such as "categorical perception." The results of these studies show, surprisingly enough, that monkeys do demonstrate categorical perception (see Kuhl 1987 for recent summary). These results are not the issue here, but the experimental tasks used to test animals' and infants' speech discrimination abilities are of interest. Each affords an opportunity to examine aspects of the hypothesis put forward by MacNeilage et al.

Consider our tests on animals. The task requires primates to use their hands in a controlled laboratory situation. Young juvenile animals (8 months to 3 years) sit in a standard primate chair and listen to auditory signals (speech syllables such as /ba/ and /da/) through earphones. The task involves same-different discrimination. The monkeys are trained to depress a standard telegraph key to initiate a trial and the trials consist of the presentation of two syllables that are either the same or different. If the stimuli are different, the animal has to lift the telegraph key. When he does so he receives a squirt of applesauce out of a tube near his mouth. If the syllables are the same, the animal has to hold the telegraph key until the end of the trial, and this too is reinforced with a squirt of applesauce.

The question that arises naturally from MacNeilage et al.'s piece is this: What hand does the monkey use to depress and lift the key? Before one can make a prediction based on the hypothesis of left-handed reaching and right-handed manipulation, some further details of the situation need to be described. First, animals cannot see the telegraph key. It is directly in front of them, but at waist level, and the earphone apparatus keeps the monkey's head in a fixed upright position so the monkey cannot easily look down at its hands. Moreover, there are two Plexiglas

trays, one at the neck and the other at the waist, that are difficult to see through. Thus, the animals can feel but not see the key.

A second feature of the task is that pressing and lifting the key appropriately requires the animal to watch an array of lights placed at eye level. The lights signal various things to the animal: A green blinking light means the animal is free to initiate a trial by pressing the key. Once the trial is initiated, the green light remains steady. When the trial ends, either because the animal has correctly lifted the key on a "different" trial or continued to press the key until the end of a "same" trial, the light goes out for 500 ms, during which time the animal must release the key. If he does so, the green light, once again signaling the opportunity to initiate a trial, begins to blink. In addition, if the animal makes a mistake by lifting or holding inappropriately, a red light comes on, signaling a 5-sec "time out." No trials can be initiated during these time-out periods, and if the key is depressed during this period, "time-out" is extended.

Thus, the task is fairly complex. It involves visual monitoring of the lights, but not visual guidance of the hand approaching and reaching the target. And speed is important. The faster the monkey initiates trials, the more often he has the opportunity to get applesauce. The practiced animal becomes highly adept. His hand never leaves the key, and he repeats quickly and fluidly the sequence of watching the lights, initiating a trial by depressing the key, listening to the sounds, lifting or holding the key depending on the auditory stimuli, and releasing the key so that a new trial can be initiated.

The telegraph key is located at the center. Either hand *could* be used. Which hand is? The right hand. In ten years, we have not seen a single animal use the left. This is true for all species tested, the Japanese monkey (*Macaca fuscata*), the rhesus monkey (*Macaca mulatta*) and the pigtailed monkey (*Macaca nemistrina*). We have tested some 30 animals ranging in age from 8 months to 3 years. Each animal is tested daily for about two years, and we have never seen an animal reverse this hand preference.

The MacNeilage et al. hypothesis correctly predicts primates' use of their right hands. The features that form the basis of a right-hand prediction are: (1) The action does not involve visually guided behavior. Animals monitor lights indicating where they are in the trial's temporal sequence, but pressing and lifting the telegraph key is not guided by visual information of the hand and the target. (2) Pressing, holding, and lifting the key are manipulative acts, and, according to the hypothesis, manipulation is a right-handed activity. (3) The practiced action becomes highly stereotypic, and this too is characteristic of right-handed activity according to the hypothesis.

One could presumably increase the left-handedness of the task using the MacNeilage et al. rules by requiring the monkey to remove its hand completely from the key after each trial, placing it at a specific distance from the key, and allowing the monkey to see the key. Each trial would then require a reaching response. Under these conditions the task comes closer to the description of left-handed activity and should result in more left-hand use. We have not attempted to follow these conditions, but manipulations such as these could provide quite informative tests of the hypothesis.

Two additional points should be made. First, although we have no systematic data, we know that these animals are not exclusively right-handed. They do use their left hands in other tasks. In fact, during the shaping phase of the experiment, when animals are reinforced with applesauce for approaching and pressing the key with their hands, we have seen animals use both of their hands. But once the act has become highly organized, an exclusively right-hand use is exhibited. Second, these same animals use either hand to pick up monkey chow during the feeding period after each day's testing and to take apples from us when they are handed to them. The important point is that whereas the telegraph key is manipulated exclusively with the right hand, grabbing monkey chow from the feeder or taking

apple pieces from a human hand are certainly not. The difference is intriguing.

In summary, our observations on primate handedness may provide some support for the MacNeilage et al. hypothesis. Primates use their right hands when performing a highly stereotypic manipulative act. The choice of hands is uniform across all animals we have seen. Once established, these hand preferences never change.

A second observation from our laboratory, this one involving human infants, is also pertinent. As cited by MacNeilage et al., infant postural asymmetries favoring the right side have been reported. We have an example that illustrates how difficult it is to counteract this tendency.

The test again involves speech-sound discrimination and the task requires a conditioned head-turn response (Kuhl 1983). The infant sits on a parent's lap and watches an assistant manipulate toys. The assistant sits at a 45° angle to one side of the baby. While this is going on, a syllable is being presented repeatedly from a loudspeaker. The loudspeaker is located at a 45° angle on the side opposite the assistant. On top of the loudspeaker is a black Plexiglas box that houses a toy animal (a bear with a drum). The infant is conditioned to turn away from the assistant, producing a head-turn response toward the loudspeaker and the bear, whenever the syllable changes to a new one. If the infant does so correctly, the Plexiglas box is illuminated for a short time and the toy bear inside is activated and pounds his drum. An equal number of control trials is run in which the sound is not changed but in which the infant's head-turn responses are monitored. If head turns occur during these control periods, they are scored as false alarms.

The task is a delicate one because the assistant has to maintain sufficient attention on the part of the baby to keep infants from constantly turning to check whether they can see the bear, which greatly increases false alarms. Yet, if infants become too fascinated with the assistant, they fail to make head-turn responses toward the bear at the appropriate times. These failures to produce head-turns are also errors. When infants are under perfect stimulus control, they produce almost no false alarms; that is, they never produce head turns on control trials and always produce them on change trials. As complex as the task sounds, six month olds are very adept at it.

The point of interest to this discussion is that we again have a complex task and a choice regarding the placement of the loudspeaker and visual reinforcer, versus the assistant with her toys. Is it best to put the visual reinforcer on the right and the assistant on the left, or vice versa? During the original pilot work on the head-turn technique, the loudspeaker/visual reinforcer was placed on the infant's right and the assistant on the infant's left. But this arrangement made it look as though infants could not perform very accurately. It was very difficult to get infants to refrain from constantly turning their heads toward the right to check on the bear, no matter how fascinating the assistant attempted to be. Infants thus produced large numbers of false alarms and scored poorly on the discrimination test. Yet watching these infants suggested that they were capable of making the discrimination and of associating the sound change with the presentation of the visual reinforcer.

Subsequently, the left-right placement of the set-up was reversed. The assistant was placed to the infant's right and the loudspeaker/reinforcer to the infant's left. Now infants were oriented to the right, watching the assistant, and were required to produce a head turn to the left only when the sound changed. The effect was dramatic. False alarms could be virtually eliminated, and yet infants still produced head-turn responses reliably when the sound was changed.

Our interpretation of this is that human infants' tendency to orient toward the right is so strong that they will produce many spurious head turns if the reinforcer is on the right. These same infants will refrain from producing spurious head turns and will perform nearly perfectly when the reinforcer is moved to the left

side. This supports the data of others (Harnad et al. 1977; Kinsbourne 1972) and the MacNeilage et al. view that the right-postural bias is exhibited very early in human infants, and is quite strong.

One final point regarding both of our observations should be mentioned. In both cases, the auditory signals being presented are speech. What effect does the signal itself – the fact that it is an auditory event, and in particular that the auditory signal is speech – have on primates' choice of hands and human infants' head-turn biases? It is quite possible that the hand/postural preferences we observed are influenced by the nature of the signal, but at this point we do not know.

In conclusion, we have cited two observations on handedness. Primates use their right hands exclusively in a manipulation task that is nonvisually guided. Human infants display a strong postural bias toward their right sides. Both observations can be taken as support for the MacNeilage et al. view, but in order to be supported strongly, further hypothesis-based predictions will need to be developed and tested in laboratory settings.

The primate mouth as an agent of manipulation and its relation to human handedness

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MacNeilage et al. (1987) have shown to everybody's satisfaction that handedness in subhuman primates is an elusive thing. This comes as no surprise because the hands in subhuman primates are rarely used to manipulate and explore things independently of the mouth; the hands by and large serve the same support function relative to the mouth that the nondominant hand in human adults serves relative to the dominant hand in bimanual skilled activities. This is even the case for those prosimians (e.g., the galagasines) that do have a clear lateral preference in reaching for their prey because after the "reach and grab" the fine dismantling of the prey is performed with the mouth while the hands hold and position the prey for the mouth. If the hands play a role subordinate to that of the mouth in manipulation, with little functional specialization worthy of the name, preferences becomes a matter of chance and habit. Indeed, one can even find human data similar in its inconclusiveness to those for subhuman primates if the manual activities are sufficiently inconsequential (Suchenwirth 1969). Nevertheless, there is a link between human handedness and lateral specialization in subhuman primates. I begin with the assumption, shared by many, that there is a unilateral cerebral specialization favored by the demands of operating the vocal apparatus (Falk et al. 1986; LeMay et al. 1982). In addition, however, I stress the role of the mouth in the exploration and manipulation of food. There are a number of parallels between oral and manual manipulation that are striking, including even the fine regulation of jaw pressure in delicate probing (cf. Preilowski's 1979 observations on fine manual pressure regulation in monkeys). If a lateral specialization exists for motor control of the oral region in vocalization and oral manipulation, it follows that a laterally biased path for focusing attention along similar lines also exists: Functional and structural specializations are optimally exploited only if supported by attentional specializations. I suggest that the link between oral and manual manipulation is given by an attentional bias that results in a preferential allocation of attention to the activities of the right hand, assuming a left-hemisphere specialization for motor functions of the oral region (Falk et al. 1986). In humans, a right-hand preference for unimanual activities requiring focused attention (and this includes both manipulative activities and those requiring fine timing) is clearly expressed, and this attentional bias can be demonstrated when motor variables are removed (Peters 1985).

Two principal factors weaken the expression of compelling hand preferences in subhuman primates. First, the hands are not sufficiently emancipated from the mouth to become themselves an exclusive focus of attention in manipulation (note here the unclear situation with regard to human infants, who also still use the mouth as an important agent of manipulation). Second, unimanual movements that do not require particular skill permit considerable flexibility in terms of which hand is chosen. We agree with Steklis and Marchant (1987) in their support of Heuer's (1987) preference/performance distinction: It would be unfortunate if prosimians with a lateral reach-and-grab preference would have to forego prey that passed on the other side. This even applies to humans. Goodale (1987), for instance, extols the virtues of right-handed reaching but thousands of right-handed baseball players reach and catch wonderfully well with the left arm and hand in spite of whatever functional and structural adaptations predispose humans to reach with the right. As far as activities like reaching in experimental situations are concerned, MacNeilage et al. (1987, p. 294) themselves recognize that the purpose of reaching rather than its membership in a certain class of movements may be an important aspect of lateral preference.

Handedness in subhuman primates is also not compelling because skilled bimanual activities in the sense in which they occur in humans (Guiard 1987; Peters 1985) are only weakly developed. In humans, skilled bimanual activities require a role differentiation of the movements of the hands, and a differential allocation of attention. Again, it is perhaps the allocation of attention that is more important than the movement characteristics or the dimension of complexity of movement of the component tasks. For instance, few would argue that the fingering movements in violin playing are less complex in terms of timing and topography than the bowing movements. Nevertheless, it is the (right) bowing hand through which the musician's will expresses itself (Whone 1972) and this is the hand that receives focused attention in the accomplished player.

I cannot think of any naturally occurring activity in subhuman primates that would require a role differentiation of the hands similar to that seen in humans. However, there are two activities that would merit closer investigation. In grooming, both hands are used to spread the fur (but it is usually the mouth that picks up the lice). The other activity is nest building, done by some anthropoid apes that build temporary sleeping nests. Here, it would be of interest to study a potential role differentiation of the hands.

In summary, it is suggested that the antecedents for handedness in humans are laid down in subhuman primates but that these antecedents are more closely linked to the use of the mouth as agent of volition and manipulation than on the use of the hand. Hand preferences in subhuman primates are weakly expressed because the manipulating primate hand has not become fully emancipated from the mouth. I cannot resist a comment on footedness in parrots in this context because several commentators, including MacNeilage et al. 1987, have misinterpreted the role of the foot in parrots. The foot in parrots has the same status as the hand in subhuman primates: The foot holds and positions the food so that the beak can manipulate it! It is the beak rather than the foot that is the primary agent of manipulation.

Primate handedness: A paradoxical link to humans?

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MacNeilage et al.'s *BBS* target article (1987) offers an interesting reexamination of the origins of primate handedness that chal-

lenges traditional claims that hemispheric specialization and handedness evolved *de novo* in human primates (see Warren's commentary accompanying MacNeilage et al.'s original target article). They claim that two contrasting lateral preferences coexist in monkeys and that these represent potential phylogenetic precursors to human handedness. The first is a left-hand (right-hemisphere) preference for visually guided movement (Hypothesis 1) and a right-hand (left-hemisphere) preference for manipulation (Hypothesis 2). MacNeilage et al. suggest that both handedness patterns "may have evolved as feeding adaptations following release of the primate forelimbs from the locomotor demands made on their quadrupedal terrestrial ancestors." The first specialization – left-sided reaching – represents a prehensile movement for food that probably began with the prosimians. The second specialization – right-sided manipulation – probably occurred later in evolution, primarily in monkeys, with the development of the pseudo-opposable and opposable thumb and the precision grip.

Despite the claims for phylogenetic continuity in hand preference, the data marshalled in support of both hypotheses can be criticized on both methodological and conceptual grounds as witnessed by the peer commentaries accompanying the target article. One of the major flaws noted was the exclusion of the larger subset of animals (or tasks) showing *no preferences* in the statistical test of manual asymmetries (see the first-round commentaries by Annett, Cicchetti, Corballis, Jerison, McKeever, Steklis & Marchant, and Warren). This artifact is analogous to a tachistoscopic experiment using nonverbal stimuli in which the hypothesis of superior left visual half-field perception is being tested (e.g., Hypothesis 1). Assume that the following lateral frequencies were observed: left = 30%, right = 10%, none = 60%. To conduct one's test only between the first two groups (L vs. R), excluding the third (no preference), could provide misleading implications about hemispheric specialization, even though there was, compatible with the hypothesis, a three-fold increase of left-sided superiority on this task. Notwithstanding, this result would not allow the conclusion that the right hemisphere was specialized for this task.

Although MacNeilage et al. (1987r) acknowledge in their response to the first-round commentaries that their position lacks firm affirmation, they still argue that those who wish to demonstrate a lack of hemispheric specialization in monkeys are in the uncomfortable position of trying to prove the null hypothesis. I would like to argue that, paradoxically, MacNeilage et al.'s search for a putative phylogenetic precursor to human handedness may have been strengthened by attention to the one phenotype they excluded from all analyses, namely, the animals showing no consistent lateral preference. In each of the studies discussed in the target article, the incidence of this phenotype ranged from 32.8% (Table 1) to 50.4% (Table 2). A similar frequency of ambilateral preference (43%) was reported independently in one of the commentaries on the target article using a number of different reaching and visually guided tasks (Deuel & Schaffer). Warren's commentary also included a re-analysis of the Beck and Barton (1972) study, which contained no information regarding the no-preference group; on the visual reaching tasks, the incidence turned out to be 31%.

My argument is the following: The incidence of this *no-preference* manual phenotype in monkeys (approximately 40%) is quite similar to the frequencies noted in recent studies on human handedness in two seemingly contrasting populations, one neuropathological – namely, *autistic and nonautistic mentally retarded* subjects (Fein et al. 1984; Lucas et al. 1988; Soper & Satz 1984; Soper et al. 1986; Soper et al. 1987; Tsai 1982), and one developmental – primarily *infants* (Gottfried & Bathurst 1983; Liederman 1983; Michel 1983; Treves et al. 1983).

Autism and mental retardation (MR). With respect to autistic and nonautistic mentally retarded subjects, this ambiguous handedness subgroup (AH) (approximately 40%) was first iden-

tified (Soper & Satz 1984) by varying procedures typically used in the assessment of human adult handedness. Subjects are asked to demonstrate their manual preference for eight relatively simple items requiring skilled movement (e.g., spoon, crayon, dime, hammer). The items are administered three times each in a quasirandom order within each of two sessions spaced a week apart in order to determine whether the response preference, especially in developmentally disabled subjects, is stable within and between tasks (items) over time. In normal adults, this ambiguous handedness subtype has not heretofore been reported because of the implicit assumption that human lateral preferences for the same task are stable and consistent over time (Soper & Satz 1984). Two recent studies, using a similar test-retest procedure, reported the incidence of AH to be rare in normal adults (approximately 3%) (Green et al., in press; Liederman & Healey 1986).

We have hypothesized that the AH subtype represents a pathological alteration or developmental arrest in the establishment of manual dominance and cognition. Although the putative neural substrate remains to be confirmed by anatomic or metabolic imaging techniques, three recent autism studies have shown that this ambiguous handedness subtype (approximately 40%) represents a more cognitively impaired subgroup compared to autistic individuals with established dominance (left- or right-handed) (Fein et al. 1984; Soper et al. 1986; Tsai 1982). This subtype (AH) has also been shown to correlate with the presence of severe expressive and receptive language deficits in institutionalized mental retardates (Lucas et al. 1988).

Human infants. The ontogeny of manual specialization in children provides another framework for thinking about the phenomenon of ambiguous handedness in both humans and infrahumans. It is compatible with Palmer's (1964) concept of an undifferentiated handedness (ambilaterality), which he claimed should be distinguished from left-handedness or ambidexterity (i.e., within-task consistency). According to this theory, handedness evolves from originally undifferentiated movement patterns of infancy to progressively more differentiated and asymmetric skilled movement patterns of adulthood. This hypothesis is compatible with current views of lateral specialization in infants and preschool children (Young et al. 1983). However, some primate investigators still claim that hand preference is stabilized during infancy in humans (see Warren's commentary).

Although evidence now favors a right-sided manual bias, even during the first year of life, the development of this lateral preference follows a variable and unstable course until about eight years of age, at which time the vast majority of children (approximately 90%) reveal a *consistent* preference for the right hand (Fennell et al. 1983; Liederman 1983; Michel 1983; Treves et al. 1983). In fact, the longitudinal study of Fennell et al. (1983) showed that the expression of right-handedness in children at age 5 predicted with near certainty (97%) the same preference at ages 8 and 11. In contrast, the expression of left or mixed preference at age 5 was less predictive, especially for the mixed group, the majority of whom became right-handers by age 11.

With respect to the construct of ambiguous handedness (AH) it has recently been shown that a number of infants and young children between the ages of 1 and 3 years (approximately 40%) reveal similar variability and instability in lateral preference (within task). Gottfried and Bathurst (1983) reassessed lateral preference for one task (draw) at six follow-up intervals in a longitudinal sample of normal infants between the ages of 12 and 42 months. Approximately half of the subjects revealed inconsistent hand preference for the same task over time. The authors reported that stability of lateral preference was associated with more precocious intellectual development, but only in females. Treves et al. (1983) investigated the manual preference of 61 normal children between the ages of 1 and 3 years on eight consecutive trials of a single measure. They reported that 33% of

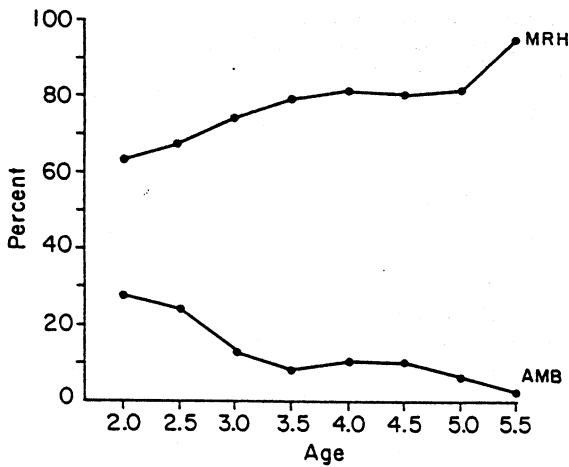


Figure 1 (Satz). Percent handedness phenotypes across age. MRH = manifest right handedness; AMB = ambiguous handedness (AH in commentary text).

the children showed no hand preference. However, they were unable to find an association between laterality and cognition, although verbal scores were pooled across sex in this study.

We have recently investigated the association between age and manual specialization in a larger cross-sectional study of normal children between the ages of 2 and 6 years (Soper et al., in preparation). Using the same assessment procedure employed in the autism and mental retardation studies, we found that the incidence of AH was inversely associated with age, peaking in the 2- to 2.5-year-old age group (28.6%) and decreasing in linear fashion to 2.4% in the 5.5- to 6-year-old age group. If a younger group of 1-year-olds had been tested, the incidence of AH would have been approximately 40% to 50% based on the frequency slope across ages. Note that the incidence of AH in the 5- to 6-year-old age group is almost identical to the estimates reported for normal adult samples (Green et al., in press; Liederman et al. 1986). It should also be noted that this linear age decrease in the incidence of AH was associated with a corresponding increase in the incidence of consistent right-handedness (ranging from 63% [ages 2 to 2.5 years] to 95% [ages 5.5 to 6 years]).

Conclusion. The expression of an anomalous or ambiguous handedness phenotype (approximately 40%) in infrahuman primates (monkeys) and in two seemingly contrasting human populations, one neuropathological (autistic and MR) and the other developmental (infants), raises the question of a possible paradoxical link in MacNeilage et al.'s search for a phylogenetic precursor to human handedness. Rather than trying to demonstrate the existence of an asymmetric phylogenetic precursor (hand/brain), for which the data do not warrant rejection of the null hypothesis at this time, the authors might consider the excluded case of ambiguous handedness as a potential bridging link in primate lateralization.¹ In this context, one might hypothesize a basic randomness in the distribution of primate handedness (commentaries by Glezer, Deuel & Schaffer, Warren) which is observed briefly in humans during the earlier stages of normal infancy and childhood when the central nervous system is maturationally less differentiated (ontogeny recapitulating phylogeny), and more permanently in cases of severe pre- and early postnatal brain insult (autism and MR).

One final comment regarding the expression of randomness in infrahumans. Typically, lateral preference (L or R) is defined by consistent unilateral responding on 70% or more of the trials of a single task. Subtype frequencies are then calculated separately for each task rather than for all tasks combined (as in humans), which is bound to mask the true incidence of AH, as well as randomness, in infrahuman primates.

NOTE

1. The hypothesis of two asymmetric primate phenotypes should have been tested to see whether this type of lateralization conferred an advantage in terms of learning compared to the nonlateralized subtype.

Language, handedness, and the larynx

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In their response to the Commentary on their target article, MacNeilage et al. (1987, p. 297) agree that "if language originated first, subsequent left-hemisphere control of praxis could easily be motivated." However, they resist the suggestion that human handedness is secondary to language. They retain their original hypothesis that human handedness evolved directly from general primate manual and postural asymmetries, the interaction between language skills and handedness being confined to the hypothesis that prior left-hemisphere specialization for manipulation influences subsequent hemispheric asymmetries in speech production. Several aspects of the data on both primate handedness and human hemispheric specialization suggest much more strongly that speech production specializes in the left hemisphere first and right-handedness comes second, both phylogenetically and ontogenetically.

MacNeilage et al. admit that the evidence for nonhuman primate population asymmetries in hand usage remains ambiguous at best. If other primate species had clear precursors to human handedness, but no language, this would be strong evidence for handedness first, then language. But systematic species handedness, so readily measurable in *Homo sapiens*, remains remarkably elusive in our extant relatives. If other primate species appear to be equally lacking in both handedness and natural language, no conclusions can be drawn about relations between these features in humans. However, there are other reasons for regarding cerebral asymmetries in language skills as being in some sense prior to handedness. One is the greater skew of the statistical distribution of left-hemisphere specialization for language. Estimates vary but, as Annett (1987) has emphasized in her commentary on the target article and elsewhere, only about 9% of the human population at most are not "left-brained speakers" (that is, would not suffer language impairments from left rather than right unilateral brain damage); and 30% to 40% have some left-hand preferences (Annett 1985). That is, far more people have some left-hand preferences than have resistance to the effects of left-hemisphere damage on language functions. Direct physiological assessment of speech lateralization has been taken to suggest that more than 90% of right-handers are left-dominant, with 65% to 70% of left-handers also left-dominant for language (Branch et al. 1964; Warrington & Pratt 1973). It is arguable that manual skills are much more flexible with respect to hemispheric specialization than language skills: Relearning manual skills with a different hand is far easier for adults than relearning language skills with a different hemisphere, and many manual skills in bimanual tasks (in particular those of the left hand for the playing of stringed instruments) may be performed satisfactorily by the right hemisphere even of those with no left-hand preferences (Haaland & Delaney 1981; Oldfield 1969).

These details are more consistent with the view that human population handedness derives from a biasing factor imposed on the random variation in individual limb preferences typically found in mammalian species (Walker 1980) than with MacNeilage et al.'s position that manual asymmetries are consistent enough to have been the precursors of other aspects of human hemispheric specialization. Few would wish to introduce any-

thing in addition to a factor that predisposes the left hemisphere to language. Annett (1985) has suggested that there is a single dominant gene whose possession raises the probability of left-hemisphere language specialization above 50%, but there are several difficulties in supporting a Mendelian account of lateralization, and this theory fails to explain the apparent bias against bilateral language control.

An alternative theory, based on the completely unambiguous anatomical fact of asymmetrical laryngeal innervation, was briefly put forward in my initial commentary (Walker 1987b), but finessed by the authors' response in favour of a fuller rejection elsewhere, with the suggestion that the hypothesis would have no implications for behaviour and is unsupported by neurological evidence. I would wish to add here only a brief reaction to these points. First, in the context of the contrast between primate grunts and squeals (anthropoid apes can in many cases produce them as easily by inhalation and exhalation) and the complexities of articulate speech, and the known bilateral brain control of nonhuman primate vocalization (see Walker 1987a for a review), the hypothesis accounts both for a move to unilateral control of speech production, and for a bias towards the left-hemisphere (influenced to some extent by the individual variations that exist for laryngeal innervation). It explains the elusiveness of the behavioural evidence for population handedness in nonhuman primates by suggesting that this should only be observed in primates with speech; and it accounts for the variability in human manual preference and skill. Independent neurological evidence that there are problems because the left and right output pathways to the larynx are of different lengths is more difficult to come by, but some support may be derived from the literature on stuttering, which suggests both that stutterers have less complete language lateralization than non-stutterers and that difficulties in laryngeal control contribute to the disorder.

The suspicion that stutterers have incomplete language lateralization has frequently been expressed (e.g., Orton 1927). It is fair to say that it has been dismissed equally frequently, but evidence has been accumulating recently that there are reliable differences between stutterers and control groups on a variety of measures of laterality (e.g., Rastatter & Dell 1987; Sussman & MacNeilage 1975; see Strub et al. 1987 for a review). The idea that laryngeal control (or coordination of the larynx with supra- and subglottal activities) is impaired in stutterers has also long been supposed, because it has always been known that a reduction of voicing variation (as in whispering, singing, or mouthing words) radically alleviates dysfluency. Systematic experiments with speech tasks having varied voicing requirements adds weight to this idea, and there is increasing confirmation of abnormality from more direct measurement of laryngeal activities in stutterers (Adams & Reis 1971; Conture et al. 1986; Dalton & Hardcastle 1977; Perkins et al. 1976; Shapiro 1980; Watson & Alfonso 1987). These findings are consistent with the notion that bilateral control of the larynx causes difficulties that are normally resolved by left-hemisphere specialization.

More generally, the challenge to brain mechanisms presented by the rapid and elaborate serial ordering of human speech has been remarked on by many others apart from Lenneberg (1967), including MacNeilage (1970). It would surely be surprising if asymmetries in output pathways did not complicate this task, especially if, as is probably the case for the larynx, the same pathways contain closed-loop feedback circuits. There is thus ample reason to look to speech itself as the prime mover in the development of human cerebral lateralization, instead of seeking its origins in a universal primate postural asymmetry, which now, because of the very thoroughness of MacNeilage et al.'s review, seems increasingly chimerical.

Left-hand reaching preferences in prosimians

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The multidimensional view of hand use advanced by MacNeilage et al. (1987) has opened the way for a comprehensive theory of primate lateralization based on comparative studies and phyletic history. Geschwind (1985) observed that the study of the biological basis of laterality was retarded by the popular assumption that neural and behavioral laterality occur only in human primates. This "homocentric" view has been supported by studies that used a limited sample of primate species as illustrated in the examples of MacNeilage et al. Clearly, a broader species data base is required to resolve the question of nonhuman primate laterality.

In the few years since we reported the first systematic study of prosimian hand preference (Sanford et al. 1984), my students and I have completed assessment of hand preference in food reaching for subjects of four prosimian species. The results of this work, summarized in Table 1, show that the left-hand bias in food reaching described in the first study for the lesser bushbaby (*Galago senegalensis*) appears to be a characteristic that extends across several species of prosimians.

Two of the first-round commentaries on MacNeilage et al. (Cicchetti 1987; McManus 1987) addressed the question of the appropriate statistical analyses to be used for assessing group hand preference. The classification of individual subjects should be a prior concern, however, because decisions about group laterality are ultimately based on classifications of the individual subjects that compose a species sample. Most studies have expressed left- and right-hand responses as a percentage of the response sample and then selected a criterion value to determine hand preference for each subject. In our recent studies binomial z-scores have been used to characterize hand preference for each subject. The sign of the z-score indicates the direction of lateral preference and the magnitude determines whether the measured preference is statistically significant. A chi-square test is used to determine whether the distribution of subjects into left, right, and ambipreferent categories is different from chance. This analysis was used for the data in Table 1.

The three lemur species were housed in zoos (Memphis, Tenn.; New Orleans, La.; Monroe, La.) or the Duke Primate Center, Durham, N.C. Thus, most lemurs were scored for hand preference while eating their usual diet in their standard living quarters, either cages or outdoor enclosures. For the ring-tailed lemurs (*Lemur catta*) and one subset of 5 black-and-white ruffed lemurs (*Varecia variegata variegata*) living on a moated island, food was thrown onto the surface of the island or into the

Table 1 (Ward). Number of individuals classified by z-scores as left-hand preferent (LH), ambipreferent (A), and right-hand preferent (RH) with chi-square values for each sample of four prosimian species and the total sample

Species	LH	A	RH	Chi square
<i>V.v.variegata</i>	9	6	1	6.16*
<i>Lemur macaco</i>	20	1	12	16.54*
<i>Lemur catta</i>	7	3	3	3.82
<i>G.s.moholi</i>	7	0	3	6.60*
Prosimian total	43	10	19	24.25*

* $p < 0.05$

adjacent moat. The mean number of responses per subject for the 16 black-and-white ruffed lemurs was 85.8; for the 33 black lemurs (*Lemur macaco*), 118.9; and for the 13 ring-tailed lemurs, 60.4.

Data for the 10 lesser bushbabies (*G. senegalensis moholi*) were collected in the laboratory under 14 different test conditions with a total of 780 responses per subject. The tests varied posture, angle of reach, visibility of prey, and angle of approach; the required response for all tests was capture of a mealworm (*Tenebrio* larva). This study (Larson et al., submitted) confirmed the earlier finding (Sanford et al. 1984) that bipedal posture enhances the use of preferred hand. In this study, whole body turning was also assessed. It was found that 9 of 10 subjects had a turning bias: 8 to the left and 1 to the right. This result was particularly interesting in light of the recent finding of a leftward turning bias in children 7 to 9 years of age (S. D. Glick, personal communication).

The theoretical proposal of MacNeilage et al. (1987) is supported in part by the data in Table 1. Evidence for the specific hypothesis of a relationship between left-hand specialization and right-limb postural support was found in an analysis of food handling patterns of the ring-tailed lemurs in the form of duration of food holding with the left hand, right hand, or bimanual grasp (Milliken et al., submitted). Ambipreferent and right-preferent lemurs engaged in more bimanual holding and did not favor either hand when holding food unimanually as compared to left-preferent subjects that held food bimanually less often and favored the left hand in unimanual holding. The unimanual left-hand food holding was particularly pronounced in three lemurs that habitually used the right forelimb in postural support. It will of course be necessary to test this hypothesis with other species because there are many adaptive specializations among prosimians.

At this early date in our studies we have already begun to identify factors that may affect the measurement of laterality and conclusions about species laterality. For example, some species have a greater propensity to pick up food with the mouth than with the hand and that propensity is influenced by food type. In the black lemur study, the younger animals were more likely to be left-hand preferent whereas the five oldest subjects were all right preferent (Forsythe & Ward, 1988). In the matriline of ring-tailed lemurs there was a sex link, with males left-hand preferent and females right-hand preferent or ambipreferent (Milliken et al., submitted).

Ultimately, the most productive insight to emerge from this work may concern the role of postural mechanisms in lateralized behavior as suggested by both MacNeilage et al. (1987) and the accompanying commentary of Michel and Harkins (1987). Evidence of bipedal posture as a setting condition for the use of the preferred hand in the first prosimian study led me to suggest that bipedalism results in increased neuromuscular complexity in problems of postural and locomotor equilibrium and that lateralization of modes of action may be the consequence and resolution of these problems of increased complexity (Sanford et al. 1984). The prosimian studies continue to show the effect of extreme postural adjustments on the manifestation of hand preference; for example, a study of the black-and-white ruffed lemur found slight hand preference in casual foraging for the same subjects that expressed extreme left-hand preference when food reaching was preceded by a whole body postural adjustment (Forsythe et al. 1988). This result makes one wonder what effect the restriction of an animal's movement (as in a primate chair) may have on the expression of hand preference. Other behaviors of this species that suggested a neuraxial basis for lateralization were a right leading limb in the initiation of locomotion and a leftward bias in tail positioning.

Geschwind (1985) proposed two levels of lateralization for the human nervous system: a pyramidal and an axial system. Other workers have found reason to look to subcortical regions for

reaching "programs" (Humphrey 1979) and sources of lateralization (Tucker & Williamson 1984). If neural lateralization is indeed not a homogeneous phenomenon, as the varied patterns of human lateralized behaviors suggest, then the study of non-human primates with their wide range of adaptive behaviors and systematic variations in forebrain development should lead to the identification of the neural mechanisms of primate laterality as well as illuminating their evolutionary origins.

Many hands make light work: Integrating research on primate handedness

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Over the last decade, statistically rigorous techniques for combining the results of scientific studies have been developed that allow for a meta-analytic overview of the state of evidence on research questions (Glass et al. 1981; Hedges & Olkin 1985). [See also Rosenthal & Rubin: "Interpersonal Expectancy Effects" *BBS* 1(3) 1978; and Prioleau et al.: "An Analysis of Psychotherapy versus Placebo Studies" *BBS* 6(2) 1983.] This commentary is intended to give a brief account of one way that such techniques might be applied to some of the evidence presented by MacNeilage et al. (1987).

To support their case for the existence of primate handedness, MacNeilage et al. (1987) twice selectively combine the data from different studies to achieve statistically significant results. This practice was strongly and justly criticized in the accompanying commentary of Steklis & Marchant (1987). A second problem with their approach is that the focus on significance levels has obscured the real issue in investigating the direction of primate handedness. Researchers are well aware that no matter how large an effect is, if little evidence is gathered the effect may not be detected; equally, and perhaps more important in this case, if the effect is not strong then large amounts of evidence may be gathered and the effect may still not be detected. However, the significance level, or "p-value" is a function of both the magnitude of the effect being considered and the amount of evidence collected (Hedges & Olkin 1985, pp. 3-6).

One can measure the direction of handedness in a population with

$$\pi_{LR} = \pi_L / \pi_R, \quad (1)$$

the ratio of those in the population with a left-handed preference to those with a right-handed preference. This can be estimated by

$$P_{LR} = L/R, \quad (2)$$

the ratio of the number in the sample with a left-handed preference (L) to the number in the sample with a right-handed preference (R), which I will call the directional ratio. A $(1 - \alpha)\%$ confidence interval for this estimate is given by

$$(P_{LR}/\exp[BC], P_{LR}\exp[BC]) \quad (3)$$

where B is the Chi-square value, with one degree of freedom, that yields $p = \alpha$, and C is the square root of $(1/L) + (1/R)$ (Goodman 1965).

A suitable "effect size" to use as a basis for combining directional ratios in k studies is the natural logarithm of the directional handedness ratio.

$$h_i^{\wedge} = \log P_{LR} = \log (L/R), \quad i = 1, 2, \dots, k. \quad (4)$$

This has the advantage of having a conveniently large sample estimate of standard error that is given by:

$$\sigma^2(h_i^{\wedge}) = (1/L) + (1/R) \quad i = 1, 2, \dots, k. \quad (5)$$

Table 1 (Wilson). Calculation of the log directional ratio for Old World monkey studies

Study	L_i	R_i	h_i	W_i	$h_i W_i$	$h_i^2 W_i$
Itani (1957)	30	16	.63	10.43	6.56	4.12
Itani et al. (1963)	149	118	.23	65.85	15.36	3.58
Tokuda (1969)	17	8	.75	5.44	4.10	3.09
Deuel & Dunlop (1980)	2	8	-1.39	1.60	-2.22	2.07
Deuel (1975)	6	1	1.79	.86	1.54	2.75
Ettlinger (1961)	17	6	1.04	4.43	4.62	4.81
Ettlinger & Moffett (1964)	7	4	.56	2.55	1.42	.80
Milner (1969)	17	9	.64	5.88	3.74	2.38
Gautrin & Ettlinger (1970)	8	6	.29	3.43	.99	.28
Brookshire & Warren (1962)	13	6	.77	4.11	3.17	2.45
Cole (1957)	14	19	-.31	8.06	-2.46	.75
Cole & Glees (1951)	9	8	.12	4.24	.50	.06
Hall & Mayer (1966)	2	3	-.41	1.20	-.49	.20
Kruper et al. (1966)	11	6	.61	3.88	2.35	1.43
Kruper et al. (1966)	3	4	-.29	1.71	-.49	.14
Lehman (1970)	12	11	.09	5.74	.50	.04
Lehman (1978)	91	80	.13	42.57	5.48	.71
Lehman (1980)	23	35	-.42	13.88	-5.83	2.45
Trevarthen (1978)	2	3	-.41	1.20	-.49	.20
Warren (1953)	26	27	-.04	13.25	-.50	.02
Warren (1977)	7	6	.15	3.23	.50	.08
TOTAL				203.54	38.36	33.41

Note: For interpretation of symbols see text.

Where samples are small, Cicchetti's (1987) commentary suggested a continuity correction (Yates 1934), but this procedure has been criticized by Fienberg (1977). One alternative way to control for small sample size is to use a linear estimator weighted according to sample size (Hedges & Olkin 1985, p. 129). Giving more weight to more precise estimates, a weighted linear estimator of log π_{LR} is

$$h = \frac{\sum_{i=1}^k w_i h_i}{\sum_{i=1}^k w_i} \quad (6)$$

where

$$w_i = 1/\sigma^2(h_i). \quad (7)$$

A large sample confidence interval for h is

$$(h - Z_{\alpha/2}\sigma(h), h + Z_{\alpha/2}\sigma(h)) \quad (8)$$

where $Z_{\alpha/2}$ is the two-tailed critical value of the standard normal distribution at an α significance level and the sample variance of h is (Hedges & Olkin 1985, pp. 110-12)

$$\sigma^2(h) = \left\{ \sum_{i=1}^k \sigma^{-2}(h_i) \right\}^{-1} = \left\{ \sum_{i=1}^k w_i \right\}^{-1}. \quad (9)$$

A homogeneity statistic can be used to determine whether the studies share a common directional ratio:

$$Q = \sum_{i=1}^k (h_i - h)^2 / \sigma^2(h_i) \quad (10)$$

$$= \sum_{i=1}^k h_i^2 w_i - \frac{\left(\sum_{i=1}^k h_i w_i \right)^2}{\sum_{i=1}^k w_i}. \quad (11)$$

If they do share a common directional ratio then the statistic Q has an asymptotic chi-square distribution with $k - 1$ degrees of freedom (Hedges & Olkin 1985, pp. 122-28).

In combining the directional ratios for the Old World monkeys as reported in MacNeilage et al.'s target article, all relevant studies of reach reported by the authors have been used. Not all studies are suitable, however. One was not suitable because of missing data (Kawai 1967). In others (Brookshire & Warren 1962; Ettlinger 1961; Ettlinger & Moffett 1964; Gautrin & Ettlinger 1970; Lehman 1970; Milner 1969; Warren 1953) only one result could be used because of the problem of lack of independence of the results. In all, 21 studies were included; they are listed here in Table 1.

Inserting the totals in Table 1 into equation 11, the homogeneity statistic, Q , is 26.65, which is nonsignificant compared to the 95th percentile of the chi-square distribution on 20 degrees of freedom. In fact, it lies between the 80th and 90th percentiles of that distribution. Thus, having established that the directional ratios form a homogeneous set, one can proceed to estimate an overall log effect ratio and its confidence interval. Using equation 6, the estimate of the log directional ratio is 0.19, and equation 8 gives its 95% confidence interval as (0.05, 0.33). This does not include zero, so the conclusion is that, at a 5% significance level, the log directional ratio is not equal to zero. Reverting to raw ratios, this means that the weighted estimator of the effect ratio is 1.21 and that, at a 5% significance level, this is different from and greater than one.

Two commentators, Guiard (1987) and McManus (1987), mention the "file-drawer problem" (Rosenthal 1979) - the fact that studies reporting statistically nonsig-

nificant results often go unpublished, and so languish in a file drawer. The results reported above may be manipulated to address this problem. For example, one might ask how many unpublished studies with a directional ratio of unity would have to be found to reduce the meta-analytic result to statistical nonsignificance: If the size of the sample were $R = L = 20$ (approximately average), then there would need to be 18 such unpublished studies. That is, almost half the studies undertaken would have to have been overlooked, which would appear to be a highly unlikely surmise. However, this result is sensitive to the size of the studies: If each of the neutral studies were large, say $L = R = 100$, then there would only have to be 4 such studies.

Meta-analytic techniques have permitted the integration of mild results from a number of studies, several with small sample sizes, to give an overall result supporting one of the contentions of MacNeilage et al.'s target article: There is a consistent left-hand preference shown by Old World monkeys in studies of reaching behavior. This commentary has not addressed the issue of whether a directional ratio of 1.21 is substantively interpretable. The studies that show a left-hand preference have predominated because, relative to the others, they have been the ones with larger log directional ratios and larger numbers of cases. Note that the technique does not relieve the reviewer of the obligation to consider each study's acceptability and relevance (Slavin 1986). The editing down to a valid set of effect ratios is a task that must be undertaken according to the knowledge and beliefs of the reviewer, and different decisions at this point will yield different results in the final analysis. The choice of the particular set of results (given in Table 1) for analysis may be disputed by those with theoretical perspectives on such a choice. These techniques can, in that case, be applied to the altered set of results, and different substantive conclusions may emerge.

Hand preference: Basis or reflection of hemisphere specialization?

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MacNeilage et al. (1987) describe population-level hand preferences for different types of tasks in nonhuman primates based on their review of the literature, and suggest that these hand preferences imply hemisphere specializations for manual preferences. They further suggest that such a hypothetical central motor lateralization is an evolutionary precursor of hemisphere specialization in humans. The presence of a strong correlation in humans between laterality in hand preference and the pattern of hemisphere specialization for cognitive functions, particularly language, or between the hemispheric representation of praxic functions and other cognitive skills would provide support for this hypothesis. These issues are not developed by MacNeilage et al., but they may be worthy of consideration if an evolutionary role in human hemisphere specialization is to be attributed to hand preference in nonhuman primates.

Hemisphere specialization in humans has long been linked to speech and language, and hand preference has been recognized as a relevant factor from the time of the discovery of cerebral dominance. Initially, language functions were considered essential for hemisphere specialization; more recently, even

though not viewed as the basis, speech and language functions are considered inextricably intertwined with brain lateralization. In the last decade, several sets of findings have emerged that corroborate the recent notion that language functions are not necessary for hemisphere specialization. (1) The diversity of cognitive skills shown to have asymmetric representation in the human brain (e.g., Bradshaw & Nettleton 1981) illustrates that the simple language/nonlanguage dichotomy can no longer account for all the empirical data. (2) Evidence that hemisphere specialization for cognitive skills exists soon after birth, with little indication that it increases over development (e.g., Kinsbourne 1975; Witelson 1977a; 1987, for reviews), suggests that hemisphere specialization is not dependent on the presence of speech. Hence hemisphere specialization may not be unique to humans. (3) The increasingly compelling evidence of hemisphere specialization for various cognitive skills in nonhuman primates (e.g., perception of species-specific vocalizations [Heffner & Heffner 1984] and facial discrimination [Hamilton & Vermeire 1985]) again demonstrates that speech per se is not essential to hemisphere specialization and, as MacNeilage et al. point out, that hemisphere specialization does not arise de novo in humans. (4) The documentation of neuroanatomical asymmetries in nonhuman primates, similar to though less marked than those in humans, does not demonstrate but is consistent with the position that hemisphere specialization does not arise de novo in humans; that brain lateralization is not dependent on the presence of speech; and thus that the essence of hemisphere specialization must lie elsewhere, possibly with more elementary or basic mental functions.

In the context of these recent data, the finding of hand preference in nonhuman primates fills a logical gap in what is known about hemisphere specialization in nonhumans, as noted by MacNeilage and his colleagues. The question remains, however, whether the suggested hand preferences reflect a central motor specialization that serves as the basis or an *anlage* for human hemisphere specialization as hypothesized by MacNeilage et al., or whether the hand preferences themselves are manifestations, or epiphenomena, of hemisphere specialization in monkeys for different types of cognitive processes.

Specifically, MacNeilage et al. suggest that there exists in nonhuman primates a left-hand preference for visually guided reaching and a right-hand preference for manipulation and practiced performance. These may be related to the right- and left-hemisphere specialization in humans for visuospatial and manipulative movements, respectively. If the hypothesized central motor specializations in monkeys evolved into the hemisphere specialization of humans, then one might expect the pattern of hemisphere specialization for cognitive skills in humans to be closely tied to hand preference. The available data do not completely support this position. The low correlation between speech lateralization and hand preference has posed a long-standing riddle, as exemplified by Roger Sperry's query: "How do left-handers with verbal processes in the left hemisphere regulate writing with the left hand? . . . and why would such abnormal regulatory systems be used?" (Levy 1986, p. 511).

Speech and language functions, regardless of hand preference, are known to be either exclusively or predominantly lateralized to the left hemisphere in about 90% to 95% of the total population as determined on the basis of the incidence of aphasia after unilateral brain damage and on the results of Amytal testing (e.g., Witelson 1983, p. 129). However, if we use the writing hand as the criterion of hand preference, proportionately more left- than right-handers have bihemispheric or right-hemisphere representation of at least expressive language: On the basis of Amytal studies, the respective figures are 30% of left-handers, compared to, at most, 5% to 10% of right-handers. Yet the data from Amytal studies, the incidence of aphasia after right- and left-hemisphere damage in right- and left-handers (e.g., Hécaen et al. 1981; Kimura 1983), and the study of

neurologically intact individuals (e.g., Bryden 1982, Chapter 10) all indicate that the majority of left-handers still have left-sided language representation. Moreover, in absolute numbers, there may even be more right- than left-handers who have right-hemisphere speech representation (5% to 10% of the 90% of the population who write with their right hand [e.g., Rasmussen & Milner 1977; Hécaen et al., 1981, as calculated in Witelson 1983, p. 136] versus 30% of the 10% of the population who write with their left hand). The fact that hand preference is correlated to some degree with neuroanatomical asymmetries supports the hypothesis that the anatomic asymmetry is a biological substrate of functional asymmetry, but anatomic asymmetry appears to be less tied to hand preference than to speech lateralization (e.g., Witelson 1980; 1983, for reviews).

Furthermore, the preferred hand for writing is not necessarily the one preferred for other manipulative tasks. In fact, studies of large samples indicate that only 65% to 70% of the population show consistent right-hand preference (Annett 1972). It is not clear what the valid definition of hand preference may be with respect to cerebral dominance. Recent work on the size of the corpus callosum, the main fiber tract connecting the two hemispheres, has revealed that the callosal area in the midsagittal plane is related to hand preference, with consistent right-handers having a smaller callosum than mixed-handers, regardless of their degree of left-hand preference (Witelson 1985). This difference is particularly marked in the posterior region of the trunk of the callosum (Witelson 1986), a region documented in animals to connect the parietotemporal cortical regions of the two hemispheres, which in man are relevant to the lateralized functions of language, praxis, and spatial perception. Such results support the biological validity of the category of consistent right-hand preference in relation to hemisphere specialization. If only 70% of the population are considered right-handed, then there is even less correlation between hand preference and speech lateralization.

Hand preference has long been considered to be a reflection of the asymmetrical neural representation of some overall motor programming or praxis – frequently defined as the processes involved in the execution of learned skilled movements, excluding such general factors as comprehension and attention. Although there is incomplete documentation of the motor behavior subsumed under praxis, and of the neural regions involved in praxis, with some current models focusing on premotor association areas (Geschwind 1975) and others on posterior parietal regions (Heilman et al. 1985; Kimura 1979), it is generally agreed that praxis is usually left-hemisphere based. In considering MacNeilage et al.'s hypothesis that a central motor lateralization in monkeys evolved into human hemisphere specialization, it may be useful to consider the correlation between brain lateralization of praxis and language skills. For most right-handers, praxic abilities are lateralized to the left hemisphere, which is also usually the language dominant hemisphere; surprisingly however, most left-handers also show left-hemisphere dominance for praxic functions other than writing (Hécaen & Sauguet 1971; Kimura 1983). The possible dissociation between brain lateralization of praxic and language skills is highlighted by individual cases with unilateral brain damage such as that of a left-hander whose praxic control was lateralized in the right hemisphere but whose language was lateralized in the left hemisphere (Heilman et al. 1973) and a right-hander with praxic control in the left hemisphere and language in the right (Heilman et al. 1974).

In summary, the existence of some dissociation of both hand preference and brain lateralization of praxis from language lateralization does not support the hypothesis that a phylogenetically early central motor lateralization served as the framework for human hemisphere specialization. Rather than hemisphere specialization for hand preference per se in nonhuman primates evolving into human hemisphere specialization as MacNeilage et al. suggest, an alternative possibility is that the

phylogenetically early hand preferences do imply a functional brain asymmetry, but are merely a manifestation of it, rather than the precipitating cause. The perceptual asymmetries for the discrimination of conspecific vocalizations and faces are not readily subsumed under a motor scheme, but are compatible with the postulate of asymmetrical representation of some cognitive skills, such as spatial- and sequential-type processing, as hypothesized by various other authors (e.g., Levy 1977; Witelson 1977b, pp. 348–49). In such a model, hand preferences would be a manifestation of such neural asymmetries. How such hemisphere specialization may have evolved is another issue.

Moreover, even the description assigned to the hand preferences noted by MacNeilage et al. may require reference to nonmotor cognitive processes. For example, the dichotomy of visually guided reaching versus manipulative behavior for the left and right hands, respectively, would be difficult to maintain had the authors incorporated the findings of Ettlinger and colleagues in which a left hand preference was observed in monkeys for haptic perception involving *manipulative* behavior (see target article, Footnote #1). This left-hand haptic preference is not dissimilar to that observed for right-handed children as young as 2-years-old, who showed more accurate perception of objects palpated with the left hand, than with the right, which is considered to be a manifestation of right-hemisphere specialization for form perception (Rose 1984). The findings of Ettlinger and colleagues, and the results of the other studies of hand preferences in nonhuman primates, are all consistent with right-hemisphere specialization in monkeys for aspects of form and space perception, with the left-hand preference for the activities that draw on these processes being a result, or a reflection, of the contralateral hemisphere's functional specialization. In addition, the results of Ettlinger et al. render it more difficult to attribute a unique manipulative aspect of manual behavior to the right hand/left hemisphere system.

A model of central motor lateralization as the basis of cognitive hemisphere specialization may not account for all the data. In fact, MacNeilage et al. themselves appear at times to cast their model in nonmotor cognitive terms, at least for the right hemisphere, for example when they write: "Left-handedness for reaching may *reflect* [italics added] a spatiomotor specialization of the right hemisphere related to the right hemisphere's visuospatial specialization in humans" (sect. 6.3, para. 2), or "the initial specialization may have been primarily for the use of visual information in preprogramming of ballistic reaching movements" (sect. 6.4, para. 1). MacNeilage et al. appear less receptive to the notion that a nonmotor cognitive factor may operate for the right hand/left hemisphere asymmetry, which may have led them to posit that central motor lateralization evolved first on the basis of adaptations to feeding. The existence of hemisphere specialization for some perceptual skills in nonhuman primates has empirical support, and the current review supporting hand preferences adds further support to this finding. However, the evidence may not clearly favor a hypothesis of motor over other cognitive factors as the basis of phylogenetically early hemisphere specialization.

Editorial note

The preceding commentary was submitted in the first round of commentaries but was received too late for copublication.

Authors' Response

Primate handedness: A foot in the door

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We begin our response with the main conclusion: Evidence accumulated since the publication of the target article (MacNeilage et al. 1987) makes it no longer possible to deny the existence of handedness in nonhuman primates. (This fact partly prompts our title.) This conclusion is relevant to those first-round commentators who expressed more or less unequivocal disbelief in the earlier evidence (Annett, Corballis, Deuel & Schaffer, Jerison, Kolb & Fantie, Lehman, McKeever, Steklis & Marchant, Walker, and Warren) and to the smaller number who found the earlier evidence persuasive (Bradshaw, Goodale, and LeMay). It is most relevant to Annett, who has the best developed alternative view of the evolution of human handedness (Annett 1985). This theory states that not only handedness but hemispheric specializations of *any* kind first evolved in hominids. Our conclusion is also particularly relevant to Hamilton & Vermeire, Peters, and Walker among the contributors to Continuing Commentary, as their skepticism about the existence of handedness in primates is one reason they prefer different views of the origin of primate specializations. We will summarize the new evidence and then discuss it in more detail.

Evidence presented by Ward firmly establishes left handedness in a large group of prosimians. Evidence provided by King and Landau (in preparation) and by Fagot and Vauclair (1988a; 1988b) reinforces our earlier conclusion that left hand choice will be found in monkeys in situations which place a priority on visual guidance. Fagot and Vauclair (1988b) found a similar result in gorillas, suggesting that the generalization might extend to the great apes. There is also additional evidence for *right* handedness in anthropoids, including a further case, reported by King and Landau (in preparation), in which the same monkeys show opposite hand preferences for different tasks (the other instance is reported in Beck and Barton 1972). There is also further morphological evidence for a larger right side of the body in monkeys, as in humans, which adds support to a "postural origins" theory (to be discussed in more detail in MacNeilage, in preparation; aspects of this theory involving footedness also prompt our present Response title). Perhaps most important, the hope we shared with some earlier commentators that our review would stimulate more and better work in this area has been realized.

Current status of the evidence

Three studies of prosimians are reported by Ward in which there is a significantly nonuniform distribution of animals across the three handedness subgroups (left, right, and none). As all studies used the same meth-

odology it is presumably acceptable to test for the significance of the difference between the total number of animals with significant left and right hand preferences. This difference is significant (Chi Square 8.54; $p < .01$, corrected for the two-cell case as suggested by Cicchetti's original commentary). What is perhaps more important than these preliminary results is that Ward and her colleagues are pursuing their hypothesis that handedness is best viewed in a postural context; they are studying a broad spectrum of behaviors from the standpoint of bodily asymmetries in general. Perhaps the most spectacular result of this work so far, to which Ward briefly alludes, is the finding that a group of 5 ruffed lemurs, who showed only slight hand preferences for reaching during foraging (100 reaches per animal), made 514 out of 515 extended reaches for food floating in a moat with their *left* hands (Forsythe et al. 1983).

King and Landau (in preparation) have reported extremely strong left hand preferences in a group of 18 squirrel monkeys in two tasks which involved catching goldfish. In one task, fish were caught from a bowl and in the other they were caught in a wading pool. Median tests evaluating the amount of left hand preference in the population were significant in each case beyond the .001 level; the correlation between amount of left hand preference on the two tests was significant beyond the .01 level. These results can be contrasted with the absence of significant population-level hand preference in a task involving reaching for a static target. In this case, the animal reaches through a small slot to obtain a piece of food resting in the end of a polyvinyl chloride (PVC) pipe four inches outside the cage wall. Results were negative whether the reach required a quadrupedal or a bipedal posture. It seems likely that the moving target is what evokes the lateralized preference pattern in the goldfish-catching situation; we would classify the situation as one that puts heavy demand on visual guidance.

Fagot and Vauclair (1988a) have shown a significant left hand preference in all six of a group of baboons in a task requiring precise alignment of a window in a sliding vertical Plexiglas panel with another aperture leading to a food reward (binomial two-tailed test L Vs R , $p = .03$). They obtained a similar result in 7 of a group of 8 gorillas (Fagot & Vauclair 1988; $p = .07$). As in the King and Landau study, simple reaching tests did not evoke a population-level hand preference in either of these experimental groups.

One thing that is remarkable about both these results and the King and Landau results on monkeys fishing for goldfish is that the percentages of animals showing handedness are much higher than in most of the monkey studies reviewed in the target article. We attribute this to the focus on visuospatially demanding tasks in these experiments.

The strongest right hand preference to be reported since the target article was written is described by Kuhl. She found that all 30 of a group of macaque monkeys tested on auditory discrimination tests over a several-year period chose the right hand to make the keypress response, which Kuhl describes as manipulative. This finding was discussed in the response to the initial commentaries. However, it is worth reiterating Kuhl's point that the relative role of manual and auditory factors in this lateralized behavior needs to be explored. Denenberg

has also emphasized the evidence for a left hemisphere specialization for auditory function, including communication, in monkeys.

Statistically significant right hand preferences and higher levels of right hand performance have been observed by Hopkins, Washburn, and Rumbaugh (1988) in a group of 2 rhesus monkeys and 3 chimpanzees in a task in which the subject must hit a moving target stimulus on an oscilloscope screen with a manually controlled cursor. Two of the chimpanzees tested (Sherman and Austin) also showed a left visual field advantage in a visual discrimination task with tachistoscopic presentation of small lines in several locations in a geometric form (Hopkins & Morris 1988). Sherman, who is more strongly right handed in everyday activities, showed the left visual field advantage in responses with both hands, but Austin only showed the advantage in responses with the left hand. This combination of results suggests that the distribution of both manual and visuospatial function in the cerebral hemispheres of these chimpanzees may be similar to the typical distribution in man.

The findings hint at an answer to Hardyck's question: Why are cerebral morphological asymmetries in great apes similar to man, despite the fact that great apes lack language? The answer is probably that much of the distributional pattern of cerebral asymmetries in humans (including significant underpinnings to subsequent language) is also present in the great apes. In any event, these authors deserve much credit for initiating work with such sophisticated experimental techniques – work which must certainly prove profitable regardless of the specific findings. [See also Macphail: "The Comparative Psychology of Intelligence" *BBS* 10 (4) 1987.]

King and Landau (in preparation) have also found a highly significant right hand preference in a group of 16 squirrel monkeys (Median test, $p = .006$) in reaching for a piece of marshmallow on a dowel while clinging with three limbs to the steel mesh of the cage wall. This is the first finding of a statistically significant right hand reaching preference in nonhuman primates that is not contradicted by other results. The result does not fit our characterization of the right hand of higher primates as being favored for manipulation and practiced acts but not for reaching. However, it is consistent with a morphological finding of Dhall and Singh (1977) which we mentioned in our initial Response. They found that the only exception to the pattern of a number of bones and muscles of the rhesus monkey being larger on the right side was a larger left pectoralis muscle. The authors considered this muscle to be the most important one in forelimb suspension. (The finding that rhesus monkeys forelimb bones are larger on the right side has recently been replicated by Falk, Pyne, Helmkamp, and De Rousseau, 1988, with a group of 145 rhesus monkeys.) We interpreted the results of Dhall and Singh as supporting our hypothesis that the right side evolves from being the postural support side in prosimians to being the operative side in higher primates. We visualized the step as occurring with the evolution of invasive foraging. But squirrel monkeys are better characterized as gleaners than invasive foragers (Terborgh 1983). Consequently, this aspect of our view requires adjustment. For the 15 monkeys that participated in both goldfish catching and suspended

reaching there was a significant difference between the preference scores in the two conditions (Wilcoxon test, $t = 18$, $p < .02$, two-tailed test). As in the case of the Beck and Barton study (1972), we regard this reversal of hand preference for different tasks in the same animals as an extremely important finding that makes it obvious that further study of primate handedness will be very rewarding.

These various results, together with many of the findings presented in the target article, put the presence of population-level handedness in nonhuman primates beyond reasonable doubt. However, two modifications are necessary to statements made in the target article and our initial Response. The necessity for these was pointed out to us by Vauclair and Fagot (personal communication). First, in the study by Schaller (1963) cited in the target article, there were not 72 gorillas but 72 chest-beating responses made by 8 gorillas. Second, the highly significant right hand preference for gorillas reported in the first-round commentary by Brésard & Bresson was obtained by summing results of a number of small-scale studies of various kinds in the literature. We briefly reviewed many of these studies, but concluded that it was unjustified to pool them.

Wilson and Hardyck raise some further statistical questions about data in the target article. Wilson presents what appears to be a useful statistical method for analyzing several studies of the same question. As he points out, the criterion for pooling studies is a critical issue, one in which we have not been held blameless. It would be tempting for us to accept the significance level that Wilson obtained in his meta-analysis of reaching studies. However, these studies are unfortunately not homogeneous, as some of them include various other acts in addition to reaching. Furthermore, the studies of King & Landau and of Fagot & Vauclair mentioned earlier make it increasingly clear that monkeys at least do not show population-level simple reaching preferences in laboratory situations.

Hardyck makes an additional statistical point. With respect to Tables 1 and 2 in the target article, he points out that there are two questions of interest. The first is whether there is a difference between the three groups: left, right, and nonhanded. The second is whether there are more left handers than right handers. Given the relatively large number of animals with either no hand preference or with a hand preference that could not be determined under the given experimental conditions, we treated the first question as moot and confined our attention to the second. Hardyck doubts the validity of this procedure, arguing, if we understand him correctly, that we are not entitled to ask the second question until we have answered the first in the affirmative. He argues that the effect of our procedure is to reduce the degrees of freedom for the Chi Square and so to increase the claimed level of significance. Perhaps he is right. Nevertheless, although he takes with one hand he gives with the other, and we are grateful to him for pointing out that certain types of study (e.g., study C of Table 1) do offer a straightforward procedure for addressing the first question.

Hamilton & Vermeire present further negative evidence for handedness in rhesus monkeys in an experi-

mental situation. They used tasks classified by us as simple reach, complex reach, and manipulate (once) and reach – tasks of the kind that have been shown by numerous other experimenters (see target article, Table 4) to fail to evoke population-level hand preferences. They suggest that we would predict hand preferences in the latter two situations. If we have given the reader the impression that we would predict hand preferences in situations that have so far repeatedly failed to evoke them, it was a mistake on our part. Hamilton & Vermeire argue that the youthfulness of their monkeys cannot be taken by us as a reason for their lack of preference as they are as old as the monkeys in the Beck and Barton study (1972) which did show preferences. We argued that Beck and Barton's monkeys' experience with a large number of different complex tasks was also an important variable. We regard as extremely implausible Hamilton & Vermeire's suggestion that "inadvertent asymmetries" in the experimental arrangements for 17 different tests could have produced the significant dissociation between left hand reaching and right hand manipulation in the Beck and Barton experiment. We also wonder whether "wild caught and experimentally naive monkeys" first subject to 90 trials in which food position was intentionally randomized (something that has been shown to produce position-specific reaching) might be expected to show hand preferences within subsequent 30 trial blocks under two new conditions. Nevertheless, Hamilton & Vermeire have raised some important methodological and theoretical questions. We would concede the point, also made by other commentators, that there has been an appreciable component of ad hoc and post hoc theorizing on our part. This is perhaps inevitable at this stage of the reappraisal of this area. The most important thing we can say to experimenters at this point is "Make the tests challenging!" Concepts such as "need for visual guidance" and "manipulation" definitely have their problems, but we hope that they will help us arrive at a theory of primate handedness that is biologically plausible and has predictive power.

Human–nonhuman relations

Satz wishes to interpret the large proportions of non-human primates without hand preference, found in many studies, in terms of

a basic randomness in the distribution of primate handedness . . . which is observed briefly in humans during the earlier stages of *normal* infancy and childhood when the central nervous system is maturationally less differentiated (ontogeny recapitulating phylogeny), and more permanently in cases of severe pre- and early postnatal brain insult (autism and MR).

It is our belief that high proportions of nonhuman primates without handedness are only observed in studies not capable of evoking their handedness. Kuhl, in an intensive study (2 years per animal) found a hand preference in all 30 of her animals. In recent work by Fagot and Vauclair (1988a; 1988b), Hopkins et al. (1988), King and Landau (in preparation), and Ward, 15% or fewer of the animals studied have been found to lack preference. We would prefer to believe that all or virtually all normal

primates beyond a certain age will develop consistent hand preferences of some sort, which implies hemispheric specialization; the lack of handedness will therefore be virtually confined to subjects with an abnormal medical history.

Harris & Carlson present valuable information on reaching in humans, thus allowing, at this remarkably late stage, a comparison of human reaching with reaching in nonhuman primates. They find that one-year-old infants and adults are like monkeys in not showing *strong* hand preferences in laboratory reaching situations with variable target locations. Nevertheless, even the one-year-olds have a population-level right hand preference in this situation which is different from the behavior of other primates. In our opinion, this result is consistent with our conclusion that the pre-emption of the left hand by the right which we hypothesized for hominids is present at this early age. Harris & Carlson correctly bring up the question of the importance of visual guidance in this situation. But however important it is, no other primate group has consistently shown a right hand reaching preference in situations that presently appear roughly comparable to the one used by Harris & Carlson. This does not necessarily mean that the pre-emption took place earlier in development, unless one holds an "ontogeny recapitulates phylogeny" hypothesis, as Harris & Carlson seem to. Regardless of the interpretation of these results, we consider the type of work presented by Harris & Carlson essential for the comparative approach to handedness that we are pursuing.

Harris & Carlson also bring up the important question of object size and its relation to grip type in reaching studies. This issue is further developed in the discussion of Frigaszy & Adams-Curtis, who also sketch out a number of other research questions which arise from the framework we presented in the target article. In particular, we would second their motion for more work on the relation between grips and both hand preference and performance. With regard to development, we wish to correct these commentators' impression that it was an oversight that led to our neglect of this area. We were severely handicapped by the lack of data on nonhuman primate handedness development. In the human realm there is much more information and we briefly attempted to suggest a coherent interpretation of it in our first-round Response. At present we would suggest that all the well-known rightward biases in infants, including the communication-related bias noted by Kuhl and also by McKain, Studdert-Kennedy, Spieker, and Stern (1983), may be relatable to our hypothesis of the evolution of a whole body postural control specialization in the left hemisphere (see our response to Witelson).

Alternative scenarios for the evolution of hemispheric specialization

Walker has again raised the possibility that length differences between the Recurrent Laryngeal Nerves (RLN) serving the left and right sides of the larynx together with increased pressures toward a larger vocal message set (taking us beyond "primate grunts and squeals") may first have induced left hemispheric specialization. Right handedness in humans would thus be a secondary conse-

quence of left hemispheric language lateralization. Walker's persistence with this idea is in part related to the brevity of our initial response to it, on the grounds that its linguistic implications would take us well beyond the main task at hand. However, further consideration of Walker's hypothesis suggested that it can be addressed in a response of limited scope.

The specific motivation suggested by Walker for left hemisphere language was that the shorter length of the right RLN meant that signals from the left hemisphere would reach the larynx earlier than signals from the right and this would give the left hemisphere an advantage in controlling phonation. Why the *earlier* arriving subsystem would have an advantage over the later is not addressed. It has always been a mystery to us why Lenneberg (1967) and others have assumed that pathways of different lengths would impose a special coordination problem on a brain (e.g., in the case of coordination of forelimbs with hindlimbs in the elephant). However, prompted by Walker, we have made an attempt to understand the functional consequences of the length asymmetry in the recurrent laryngeal nerves. According to Krmptotic (1959), the right branch of the nerve is approximately 3/4 the length of the left branch. However, Krmptotic also reports that the mean axon diameter of the left branch is approximately 4/3 as great as the right. It can thus be inferred that the greater average conduction velocity of the right branch would exactly compensate for its greater length and the time of arrival of signals at the termination of each branch would be exactly the same, given a synchronous origin of the signals in the brain stem. This result suggests that there is no problem in synchronizing inputs to the left and right sides of the modern adult larynx, as far as the length of the recurrent laryngeal nerve is concerned. (We thank James Abbs for bringing these findings to our attention.) If only Lenneberg (1967), who used the figures for the right RLN fiber diameters in his computations, had noticed that the left RLN diameters were different, the recent history of thought on this topic might have been different.

The main basis for Walker's hypothesis was the likelihood of anatomically induced asymmetries in laryngeal control; hence, our failure to find such asymmetries in inferred transmission characteristics leaves the hypothesis, in our opinion, without a center. One could argue that the balancing of the length differences by the transmission differences shows that the length difference is a problem that needs to be solved. But there is no evidence that the problem is one of any great difficulty. In addition, the evidence cited by Walker for the co-occurrence of laryngeal control problems and anomalous hemispheric specialization patterns does not allow conclusions to be drawn about the direction of causality – although the corticofugal direction would certainly be more likely for most cases.

Like Walker, Peters believes that human handedness (though not the left handedness of prosimians) was a secondary development. He is apparently driven to this belief by his dissatisfaction with the evidence for nonhuman primate right handedness (which the evidence summarized earlier should diminish) and his belief in the importance of the mouth but not the hands as manipulative organs in nonhuman primates.

We share Peters's view that the role of the mouth in noncommunicative acts such as food processing and feeding may be an important factor in nonhuman primate evolution. It is certainly a thoroughly neglected factor. (Evolution of facial expression is also neglected.) This is presumably due partly to the fact that normally neither the process nor the output of the oral phase of digestion is readily available for inspection and that the externally visible food processing operations prior to mastication and swallowing have not captured the imagination of anyone interested in the evolution of action systems. Elsewhere, one of us has attempted to draw attention to one aspect of oral vegetative function we believe has important evolutionary implications (MacNeilage 1987). It was claimed that feeding with the assistance of both hands, as seen in nonprimate mammals such as squirrels, and feeding with the assistance of one hand, which evolved in the earliest primates, were two early stages in the evolution of the main mode of organization used in complex output systems – the frame/content mode. This mode is defined as two complementary output subsystems, one more general-purpose than the other, with a lock and key relationship, manifest in output. Bimanual coordination was a further development of this mode in the manual system and two instances of the evolution of human language from nonlanguage, inferrable from speech errors, also adopted an analogous (not homologous) role. At the phonological level vowels and consonants are inserted into syllable structure frames; and at the morphosyntactic level content word stems are inserted into frames composed of closed class (grammatical) morphemes.

In the hand-mouth instances of the frame/content mode, the mouth, as Peters points out, usually plays the manipulative role. Peters did not say exactly when he thought the specialized left hemisphere oral system might first have evolved, but if it is present in prosimians Peters would be expected to predict *right* hand-mouth interaction, which would certainly be testable. It is of interest that Post, Hausfater, and McCuskey (1980) have reported a significant right hand preference for hand-mouth interaction in yellow baboons. We would regard this result as a consequence of the left hemisphere's having evolved a specialization for motor control of the whole body, which would be manifest in both right handedness and vocal communication lateralization. Perhaps an oral noncommunicative specialization might also have evolved. Thus, while we assume that Peters would only expect these animals to show right handedness in interaction with the mouth, we would expect that these animals would also show right hand preferences in manipulative tasks that do not involve the mouth. It would be interesting to know how Peters would account for the body asymmetries which favor a larger right side found in monkeys by Dhall and Singh (including the lower limbs) and by Falk et al. (1988).

Peters would presumably share our belief that both the mouth and the hand, under left hemisphere control, become increasingly important for manipulative purposes in hominids. Despite the evolution of tool use, the teeth have no doubt been used extensively in conjunction with the hand throughout human evolution, not only in chewing, but also in the preparation of a large range of

utilitarian objects (e.g., fiber baskets, textiles, etc.; see Larsen, 1985, for a discussion of this theme). The prominence of teeth in the paleontological record will probably lead to a much more thorough documentation of this important thread of hominid evolution.

While we agree with Peters about the importance of nonvocal oral evolution, we strongly disagree with his conclusion that the hands have been unimportant in nonhuman primates. The descriptions of primate tool use by Beck (1980), numerous descriptions of manual invasive foraging (e.g., Terborgh's 1983 description of cebus monkeys), the descriptions of chimpanzees using stones to crack open nuts in the wild (Boesch & Boesch 1981), Trevarthen's (1978) descriptions of baboons manipulating objects at a rate of 7 1/2 acts per second, and a number of other sources of evidence conclusively show an impressive level of nonlocomotory manual function in many primates. [See also Chevalier-Skolnikoff: "Primate Tool Use" *BBS* 12(1) 1989.]

To conclude, although we agree with Peters about the importance of noncommunicative oral function in the development of hemispheric specialization, neither he nor anyone else has yet provided much hard evidence of this role. On the other hand, there is a good deal of evidence not only that there is handedness in higher nonhuman primates but that naturally occurring hand function in these animals can reach a very high level of sophistication. A footnote: We regard Peters's recent review of footedness (1988) as a valuable contribution to the question of evolution of handedness, for reasons which will become clear later, although Peters himself does not place this topic in an evolutionary perspective.

Denenberg accuses us of species snobbery because we concentrated our attention on the zoological order which was the topic of our paper. He thus lays himself open to the same charge. In our first-round reply to Bradshaw, we summarized our position on the relation between primate handedness and asymmetries in other mammals:

Orientation (turning) preferences in rodents (Glick & Shapiro 1985) seem relevant to the putative primate postural asymmetry but no population-level asymmetries in these animals have been established. Nor does there seem to be any way to reinterpret studies of paw preferences in rodents in order to claim population-level asymmetries. We are intrigued by the evidence mentioned by Bradshaw for a right-hemisphere spatial specialization and a right-hemisphere emotional-control specialization . . . possibly related to predation. However, although we suspect that there were preadaptations to the putative prosimian asymmetries, we see no clear evidence of this at the moment. (MacNeilage et al. 1987r, pp. 295-96)

It is clear from this reply that we do not believe functional asymmetries began in primates. It is also clear that we do not believe that asymmetries in other taxa are irrelevant to asymmetries in primates. The choice of at least one of the prosimian asymmetries that we propose was presumably determined by asymmetries in ancestral forms. Our problem with this material arose from our inability to find population-level asymmetries that were consistent across strains of rats, and could therefore be related to the particular population-level asymmetries we observed in primates. We find it surprising that Denen-

berg does not mention this problem in his commentary, for it was he and his colleague Yutzey who drew our attention to it with the following statements (Denenberg & Yutzey 1985, p. 130):

With respect to postural asymmetries:

Glick's laboratory was the first to report that the neonatal rat has postural asymmetry which they measured by noting tail position. Their females are right tail biased in infancy and they are also right biased in adulthood for side preference and rotational behavior. We have confirmed the finding of neonatal tail posture asymmetry. In our population, both sexes are left biased.

Next with respect to affective behavior:

The research to date find that affective behaviors are lateralized in the right hemisphere. However, all these experiments have come from our laboratory using our strain of rat and thus it is difficult to know how widely this conclusion can be generalized.

Finally with respect to spatial behavior:

studies from our laboratory and from T. Robinson's both concur in finding that handling in infancy brings about a left sided behavioral preference thereby implicating the right hemisphere as controlling this behavior. However, research from Glick's laboratory with his strain of rat finds right sided biases in two different behavioral tasks. Thus there is clear evidence of strain differences.

Another thing we found rather daunting about the nonprimate mammal literature, though Denenberg failed to mention it in his commentary, is the magnitude of the sex differences in many studies. For example, Robinson, Becker, Camp, and Mansour (1985), in a summary of their review of sex differences in postural/motor asymmetries, state: "There appears to be no consistent bias for one direction across a variety of different tests of postural/motor asymmetries" (p. 195). How does one relate this conclusion to studies of primate handedness where sex differences have so far failed to play a significant role?

Part of Denenberg's difficulty with our position seems to come from his mistaken belief that we think primate handedness evolved *before* hemispheric specialization. We believe that handedness, and hemispheric specialization related to it, were subject to evolutionary changes *in parallel* in the earliest primates in response to selection pressures for unimanual predation in an arboreal habitat. But we are unsure what the neural or manual substrate for these lateralized developments was. To repeat: Our problem is that the evidence for *population-level asymmetries* in the ancestors of the first primates is simply not there. We may be in a better position to guess about this substrate when the lateralized *mechanisms* documented for modern nonprimate mammals are more closely related to the lateralized mechanisms of primates. The finding of Glick, Ross, and Hough (1982) that neurochemical asymmetries in the nigrostriatal system showed the same relation to body orientation preferences in rats and humans (if one takes handedness as indicating body orientation preference) is a promising lead. But in the case of detailed properties of manual function and other functions (e.g. muricide), it is more difficult to compare dependent variables across major taxonomic groups. Another current barrier, pointed out by Robinson et al.

(1985), is that while most of the neuropsychological work on action asymmetries in nonprimate mammals has focused on subcortical neural substrates, most work on primates has focused on the neocortex. This is unfortunate, because postural asymmetries in primates, including the well-documented ones in human neonates, obviously have very important subcortical substrates. Perhaps more attention will be given to subcortical asymmetries in primates as a consequence of the recent finding of Kooistra and Heilman (1988) that the left globus pallidus is larger in humans than the right.

To summarize our response to Denenberg: We feel that it is essential to try to develop a unified theory of the evolution of neurobiological asymmetries in *vertebrates*, though in terms of population-level patterns of primate handedness we see little in the way of straightforward links to other taxa at the moment. Our ultimate aim will perhaps be served in part if we can convince Denenberg of the relevance of primate handedness to *his* concerns.

Witelson expresses some doubts as to whether a "central motor lateralization" (her term for our view) should be accorded a major evolutionary role, suggesting instead that the initial specialization(s) may have been cognitive, and that handedness may be a reflection of cognitive specializations rather than a crucible for them. In order to respond adequately to her wide-ranging discussion it is necessary that we begin by summarizing our present views in overall terms. We now hold what can be called a "postural origins" theory of the evolution of primate hemispheric specializations (MacNeilage, in preparation), nonlinguistic aspects of which were briefly alluded to at the end of the target article and in the initial response to the commentary. Left hand reaching preferences in prosimians, and the likelihood that the earliest prosimians were vertical clingers and leapers, lead us to believe that two complementary specializations developed (or perhaps developed further - see our reply to Denenberg) in ancestral prosimians:

(1) A left-hand, right hemisphere perceptual-motor specialization for unimanual predation with visual-spatial (and probably auditory) perceptual components

(2) A left hemisphere specialization for whole-body postural organization particularly involving the right side of the body.

With the advent of quadrupedalism, and the consequently increased freedom of the upper limb from postural demands in bipedal postures, the right side of the body became the operative side for the forceful interactions with the environment associated with invasive foraging. Thus the upper limb makes contact with objects and applies force as necessary and the lower limb plays a complementary role. And in a role reversal relative to the initial prosimian configuration, the left side of the body becomes the supporting side. As a consequence of this, the right hand becomes the favored hand for manipulation and practiced acts.

We believe that the putative left hemisphere specialization for whole-body postural organization may also have been associated with the left hemisphere specialization for, first, vocal communication (present in monkeys), and later, language. There are two reasons for this belief. First, vocal production involves a sizeable proportion of the body musculature and such production, in the posturally demanding and variegated arboreal milieu, may

require a lateralized controller with bilateral control capability. Second, in most nonhuman primates, communication, including vocal communication, is frequently associated with whole-body postural configurations, which may also require lateralized control.

Witelson is approximately right in characterizing our view as one of central motor lateralization. We would call it perceptual-motor. Witelson, like Hamilton & Vermeire, prefers a cognitive origin for primate hemispheric specializations. Hamilton & Vermeire are apparently motivated by skepticism about the evidence for primate handedness, a skepticism we believe unjustified in the light of the most recent evidence. Witelson is mainly motivated by evidence against common lateralization of language and manual function. Whatever the motivation, we believe postulating the evolution of purely cognitive specializations has a major problem. If one believes, with Mayr (1982), that behavior is the great "pacemaker of evolutionary change" then the question that Hamilton & Vermeire and Witelson have to answer is what was the behavior which was selected for, thus leading to the cognitive adaptation in one hemisphere. Witelson does not take up the question. However Hamilton & Vermeire offer a "brain first" example based on interhemispheric differences in the "effective dendritic spread of sensory neurons." Even if living organisms were shown to have such differences, one would not know whether these were a cause of a consequence of a functional difference; and the question of how this difference could have first developed, independent of behavior, only in sensory systems, and on one side, seems to have limited heuristic value. Our emphasis on behavioral selection pressures such as unimanual predation in vertical clingers and leapers (which gives a rationale for hemispheric division of labor) invasive foraging, and communication under demanding arboreal postural conditions seems to be more compatible with current evolutionary theory and is at least to some extent testable.

We also believe that the evidence against our theory, based on individual differences in the distribution of hemispheric specializations in modern humans, is not as great as Witelson and others might suppose. Hemispheric dissociations between handedness and language control have long been a thorn in the side of those who wish to argue for a common basis for the two functions. Left handers with left hemisphere language have been the subgroup most commonly focused on in this respect. But, as Witelson has pointed out, many of these cases appear to have control of manual praxis in the left hemisphere, so one need only explain the "switch" in the output organ, not a hemispheric dissociation of control between language and manual function.

From our perspective, an important additional variable in assessing constellations of specializations is footedness. Footedness dissociates from handedness often enough (as we will see later) to lead one to believe that it is not simply a secondary consequence of handedness. However, nobody has advanced an adequate alternative theory. We believe footedness can be taken as indicating that a postural control specialization is in the contralateral hemisphere. According to Peters (1988), about 50% of left handers are right footed, a percentage that approximates the percentage of left handers estimated to have left hemisphere language (about 67% according to Witelson).

In a study of 40 such right footed left handers, Searleman (1980) showed that 39 of them had a right ear advantage on the dichotic listening test. (Incidentally, this result is a major problem for Annett (first round) who assumes a random distribution of the various hemispheric specializations in left handers in the absence of the organizing right shift factor.) We conclude from this that left handers who are right footed tend strongly as a group to have left hemisphere specialization for language and that their language control is not dissociated from their control of whole-body posture. Some additional facts support this hypothesis. Chapman, Chapman, and Allen (1987) report that subjects who are totally left handed are also most likely to be left footed. And Healey, Liederman, and Geschwind (1986) have shown that subjects who are not totally left handed are most likely to depart from unanimity by being *right* handed for operations that involve the whole body such as swinging a bat or racquet. This of course fits with the tendency inferrable from the evidence presented earlier for these subjects to be right footed, and it reinforces the conclusion that footedness is related to whole-body postural organization. We conclude that few of the approximately 7% of the population who are left handed with left hemisphere language are counterexamples to our hypothesis that language specialization and whole-body postural control are localized in the same hemisphere.

We also suggest that the subjects who are totally left handed and left footed are most likely to comprise the approximately 2% of the population consisting of left handers who have right hemisphere language. Such subjects would also not be counterexamples to the hypothesis that language control and whole-body postural control are localized in the same hemisphere. They would simply be complete mirror images of the typical right hander. We have not looked carefully into the question of right handers who have right hemisphere language. But it seems not beyond the bounds of possibility that some of them are left footed, and perhaps perform some manual acts involving the whole body with the left hand, and are therefore also not counterexamples to the hypothesis that there is an association between language control and whole-body postural control. Incidentally, it is of interest to note that right handers who depart from total right handedness are most likely to register this departure through lack of preference (Healey et al. 1986) which would not necessarily lead us to share Witelson's doubts that they have the characteristic left hemisphere language specialization.

The foregoing considerations lead us to believe that over 90% of the normal human population may have language control and whole-body postural control in the same hemisphere. This sizeable proportion of the population is thus consistent with the postural origins theory, although we have no explanation for the observed proportions of left and right hemisphere sites for that control. We feel that for a theory with this level of generality a 9 out of 10 hit rate is very creditable. We acknowledge the existence of clear counterexamples such as one of the two cases cited by Witelson. This was the subject of Heilman, Coyle, Gonyea, and Geschwind (1973) whose hand and foot preferences were both ipsilateral to the language hemisphere but contralateral to the locus of control of manual praxis. (The foot preference of the other case cited

by Witelson [Heilman, Gonyea & Geschwind 1974] was not given.) A small percentage of exceptions could be explicable on grounds that are not contradictory to our theory, especially if they were studied more carefully with respect to medical history than has typically been the case to date.

We summarize our response in the following terms: Several more recent studies, taken together with the findings we reviewed in the target article, put the existence of handedness in nonhuman primates beyond reasonable doubt. This should change the opinions of a number of commentators. We feel that most of the findings, together with evidence on the nature of human handedness and left hemispheric specialization for vocal communication in primates, are consistent with a "postural origins" theory. In this emphasis we follow the lead of Ward. According to this theory, a left hemispheric specialization for whole-body postural organization developed (further?) in early prosimians, together with a complementary right hemispheric specialization for left handed predation. With the locomotor change from vertical clinging and leaping in prosimians to quadrupedalism in higher primates the right side (including the hand) became the operative side, leading eventually to right handedness in hominids. Postural considerations may also account for the (further?) development of a vocal communication specialization in the left hemisphere in primates. The theory is not inconsistent with instances of hand preference ipsilateral to the language hemisphere in humans, if contralateral footedness gives evidence that body posture control is in the language hemisphere. We emphasize the merits of our more orthodox approach to the explanation of the evolution of function in terms of adaptations of important behaviors to selection pressures, and contrast it with approaches in which cognition (Witelson) or local unilateral neural changes (Hamilton & Vermeire) provide the main impetus for change. We would emphasize (with Denenberg) the relevance of the mammalian evolutionary heritage of primate asymmetries. Links in terms of lateralized mechanisms may be found, though links in terms of observable population-level asymmetries are not presently obvious. We agree with Peters that noncommunicative oral specialization may be an important neglected issue, especially in higher primates, but we find persuasive counterevidence to Walker's claim that length differences in the left and right recurrent laryngeal nerves were responsible for the evolution of left hemispheric specialization in hominids.

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