

# Primate handedness reconsidered

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**Abstract:** 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.

**Keywords:** apes; cerebral dominance; evolution; feeding; handedness; hemispheric specialization; laterality; monkeys; primates; prosimians

## 1. Introduction

Roughly 90% of humans are right-handed. This right-handedness is accompanied by a left-hemisphere specialization for manual function (Kimura 1977). The precise nature of the manual specialization is not agreed upon (e.g., see Bradshaw & Nettleton 1981), but its existence is generally considered central to an understanding of left-hemisphere specialization in humans. In fact, manual specialization is often taken to be the first step in the evolution of left-hemisphere specialization in man; and left-hemisphere specialization is generally thought to be the main neural and functional development that sets humans apart from other animals.

Given this focal role of manual function in theories of human evolution the precise nature of the specialization is of great interest. For an evolutionary account the first and perhaps most important question is, What adaptive function does the specialization serve? The most common answer is that it evolved from and for *tool use* in early hominids (e.g., Corballis 1983; Kimura 1979; Steklis & Harnad 1976). A more recent view is that it evolved for *throwing* in early hominids (Calvin 1982), an instance of a supposed specialization for the timing of action sequences. Both of these views link this evolutionary devel-

opment to *quantitative* changes in an adaptive function. Throwing is often observed in chimpanzees, and there is no evidence that the principles of manual control involved in human tool construction and use are different from those underlying manual function in many other primates. Consequently, why should at least an incipient manual specialization not exist in them?

The question of whether there are precursors to human handedness patterns in nonhuman primates has received some attention, particularly in a series of experimental studies by Warren and his colleagues (Brookshire & Warren 1962; Warren 1953; 1958; 1977b; Warren, Abplanalp & Warren 1967). The unequivocal conclusion of Warren and others in several recent publications devoted to specialization of function is that nonhuman primates do not have handedness like that of humans. These publications include reviews (Bryden 1982, pp. 195-97; Corballis 1983, pp. 113-16; Walker 1980, pp. 348-51; Warren 1980, pp. 353-54) and symposia (Diamond & Blizard 1977; Harnad, Doty, Jaynes, Goldstein & Krauthamer 1977; Harnad, Steklis & Lancaster 1976), with individual papers by Diamond (1977, p. 483), Hamilton (1977a, pp. 222-23), Harnad and Doty (1977, pp. xxvi-xxvii), Steklis and Harnad (1976, p. 448), Warren (1977a, pp. 273-80; 1977b, pp. 151-72), and Warren and

Nonneman (1976, pp. 732–44). The handedness pattern most emphasized in nonhuman primate samples has been a U-shaped distribution with an approximately equal number of left- and right-handers and a variable percentage of animals without preference. This distribution has often been regarded as adventitious, perhaps the result of laboratory experience (e.g., Warren 1980). Where preferences *have* been observed, they have often been considered to be task-specific (with individual monkeys considered inconsistent, because they use different hands for different tasks), or weak and inconsistent across sessions. Little attention has been given to the possibility that nonhuman primates might display specific hand preference patterns different from those of humans (however, see Preilowski 1983; Sanford, Guin & Ward 1984).

The conclusion that nonhuman primates do not have handedness like that of humans is problematic, because it means that neither specialized manual function nor, by implication, hemispheric specialization for manual function had precursors, despite some 60 million years of prehomimid evolution during which the forelimbs were already partially free of locomotor demands. The conclusion is also problematic because it leaves unexplained the growing anatomical evidence for cerebral asymmetries in primates (LeMay, Billig & Geschwind 1982). Our review of primate handedness studies suggests that the conclusion may in fact be wrong, and that accepting the null hypothesis may be premature. In fact, as Walker (1980) has pointed out, "data on handedness in non-human primates [are] extremely limited and consist largely of studies of food reaching in the rhesus monkey" (p. 348). Furthermore, the secondary sources mentioned above confined their attention to only a few of the available studies, placing little or no emphasis on several studies in which asymmetric hand preference patterns *were* observed. Though limited by the relatively sparse and fragmentary evidence presently available, our own review suggests that, contrary to current opinion, non-human primates may display theoretically significant handedness patterns. In fact, there is evidence that both left-handed reaching and right-handed manipulation may have evolved with qualitative changes in structure – left-handedness with the prehensile hand, and right-handedness with the opposable thumb.

To support this claim, we will first present a detailed reexamination of the evidence on hand preferences in Old World monkeys, the group on which most of the work has been done. After a few preliminary remarks we will consider instances of population-level asymmetries of preference, and compare them with studies that do not find asymmetries. Then we will consider arguments against a homology with human handedness. Next we will review studies of hand preferences in other taxa. Finally, we will discuss the implications of the review for the evolution of handedness and hemispheric specialization in primates.

## 2. Old World monkeys

Almost every study of Old World monkey handedness involves reaching and grasping a food reward, either as the only act, or as the terminal act, in a task. Food rewards have been found necessary to evoke repeated manual

responses. To facilitate discussion, we have constructed a purely *descriptive* classification of the various tasks that have been studied. Simple-reach tasks (R) involve picking up single food items presented alone on flat surfaces, through cage fronts, or in food wells, and so forth, on an otherwise flat surface. Complex-reach tasks (CR) involve reaching for food placed in an immediate context that influences the details of the reach, for example, in an open box or a bottle. Expose-and-reach tasks (E&R) call for moving a loose object covering the food (e.g., a block or card) before reaching for it. Stabilize-and-reach tasks (S&R) require or strongly encourage the nonreaching hand either to hold an object in which the food is placed or to hold aside some impediment to reaching. Retrieve-and-reach tasks (R&R) involve gaining access to the food by retrieving something to which it is attached, such as a piece of string. Manipulate-and-reach tasks (M&R) require at least one movement more indirect than simply moving a loose barrier aside to make the food available: A typical task involves opening one or more hasps.

The term "handedness" denotes a more or less uniform preference for one hand in a wide variety of activities. In our analysis of the experimental results we will use the term "hand preference" to refer to greater use of one hand than the other for any act, intending it to be theoretically neutral with regard to the generality of the asymmetry. Only when we are prepared to make some statement about the generality of the observed preferences will we use the term "handedness."

### 2.1. Studies showing asymmetry of preference

**2.1.1. Japanese studies.** A number of studies have shown a left-hand preference for reaching in subpopulations of Old World monkeys. Three published field studies of Japanese macaques (*Macaca fuscata*) are unanimous in finding a left-hand preference for simple reaching (R) for food items thrown by the investigators (Itani 1957; Itani, Tokuda, Furuya, Kano & Shin 1963; Tokuda 1969). The method of determining whether there was a hand preference was not given in the studies of Itani. Tokuda used a criterion of 8 or more reaches with the same hand out of a total of 10 reaches. Table 1 shows the results. Chi square tests for the individual studies show a significant excess of left over right preferences only in the Itani (1957) study. However, if we pool the data of the larger study by Itani (which included some data from the smaller) with the data of Tokuda, we find a significantly greater number of left-than right-hand preferences [ $\chi^2(1) = 5.46, p < .02$ ]. Interestingly, Kawai (1967) also observed an excess of left- over right-hand preferences in a field study of one-handed catching of food in the Koshima troop [ $L = 17, R = 8, \text{No preference} = 16, \chi^2 L/R(1) = 3.24 \text{ N.S.}$ ].

Although these results are suggestive, it would be desirable to have further studies of this kind, in which criteria for hand preferences are given, and the possibility of bias in food placement with respect to the animal is controlled for.

**2.1.2. Studies by Ettlinger's group.** Asymmetric patterns of preference – favoring the left hand – have also been observed in several experimental studies of rhesus monkeys (*Macaca mulatta*) performing *visual* and *tactile discrimination* tasks, by Ettlinger and his colleagues



Table 1. Hand preferences in field studies of Japanese macaques picking up food

Study	Troop	Left	Right	None	N	X <sup>2</sup> L/R
A. Itani 1957	Takasakiyama	30	16	36	82	<.05
B. Itani et al., 1963	Takasakiyama	149	118	127	394	N.S.
C. Tokuda 1969	Koshima	17	8	16	41	N.S.
B and C		166	126	143	435	<.02

(Ettlinger 1961; Ettlinger & Moffett 1964; Gautrin & Ettlinger 1970; Milner 1969). In a typical visual discrimination test the animal was required to respond to one of two simultaneous stimuli by pushing a sliding lid off a food container under the correct stimulus and reaching for the reward (E&R). An instance of hand preference was scored only if the animal performed both acts with the same hand. In the tactile tests the animal was required (in the dark) to identify manually and then displace the correct object of a set of two to obtain the reward the object had covered. Both tasks can be classified as expose-and-reach tasks, but they were not simple examples of the type, because responses were conditional on perceptual discrimination. Hand preference was considered to exist if the same hand was used for both displacing the object and reaching for the food on 90% or more of a given block of trials. In all studies, a population-level trend toward left-hand preference was noted, with an approximately 2:1 ratio of left to right preference in *early* stages of the experiments (see left side of Table 2; later stages will be discussed below).

Of the individual studies only the 1961 study of Ettlinger shows a significant excess of left-hand preferences [ $\chi^2(1) = 5.24, p < .05$ ]. Here again, two studies (those by Ettlinger and Moffett and by Milner) used some of the same animals. If we exclude the smaller of these two studies and pool the remaining three, we find a significantly greater number of left- than right-hand preferences [ $L = 42, R = 21; \chi^2 L/R(1) 7.0, p < .01$ ].

**2.1.3. The Beck and Barton study.** A left-hand preference in reaching for food was also observed in an experimental study by Beck and Barton (1972). This is by far the most analytically sophisticated study in the primate handedness literature and is relevant to a number of issues discussed in this paper. We will therefore describe it in some detail. Beck and Barton studied the performance of

10 stumptail macaques (*Macaca speciosa*) on 17 tasks, ranging from simple reach to complex tasks with terminal reach and involving up to four separate acts, from use of a single finger alone to simultaneous use of both hands. A list of the names of the tasks, arranged according to our classification, in Table 3, gives some idea of their nature and variety.

Median percentages of hand use were computed by Beck and Barton for each of the 31 individual acts. Each median was computed from 10 percentage values, each representing the tendency of one monkey to use a particular hand in that act. Table 3 shows the median percentages of hand use for the 31 individual acts, divided into six task categories: In general, median preference levels extended over almost the total possible range, from 100% left-hand preference for food reaching in the two-imbedded-hasp pulled container test to 96% and 97% right-hand preference for manipulation in the two single finger movements of the two-imbedded-hasp container test. If these were considered simply in terms of strength of preference for one hand, they would form a roughly normal distribution about the chance level of preference (50%). But if the subtests are considered in terms of the four types of movement represented in the table, a clear pattern emerges. Whereas 12 of the 17 food-reaching components showed a left-hand preference, only 3 showed a right-hand preference. By contrast, all 8 of the manipulative acts showed a right-hand preference. We were unable to obtain scores for individual monkeys on individual acts, which would have facilitated statistical tests of these trends. However, median hand preferences for individual monkeys were given for all food-reaching acts combined, and all other acts combined, and these are shown in Figure 1. The 5 stabilization acts presented ranged around a chance value.

Figure 1 shows that no animal departs strongly from a tendency to prefer the left hand for reaching and the right

Table 2. Numbers of monkeys with and without hand preferences in discrimination studies

Study	Early testing					Later testing				
	Left	Right	None	N	X <sup>2</sup> L/R	Left	Right	None	N	X <sup>2</sup> L/R
A. Ettlinger (1961)	17	6	19	42	<.05	9	10	6	25	N.S.
B. Ettlinger & Moffett (1964)	7	4	16	27	N.S.	12	7	8	27	N.S.
C. Milner (1969)	17	9	32	58	N.S.	15	14	29	58	N.S.
D. Gautrin & Ettlinger (1970)	8	6	13	27	N.S.	10	9	9	28	N.S.
A, C, and D	42	21	64	127	<.01	34	33	44	111	N.S.

Table 3. Median percentage of hand preference for the 17 tasks in the Beck and Barton study

Task category and name	Reach (% Left)	Expose (% Left)	Stabilize (% Right)	Manipulate (% Right)
<i>Simple reach</i>				
Reach	35			
<i>Complex reach</i>				
Elevated reach	53			
Shallow container	50			
Container	71			
Opaque container	75			
Half tube	51			
Tube	49			
	$\bar{x}$ 54.4			
<i>Expose &amp; reach</i>				
Block	33	60		
<i>Stabilize &amp; reach</i>				
Whisk	68		76	
Drawer	59		51	
Moving tube	82		(no data)	
Moving fur tube	98		44	
	$\bar{x}$ 76.8		$\bar{x}$ 57.0	
<i>Manipulate &amp; reach</i>				
One-hasp container	70			77
Two-hasp shallow container	58			77
				66
Two-imbedded-hasp container	50			96
				97
	$\bar{x}$ 59.3			$\bar{x}$ 82.6
<i>Stabilize &amp; manipulate &amp; reach</i>				
One-hasp pulled container	98		67	55
Two-imbedded-hasp pulled container	100		17	53
				61
	$\bar{x}$ 99.0		$\bar{x}$ 42.0	$\bar{x}$ 56.3
	$\bar{x}$ 64.7		$\bar{x}$ 51.0	$\bar{x}$ 72.8

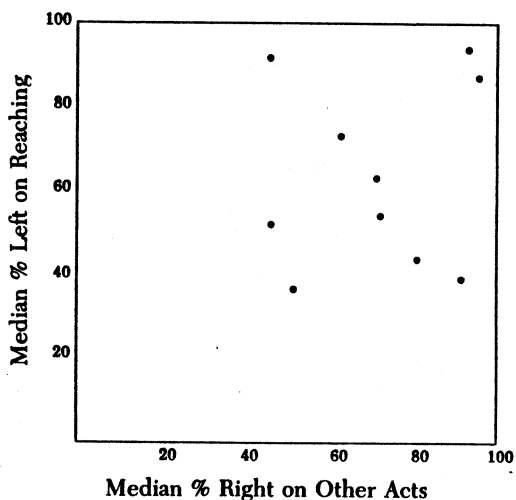


Figure 1. Median percent left-hand use for reaching for food, and median percent right-hand use for other acts, for the 10 individual monkeys of the Beck and Barton study.

hand for other acts taken as a whole, and no animal showed a reversal of both trends. The mean right-hand preference level for the other acts (estimated from the graph) is 71.2%, which is significantly different from chance performance beyond the .01 level [ $t(9) = 3.35$ ]. The mean left-hand preference for food reaching is approximately 61.9%, which falls short of significance [ $t(9) = 1.78$ , N.S.]. Despite this lack of significance for the group taken as a whole, the figures suggest that there is a tendency for at least some of these monkeys to possess a dichotomy of preferences, a left-hand preference for reaching and a right-hand preference for other activities. Table 3 suggests that the right-hand preference may be most marked for manipulation.

In the tasks that require only reaching, there seems to be a tendency for left-hand preferences to increase with the difficulty of the task. The simplest reach task actually shows a right-hand preference. The strongest left-hand preferences are on the two-container tasks demanding the most indirect reaches. There is a further tendency for the left-hand preference for food reaching to be greater when a stabilization movement is also required, particularly in the two tests in which the food was in an unstable

surround. Left-hand preferences are at their highest levels when both stabilization and manipulation are also required.

Right-hand preferences are strongest when only manipulative components are required in addition to reaching. This is especially true of the two-imbedded-hasp container test. The use of a single finger required here to open the hasp presumably involves more manual dexterity than any other subcomponent of these tasks. It is of particular interest to note that a much weaker right-hand preference is observed for exactly the same pair of acts in the two-imbedded-hasp pulled container test, where they occur in a task that also requires a stabilizing movement. This result, as well as the considerable variability in the strength of left-hand preference for food reaching in tasks that also involve other acts, makes it clear that although hand preferences can be identified for individual task components considered in isolation, the strength of these preferences is considerably affected by the overall configuration of the task.

We would argue that the results of the Beck and Barton study constitute *prima facie* evidence for population-level patterns of hand preferences in this species of Old World monkeys and that these results warrant a reexamination of the question of manual preference in primates. This study is the *only* one in the literature to have used a variety of tasks, going well beyond food reaching alone, on a fair number of subjects.

From the perspective of human handedness, the result of most interest is the finding of a right-hand preference in manipulative acts analogous to that observed in humans. The fact that this finding has received scant attention in the literature, even though it was noted by Beck and Barton, is presumably due in part to the coexistence of a left-hand preference for reaching, so that the overall pattern of manual function was unlike that observed in humans. However, we would assert that the coexistence of a right-hand preference for one class of acts and a left-hand preference for another makes both results more worthy of interest than if either had occurred alone.

**2.1.4. Deuel and Dunlop.** One significant right-hand preference for reaching has been shown. Deuel and Dunlop (1980) found that 8 monkeys out of 15 experimentally naive, adolescent rhesus monkeys showed a right-hand preference for reaching in the Wisconsin General Testing Apparatus (WGTA), whereas only 2 showed a left-hand preference (binomial  $p < .05$ ) (the results of this study are similar to those given in an earlier, often-cited abstract, Deuel 1975). However, this test was preceded by another reach test using the primate chair in which the same monkeys showed a nonsignificant left-hand preference (6 left, 1 right, 8 no preference: binomial N.S.). Subsequently, 20 monkeys, including 3 of the group already described, were tested on five tasks, including reaching from the primate chair. No obvious trends toward left- or right-hand preference were observed on any of these tests. In addition, the finding of a right-hand preference in this study conflicts with the outcome of two other findings from simple-reach testing using the WGTA (Brookshire & Warren 1962; Warren 1953). In these two studies no significant differences between animals with left and right preferences were observed (see Table 4).

**2.1.5. Preference and ability.** One other example suggesting a specialized use of the right hand can be cited, although, strangely enough, it does not involve preference. Preilowski (1979) reports in an abstract that a group of eight rhesus monkeys all showed greater ability to produce specific pressures between the fingertips of the right hand than the left at the higher levels of difficulty ( $1/2^8 = 1$  in 256,  $p < .01$ ), a result "unpredicted by demonstrated hand preferences" (p. S89). The possible importance of differences between preference and ability for an understanding of manual action is strengthened by the results of Brinkman (1984a). Brinkman reports the relation between hand preferences of adult crab-eating macaques (*Macaca fascicularis*) and their offspring for the hand (finger) used to push a raisin through a hole in a Plexiglas screen so the raisin could be obtained by the other hand on the other side. In a personal communication updating the figures in the 1984 abstract, Brinkman reports that of 37 offspring whose parents differed in hand preference, 31 showed the handedness of the female parent [ $\chi^2$  (1) 16.88  $p < .01$ ]. Taking into account the maternally oriented child-rearing milieu in this species, these results suggest that a tendency to learn hand preference from the mother may sometimes override a hereditary contribution, if we assume that contribution to be the same from both parents.

## 2.2. Studies showing no asymmetry of preference

Table 4 is a summary of a number of other studies of Old World monkeys in which population-level asymmetries were not found. Certain studies in this group have received the bulk of the attention in the literature. (There are also a few studies in which the relative frequencies of left- and right-hand preferences are not given: Cronholm, Grodsky & Behar 1963; Warren 1958; Warren et al. 1967.) Two studies (Brookshire & Warren 1962; Kruper, Boyle & Patton 1966) show an obvious, though not significant, tendency toward a left-hand preference. Two studies (Cole 1957; Lehman 1980a) show a nonsignificant tendency toward a right-hand preference.

What is most striking when we compare studies that have obtained asymmetrical hand preferences with studies that have not are the differences in their chosen tasks. Most studies failing to find hand preferences have used relatively straightforward laboratory tasks (simple reach, complex reach, expose and reach) and, unlike most studies in which hand preferences were obtained, have included none of the following: (1) field observations; (2) tasks in which visual discrimination was a condition of food reward; (3) tasks of the kinds that elicited strong left-hand reaching preferences (e.g., stabilize-manipulate-reach); (4) tasks of the kinds that elicited strong right-hand preferences for manipulation, for example, two successive single finger manipulations without stabilization (Trevarthen's 1978 study is an exception, but he used only five monkeys); (5) tasks measuring precision of manual control; (6) a relatively large number of different, complex tasks. This last factor is of interest, because a large number of tasks (as in Beck and Barton's study) may encourage some monkeys, at least, to develop a systematic division of labor between the hands on the individual acts within a task. Such a division of labor may be natural

Table 4. Summary of studies not showing asymmetrical distributions of hand preferences

Study	N	Age information	Preferences			Criteria
			L	R	None	
Brookshire & Warren 1962	19	1.2-2.5 kg initially. Estimated ages: 12-18 months	9	4	6	50% ± 3σ%
Cole 1957	33	—	13	6	0	>50%
Cole & Glees 1951	17	—	14	19	—	—
			9	8	0	—
Hall & Mayer 1966	7	4 adults, 2 young adults, 1 juvenile	2	3	2	Arbitrary
Kruper, Boyle & Patton 1966	19	2.5-3.4 kg	11	6	2	50% ± 2σ%
Kounin 1938	7	4.5-7.3 kg	3	4	—	50% ± 2σ%
	4	1 pubescent 3 prepubescent	Task specific			Arbitrary
Lehman 1970	24	2.4-4.8 kg "immature"	4	2	18	>90%
			7	4	13	>80%
			12	11	1	>50%
Lehman 1978	171	1.36-7.0 kg	91	80	—	>50%
Lehman 1980	58	.8-5.3 kg	23	35	—	>50%
Trevarthen 1978	5	"Juvenile"	2	3	—	—
Warren 1953	84	Adolescent & mature	23	23	38	>90%
			26	27	31	>80%
Warren 1977b	14	2-4 years (over the test period)	7-8	6-7	0-1	—

in the demanding conditions of the wild, but may only emerge in the laboratory under conditions of sufficient pressure.

### 2.3. Discussion

**2.3.1. Warren's position.** We can now consider explanations for the data on hand preferences in Old World monkeys that have led to the consensus that the hand preferences have no theoretical significance.

In a comprehensive review of primate hand preference studies, Warren made the most explicit attempt so far to explain these preferences (1980). He concluded "that the appearance of handedness in monkeys is an artifact produced by the methods that have been used in chronic experiments" (p. 356). He believes that three factors underlie the initial establishment of a preference when the naive monkey is first faced, as it typically is, with extensive practice on a simple task (p. 354):

1. "A detectable disparity between the hands in skill." (Note that the brain appears to be specifically excluded here, and there is no implication that one hand might be favored more than another in the population in general.)

2. "The effort required for a given manipulation."

3. "An environmental asymmetry that militated against equal practice with both hands."

Warren believes that, in the presence of one or more of these variables, "a differential delay of reinforcement for responding with the left hand and right hand would develop, and monkeys would shape themselves under this contingency to use one hand exclusively to make particular manual responses" (p. 354). He notes, howev-

er, that as "monkeys have a limited range of response generalization" (p. 354) their preferences on different types of tasks introduced later tend to be uncorrelated with the initially established preference. The view that hand preferences in nonhuman primates are to some significant degree artifactual has also been voiced by others (Cronholm et al. 1963; Deuel & Dunlop 1980; Steklis & Harnad 1976).

Results already reviewed suggest that the conclusion that hand preference is simply an artifact of laboratory experience is incorrect. Preferences were noted in four Japanese field studies in animals without laboratory experience. Preferences were also noted by Lehman (1978; 1980a) at the onset of his studies of experimentally naive monkeys. In addition, the systematic pattern of asymmetries in the experimental studies described above does not appear to be explicable on the basis of differential reinforcement.

With respect to the role of "environmental asymmetries," there is certainly evidence that they can influence hand preferences by making a movement of one hand more straightforward than the other. For example, Deuel and Dunlop (1980) found a left-hand preference for reaching in monkeys housed in cages with a steel plate covering the part of the cage front adjacent to the monkey's right hand when it looked out of the cage. In addition, the typical use of a spatially balanced presentation of stimuli to the left, right, and center of the front of the cages is predicated correctly on the assumption that most animals tend to favor reaches that do not cross the body (Cronholm et al. 1963; Lehman 1970). However, these types of response bias no doubt have parallels in human behavior

Tests and categories					
Simple reach	Complex reach	Retrieve & reach	Expose & reach	Stabilize & reach	Manipulate & reach
Reach	Bottle	Wire	Blocks	Hasp	Handle box
Reach	Tactile discrimination				"Matchbox" "Matchbox" Problem box
Reach 1	Jar				
Reach 2	Thread				
Reach	Cylinder		Block		
	Vertical hole	Rake	Trapdoor		
Reach					
Reach					
Reach					Puzzle box
Reach	Trough Horiz. bottle Vert. bottle	Wire Chain	Block Card Extension		Handle box

and should not in themselves be taken to mean that monkeys do not have significant hand preferences.

The use of different hands for different simple reaching tasks in the *absence* of any obvious environmental constraint certainly seems to be unlike human behavior and is hard to reconcile with the concept of handedness. Warren (1980) accordingly draws attention to the finding of Deuel and Dunlop (1980) that monkeys tend to use opposite hands on two simple reaching tasks depending on whether they are in a primate chair or in the Wisconsin General Testing Apparatus. However, as we pointed out earlier, the right-hand preference found by Deuel and Dunlop in the WGTA was not replicated in other studies. Moreover, the consistency with which studies of Old World monkeys have shown a left-hand preference for reaching suggests that such reaching is indeed an example of handedness, even if it is unlike human behavior. The evidence for right-hand preferences that we have reviewed also suggests handedness. The coexistence of left- and right-hand preferences argues that Warren's criterion for handedness – that the same hand be used for all acts (Brookshire & Warren 1962, p. 222) – may be inappropriate for Old World monkeys.

The criterion also seems inappropriate for humans, especially in bimanual tasks. In tasks that require, or simply allow, the use of two hands, humans tend to use the right hand for the most demanding manipulative components of acts, and the left either in a supportive or stabilizing role or for concurrent acts that require lesser capacity (Peters 1981). Quite similar behavior has been observed by Trevarthen (1978) in a detailed analysis of the performance of five individual baboons (species not

given) in opening a puzzle box in three stages to obtain a reward. Four of the five monkeys evolved a consistent tendency to use one hand for certain acts and the other hand for others. Trevarthen also noted a tendency to prefer a dominant hand (3 right, 2 left) for the more difficult acts, and a subordinate one for the easier acts, as one would typically observe in humans.

Warren has asserted that the "task-specific" preferences observed in his and in Beck and Barton's studies of multi-act tasks rule out an "organismic" (innate) basis for handedness (Warren 1977b), implying that somehow the tasks artificially induce the preferences. (These preferences might more properly be described as *act-specific* because they involve individual acts within tasks.) By contrast, our own hypothesis is that these act-specific preferences reflect two distinct types of handedness: (1) a dichotomy of hand preference involving the left hand for food reaching and the right hand for manipulation; (2) a division of labor between a dominant and a supportive hand typical of human bimanual coordination.

**2.3.2. Age, task difficulty, practice.** We have suggested that whether or not an asymmetric hand preference pattern will be observed in Old World monkeys may depend on what type of task is studied. But does this mean that animals that do not show hand preferences on tasks showing population-level asymmetries do not possess handedness? And does it mean that the tasks on which asymmetric hand preference patterns are not revealed are not capable of revealing handedness?

An alternative possibility is that both numbers of hand preferences and asymmetries of hand preference would

have been higher if young monkeys had not been typically used in the studies we have reviewed. Macaque monkeys are considered to have an infant stage of 1½ years and a juvenile stage of 6 years. Although age information is not always given directly in the studies we have reviewed, weights of the animals are sometimes given and can be used to estimate age. Estimates can be made from average relations between weight and age, from data provided by Tanner (1962): birth, 1.9 kg; 1 year, 3.3 kg; 2 years, 4.5 kg; 3 years, 6 kg; 4 years, 7.6 kg. Examples of ages and weights of monkeys used in experimental studies leading to negative conclusions about asymmetries of hand preference are given in Table 4. It can be seen that many animals used were quite young.

There is some evidence that the number of monkeys showing a hand preference increases with age. In a study by Warren et al. (1967) no differences in preference levels of immature and adult monkeys were found. However, in two studies by Lehman (1978; 1980a) the heavier and thus presumably older monkeys showed significantly stronger hand preferences at early stages of testing. Furthermore, Kruper et al. (1966) observed a significantly higher level of preference in a group of older monkeys than in a group of younger ones. A monotonic trend toward more preferences in older animals was shown by Itani et al. (1963; see Table 5). As to the possibility that asymmetries of preference increase with age, a trend in this direction was also observed by Itani et al. (1963). The percentage of animals showing a left-hand reaching preference increased from 35% to 54% between the youngest (.5–3.5 years) and the oldest (16.5 years and above) age groups, whereas right-hand reaching preference decreased from 29% to 23%.

Age may also be a factor in the inconsistency of preference across sessions, which has sometimes been taken to mean that humans and nonhumans are unlike in handedness. For example, a major reason for Warren's reversal of his earlier conclusion that monkeys possess "organismic" (i.e., innate) hand preferences (Warren et al. 1967) was his finding that hand preferences in a subset of acts in his later study (1977b) were uncorrelated across sessions. It is possible that such inconsistencies are more prominent in younger animals, on more difficult tasks. For example, Trevarthen (1978) observed that consistent preferences took some time to develop in "juvenile" baboons performing a relatively difficult puzzle box task. Such effects might also be present in human children. Another possibility is that some of the changes, described as evidence of inconsistency, are in fact systematic trends of some sort. For example, a significant shift toward right-hand preferences between Session 1 and Session 3 can be

deduced from Figure 1 in Warren (1977b) ( $t = 2.16, p < .05$ ). In the studies of Ettlinger's group (Table 2), the significant trends toward larger numbers of left-hand preferences in early testing disappear in later testing.

In some cases it is not clear whether serial trends are related to age or to practice on the same or related tasks, or to both. In the Warren (1977b) study, more than two years elapsed between earlier and later testing, but the animals performed tests requiring manipulation during the intervening period. In one of the studies from Ettlinger's laboratory (Ettlinger 1961) variable intervals of up to a year intervened between earlier and later testing and the activities of the animals in the intervening period were not described. But in the other three studies, later testing immediately followed earlier testing. Gautrin and Ettlinger (1970) also report *within-test* changes in number of significant hand preferences for two visual discrimination tests from their own study and two tactile tests from Milner's (1969) study. Numbers of animals showing significant right-hand preferences increased in both visual (+5) and tactile (+7) tests, whereas an increase in left-hand preferences in the visual tests (+3) was canceled by a decrease in preferences in the tactile tests (-3). The net difference in intratest preference changes is obviously significant, and shows that right-hand preferences may increase as a short-term effect of practice. In the tactile case this result may be due to a greater ability of the right hand in haptic manipulation. The study of Itani et al. (1963) suggests, indirectly, that practice does not increase right-hand preferences in reaching in field studies. In this study, as mentioned earlier, the number of right-hand preferences was relatively smaller in older groups of animals, whereas the number of left-hand preferences was relatively greater.

Although it is undeniable that hand preferences in Old World monkeys seem weaker than in humans, as Warren (1977b) claims (see also McGonigle & Flook 1978), we conclude that the predominantly negative conclusions about monkey handedness in the current literature may be largely due to several factors: (1) using tasks not conducive to the demonstration of handedness; (2) using a handedness criterion demanding that the same hand be used for all acts (this criterion tends to obscure systematic differences in the use of the two hands, either of the kind we have noted - left for reaching, right for manipulation - or of the kind shown in human bimanual coordination); (3) using young monkeys with relatively undeveloped strength and asymmetry of preference; (4) a tendency to regard intratask inconsistency as evidence against handedness, when it may be due to some combination of task difficulty, ages of the experimental subjects, and systematic trends induced by practice.

In conclusion, if some tasks are indeed more conducive to revealing hand preferences than others (in the absence of obvious physical biases), we must ask what this tells us about the monkeys, not about the tasks. Before discussing this issue, we will summarize the findings on hand preference in other nonhuman primate taxa.

### 3. Prosimians

We are aware of only two studies of hand preference in the prosimian suborder. Sanford et al. (1984) studied

Table 5. Relation between age and percentage of monkeys showing significant hand preferences in picking up food

Age (years)	N	% With pref.
0.5-3.5	177	64
4.5-7.5	127	69
8.5-15.5	58	72
16.5+	32	75

Source: Itani et al. (1963).



preferences in bush babies (*Galago senegalensis*) in two types of tasks involving reaching for food. In the first part of the study, 25 adult animals were required to assume their typical vertical posture to reach a worm positioned 1½ in. outside the cage wall by grasping a rod on which the worm was impaled. Each animal received 54 trials. The worm was presented equally often through each of three small openings: a central opening 6 in. above the floor of the cage, an opening 4 in. to the left of the central one, and one 4 in. to its right. A strong left-hand preference was observed in the population. Twelve animals made more than 80% of left-hand responses and the other 13 were distributed fairly evenly across other preference levels. Subsequently, 12 animals from the original study were tested in the horizontal posture adopted to pick up mealworms from the floor of the cage. No systematic trends were noted in the distribution of preferences in this second test. Hand preferences on the two tests were found to be uncorrelated, but performance on both tests was highly consistent on retesting ( $p < .01$ ). Subramoniam (1957) studied reaching for food in 8 slender lorises (*Loris tardigradus*). Although she reports no numerical data, she states that small insects were taken "always and consistently by the left hand" (p. 388) ( $1/2^8 = 1$  in 256,  $p < .01$ ). This was true "whether the insect lay on the ground or was placed on the branches or was proffered in the cage at the end of a pair of forceps" (p. 388).

#### 4. New World monkeys

Three of the five studies known to us are on the common marmoset (*Callithrix jacchus*). The most explicitly reported large-scale study was conducted by Box on eight subjects (1977). She studied relative hand use in a number of spontaneous activities: reaching for food in a food bowl, holding food, initiation of climbing up, reaching up, reaching down, walking initiation, and pushing or boxing another animal. (Care was taken to tabulate only acts made from a neutral stance.)

One hundred instances of each activity were observed for each animal. A marked distinction can be observed between reaching and holding and the other acts. There was a trend toward left-hand preferences for reaching and holding, significant in the former case (mean left reaches = 66.6,  $t = 2.76$ ,  $p < .05$ ) but not the latter (mean left holds = 59.3, N.S.). As to individual animals, the same six animals showed a significant left-hand preference for reaching and holding, and the same single animal showed a significant right-hand preference for both acts. This distribution of preferences is not significant when tested against the binomial distribution. (Note, however, for later reference, that there was a highly significant rank order correlation between hand use for reaching and for holding ( $\rho = .93$ ,  $p < .01$ .) Mean preferences for the other activities ranged from 44 (left reaches) to 49 and did not depart from chance levels. Mean preference levels for the individual animals on the other tasks ranged from 29 (left reaches) to 61. Scores on these other tasks were uncorrelated with each other, or with scores on reaching and holding.

Rothe (1973) studied hand preference in spontaneous activities and seven test situations in 21 common marmosets. Spontaneous activities were "grooming, play, feed-

ing, object exploration, etc." (p. 501). Tests were complex reach (tests 1-4 and 6), expose and reach (test 7), and a test perhaps best described as find and reach, involving mealworms concealed in a box among other materials (test 5). In laboratory tests, animals were given a total of 810 to 1,210 trials, and thus could be considered to have been highly practiced by the end of the set of tests, which were apparently given in the numerical order mentioned earlier. Unfortunately, results were not reported for separate acts except for test 1, which involved reaching for food within glass cylinders. Results are given in Table 6. Preferences listed in the table for individual animals, on spontaneous activities and test 1, are all significant beyond the .01 level, but no criterion for determining the significance of preferences listed for tests 2-7 is given.

Although there are trends toward population-level hand preference in these results (significant for tests 2-7), it is difficult to interpret them in the absence of results for most separate acts. This is particularly so because the author places much emphasis on the intratest and intertest variability of the animals. It is conceivable that this resulted partly from testing the animals in communal cages, in which the details of their performance could easily be influenced by other animals. However, there is a significant population-level right-hand preference in these animals for a set of four complex-reach tasks and two tasks also involving acts preceding reach.

Stellar (1960) found a nonsignificant trend toward right-hand preference in an expose-and-reach task involving the displacement of an object over a food well. Five of eight animals preferred the right hand for both acts (four on over 90% of trials) and three preferred the left (two on over 90% of the trials).

To summarize these three studies of marmosets, a significant left-hand reaching preference has been observed for simple reaching in marmosets (Box 1977) and a significant right-hand preference has been found for a complex of laboratory tasks in another study (Rothe 1973). The left-hand preferences appear consistent with those found in prosimians and Old World monkeys. The extent to which the right-hand preferences might be related either to manipulative demands (greatest in tasks 5 and 7) or to a trend toward right-hand preference with task experience - both of which are observed in Old World monkeys - cannot be determined. But the large number of trials given makes the possibility of a right-hand preference trend with task experience a viable one.

Another group of New World monkeys, the cebus, is known for its manipulative skills. Kounin (1938) found that three cebus monkeys exhibited stronger hand preferences than a small group of rhesus monkeys when performing three tasks. The tasks involved retrieving food from a hole in the cage wall, a hole in the cage floor with a

Table 6. Distribution of marmoset hand preferences in the study of Rothe (1973)

	Left	Right	None	X <sup>2</sup> L/R
Spontaneous activities	2	6	13	N.S.
Test 1	7	12	2	N.S.
Tests 2-7	5	14	2	<.05

trapdoor, and by means of a rake. Two monkeys preferred the right hand and one the left.

Fragaszy (1983) studied 14 squirrel monkeys (*Saimiri sciureus*) in the act of grasping objects of various sizes, shapes, and states of motion. Only 6 animals were reported to prefer one hand on 60% of the occasions or more. How hand choices were distributed among the 6 animals and how many reaches each animal made were not reported.

## 5. Apes

No studies of hand preferences in lesser apes are known to us.

The experimental study of great ape handedness most often cited is that of Finch (1941). He tested 30 chimpanzees (*Pan troglodytus*), 26 of them adults, on four tests involving only unimanual responses. Results were pooled from tasks in which animals procured food: (a) directly, (b) by pulling on a string, (c) by displacing a box. He reported a U-shaped distribution, with 25 animals making more than 80% of their responses with the preferred hand; 11 preferred the right hand and 14 the left.

A similar lack of population-level asymmetry in hand preferences was observed by Preilowski and Leder (1984) in six lowland gorillas (*Gorilla gorilla*), two males and four females. Only one animal was under 10 years of age. They studied five activities: (a) picking up food, (b) bringing food to the mouth, (c) picking up branches, (d) picking or stripping leaves from the branches and bringing them to the mouth, (e) picking up sunflower seeds and bringing them to the mouth. The average number of observations per animal, per act, was 640. They reported that "the direction of preferences showed no interindividual consistency and no task specific effects." However, they noted that strength of preference varied with the task; the strongest preference was shown in task (d), with the highest scores produced by those animals that demonstrated an equally strong preference for the opposite hand in collecting the branches.

A quite different conclusion comes from a study of four adult female lowland gorillas by Fischer, Meunier, and White (1982). A total of 619 assessments were made over a 3-month period in the following categories: (a) reaching for apple wedges (120 tests per subject); (b) interacting with objects (43 incidental observations); (c) using one hand while holding an infant with the other hand (96 observations). All animals exceeded the handedness criterion of using the right hand for grasping objects and food at least 80% of the time, and the mean value for right-hand grasping was 96%. If one makes the most generous estimate as to the variability of these animals – namely that three made 100% right-hand responses and the other 84% right-hand responses – this result is significantly beyond chance [ $t(3) = 11.50, p < .01$ ]. Left-arm support for the baby was observed on 64% of occasions. The authors conclude that "the consistency of dextral preference across all tests is amazing and comparable to the human data" (p. 1093). However, four subjects are not enough to give a statistically significant hand preference asymmetry in the sample.

In a recent study, groups of chimpanzees, gorillas, and orangutans (totaling 21) were all found to favor the left

hand for face touching, significantly so in the case of chimpanzees and gorillas (Dimond & Harries 1984). This result has also been found for English-speaking human subjects but not for Japanese speakers (Hatta & Dimond 1984). Monkeys were reported to rarely engage in face touching (Dimond & Harries 1984).

All other reports known to the authors are subject to one or more of the following problems: (a) very small numbers of subjects; (b) very limited sampling of tasks; (c) relatively casual observation; (d) averaging of preference levels across tasks; (e) inadequate description of tasks. We will nevertheless briefly summarize the findings of these reports. First, consider other reports on gorillas. Haas (1958) found that three gorillas were "predominantly right handed," but that one was left-handed in certain activities. LeGros Clark (1927) reported strong right-handedness in a gorilla named "John Daniel." On the basis of 497 observations of two gorillas, Reiss, Ross, Lyerly, and Birch (1949) reported that "the right hand was more frequently used regardless of the nature of the activity" (p. 114). The overall relative frequency reported was 54%. Schaller (1963) reported that 59 of 72 gorillas giving chest-beating displays began with their right hand [ $\chi^2(1) = 29.4, p < .001$ ]. He also reported that gorillas reached with the hand nearest to a food reward, and if food was equally near to each hand they were ambidextrous. Yerkes (1927) noted a right-hand preference in one gorilla for various types of stick problems. He also noted a right-hand preference for reaching for food, but a left-foot preference if the food was out of arm's reach.

There are a few observations on chimpanzees. Goodall (1970) reported that about as many chimpanzees preferred the left as the right hand while fishing for termites with twigs. Taalman Kip (1916) reported right-handedness in chimpanzees for precision movements. Yerkes (1943) found that chimpanzees showed general individual hand preferences, although he also noted task specificity in some instances. He made no observation on the distribution of preferences for the two hands in the population.

Apart from the study of face touching, the only published observation on orangutans that we are aware of was made by Grzimek (1949). He remarked that in both orangutans and chimpanzees hand choice was situationally determined.

In summary, the relatively large-scale studies of great apes have a variety of results, one finding a right-hand preference for gorillas, two others finding no clear tendency toward an asymmetrical distribution of preferences, and one showing a left-hand preference for face touching. Although the smaller-scale studies show some consensus on right-hand preferences for gorillas, they provide no real basis for making statements about intraindividual patterns or for noting population-level trends (with the exception of the study of Schaller 1963).

## 6. General discussion

We have found a number of statistically significant asymmetries of manual function in 8 of the 181 species of nonhuman primates, most of which are uncontradicted by other findings. These are summarized in Table 7. All but one of the left-hand preferences involve reaching,

Table 7. Summary of asymmetries of hand preference in nonhuman primates

Group and species	Left preference	Right preference
<i>Prosimians</i>	Simple food reaching (bush babies, Sanford et al. 1984; lorises, Subramoniam 1957).	
<i>New World monkeys</i> (common marmosets)	Simple food reaching (Box 1977)	Reach and act-and-reach tasks; results pooled; practiced subjects (Rothe 1973)
<i>Old World monkeys</i> (macaques, 3 species)	Simple food reaching; Japanese field studies Expose-and-reach sequence: early trials, 2-choice discrimination studies  Food reaching in various single and multi-act situations (Beck & Barton 1972)	Simple food reaching WGTA <sup>a</sup> (Deuel & Dunlop 1980) Trend in later trials: a. Expose-and-reach sequences, 2-choice discrimination studies b. Various reach and act-and-reach tasks; results pooled (Warren 1977b) Manipulation in multi-act situations (Beck & Barton 1972) Precision in finger pressure maintenance (Preilowski 1979)
<i>Great apes</i>	Face touching (Dimond & Harries 1984)	Initiation of chest-beating displays (gorillas, Schaller 1963) Reaching and other use <sup>b</sup> (gorillas, Fischer et al. 1982)

<sup>a</sup>Wisconsin General Testing Apparatus. This finding was not replicated in two other studies.

<sup>b</sup>This finding was not replicated by Preilowski and Leder (1984).

whereas the results favoring the right hand are in various categories.

**6.1. Left-hand preferences.** Left-hand preferences have been observed for simple reaching in prosimians, New World monkeys, and Old World monkeys, and for reaching preceded by other activities in Old World monkeys. Of all the actions we have considered, reaching in the field studies of Old World monkeys would seem to be most dependent on visual guidance. In the reaching studies, the food can be placed anywhere in a 360° field and at various distances from the monkey. The monkey is in principle in the center of the field and facing in one particular direction. In order to get the food, it must first determine the direction and distance of the food on the basis of visual information and then execute a movement based on this information. We suggest therefore that the finding of left-hand reaching preferences in the field studies reflects a left-side preference for visually guided reaching. A similar explanation may account for the left-hand reaching preferences found in lorises and marmosets in what were apparently free field situations involving different approach routines based on visual information at different times.

The tendency for left-hand preferences to be absent in simple reaching situations in the laboratory can perhaps be explained as follows: On a typical trial, in these studies, a food item is placed in one of a small number of locations in the front of the cage. Presumably the animal is usually facing the cage front and has to move only a small distance in a predominantly frontward direction to

get the food. Given the small number of possible food locations and the small range of required movements, the animal can plan and execute its reach with minimal visual information. Consequently the left-side specialization is not necessarily invoked. But if this line of reasoning is correct, further explanation is required for the strong left-hand reaching preference shown by bush babies for simple reaching in a laboratory situation. Facts relevant to this result are that the bush baby is a nocturnal insectivore that locates its food with heavy use of visual information, and often catches flying insects with a one-handed ballistic "smash and grab" movement, which is faster than the human eye can follow (Bishop 1964). In this context, the left-hand preference can be seen as reflecting a left-sided visuomotor specialization for feeding, revealed even in stereotyped situations involving stationary prey, which might require little visual guidance for a monkey in the daylight. The fact that the bush baby's left-hand preference is *not* shown in the quadrupedal posture suggests that the specialization is restricted to the typical upright feeding posture.

We believe that the hypothesis of a left-side specialization for visually guided movement also accounts for the results of those more complex laboratory studies in which left-hand reaching preferences were observed. Thus, left-hand preferences may have been observed in the studies of Ettliger and his colleagues and not in otherwise similar expose-and-reach tasks because of the additional visual demands in the discrimination paradigm.<sup>1</sup> In the Beck and Barton study, two of the highest left-hand reaching preferences were on the moving tube tests.

These tests required the monkey to match the spatial target of its reach to the position of a tube swinging in response to the animal's touch – again, a visually guided action. Finally, Beck and Barton reported an increase in left-hand reaching preferences as the number of different acts in the task increased. Here again, as soon as a task calls for more than one act, a minimally guided grab will not suffice: Visuomotor control is increasingly called for.

As to the left-hand preferences for face touching, Diamond and Harries consider that it may be related to the special role of the right hemisphere in emotional behavior. Another possibility is that it is related to the special role of the right hemisphere in apprehension of the body image, indicated by the body neglect symptoms that often follow right-hemisphere damage. In any event, the results suggest some evolutionary continuity between great apes and man in right-hemisphere function.

**6.2. Right-hand preferences.** The hand preference perhaps most recognizable to the human observer is the right-hand preference in the Beck and Barton study. It was found to be greatest on a task involving two single finger manipulations, and unlike many of the tasks favoring the left hand, appeared to be reduced by differential concurrent demands. We suggest that this preference is homologous to the right-hand preference of humans, in whom the right hand is typically preferred for the most demanding manipulative acts. The fact that this preference has revealed itself clearly only in part of a single study is perhaps due to insufficient separation between manipulative acts and other concurrent demands in other studies. But how can the apparent trend toward increasing right-hand preferences with practice be explained? We are handicapped here by not knowing how this trend was distributed across the different tasks of the Warren (1977b) study, and whether the trend in fact occurred in tests 2–7 of the study of Rothe (1973). But as both these studies included tasks involving movements in addition to food reaching, we raise the possibility that the observed trend (in these and in the discrimination studies) reflects an increasing role of the right-sided specialization for manipulation noted in the Beck and Barton study, as practice on the tasks increased. Although the manipulative demands in these various studies were not great, the possibility that they were a factor in the performance changes is suggested by the fact that no trend toward a right-hand preference seems to have been observed over 600 simple reaching trials in the studies of Lehman (1970; 1978; 1980). However, even complex reaching tasks could still show a trend toward right preference as the need for visual information decreases in these stereotyped situations.

We would also point out that the age-related trend toward increasing left-hand preference in the study of Itani et al. (1963) is consistent with our hypothesis about both left- and right-sided specializations. The absence of a trend toward right-hand preference may be because there is no significant manipulative component in the task, and the continued left-sided trend may be because of the continued importance of visual guidance in food reaching in field situations, regardless of age or experience.

To summarize what has been said so far: We suggest that monkeys have a left-hand preference for visually

guided movement and a right-hand preference for manipulation, broadly defined. Hand use in a given instance will depend on the balance of the two preferences in the individual subject and on the balance of factors evoking the two specializations. If visual information is important though the task is not inherently complex, as in simple reaching in the field, left-hand preferences will tend to be elicited and maintained. Beyond a certain minimum of movement complexity the right-hand preference will either be initially invoked or will be engaged as the need for visual information decreases with practice on stereotyped tasks. Simple reaching tasks in the laboratory initially bring out neither preference in the majority of monkeys, but because of the simplicity of the task, the manipulation specialization is not engaged as the need for visual information decreases with practice. Thus, we would characterize the four "switch-reaching" monkeys noted by Ettlinger et al. (note 1) as animals in which the left-hand reaching preference is engaged by visual information, but the right-hand manipulative preference is engaged by haptic demands in the absence of visual information.

Finally, we wish to suggest that the greater right-hand capacity for finger pressure maintenance in Old World monkeys (Preilowski 1979) and the trend for right-hand initiation of chest beating in gorillas (Schaller 1963) may be related to a right-sided posture-strength specialization which first evolved in prosimians. This possibility will be discussed in a following section.

**6.3. Neural implications.** We know of no reason to believe that the left- and right-handedness we have described simply result from learning. The asymmetries presumably have an innate component and imply asymmetries of neural control. There is apparently no asymmetry in the major efferent transmission pathway in Old World monkeys. Warren and Nonneman (1976) report that "Dr. Norman Geschwind examined the brain stems of 13 monkeys that had served in one of our long-term studies of handedness and could see no appreciable differences in the cross sectional areas of the pyramidal tracts in any of the monkeys, even those which had very strong and consistent manipulatory preferences" (p. 743). Such asymmetries might not even be expected, if individual animals have two opposite hand preferences. We suggest, then, that the asymmetries reflect specialization of the contralateral hemisphere.

Left-handedness for reaching may reflect a spatiomotor specialization of the right hemisphere related to the right hemisphere's visuospatial specialization in humans. Variou motor correlates of the human spatial specialization have been reported (e.g., Guiard, Diaz & Beaubaton 1983; Kimura & Vanderwolf 1970; LeDoux, Wilson & Gazzaniga 1977; Roy & MacKenzie 1978; Todor & Doane 1978). These do not presently lend themselves to a unitary functional explanation, and some findings and claims perhaps need to be more firmly established. But the possibility that some residue of the spatiomotor specialization we attribute to prosimians and monkeys may be present in humans is suggested particularly by the study of Guiard et al. (1983). They report "evidence that normal right handers perform open-loop ballistic aimed movements with a smaller constant error when using the left rather than the right hand. In addition, constant error

is found to be minimal for movements directed towards the left half field" (p. 111). The reaching movements in the studies we have reviewed are presumably not ballistic. But, as noted earlier, the typical prey-catching movements of the bush baby *are* ballistic. The right-hand preferences we have observed are presumably associated with a left-hemispheric specialization for manipulative movements. We take it to be related to that found in humans.

A dichotomous pattern of preference – left for reaching, right for manipulation – with associated hemispheric specializations may be the modal handedness pattern for monkeys capable of good bimanual coordination. It is premature to speculate about the proportion of animals displaying this pattern, or about what other patterns might exist in what proportions. The Japanese field studies suggest that certain adult macaques may be strongly right-handed for reaching. Do they have a reverse dichotomy of preferences, and are there adult monkeys that prefer one hand for both types of activity? Certainly animals can be found in experimental studies (other than the Beck and Barton study) that use the same hand for both reaching and manipulation in a few tests [e.g., Brookshire and Warren's monkeys 17 and 12 (left) and 2 and 10 (right)]. But the question can be raised as to whether these are temporary strategies of young monkeys and/or they are conditioned by experimental regimes, without parallels in the wild. Since humans do not have uniform arm-hand preferences (we are not all right-handed), it would not be surprising if other primates did not have a uniform pattern either. The question of how the nonuniform patterns of humans and other primates relate to each other may become a very important one in the future.

**6.4. Evolutionary Implications.** What can be said about the evolution of primate handedness on the basis of this review? We present the following speculative but testable account summarized in Table 8. Both handedness patterns that we have observed 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, specific to manual functions, was a left-hand/right-hemi-

sphere specialization for visually guided reaching for food in prosimians. It accompanied a structural adaptation also related to locomotion, whereby the ancestral mammalian paw evolved into a hand with the prehensile property. (Prehensile movements can be defined as "those by which an object whether fixed or free is seized and held, partly or wholly, within the compass of the hand"; Napier 1960, p. 647.) The left-hand preference is probably most marked in animals such as galagos and tarsiers, which are bipedal, typically have upright posture, and live primarily on a diet of insects and small animals, many of which are not easily caught. As bush babies are considered to differ little from their ancestral forms (Charles-Dominique & Martin 1970), this asymmetry may first have evolved over 50 million years ago. If so, then the initial specialization may have been primarily for the use of visual information in preprogramming of ballistic reaching movements. In other species with less specialized feeding behavior, visual information may be important for both preprogramming and on-line guidance.

We suspect that a right-hand preference for manipulation is not present in prosimians. They possess minimal structural adaptations of the hand for manipulation and manipulation is not a prominent component of their behavior (Bishop 1964). Manipulative specializations developed in the continuing course of primate evolution with the development of the pseudo-opposable and opposable thumb and the consequent ability to use the precision grip (Napier 1962). As this development occurred, primarily in monkeys, a second, right-hand/left-hemisphere specialization may have come to coexist with the first. This may also have been primarily an adaptation for feeding, but this time for foraging and for processing food before eating it – husking nuts, peeling fruit, and so on. The specialization would therefore have developed partly in the context of the evolution of bimanual coordination.

Kimura has made an analogous suggestion regarding the role of bimanual coordination in the evolution of left-hemisphere specialization: "It seems not too far-fetched to suppose that cerebral asymmetry of function developed in conjunction with the asymmetric activity of the two limbs during tool use, the left hemisphere, for rea-

Table 8. *Evolution of asymmetric upper-limb specializations in primates*

Group	Left side	Right side
<i>Prosimians</i> (circa 65 million years)	Visually guided reaching, initially in upright feeding posture (right-hemisphere control)	Part of a complementary postural control system (left-hemisphere control)
<i>Monkeys</i> (circa 40 million years)	<ol style="list-style-type: none"> <li>1. Generalization of the prosimian asymmetry (right-hemisphere control)</li> <li>2. Subordinate role in bimanual coordination (primarily left-hemisphere control)</li> </ol>	<ol style="list-style-type: none"> <li>1. Fine hand-arm movement control (left-hemisphere control)</li> <li>2. Dominant role in bimanual coordination (left-hemisphere control)</li> </ol>
<i>Great apes</i> (circa 18 million years)	Intermediate between monkey and man?	
<i>Hominids</i> (circa 7 million years)	Left-side reaching preference disappears	Right hand-arm becomes dominant for all unimanual tasks

sons uncertain, becoming the hemisphere specialized for precise sequential limb positioning" (1979, p. 203). Although we agree that bimanual coordination may have been one motivating factor for the left-hemisphere motor specialization, we suggest that it may have predated intensive tool use. We also suggest that the specialization came to occupy the left hemisphere partly because of the existence of a complementary specialization in the right hemisphere.

Of course, we have no direct evidence that the right-hand preference evolved in the context of bimanual coordination. At first glance, it seems natural that the right hand should act on an object in the other, retrieving hand. But then one notes that where the left hand is favored for reaching, it also probably does most of the interaction with the mouth in feeding (recall the reaching-holding correlation in the Box 1977 study). Thus the left hand might initially possess all the manual skills. If so, it would seem natural for the right, unskilled hand to hold an object, while the left manipulated it in cases requiring bimanual coordination. Why then are we not fully left-handed?

We suggest that the answer lies in the postural preadaptation of the right arm-hand that accompanied the evolution of the left-hand reaching preference. Sanford et al. (1984) present the provocative hypothesis that the assumption of the upright stance in primates led to profound postural control problems and that the development of asymmetrical manual specialization may have been part of a response to these problems. The typical feeding situation in many prosimians, including bush babies and lorises, is to cling to a vertical support with the legs and one arm while the other arm is involved in feeding (see for example Jolly 1972, Figs. 30 and 33). A capacity for fine somatic sensorimotor control may then have evolved in the (right) holding limb, together with other bodily structures, as one aspect of the asymmetric posture-related adjustment that Sanford et al. (1984) hypothesize. This preadaptation might have predisposed later evolving animals, less dependent on vertical postural support, to prefer the right hand for tasks requiring fine somatic sensorimotor control. This view of the origin of right-handedness is consistent with the greater skill of the right hand in producing and maintaining specific pressures between the fingertips, reported by Preilowski (1979) for the rhesus monkey. The likelihood that a postural specialization is accompanied by an asymmetry in strength leads us to the suggestion made earlier that the right-hand preference for the initiation of chest beating in the gorilla may have postural implications. Presumably the animals favor the stronger hand for this aggressive display.

Although it is no doubt an oversimplification to consider posture a unitary concept, there is a good deal of evidence of postural asymmetries favoring the right side of the body in human right-handers. Neonatal postural asymmetries favoring the right side of the body are well known (Young, Segalowitz, Corter & Trehub 1983; see summary in Chapter 1). These include a tendency to orient the head toward the right when in supine position and to sustain a stronger right-hand grasp for a longer duration. (The head orientation preference is strongly correlated with later handedness; Michel 1983.) Harris (1983) has pointed out that a frequent observation in

earlier studies of child development was that a right-hand preference was seen for extreme, but not for shorter, reaches. It may be that the postural demands of extreme reaches are more likely to engage a posturally specialized system. In adults, Tan (1985) has found asymmetries of responsiveness in the leg's posturally specialized soleus muscle which are correlated with hand preferences. Robinson, Becker, Camp, and Mansour (1985) have discussed evidence for a special role of the nigrostriatal complex of the left hemisphere in postural control in Parkinsonian patients, and Glick and Shapiro (1985) draw an analogy between human nigrostriatal asymmetries and those observed in rats with postural asymmetries.

One final implication of the present account is that a left-hand specialization for holding also developed in the context of bimanual coordination. Thus, in addition to a specialization for visually guided movement, we attribute to the left hand a special role in liaison with the right hand. But this time the control is vested primarily in the left hemisphere. In future experimental studies of Old World monkeys a left-hand preference for holding might be observed, if the experimental situation does not produce a conflict between left-hand holding and left-hand reaching.

We have argued that both the left- and the right-hand preference patterns observed in nonhuman primates may be precursors of human specializations. However, monkeys and humans would seem to be separated by an evolutionary 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 now normally preempts the left, even for visually guided movement. A vestige of the earlier left-hand reaching specialization may be revealed in the study of Guiard et al., whereas experiments showing greater left-hand precision in static positioning (e.g., Kimura & Vanderwolf 1970) may indicate the continued existence of a holding specialization. And the finding that left-hemisphere damage affects the function of the left as well as the right hand in humans (Kimura 1977) may reflect the evolution of left-hemisphere control of the left hand in bimanual coordination.

There is not enough functional evidence to place the hand preferences of great apes into an evolutionary perspective. On evolutionary grounds one might expect them to share manual specializations of their ancestors among Old World monkeys. However, similarities in hemispheric structural asymmetries between great apes and right-handed humans (to be discussed later) raise some expectations of a humanlike functional pattern.

**6.5. Functional hemispheric specialization: Apparent counterevidence.** We have argued that two types of handedness found in nonhuman primates are indirect evidence for two types of functional hemispheric specialization. This claim must be placed in the historical context of a negative consensus against hemispheric specialization in nonhuman primates derived from more direct neuropsychological investigations. (Again, studies have been mostly on Old World monkeys.) Conclusions have been negative with regard both to hemispheric specialization in general (e.g., Hamilton 1977b; Jung 1962) and to manual function in particular (e.g., Warren



1980). However, evidence has been accumulating for hemisphere specializations (e.g., Ettliger 1984), particularly for left-hemisphere specialization in auditory function (Dewson 1977) and vocal communication (Beecher, Petersen, Zoloth, Moody & Stebbins 1979; Heffner & Heffner 1984). And in the past few years, evidence of specialization in the hemisphere contralateral to the preferred hand has been reported (Garcha, Ettliger & MacCabe 1982; Hamilton & Vermeire 1982).

There are also general reasons for doubting that the negative consensus is justified. A first point, made by Hamilton (1977b), is that those who wish to show that there is no hemispheric specialization in monkeys are in the uncomfortable position of trying to prove the null hypothesis. A second point is that, for practical reasons, most neuropsychological studies use a very small number of monkeys per lesion condition. The resulting problem for making population estimates of specialization is sometimes acknowledged by the authors themselves: "With our small sample of animals no firm conclusions can be drawn" (Ettliger & Dawson 1969, p. 166). A third point, made by Hamilton and Vermeire (1982), is that "only the more recent work with primates has used cognitive tests of a type that would be expected to reveal hemispheric specialization in *man*" (Hamilton & Vermeire 1982, p. 691; our emphasis). Consequently, the possibility has remained open that if experimental paradigms analogous to those showing specialization in humans could be developed, analogous specializations in other primates could be found.

The foregoing review further suggests that in studies of the possibility of hemispheric specialization for manual function, the typical procedure of determining a single type of handedness on the basis of performance on only simple laboratory tasks could be misleading if many animals have two hand preferences that are best revealed by a combination of field studies of reaching and laboratory studies of more complex laboratory tasks. In addition, as with strength of hand preferences, hemispheric specialization may increase with age and may not be easily revealed in younger subjects. Finally, there have been no neuropsychological studies of the great apes. This group might be expected to be most like humans in hemispheric specialization for two reasons: They are considered to have shared a common ancestor with hominids more recently than did Old World monkeys and, as we mentioned, they possess structural hemispheric asymmetries more clearly analogous to human asymmetries than are those of Old World monkeys. Consequently, the absence of neuropsychological studies of this group may result in the impression that humans and nonhuman primates are more different in cerebral function than they really are.

The most direct evidence of hemispheric specialization for manual function in humans comes from neuropsychological studies of manual function itself, rather than from manual responses in tests of perceptual, mnemonic, or cognitive function – as in typical studies of nonhuman primates. The main finding from studies of the effects of unilateral damage in humans is that skilled performance of both hands of right-handers seems to be vested in the left hemisphere (e.g., Kimura 1977). There has been no comparable study of nonhuman primates directed specifically at the question of hemispheric specialization for manual function as such.

The most relevant evidence on the issue seems to come from the study of Trevarthen (1978), mentioned earlier, in which baboons learned to open a multi-act problem box by means of bimanual coordination, achieving speeds of up to 7.5 acts per second. Two of the animals were studied further after division of the optic chiasm and section of the anterior commissure and the corpus callosum. Trevarthen found that "when tested within a few days of surgery both subjects first performed the task spontaneously with the dominant hand alone. The subordinate hand remained inert even for steps in the manipulation that had been performed by it before surgery" (p. 347). This and other observations led Trevarthen to conclude that "the schema governing the serial and spatial ordering of fine movements of both hands in response to the sight of the box in one of the two orientations was laid down at the end of learning the skill in one side of the brain more fully than in the other" (p. 371). Trevarthen's study of two subjects does not allow conjectures as to the distribution of this type of asymmetry of function in the baboon population. In addition, instances of an inability to use the nonpreferred hand in human commissurotomy cases have not been reported. The observation is nevertheless of interest because it suggests that in bimanual tasks normally both hands are controlled primarily by the hemisphere contralateral to the preferred hand in these monkeys, just as in humans (Wyke 1971).

As mentioned earlier, a specialization in the hemisphere contralateral to the preferred hand in monkeys has been observed in some studies. For example, Garcha et al. (1982) found a bilateral tactile deficit after lesions of somatosensory area S II contralateral to the preferred hand, whereas Hamilton and Vermeire (1982) showed better learning of discriminations based on sequentially presented visual stimuli in the contralateral hemisphere of split brain preparations. It is difficult to fit these studies into the framework being developed here without knowing more about the handedness of the animals. However, they do show directly that hemispheric specialization can be associated with hand preferences in Old World monkeys. In addition, the bilateral deficit in the study of Garcha et al. suggests unilateral control of bimanual function.

**6.6. Structural hemispheric asymmetries: Current evidence.** Although it is a far from straightforward task to relate structural asymmetries to functional asymmetries, it is generally agreed that there should be some relation. Coexisting with the earlier consensus against functional hemispheric asymmetries in nonhuman primates was good evidence for the existence of structural asymmetries in great apes, and some evidence in other taxa. This evidence has been added to in recent years (see Geschwind and Galaburda, 1985, for a summary of studies of both humans and other mammals). In humans, most attention has been given to asymmetries in overall brain shape and the topography of the sylvian fissure and its immediate surround (LeMay et al. 1982). With respect to overall brain shape of right-handers there is a tendency for an anticlockwise torque "with the left occipital pole longer and often extending across the midline toward the right, and a wider right hemisphere in its central and frontal portions, and frequent forward protrusion of the

right frontal pole. This is found also in newborns" (LeMay 1976, p. 363). There have been a number of findings regarding the sylvian fissure and perisylvian cortex. Falzi, Perrone, and Vignolo (1982) found the cortical surface area of *pars opercularis* and *pars triangularis* of the 3rd frontal convolution (Broca's area) to be larger in the left hemisphere of right-handers than in the right. The sylvian fissure is longer in the left hemisphere in humans (Yeni-Komshian & Benson 1976) but terminates posteriorly at a superior location in the right hemisphere of right-handers (LeMay 1976). In addition, in humans the *planum temporale* posterior to Heschl's gyrus was found to be longer on the left side in 65 of 100 brains (Geschwind & Levitsky 1968). (The right *planum* was larger in 11 cases.) A similar tendency has been observed in fetal brains (Wada, Clarke & Hamm 1975).

The asymmetry in the *planum temporale* in particular has been widely interpreted as reflecting left-hemispheric specialization for linguistic function, because it is considered to be part of the surface of Wernicke's area. But sylvian fissure topography on the left – the longer and lower fissure and even *planum temporale* dimensions – can perhaps also be related to inferior and posterior expansion of the left parietal lobe (Jerison 1976). LeMay (1976) reports as follows: "Associated with a lower sylvian point, the left postcentral gyrus, especially in its lower portion, is wider than on the right and there is a greater degree of fissuration on the left between the central sulcus and the posterior end of the sylvian fissure" (p. 357). The left parietal lobe has an important role in language, but it also has an important role in the control of human manual function (Kimura 1982), and has been specifically implicated in the control of bimanual coordination (Wyke 1971). The parietal lobe is also important for manual control in monkeys (Mountcastle, Lynch, Georgopoulos, Sakata & Acuna 1975), but monkeys have no language, as conventionally defined.

Thus it becomes appropriate to raise the question of the relative role of language and hand control specialization in cerebral structural asymmetries. The question can be addressed in a rather gross way by considering hemispheric asymmetry data on left- and right-handers. If we consider preferred hand control to be primarily from the contralateral cortex, then we would expect hemispheric asymmetries related to hand preference to show opposite distributions in left- and right-handers. Language specialization is considered to be primarily in the left hemisphere in virtually all right-handers. But approximately two-thirds of left-handers are also considered to have

language control primarily in the left hemisphere (Milner 1975). Thus, to the extent that human hemispheric asymmetries are related to language specialization we would expect asymmetries in a population of left-handers to be similar to those in a right-handed population, but less marked. An evaluation of these rather different expectations can be made from other data provided by LeMay and her colleagues (LeMay 1976; LeMay et al. 1982) and summarized in the first two lines of Table 9. Neither expectation can be strongly confirmed or disconfirmed. On the five variables for which direct comparisons can be made, the left-handers show an asymmetry similar to that in right-handers in two (right frontal lobe width and left occipital lobe length), an opposite asymmetry in one (occipital lobe width), and no definite trend in the other two variables.

Line 3 of Table 9 shows results for great apes. It can be seen that asymmetries here coincide more with those of right-handed humans than with left-handers on the variable on which left- and right-handers differ (occipital lobe width). In addition, Yeni-Komshian and Benson (1976) also showed that great apes parallel humans in having a longer sylvian fissure on the left side. And as the human brains in that study were not selected for handedness, the human result presumably reflects the situation in right-handers. The analysis of the last paragraph does not entitle us to attribute the similarities between apes and right-handers more to manual function or to language-related function. But in the absence of close parallels between human language and other primate communication, the possibility that these similarities are attributable, at least partially, to shared asymmetries in manual function should certainly be explored.

It is difficult to relate human hemispheric structural asymmetries to those of nonhuman primate groups, other than the great apes, partly because structural homologies are in many cases hard to establish. Some suggestive findings of asymmetries in Old World monkeys have been presented (Cain & Wada 1979; Falk 1978; LeMay 1976; LeMay et al. 1982). However, it is not clear what kinds of structural asymmetries related to manual function we might expect in monkeys, given our hypothesis that the modal handedness pattern is dichotomous, and our uncertainty as to the distribution of preferences in entire populations. In the prosimians we would not expect hemispheric asymmetries related to manual function to be analogous to those in man. We would not expect them, because we do not expect these animals to have evolved right-hand preferences and left-hemisphere specializa-

Table 9. Patterns of cerebral hemispheric asymmetries observed in right- and left-handed humans and in great apes (figures expressed in percentages)

	Frontal width	Frontal length	Occipital width	Occipital length	Sylvian-point height
	L> = R>	L↑ = R↑	L> = R>	L↓ = R↓	L↑ = R↑
Right-handed humans	9 21 70	7 63 30	64 20 16	69 22 9	8 25 67
Left-handed humans	20 41 39	21 60 19	22 32 46	56 24 19	7 71 21
Great apes	8 50 42	4 25 71	50 50 0	61 39 0	6 0 94

Source: LeMay (1976) and LeMay et al. (1982).

tions for manipulation and bimanual coordination without an advanced ability to oppose the thumb to the rest of the hand.

**6.7. Conclusion: Features of the present view.** Although it is obviously speculative, we believe that our presentation of a comprehensive testable view of the evolution of primate handedness has heuristic value. The view has the merit of suggesting a plausible adaptive sequence. Left-handed reaching and right-handed manipulation are hypothesized to have been functional perceptual-motor adaptations to selection pressures of feeding, accompanied by important structural adaptations – the prehensile hand and the opposable thumb, respectively. A view stressing functional adaptation as the initial step in manual specialization is considered preferable to a view favoring the evolution of metafunctional capacities such as sequencing (Calvin 1982) or an analytic-synthetic dichotomy (Levy 1977a), as the kind of causal chain of events that would have to be conjectured to underlie the latter type of development would seem more tenuous. 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; this view also seems preferable to scenarios in which one hemisphere initially achieves a specialization and the other either does not possess one or achieves it later by default (Bradshaw & Nettleton 1981). The (probably close) relationship between the evolution of manual specializations and language, which is beyond the scope of this paper, has been considered elsewhere (Lindblom, MacNeilage & Studdert-Kennedy, in preparation; MacNeilage, Studdert-Kennedy & Lindblom 1984; 1985).

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#### NOTE

1. An important qualification needs to be made at this stage. Our suggested explanation for the reaching preferences in the field studies includes the property of visual guidance. But a number of studies by Ettlinger and his colleagues were of tactile discrimination, and no clear differences in proportions of monkeys showing particular hand preferences were found in visual and tactile studies. However, two factors suggest to us that we should not extend our generalization about left-hand preferences to include tactile guidance. First, animals had visual shaping trials before tactile discrimination tasks were begun in two of the three studies involving tactile discriminations (Ettlinger & Moffett 1964; Milner 1969). In the other study, which included tactile discriminations (Ettlinger 1961), neither visual pretraining nor the order in which animals were exposed to visual and tactile tasks (in the same apparatus) was mentioned. It is therefore possible that a preference related to visual guidance was initially established in many cases and could have tended to persist in the tactile tasks. Second, during the overall period during which several discrimination studies were carried out, Ettlinger, Blakemore, and Milner (1968) noted that of 50 monkeys that performed both visual and tactile tasks, 4

monkeys preferred one hand for one type of task and the other for the other type. In all four cases it was the left hand that was preferred for visual tasks. Furthermore, all of *these* animals first performed tactile tasks without visual pretraining – that is, in the dark. Although the direction of this dichotomy of preferences is not statistically significant in four subjects ( $1/2^4 = .0625$ , N.S.), the sheer existence of these examples of a dichotomy of preference in two tasks in which conditions for the motor response are virtually identical seemed worthy of note to the authors and to us. And in that context the fact that the pattern of preferences is always in the same direction may be important. In the light of these two considerations – the use of visual shaping trials preceding tactile testing and the fact that dichotomous preference patterns involve left-hand preference for visual but not tactile tasks – we prefer for the moment to conclude that the left-side preference is related only to visually guided movement.

## Open Peer Commentary

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### Handedness as chance or as species characteristic

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The human pattern of manual and cerebral asymmetry is introduced in MacNeilage et al.'s target article, as in so much of the literature, as though it can be treated as a human species characteristic. But right-handedness and left-brainedness are not human universals. About 10% of humans show a strong preference for the left hand, and about 30–40% show at least one left-hand preference when several actions are considered. What does seem to be universal in human *groups* is that about 60% develop consistent right-handedness, when only about 25–50% (depending on criteria of assessment) would be expected to do so by chance. Similarly, although speech is a human universal, the tendency for speech to depend on the left hemisphere is not. Estimates from several sources suggest that about 9% of humans are not left-brained speakers (Annett 1975; 1985). The 10% left-handers and 9% right- or bilateral-brained speakers are *not the same*; there are more right- than left-handers among the latter. Hence, there is considerable natural variation in humans for lateral asymmetries of hand and brain, and underestimation of this variation has hindered the analysis of questions about lateral asymmetries.

The evidence cited here concerns handedness in nonhuman primates and is used to argue for changing patterns of hemisphere specialisation in the course of primate evolution. The strong argument that such asymmetries are species universals is clearly not tenable, so the argument must be presumed to rest on the demonstration of biases toward one side significantly greater than expected by chance. There can be no doubt that nonhuman primates and other mammals may develop handedness. A tendency to develop preferences for one hand or the other is probably inherent in all complex, bilaterally sym-

metrical nervous systems. It is also probable that patterns of cerebral asymmetry tend to develop in primates. These biases of hand and brain can be expected to develop as ontological variation in the growth of each individual. If it is to be argued that there are species biases like those observed in man, it must be demonstrated that there are inequalities in the proportions biased toward left or right in samples large enough to allow tests against the null hypothesis.

Only two large data sets are cited in the target article for which a significant excess of left- over right-handed animals is claimed. In the first, Japanese macaques, the percentages recorded as left- and right-preferent were 38% and 29%, respectively. In the second, monkeys during early testing by Ettlinger et al., the corresponding percentages were 33% and 16%; later testing of these same animals found percentages of 31% and 30%. There is no convincing reason for accepting the early findings as more valid than the later ones, especially when it is argued elsewhere that lack of bias might be due to the use of immature animals.

The main reason for rejecting the claim of significant bias toward the left hand is that the very large proportions of animals showing no consistent preference, 33% and 50% in the Japanese and Ettlinger data, respectively, are omitted from the statistical calculations. It often happens in the treatment of human samples that "ambidextrals" are omitted, on the assumption that they are rarities who can be safely ignored, the variation in humans discussed above being unrecognised. There can be no justification for omitting half the animals here, when it is argued that a majority are left-handed. If bias toward the left hand for reaching is not true of a substantial majority, but only of about one-third of animals, then speculations about evolutionary advantage are not worth consideration. The Beck and Barton (1972) data cannot contribute to a serious assessment of species trends, because only 10 animals were involved and these are not described as individuals. When hand preferences range between left-, right-, and none, it is obvious that sampling factors could produce apparent, but illusory, biases among so few cases. The vast majority of studies, as indicated in Table 4 of the target article, show no evidence of species biases for hand preference.

In what sense is the argument supposed to be compatible with the theory of evolution? What selective advantages could be conferred by strong biases toward one hand or the other in animals that run along branches on four hand/feet (Napier 1980), when loss of skill in either hand would increase the risk of falling? If natural selection can be supposed to give rise to various patterns of cerebral specialisation, which change between primate genera, why could not the human pattern arise as a special *Homo* adaptation? It is sensible to look for precursors of human adaptations, but also sensible to recognise that cerebral specialisations could be linked with genes we do *not* share with our primate cousins. There must be some genes associated with unique human adaptations, and because man is the only primate that *talks*, it seems not unlikely that a bias toward left-hemisphere speech could have arisen in a hominid ancestor.

Whatever the advantages of the human biases toward left hemisphere and right hand, they are not so great as to have made these characteristics universal in *Homo sapiens sapiens*. This observation raises the possibility that there are disadvantages as well as advantages associated with human asymmetries. An association with variation in brain anatomy has been found by Witelson (1985a), in that nonright-handers (mixed- and left-handers) tend to have a larger corpus callosum than do consistent right-handers. Perhaps strong right-handedness is associated with costs to overall cerebral power that can be tolerated in a large-brained primate but that would not be acceptable in one with a smaller brain.

This is not to deny the possibility that nonhuman primates could have diverse patterns of cerebral specialisation. It is possible that the human pattern itself arises as a slight modifica-

tion of some basic mammalian or even vertebrate pattern of embryological development. However, arguments for any such asymmetries need to be made in the light of the possibility that the most powerful determinant of asymmetry is chance. Human asymmetry could be due to chance, plus a constant in some but not all people, which weights the odds in favour of the left hemisphere (Annett 1972; 1985).

## But what about nonprimate asymmetries and nonmanual primate asymmetries?

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MacNeilage et al.'s thesis suggests that human asymmetries may have a far more ancient origin than currently thought, and it is certainly inconsistent with arguments (Bradshaw & Nettleton 1981) that tool use provided the original evolutionary pressure. The argument that nonhuman primates should show some manual asymmetries because their manual dexterity with implements resembles human tool use, however, is to ignore the role of learning by observation and imitation in acquiring tool skills. Thus, two such individuals, a teacher or model and a learner, of opposite handedness would interact far less efficiently than they would if both were dextrals (or sinistrals), as has been shown recently with learning to tie knots (Michel & Harkins 1985a). Nonhuman primates are not known to impart or acquire such complex manual skills in such a structured fashion.

Yet we do agree with MacNeilage et al. that visually guided reaching by the left hand and right-hand manipulation occur in nonhuman primates, perhaps stemming from feeding adaptations and the development of prehensile hands and opposable thumbs. Why then, the authors ask, are not *both* functions now subserved by our right hands? If we plan to pick up and work on an object, we may well reach for it with the left (holding or stabilizing) hand, to leave the right hand free to work on it, rather than reach with the right hand and then have to swap hands and possibly fumble it. This idea may not yet have been tested, but our manual specialization may encourage left-hand reaching whenever complex bimanual interaction is planned, just as manual asymmetries may emerge with nonhuman primates only with complex tasks. The same need to avoid swapping hands may also answer MacNeilage et al.'s question about why we are not fully *left-handed* if the left hand initially possessed all manual skills.

The argument that these feeding-driven selection pressures result in simultaneous specialization of both hands/hemispheres (stabilization and manipulation) may seem to dispose of the scenario wherein one hemisphere (the left) specializes for sequential manipulative function, while the other (the right) becomes specialized by default for a loose collection of "left-over" functions. Right-hemisphere functions might even specialize first (e.g., territoriality, arousal, spatial processing, emotionality - all of survival value and possibly present in nonprimate lateralization, see below). MacNeilage et al. retain the by-default argument by suggesting that left-hand/right-hemisphere spatial reaching might precede right-hand/left-hemisphere manipulation - even if, in turn, right-hand/left-hemisphere posture stabilization was itself a prerequisite for left-hand guided reaching.

The evidence for nonmanual behavioral asymmetries in nonprimate mammals (briefly mentioned by MacNeilage et al.) might force us to look behind the particular stabilize-reach-manipulate scenario proposed, and even the general thesis that primate handedness stems from feeding adaptations after the release of primate forelimbs from locomotor demands. At the

behavioral level, Robinson and Coyle (1980) found that right-hemisphere damage in rats led to spontaneous hyperactivity and widespread catecholamine decreases. Sherman, Garbanati, Rosen, Yutzey, and Denenberg (1980) noted that rats handled in infancy tend to turn left which, together with certain other findings, implies right-hemisphere control of both spatial preference and emotional behavior (Denenberg 1981). The right cortex may be thicker in male rats (the more exploratory sex) and vice versa in females (Diamond, Johnson & Ingham 1975). The rat, cat, rabbit, and mouse apparently have bigger right hemispheres (Kolb, Sutherland, Nonneman & Whishaw 1982). Bianki (1983) even claims that in the rat the right hemisphere dominates for space perception, simultaneous information processing, perception of concrete characteristics, and deductive processing, whereas the left dominates for time perception, successive information processing, perception of abstract characteristics, and inductive reasoning. This might seem suspiciously similar to the human model called into question by MacNeilage et al. [although the left-side control of song in certain passerines should also be noted (Nottebohm 1979)]; but the possibility must be considered (Geschwind & Galaburda 1985; although cf. Corballis & Morgan, 1978, for the opposite scenario) that precocious development of the right hemisphere in the survival-related functions discussed above recapitulates the course of evolution.

What do we make of behavioral asymmetries in the monkey then? Most appear to involve left-hemisphere advantages: for discriminating species-specific vocalizations (Petersen, Beecher, Zoloth, Green, Marler, Moody & Stebbins 1984) and other auditory signals (Dewson 1977), and for discriminating photographs of monkey faces (Hamilton & Vermeire 1983), lines differing in slope (Hamilton 1983), and squares containing a center or off-center dot (Jason, Cowey & Weiskrantz 1984). Two involve right-hemisphere advantages: for auditory gap detection and syllable discrimination (Pohl 1984), and for superior tactile discrimination (Horster & Ettliger 1985) by monkeys spontaneously preferring the left hand (78) compared to the right (77); the 82 without consistent preferences were fastest of all (although cf. Zimmerberg, Strumpf & Glick, 1978, where rats without consistent turning preferences were the poorest performers). Of course the existence and nature rather than the direction of asymmetries may be more important when comparing across species, and apparent hemispheric advantages may merely reflect which hemisphere is able to assume control. Nevertheless, it is not immediately easy to see how such behavioral asymmetries within the primates square with the proposed hypothesis; it may explain the case of monkey handedness, but possibly not the human case.

Some final points:

1. MacNeilage et al. observe that the "more recent" view is that asymmetries evolved for throwing in early hominids. This suggestion goes back at least to Kolakowski and Malina (1974).

2. MacNeilage et al. regret being unable to draw conclusions from the data available to them (LeMay, Billig & Geschwind 1982) about the relationships between morphological asymmetries in the brain and handedness and language lateralization. Posterior asymmetries [ascertained by Nuclear Magnetic Resonance Imaging (NMRI)] do seem to correlate with handedness, however (Kertesz, Black, Polk & Howell 1986; although cf. Koff, Naeser & Pieniadz, Foundas & Levine 1986); sinistrals do show reduced morphological asymmetries overall (Bear, Schiff, Saver, Greenberg & Freeman 1986); such asymmetries may be poor predictors of language lateralization (Henderson, Naeser, Weiner, Pieniadz & Chui 1984).

3. MacNeilage et al. agree that the failure to observe manual asymmetries in some studies stems from using young animals. This implies that asymmetries develop maturationally. This is certainly not true in the human case (Witelson 1985b), although the ontogenetic unfolding of lateralized skills may give that false

impression. Conversely, MacNeilage et al.'s claim that expected nonhuman asymmetries may take time to develop with practice (presumably via the establishment of appropriate processing sets) closely parallels the human case (Bradshaw & Nettleton 1983).

4. According to Guiard, Diaz, and Beaubaton (1983), when dextrals perform a fast movement aimed toward a visible target (reaching<sup>p</sup>), the left hand is indeed more accurate (although cf. Todor & Cisneros 1985).

## Reaching or manipulation: Left or right?

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MacNeilage et al. emphasize left-hand function in visually guided movement. This accounts for the bush babies' open-loop ballistic "smash and grab" capturing of flying insects. It also accounts for the better accuracy of left ballistic pointing by adult humans (Guiard, Diaz & Beaubaton 1983). Although postural asymmetries favoring the right side of the body are observed from birth, as MacNeilage et al. remind us, the 5-day-old human exhibits left-hand superiority in open-loop visuomanual reaching for an object (de Schonen & Bresson 1984).

The fact that the right hand performs manipulation after ballistic capture is confirmed by early human bilateral behavior. In ballistic reaching, the eyes can stop to fixate an object once the movement has started. In holding for manipulation, visual control of the fingers of the right hand is continuous (i.e., it involves the nonballistic system). When a 5-month-old child tries to take a small object from a rectangular tray (21 × 29 cm), the child always puts its left hand on the edge of the tray first, and then reaches for the object with its right hand. This behavior ceases with the onset of unimanual reaching when the child is about 6 months old (Bresson, Maury, Pieraut-Le Bonniec & de Schonen 1978). Was the left ballistic system a necessary condition for transferring manipulative activities to a right hand that could no longer be used to maintain the functional posture in insect-catching (Sanford, Guin & Ward 1984)?

The postural aspects of limb dominance outlined by MacNeilage et al. appear early in phylogeny, as Megirian, Weller, Martin, and Watson (1977) showed in another taxum (the marsupial mammal *Trichosurus vulpecula*). Yet, some cases of manipulation by the left hand do occur in taxa other than primates (e.g., Psittacidae) at the population level. Several species of parrots manifest fully lateralized prehension patterns in their two limbs. They probably do not use their left limbs in ballistic reaching. Most of them, from the New World as well as the Old World, carry their entire body weight on the right leg, whereas they manipulate food with the left. Out of nine species of Australian parrots, Rogers (1980) found only one psittaciforme (*Platyercus elegans*) to be "right-footed." Friedman and Davis (1938) studied 20 individuals from 15 species of American parrots, using 20 presentations of food in pieces of equal size under standard conditions. They found that only 3 of the birds, of 3 different species, were right-handed. We calculated that for only 1 of these 3 parrots did the preference reach significance ( $\chi^2 = 16.2$ ,  $df = 1$ ,  $p < .001$ ). Left-footedness was found to be statistically significant for 14 out of 17 parrots (the value of  $\chi^2$  ranges between  $p < .06$  for 1 bird, and  $p < .001$  for 9 birds); these results held true in the retest one year later.

In another parrot (*Amazona amazonica*) Nottebohm (1980) reported an absence of hypoglossal dominance, either left or right; yet, the left-footedness established for this parrot by



Friedman and Davis (1938) is significant at  $p = .006$ . In passerine birds, which do not exhibit such lateralized manipulative activity with their legs, vocalizations are controlled by the left cerebral hemisphere (Lemon 1973; Nottebohm 1980). Analogous findings concerning species-specific call perception have been reported in Japanese macaques (*Macaca fuscata*) (Beecher, Petersen, Zoloth, Moody & Stebbins 1979). MacNeilage et al. have conflated this fact with left-hemisphere specialization for auditory function in some monkeys (Dewson 1977). In order to understand the shift from left- to right-limb preference, as well as the lateralization of auditory and vocal functions, much more species-specific data are needed. If we consider only primates, species-specific differences in lateralization may still need to be explained.

MacNeilage et al. link right-handedness with control of fine movements of the fingers in manipulation and with specific fingertip pressure and strength (Preilowski 1979). They also juxtapose this with right-hand preference in initiating chest-beating in adult male mountain gorillas (*Gorilla gorilla beringei*). Gorillas (*Gorilla gorilla*) appear to be mostly right-handed. Data on handedness in 27 gorillas indicate that only 3 were left-handed ( $\chi^2 = 20$ ,  $df = 3$ ,  $p < .001$ ); the pattern is similar in the small number of orangutans studied. However, chimpanzees (*Pan troglodytes*) and gorillas walk on the ground, whereas orangutans (*Pongo pygmaeus*) are almost exclusively tree-dwelling. These three anthropoid species do not manifest the same functional behavioral asymmetries. Most chimpanzees appear to be left-handed after the age of 3. Of 57 chimpanzees whose lateralization was described, 27 were left-handed and only 16 were right-handed ( $\chi^2 = 5.15$ ,  $df = 2$ ,  $p < .10$ ). The difference from the handedness pattern of the 27 gorillas was extremely significant ( $\chi^2 = 31.2$ ,  $df = 2$ ,  $p < .001$ ) (Brésard 1984).

Chimpanzees, both in their unilateral and bilateral specializations, seem to differ from the closest species in their taxum. This might serve to remind us of the case of *Platyercus elegans* among other psittaciformes. Chimpanzee handedness appears to be the reverse of that of other great apes, and less stable. And within the "chimpanzee" species, there may be a constant proportion of reverse-lateralized individuals. This may also be a characteristic of several other species, such as human beings with their fixed ratio of left-handers.

A clear difference of this sort appeared in longitudinal observations of unimanual and bimanual behaviors in an orangutan and a chimpanzee (Brésard & Bresson 1983). The young male orangutan was constantly right-handed throughout the whole set of experiments, especially for the precision grip in holding a tiny marble ( $\chi^2 = 31$ ,  $df = 1$ ,  $p < .001$ ). The chimpanzee, a female younger than 3 years old, had variable lateralization, becoming fully left-handed only when she reached the age of 4 ( $\chi^2 = 158$ ,  $df = 1$ ,  $p < .001$ ), and at 5½ she still is. Chorazyna (1976) writes about her female chimpanzee (observed between the ages of 3 days and 27 months) that "each new motor activity of our chimpanzee is initiated in the left side and subsequently shifts to the right" (p. 382). As MacNeilage et al. mention in referring to Itani et al. (1963), left-handedness appears unstable in very young Japanese macaques. But the chimpanzee mentioned above (Brésard & Bresson 1983) also achieved distal knuckle-walking using her left forelimb several months before achieving it with her right forelimb. Bimanual behavior of 5-month-old human babies is likewise transient. We ought to study behaviors that appear transiently in development.

MacNeilage et al. note that the available data on phylogenetic aspects of right and left lateralization have many gaps. Especially in the case of the apes, the data show great inconsistency. Left- and right-limb use and cerebral organization should be studied especially closely in species that turn out to differ from the closest relative in their same taxum, as should the within-species subpopulations with different limb preferences, such as left-handers in humans.

## Handedness is a matter of degree

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MacNeilage et al. have offered some interesting speculations on the evolution of manual preference and, potentially, on the genesis of hemispheric specialization. Their claim is that non-human primates show a left-hand specialization for complex visually guided reaching, while simultaneously exhibiting a right-hand specialization for manipulation. Acts involving minimal visual guidance do not show any strong preference. They see the development of lateralized behaviors as having led to the differential specialization of the two cerebral hemispheres.

Although the story has a certain degree of credibility, there are many issues on which it could founder. For instance, the Beck and Barton (1972) data may not be as compelling as MacNeilage et al. make out. We will let others who are more expert in primatology comment on this, however, and consider instead two other major points. First, does the theory have any implications for the study of human handedness? Second, does it have any implications for our understanding of human cerebral asymmetries?

The MacNeilage et al. position would become particularly interesting if it could lead to new ways of looking at human hand preference. Although the strong right-hand preference for manipulation in humans may have come to obscure other effects, as MacNeilage et al. suggest, their position does lead to several testable predictions. First, and most obvious, it suggests that there should be a strong population preference for the right hand in manipulation. Second, there should be no strong population preference for simple reaching behaviors. Third, there should be a left-hand preference for complex visually guided reaching behaviors.

People undoubtedly do show a right-hand preference for manipulative activity (e.g., Annett 1985; Porac & Coren 1981). Virtually any hand preference or hand performance test indicates that about 90% of the population is right-handed and only about 10% is left-handed. In recent years, however, there have been a number of factor analyses of hand preference inventories (e.g., Beukelaar & Kroonenberg 1983; Bryden 1977; Dean 1982; Healey, Liederman & Geschwind 1986). Each of these provides overwhelming evidence for a population-level right-hand preference for manipulation. However, these analyses are also consistent in showing two to four additional factors. One of the common subsidiary factors includes items about such behaviors as picking up a penny, petting a dog, pointing (Dean 1982), snapping one's fingers (Healey et al. 1986), picking up a glass or pitcher (Bryden 1977), turning on a light switch, and crumpling a piece of paper (Beukelaar & Kroonenberg 1983). All these activities either involve a minimum of visual guidance or are well practiced. The tendency is for these items to be performed equally well with either hand: Both left- and right-handers are more likely to give "equal" responses to them. For the sake of simplicity, these behaviors can be considered analogous to simple reaches in primates, and therefore provide at least modest support for the second prediction from MacNeilage et al.'s position.

The third prediction from MacNeilage et al.'s position would require that we find some activity that right-handers normally do with the left hand and vice versa. Although there certainly are "reverse items" (e.g., "With which hand do you hold the nail when hammering?"), they are but alternative ways of asking about dominant hand activity. In examining hand preference questionnaires, we were able to find only one factor on which people might be said to use the reverse pattern, and that is the Healey et al. (1986) Factor 3. The highest-loading items on this factor concern swinging a baseball bat, turning a cartwheel, and



carrying a heavy suitcase. Whereas the former two items might be said to involve complex visually guided movement, the latter certainly does not. However, hand questionnaires are usually constructed to identify a primary common factor; a sufficient number of questions with which to uncover a factor such as the one MacNeilage et al. propose are rarely asked.

Support for the predictions of MacNeilage et al.'s theory in studies of human handedness is therefore limited. Although there is some evidence that simple reaching behavior is less lateralized than manipulation, there is little support for the view that there is a bias to the left for complex visually guided behavior, and alternative theories may be at least as viable. Perhaps a better description of the simple reaching behaviors is that these require only modest skill, and the selection of the hand to perform them is governed by the location of the target item, the hand that is free for the moment, and so on. In other words, there may be some activities for which it is very difficult to use the nondominant hand, and others for which it is relatively easy to shift.

In fact, there may well be meaningful individual differences in the likelihood that one will use the nondominant hand for simple behaviors. Some people find it easy to shift to their nondominant hand; others do not. Thus, degree and direction of hand preference may be quite distinct factors. It is interesting to note that, in mice, one cannot selectively breed for direction of paw preference, but one can breed for degree of preference (Collins 1985). Similarly, in a three-generational study of hand preference and proficiency in humans, we have found that from grandparents to grandchildren there is only limited heritability for direction of handedness, but that there is a strong heritability for the degree of handedness (Bryden 1987). Thus, whereas left-handed grandparents are little more likely to have left-handed grandchildren than are right-handed grandparents, strongly handed grandparents produce strongly handed grandchildren. One major distinction among humans may therefore be how willing they are to shift hands as a function of environmental demands.

MacNeilage et al. also argue in their Conclusion that their theory is relevant to cerebral specialization, in that it provides a "plausible motivation for the development of specializations in both hemispheres." They suggest that such a view is preferable to one in which a hemisphere develops its specialization by default. We would agree strongly with this view as it applies to hemispheric specialization. The complementary specialization of the two cerebral hemispheres may not be a causal process, with the two being related to a common origin and/or driven by reciprocal processes. Instead, it may be a statistical byproduct of the fact that human beings show two quite different population biases. Most of us have a left hemisphere that is specialized for linguistic processing and a right hemisphere that is critically involved in visuospatial processing: We may *think* the two are causally complementary, because this is the modal pattern of cerebral organization. However, Bryden, Hécaen, and De-Agostini (1983), in a survey of aphasic and visuospatial deficits in a large sample of unilaterally brain-damaged adults, found that the incidence of aphasia was not associated with the incidence of visuospatial difficulties after right-hemisphere damage but that it was *positively* associated after left-hemisphere damage. Such a finding would suggest that left- and right-hemispheric specializations are independent of one another, appearing to be complementary only because there are opposing population biases. In fact, this appears to be what MacNeilage et al. are communicating in their Figure 1, which shows an insignificant (+.21) association between left-hand reaching and right-hand manipulation: This is what would be expected were the lateralization of reaching and manipulation controlled by systems having distinct and independent origins.

In terms of human handedness and cerebral specialization, then, the MacNeilage et al. target article offers two major

suggestions, both of which remain speculative. The first is that there is a distinct visually guided movement factor in human handedness, which shows a population bias to the left. We have been able to unearth limited support for such a notion. The second is that left- and right-hemispheric specializations have quite different origins and are therefore causally separable. Evidence is accumulating that this may in fact be the case.

## On evolutionary expectations of symmetry and toolmaking

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As Gould (1985) said, "Always be suspicious of conclusions that reinforce uncritical hope and follow comforting traditions of Western thought" (p. 401). Especially, I might add, when (1) the null hypothesis coincides with human uniqueness, and when (2) demanding enough consistency in individual performance will inevitably push the conclusion toward a null hypothesis. MacNeilage et al. have done a real service by carefully reviewing the evidence for a hypothesis about primate handedness which, because of the way the question was posed originally, had a hidden tendency to converge on human uniqueness when the data were sparse. The present turnabout in the primate handedness literature should make us reevaluate how the questions are posed in the primate language literature; its ever-escalating threshold criteria for "true language" make one worry about analogous self-fulfilling prophecies.

One need not presume that unconscious anthropocentrism has played an obfuscating role in primate handedness investigations; in this particular case, an unexamined belief in symmetry may have been sufficient to ensnare. (I was sensitized to this by a medical illustrator: My sketches of brain horizontal sections showing the frontal and occipital pole asymmetries came back looking beautifully symmetric; the artist was distressed to learn that brains weren't symmetric.) Given that a null hypothesis constitutes the unsurprising, conventional explanation, why should either functional or structural symmetry be the null hypothesis for comparing the sides in behavior and neuroanatomy? Why should we expect symmetry in any mammal, given such asymmetries beneath the skin as the right side's liver and the left side's spleen, or the size differences between our two kidneys? Economy of genes hardly seems likely: Although specifying the neuroanatomy of an average hemisphere probably takes a lot of genes, it seems unlikely to require much more to specify the changes by which the two hemispheres differ.

One can argue that once a variant on symmetry arose, the rate of divergence from symmetry accelerated in the same manner as gamete dimorphism probably accelerated 1,000 million years ago (Maynard Smith 1978, ch. 9). Same-size gametes are inherently unstable, given any variation in energy investment in gametes to knock it off dead center, so one expects anisogamy going to such extremes as the energy-rich ovum and the cheap sperm (this is what defines female and male, and such appears to be the origin of the two-sex system).

We may come to look upon symmetric hemispheric function in the same manner as isogamy – that is, as inherently unstable. Having to coordinate two separate "centers" for the same function gets expensive, dependent on that long, slow trip through the corpus callosum. Although having two centers can be important when one is damaged, such considerations are very weak in biological evolution, in comparison to increments in food-finding and offspring-rearing skills. And even in inbred strains of rats, there are substantial variations on the theme of brain anatomical asymmetry, most rats (like humans) having a somewhat larger right hemisphere, but with some having a

larger left hemisphere. Because rat behavior varies with such gross asymmetries (Denberg 1981), the rats with the larger right hemisphere being less exploratory than those with the larger left, one can see how different environments could eventually bias the population toward a favorable brain asymmetry.

Evolutionary rationales play a role in our experimental design, not merely through what we establish as a null hypothesis but in what we measure – for example, manipulative abilities associated with tool use and toolmaking. Yet, these expectations are seldom made explicit. It would not be such a problem except that our common-sense expectations regarding human evolution are so often wrong (e.g., the reasonable-sounding “bigger-is-smarter-is-better” rationale for brain size increase; see Calvin 1986a; 1986b; Gould 1981). One reason is that we attribute characteristics of the more visible cultural evolution to the more cryptic biological evolution. The right place for making substantial biological change (islands, the pockets of population on the ice age frontiers, etc.) is often quite different from the place where cultural evolution operates most readily (population centers where making a living is somewhat easier, where observational learning and the rumor mill can pass around new techniques quickly, etc.). However handy that cultural evolution is for getting things started (behavioral innovations often precede selection for the anatomical variants which make the behavior safer and more efficient), it was biological evolution that had to enlarge and reorganize the brain.

I am uncomfortable with MacNeilage et al.'s concluding statement that a “functional” adaptive rationale (the supposed long-run virtues of left-handed reaching and right-handed manipulation specializations) is preferable to a “metafunctional” one such as sequencing for throwing. I have nothing against their hypothesis as such, and think it an admirable one for stimulating relevant experiments. But by compound interest reasoning, anything can do the job given enough time; to say something might be useful is no longer enough. The associated rate of evolution is the inseparable flip side of the coin for every selection pressure. I would not be surprised if throwing has played a role only in hominid evolution, and not primate evolution more generally – but for the period that scavenging and hunting have provided selection pressures, I have argued elsewhere (Calvin 1983a; 1983b) that throwing is a particularly fast track for brain reorganization and that it helps explain neoteny (Calvin 1986a; 1986b).

Unlike hunting, toolmaking (one rationale for spending so much time testing monkey manipulative abilities) simply does not have the hallmarks of an innovation that can rapidly drive biological evolution. And there are now ethological and archaeological reasons why one might doubt that toolmaking was what drove hominid brain reorganization, including handedness.

First, chimpanzee nut-cracking skills are surprisingly human-like (see Boesch & Boesch 1981), and termite-fishing further involves a certain delicacy in toolmaking (Goodall 1970; 1986). Although human applications are obviously more extensive, it remains to be seen whether innate abilities are of an order of magnitude more complex, as they have long been assumed to be.

Second, the archaeological record now shows that flaked-rock toolmaking goes back 2.4–2.0 million years (which is also about when the ice ages and the threefold brain enlargement both started), and that a standard toolkit had become established by 1.5 million years ago (indeed, two distinctly different toolkits, the Acheulian and the Developed Oldowan). What is so interesting is that the toolkit stays almost static for a very long time, the next major developments (the early forms of the elaborate blade techniques, also hafting for attachment to shafts) not appearing in the record until more recently than 0.3 million years ago (Isaac 1972; 1976). This lack of marked improvement is most relevant to the folk notion that toolmaking drove the increase in brain size, for *Homo erectus* brain size doubled

during this Middle Pleistocene period without much invention of new tools.

If brain size could change so markedly during a stasis of tool invention, it calls into question such brain reorganization proposals as tool-driven lateralizations as well, suggesting that we should consider other possibilities. An obvious starting place is the reputation of the left hemisphere for time-sequencing aspects (Bradshaw & Nettleton 1981; Efron 1963; Mateer & Kimura 1977; Tallal & Schwartz 1980) – not just for bilateral motor sequencing of hand and face, but for detecting sensory sequences as well. Sequencing suggests specialized buffering, such as when a ballistic movement must be planned in advance and then rapidly executed without benefit of further sensory feedback (e.g., when a sequence of sounds must be held and analyzed while determining phoneme and word order).

My favorite candidate for a hominid evolutionary drive – because of its direct exposure to natural selection in a place where evolution could be rapid and insured against backsliding (most natural selection has no lasting effect) – happens to be throwing success, through its exquisite timing of projectile release (Calvin 1983a; 1983b; 1986b). But even a priori, timing tasks should be especially prone to lateralization because of the slow conduction through the corpus callosum, which would make coordination of two centers impossible for brief time frames (just as it can take a letter as long to travel across town as across the country, it can take a message about as long to travel to the neighboring hemisphere as it does to travel to the far reaches of the spinal cord).

It is interesting that the most strongly right-handed skills in humans are throwing, clubbing, and hammering (Annett 1970a). It is accordingly curious that such ballistic skills (e.g., the bush baby's fly-snatching), characterized by “get set” planning but limited feedback opportunities during rapid execution of the plan, are so seldom measured in the primate literature. Slow feedback-guided reaching and manipulative movements, which are much less strongly right-handed, have been the experimenters' favorites. We need not substitute a hunting mythology for the toolmaking mythology; it would suffice to use the conspicuous features of human-handedness and hemispheric-specialization literature as guides for experimental and field studies of primate handedness.

## On viewing the evidence for primate handedness: Some biostatistical considerations

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MacNeilage et al. present data to suggest that nonhuman primates may show evidence of handedness. Although they are careful to mention that their findings are not definitive, I would agree that their work does have important heuristic value in being consistent with the theory of evolution by natural selection.

One curious proclivity of the authors is to present data in support of either right-, left-, or no hand preferences among various nonhuman primates, but then to compare the numbers only with either left- or right-hand preferences. Although this may be a perfectly reasonable comparison, one wonders why other possibilities are not discussed. These include (among others) the following, which are presented in order of specificity:

1. An overall test of hand preference. Here one would compare the numbers of primates showing each type of handedness preference (right, left, or none).
2. A test of general hand preference (whether right or left). Here one would compare the number of primates manifesting

either right or left preferences with the number of primates showing no hand preferences.

3. A relative test of right-hand preference. Here the number of primates with right-hand preference would be compared to the number with no hand preference.

4. A relative test of left-hand preference. Here the number of primates with left-hand preference would be compared to the number with no preference.

5. The authors' specific test comparing the number of primates with right-hand preference to the number manifesting left-hand preference.

Assuming that the answers to these five questions may be necessary for developing a more comprehensive analysis of available data, several steps and assumptions need to be undertaken in order to accomplish such an objective. I will proceed as if such an objective were viable.

#### Caveats:

1. For an accurate chi-square test, the expected frequencies for each cell should be 5 or greater (e.g., Leach 1979; Senders 1958).

2. For an approximate chi-square test, the expected frequencies can be as low as 2 (e.g., Senders 1958).

3. In the 2-cell case (e.g., comparing frequency of right- vs. left-handedness), a correction will give more accurate results (e.g., Mosteller & Rourke 1973). The correction consists of subtracting .5 from each observed (O) minus expected (E) difference (O - E) in the calculation of chi square. However, the correction should not be used when its application increases the value of chi square (e.g., Senders 1958, p. 422). It should be mentioned that the authors have not used the correction in their analysis.

#### Procedure:

1. Perform an overall omnibus chi-square test comparing the frequency of primates that demonstrate right-hand preference, left-hand preference, or no hand preference.

2. If the resulting chi-square value is 5.99 or higher ( $p = .05$  for  $df = 2$ ), then do the following specific comparisons:

a. Test for overall hand preference: Compare the summed frequency of animals showing left- or right-hand preference and compare this sum to the number of animals showing no hand preference.

b. Test for left-hand preference: Compare the number of primates with left-hand preference to the number with no hand preference.

c. Test for right-hand preference: Compare the number of primates with right-hand preference to the number with no hand preference.

d. Test the difference in numbers of primates showing left- and right-hand preference.

Since four specific comparisons are being made, set the nominal level of required statistical significance at  $.05/4 \approx .01$ , rather than at .05 (in order to control for Type I error; e.g., see Leach 1979, p. 235).

**Example (or application).** The data in the authors' Table 2 are based on the numbers of monkeys with and without hand preferences in discrimination studies. For purposes of application, I shall focus on the results over studies A, C, and D (early testing). The raw data indicate the following numbers of monkeys with or without specific hand preferences: left preference, 42; right, 21; none, 64 ( $N = 127$ ).

#### Questions:

1. Is there evidence for overall hand preferences? Here chi square, with expected values of 42.33, 42.33, and 42.33 (and 2  $df$ ) produces a value of 21.84 ( $p < .0005$ ) indicating an answer of yes.

2. Is there evidence for general hand preference (i.e., left or right) relative to no hand preference? Here the observed values of 63 (left and right) and 64 (no preference) are virtually identical to the expected (E) values of 63.5. Thus, there is no evidence for general handedness (i.e., left or right, relative to none).

3. Is there evidence for left-hand preference? Because more monkeys demonstrate no hand preference than left-hand preference, the answer to this question is no.

4. Is there evidence for right-hand preference? Similarly, because 64 animals show no hand preference, compared to only 21 showing right-hand preference, there is no evidence indicating right-hand preference.

5. Is there evidence for a greater number of primates with left-hand (as compared to right-hand) preference? In this case we compare 42 animals with left-hand preference to 21 with right-hand preference. Applying the correction, we obtain a value of 6.35 ( $p < .025$ ), indicating more left-hand preference than right-hand preference.

To summarize, because the overall chi-square test was statistically significant (chi square = 21.84,  $p < .0005$ ), this enabled us to perform the four specific tests. Because we also needed to control for Type I error, based upon making four specific tests rather than one, our level of significance became  $.05/4 \approx .01$ . (Note: To indicate a trend in the data, we can use level of significance  $.10/4 = .025$ .) Applying these criteria, there is a trend ( $p < .025$ ) for more left- than right-hand preferences. [Note: MacNeilage et al. report statistical significance for left-hand preference ( $p < .01$ ) but they use neither the correction factor nor the data analytic strategies just outlined.]

These results have focused on enumeration data, rendering chi square as an appropriate test. When the data appear in counts such as the number of right-hand-to-face contacts, the same general logic can be applied to the data analysis, except that different overall tests would now be appropriate [e.g., an analysis of variance (ANOVA) design or its nonparametric analogue]. Here, again, significant results would be followed by specific comparisons controlling for Type I error.

In summary, the purpose of this commentary is *not* to suggest that MacNeilage et al.'s approach is incorrect but rather that their data analytic strategy should be better rationalized. They might be better able to defend their strategy and thus be on a more solid biostatistical foundation (produce more accurate results) if they chose to apply the correction factor to their chi-square analyses. It should also be noted that values of chi square are heavily influenced by sample size. Thus, the same proportion of right-hand over left-hand preference (e.g., 62%) will not be statistically significant when based on 50 cases ( $p > .10$ ), but will be statistically significant when based on 100 cases (here  $p < .025$ ). Given the wide range of sample sizes presented in the reported literature, this fact also needs to be stressed.

Along similar lines of reasoning, at what point does one consider the proportion of primates with left- or right-hand preferences to be of substantive or clinical significance (especially given that the proportion of right-hand preference among humans is estimated by the authors to be about .90)?

## Straw monkeys

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It seems to me that MacNeilage et al. have erected something of a straw monkey. Although there may be a weak population-level asymmetry of hand preference in some primates, this evidently bears only a slight resemblance to the phenomenon in humans. For one thing, most of the evidence seems to support a bias in favor of the *left* hand. Although MacNeilage et al. ingeniously incorporate this into a highly speculative theory of the evolution of human handedness, the fact that this bias is in the direction opposite to that in humans scarcely inspires confidence.

The evidence, moreover, is weak. In making statistical comparisons between the proportions of left- and right-handers, the authors ignore the large proportion of animals displaying no

overall preference. The data in the target article's Table 1, for instance, reveal only 37.9% of monkeys with a left-hand preference compared to 27.5% with a right-hand preference, and 34.6% with no preference. This is, of course, a far cry from the 85–90% preference for the right hand in humans. In any event, the majority of studies, summarized in MacNeilage et al.'s Table 4, fail to find consistent population-level asymmetries at all, which makes one wonder whether those that do find them may have been in some way influenced by biases in the immediate experimental environment.

The case for consistent handedness depends, moreover, upon a post hoc distinction between reaching (left-hand bias), stabilizing (no consistent bias), and manipulating (right-hand bias). The right-hand bias for manipulation, which provides the closest analogy to human right-handedness, appears in only one study (Beck & Barton 1972), but is apparently not manifest in five other studies summarized in Table 4. The left-hand bias in reaching is evident in one series (Table 2) in early, but not in later, testing – another post hoc classification necessary to sustain the argument. By juggling the evidence in this post hoc fashion, MacNeilage et al. run the risk that their conclusions represent superstition rather than fact.

The evolutionary argument presented by the authors is interesting, however, and may have testable implications. I wonder also whether the left-hand bias in reaching bears any relation to the left-hand preference that has been reported in the early reaching behavior of human infants (e.g., Gesell & Ames 1947; Seth 1973). Could this be a case of ontogeny recapitulating phylogeny?

There is little insight in the evidence marshalled here, however, into the overwhelming right-handedness of humans, and the sense of discontinuity between humans and other primates remains. There has been much argument as to whether human handedness is in some way genetically coded (for a summary, see Corballis 1983). Of course, not all humans are right-handed. Surveys suggest that the percentage of left-handers may asymptote at about 12–13% of the population when cultural pressures to right-handedness are minimized (Brackenridge 1981; Coren & Porac 1981; Levy 1974); that is, the proportion of left-handers, or nonright-handers, seems to be about one-eighth.

This proportion can be related in simple fashion to the theory proposed by Annett (1972; 1974; 1978). According to this theory, the majority of individuals inherit a *right-shift* factor and are predominantly right-handed, although the minority lack this factor and are equally divided into left- and right-handers. The presence or absence of the right-shift is determined in Mendelian fashion by a single gene locus, in which the right-shift is dominant. Now if the two alleles – coding presence and absence of the right-shift factor – are equally represented in the population, and if mating is random with respect to handedness, then one-quarter of the population should be homozygous for the lack of the right-shift factor. Assuming no environmental bias, this quarter will be divided in turn into one-eighth who are predominantly right-handed and one-eighth who are predominantly left-handed.

This simple account ignores the possibility that some left-handers may be genotypically right-handed but phenotypically left-handed as a result of some early cerebral insult, although the evidence is mounting against the idea that left-handedness in the normal population has pathological origins (Annett & Ockwell 1980; Hicks, Evans & Pellegrini 1978; Hubbard 1971; McManus 1981; Schwartz 1977). Elsewhere I have tried to extend Annett's model to incorporate cerebral lateralization for the representation of language (Corballis 1983; see also Annett 1978), and the proportion of people with right cerebral dominance for language appears to be considerably less than one-eighth. Nevertheless, the one-eighth rule has an engaging simplicity to one whose superstitions tend toward the numerical.

For a nonhuman match to the *proportion* of right-handers in the human population, we are better aped by parrots than we are parroted by the apes. Rogers (1980) summarizes evidence for consistent *footedness* in several species of parrot, including seven that are predominantly left-footed and one that is predominantly right-footed. In Rogers's sample of 342 parrots, 45 showed a footedness opposite to that of the majority of their species. This is 13.2%, very close to the magical proportion of one-eighth. It would be interesting to know whether the inheritance of footedness in parrots is consistent with Annett's model.

## Patterns of hand preference in monkeys

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MacNeilage et al. have clearly raised an interesting new question – whether monkeys demonstrate different cerebral dominance for different motor acts. Besides satisfying our hope for a smooth phylogenetic progression toward the human cerebral dominance status, the possibility of two opposite types of hand preference with corresponding opposite cerebral dominances has not been evaluated in the past, and most experiments, including our own (Deuel & Dunlop 1980), have not found motor dominance. The new question deserves experimental evaluation, and MacNeilage et al. have provided hypotheses that are amenable to testing. The hypotheses include: (1) Monkeys show a left-hand (right-hemisphere) specialization for visually guided movements; (2) they show a right-hand (left-hemisphere) specialization for postural support and stabilization; (3) when postural support and stabilization are not required, they use the right hand for manipulation; and (4) they thus show *both* left and right preference, depending on the task.

Using data on such motor performance collected recently from 41 wild-reared, naive adolescent fascicularis monkeys, we tested the hypotheses. All tasks (described in detail in Deuel & Dunlop 1980) were presented in the primate chair so that no postural support demands were placed on the upper extremities. The hypotheses predicted that monkeys would show a left-hand (L) preference for visually guided reaching toward a stationary object, for manual tracking and retrieval of constantly moving bait, for catching a dangling string in a bimanual pulling task, and for bait retrieval during bilateral simultaneous visual presentation of bait. The hypotheses predicted that the same animals would show a right-hand (R) preference in a repetitive thumb and forefinger manipulatory item, and for bait stabilization against the pull of a spring. The number of trials presented ranged from 10 to 24, depending on the task, and L or R preference was declared if 70% of the trials or more were performed with one hand. Otherwise, ambilaterality (A) was declared. In analyzing the group data, we used a one-sample  $\chi^2$  test (Siegel 1956) because slightly different numbers of animals participated in each item. The U-shaped distribution of preference generally found among monkeys would lead to about one-third being placed in each of the L, R, and A categories. As shown in Table 1, this was the expected distribution for the  $\chi^2$  test we performed.

For both of the items predicted to elicit an R preference, no deviation from an even L, R, and A distribution was found. Among the four left items,  $\chi^2$  was significant for simple reaching. This is clearly related to the high incidence of ambilaterality rather than to an increased L preference. Visually guided tracking demonstrated a minimally significant  $\chi^2$ , in this case due to a left-handed preference for retrieval of bait. This item thus provides evidence in support of Hypothesis 1. However, Hypotheses 2 and 4 were not upheld, as no opposite preference was found in the group, so this statistic becomes equally con-

Table 1 (Deuel and Schaffer). *Predicted and observed hand preferences in 41 experimentally naive adolescent fascicularis monkeys*

Task item (no. of subjects)	Predicted preference	Frequency of preference (% of n)			df, $\chi^2$	Range of probability that $\chi^2$ differs from chance
		L	R	A		
Simple reaching for stationary bait (37)	L	5 (14)	10 (27)	22 (59)	2, 12.7	.01 > p > .001
Visually guided tracking and retrieval of moving bait (27)	L	15 (56)	8 (27)	4 (17)	2, 6.9	.05 > p > .02
Catch dangling string to reel in to obtain bait at end (35)	L	12 (34)	11 (32)	12 (34)	2, .08	.98 > p > .95
Retrieve stationary bait during bilateral simultaneous visual presentation (39)	L	16 (41)	11 (28)	12 (31)	2, 1.08	.70 > p > .50
Approximate thumb and forefinger (manipulate) to retrieve bait from foodwell (28)	R	14 (52)	7 (24)	7 (24)	2, 3.6	.20 > p > .10
Stabilize bait within reaching distance so other hand may retrieve (35)	R	9 (26)	11 (31)	15 (43)	2, 1.6	.50 > p > .30

Note: Preference for left (L) or right (R) hand was declared if 70% or more of the trials were carried out with that hand. Otherwise the monkey was declared ambilateral (A). One-sample  $\chi^2$  tests were applied to determine whether the distribution of L, R, and A preferences differed significantly from 33 1/3% each.

sistent with a hypothesis of simple left-handed preference for this task. Further, when performance of the nonpreferred hand (speed in the manipulation item and force exerted in the dangling string item) was compared with performance of the preferred hand for animals that had demonstrated preferences in these items (data not shown), there was no difference in the performance level of the two hands, although in human children (Rudel et al. 1984), adolescents (Deuel & Moran 1980), and adults (Annett 1970b), performance routinely differs between preferred and nonpreferred hands.

These group statistics could mask individuals that consistently and significantly demonstrated L preference for visually guided movement together with R preference for postural support and stabilization and manipulation. To ascertain whether there were such individuals in our group, we first selected the 22 animals that had performed all four items that hypothetically elicited an L preference, as well as both items that should elicit an R preference. Of the 22, only 1 demonstrated the predicted pattern of hand preference; 15 demonstrated at least 1 right preference for a left item, whereas 2 demonstrated right preference for all left items, and another demonstrated right preference for left items and left preference for right items. We next looked among all 41 subjects and found that 7 of them demonstrated an L preference across all items attempted, 3 demonstrated an R preference across all items, and 2 demonstrated ambilaterality. Thus, our current data suggest a complex pattern of changing preferences for most individual animals.

In reinterpreting our previously reported data from rhesus monkeys (Deuel & Dunlop 1980), MacNeilage et al. cite us (Sect. 2.1.4) as finding a significant R preference for reaching among monkeys tested in a Wisconsin General Testing Apparatus.

This group of 15 animals was originally tested in a primate chair and tended toward an L preference. When subsequently tested in the Wisconsin General Testing Apparatus, the group tended toward the *opposite*, R, reaching preference as cited above. Therefore we did and still do interpret these data to mean that the observed hand preferences were a function of the situation in which the testing was carried out, rather than a function of innate cerebral dominance.

All of these considerations seem to converge to suggest that adolescent fascicularis monkeys, and the rhesus monkeys we tested previously, possess malleable, situation-dependent hand preferences. Rather than serving as evidence for the inborn, cerebrally dependent lifelong handedness seen in human beings (Bishop 1980; Joynt 1985; Michel & Harkins 1985b), all of our data suggest that if the origins of cerebral dominance are to be found in the monkey, they will not be found in hand preferences, and probably not in the motor system (Michel & Harkins 1986).

### Primate handedness: How nice if it were really so

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MacNeilage et al. are to be congratulated for their endeavors. The available reports on handedness in nonhuman primates did not add up to a meaningful data base. In the target article, the authors attempt to remedy this state of affairs by supposing that monkeys prefer to use their left and right hands for different



tasks. My comments focus on three issues raised in the target article.

**1. What might be a factor common to studies that have indicated left preferences?** MacNeillage et al. suggest that the left hand is preferred by several species of nonhuman primates when reaching. However, is reaching unitary, or might preference not vary depending on whether the animal is reaching to palpate, to retrieve, and/or to manipulate? (Reaching to show/point is probably largely a human activity.) More specifically, might the trend toward left-hand preference observed in the Japanese field studies and in the "studies by Ettlinger's group" have arisen because the monkeys were initially reaching to palpate (and only secondarily to retrieve)? (This view would not accord with the report by Ettlinger, Blakemore, and Milner, 1968.) When humans harvest soft fruit (e.g., plums), the tactile impression of soft/hard may be as important as the visual appearance; do monkeys making "simple reaches" for food not also palpate? Might this be the reason for the claimed congruence between the Japanese field studies and those by Ettlinger's group, which frequently required tactile discrimination? Similarly, might not "manipulation" ultimately be subclassified into various specific kinds of manipulation? It seems that MacNeillage et al. have (implicitly) classified reaching-to-manipulate as manipulation.

**2. The relationship between preference and ability – a further study.** MacNeillage et al. seem to imply (despite their disclaimer about the "possible importance of differences between preference and ability") that preference is equivalent to superior performance. However, Hörster and Ettlinger (1985) have reported that 78 rhesus monkeys which preferred to use their left hand had learned a tactile discrimination task ("cylinder" and "sphere") more rapidly (210 trials) than 77 monkeys which preferred to use their right hand (250 trials). Since both those animals using the left hand and those using the right hand were using their preferred hand, ability must also be related, at the very least, to a factor other than use of the preferred/nonpreferred hand. (These observations fail to support the earlier evidence of a higher incidence of left preference than of right; but all the animals in Hörster and Ettlinger's study were assessed exclusively on the very *first* discrimination task undertaken after they arrived for training. Despite earlier evidence to the contrary, it remains possible that left preferences would increase rather than decrease across tasks.)

What is missing from Hörster and Ettlinger's (1985) study, however, is information about ability with the hand *not* used. Would the monkeys which preferred to use their left hand have learned equally quickly with their right hand (as remains possible), or more slowly (as Hörster and Ettlinger imply)? If they learned equally quickly (and no direct evidence seems to be available), one might presume that left-handed monkeys are simply cleverer (in both hemispheres) at learning to make a tactile discrimination. If they learned more slowly, one might presume that the left hemisphere of left-handed monkeys is less proficient than the right at this task. Did the monkeys that chose to use the right hand use their left hemisphere? Was it the less proficient hemisphere? And why should that hemisphere then be used? Or, could the right hemisphere of the right-handed monkeys prove to be even less proficient than the left hemisphere, which has been shown, on the basis of the poor learning scores with the right hand, to be less efficient than the right hemisphere of left-handed monkeys? That is, would their performance with the left hand be inferior to their already inferior right-hand performance?

**3. The relationship between preference, ability, and hemispheric specialization.** The issues become yet more complex when hemispheric specialization is considered in the light of ablation data. The findings of Garcha, Ettlinger and MacCabe (1982) have, in general, been replicated (Hörster & Ettlinger, unpublished), although not for as many tactile tasks as in the original study (perhaps because fewer monkeys with strong

lateral preferences were available). However, in the case of the discrimination between "cylinder" and "sphere," the outcome of the replication was clear: As before, there was impairment in both hands after ablation of area SII contralateral to the hand the monkey preferred to use and less impairment or none after ablation of SII ipsilateral to the preferred hand. This suggests that the SII cortex opposite the preferred hand – whether the left or the right – is critical for performance of the tactile discrimination task described in Hörster and Ettlinger (1985), whereas the SII cortex ipsilateral to the preferred hand is not. Hence, taking the ablation studies together with the findings of Hörster and Ettlinger (1985), one would expect that in a population of monkeys the right area SII would tend to be more specialized than the left for this tactile discrimination task. However, when the insula (the next way-station beyond SII in the neural pathway originating in SI) was ablated on the side either contralateral or ipsilateral to the preferred hand, a slightly different outcome was obtained: The impairment after contralateral ablations was greater than it was after ipsilateral removals also on certain visual/auditory tasks (Hörster & Ettlinger, unpublished). This indicates that "hemispheric specialization" may prove to be too global a concept. Specific structures within a hemisphere may indeed be specialized, but others – belonging to the same neural system – may be less so. (To the extent that the positive findings of Garcha et al., 1982, applied to several different tactile tasks, it may be legitimate at this stage to speak of "hemispheric" rather than of "act-specific specialization.")

In this connection, some unpublished observations by Hörster, Rivers, Schattank, and Ettlinger may be of interest. As a control group for animals with cortical ablations, five unoperated rhesus monkeys, previously trained as in the study by Garcha et al. (1982), were injected with <sup>14</sup>C-2-Deoxyglucose and then assessed for their continued performance on a graded roughness discrimination task (described as "stage 8" in Garcha et al., whereas in the present investigation the animals were adapted to this task for weeks/months prior to injection). Of these five control monkeys, two ("Einstein" and "Zsa-Zsa") showed a spontaneous preference for the use of the left hand, although both animals had at earlier stages of their training also made some use of the right hand. Immediately before injection, Einstein invariably used the left hand; hence, the right did not have to be restricted after injection. Zsa-Zsa occasionally used the right hand, so using that hand was mechanically prevented after injection.

In these two monkeys, the effect of the injection was different from what it was in the other three (and also different from the effect in seven monkeys that had been trained before injection on a task of cross-modal recognition). In the brains of Einstein and Zsa-Zsa, all structures were more strongly labeled in *one* particular hemisphere (whenever they were not equally labeled on the two sides). In the other nine monkeys, however, labeling of some structures was stronger in the left hemisphere, whereas labeling of other structures was stronger in the right (or the labeling was equal). In the case of Einstein, the one-sided labeling was uniformly stronger in the (contralateral) right hemisphere, as might be expected. With Zsa-Zsa, however, labeling (whenever unequal) was always unexpectedly stronger in the (*ipsilateral*) left hemisphere (see Figures 1–3). These inequalities involved: sulcus (s.) principalis; the two orbital sulci; the dorsolateral cortex inferior to s. principalis; s. inferior and superior arcuatus; the frontal operculum with the upper part of the insula; areas A1 and SII; the anterior s. superior temporalis; areas TE, OB, and OA; and possibly other structures (e.g., amygdala, anterior caudate and putamen, etc.). The findings for Einstein and Zsa-Zsa illustrate how uncertain the relationship between hand use and hemispheric functioning (at least as assessed by 2 DG) can be.

Whatever the ultimate solution to these problems, MacNeillage et al. have made a worthwhile contribution: first in their



## The riddle of Carlyle: The unsolved problem of the origin of handedness

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Why (the right hand) was chosen is a question not to be settled, not worth asking except as a kind of a riddle.

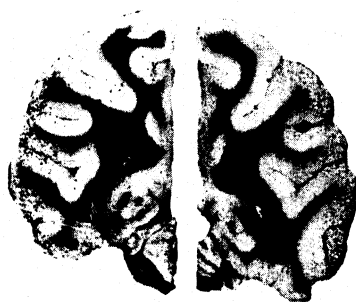
Thomas Carlyle



(1)



(2)



(3)

Figures 1-3 (Ettlinger). All figures are contact prints of the original radiographs of monkey Zsa-Zsa. The left hemisphere (indicated by a small circular hole) is always on the left. The hemispheres were separated before cutting (as the available cryostat could not cut full-width sections), but were realigned before production of the radiographs. (In aligning the two hemispheres, an error of ca. 50  $\mu$ m was made, so that at any level the left hemisphere is paired with a right-hemisphere section that was located ca. 50  $\mu$ m posterior to it.)

In Figure 1 (section 1330/1372), stronger labeling can be seen on the left in: SMA, sulcus (s.) superior arcuate, s. principalis, s. inferior arcuate, frontal operculum, and s. superior temporalis; in Figure 2 (868/896), in: SMA, A1, s. superior temporalis, TE, and possibly also in the thalamus; in Figure 3 (588/616), in: SMA, PE, s. intraparietalis, s. lateralis, s. superior temporalis, and possibly on the medial occipital surface.

novel attempt to systematize hand usage; second, in drawing attention to the methodological inadequacies of many of the relevant studies; and third, in the impetus their article will give to further research in this important area.

### ACKNOWLEDGMENT

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MacNeilage et al. have bravely attacked one of the fundamental problems of evolutionary morphophysiology: the origin and phylogeny of the functional asymmetry of the upper extremities in humans. To solve this problem one must examine the vast amount of data on physiological and morphological lateralization in subprimates and primates to sort out the causes and manifestations of the asymmetry and to answer the main riddle of Carlyle: Why were the right hand and left hemisphere chosen by the evolutionary process as dominant in humans?

MacNeilage et al. suggest an original and elegant hypothesis that can be formulated in the form of three principal postulates: (1) Human functional asymmetry of the upper extremities (handedness) has evolutionary precursors that can be detected in asymmetries of extant subhuman primates. (2) The left-handedness of extant lower primates and consequently the specialization of the right hemisphere evolved as an adaptation to performing visually guided movements (reaching and grasping). (3) Right-handedness in humans and dominance of the left hemisphere have a direct precursor in right-hand preference by subhuman primates for manipulating objects. This kind of human asymmetry is a direct consequence of movements of the right upper extremity in early anthropoids while acquiring the erect posture.

This hypothesis appears quite viable; but, like any evolutionary hypothesis based on extrapolating to extinct predecessors the data obtained in extant animals, it has its strong and weak points.

It seems appropriate to comment on both the strengths and weaknesses of MacNeilage et al.'s proposal. We can clearly accept their first postulate concerning the existence of certain phylogenetic precursors of mirror asymmetry in the handedness of *Homo sapiens*. Mirror asymmetry in morphofunctional organization is a universal biological phenomenon known as mirror isomery; this phenomenon has been described in a wide variety of organisms, starting with prokaryotes and unicellular organisms and extending up to the highest multicellular forms, including humans. It has been shown that colonies of some well-known bacteria have preferred directions of rotation (*Proteus*, *Clostridium*, and *Bacillus*; Hoeniger 1966). Blue-green algae have left/right preferences in movements on agar surface (Schmid 1918; 1919). Among unicellular eukaryotes such as *Amoeba* and *Infusoria*, the trajectory of their propelling movements is asymmetric and left/right preference varies with species (Bullington 1925; 1930; Grebecki & Micolajczyk 1968; Schaeffer 1931). Among multicellular invertebrates, left/right morphofunctional asymmetry has been found in crustaceans (Davis 1968), nematodes (Croll 1969), and insects (Wilson 1968).

It is hence evident that left/right mirror asymmetry of morphofunctional organization is of rather ancient phylogenetic origin. One accordingly wonders why this kind of asymmetry persisted through the history of the biological world, starting with the most primitive organisms and extending to the most complicated ones, including humans. Some authors have even tried, unsuccessfully, to correlate macro-asymmetry in organization and function with molecular asymmetry (left or right spiraling of protein or nucleic acid molecules, etc.; Kasinov 1973).

A more fruitful approach has been found in the concepts of selective adaptation. The conclusion is obvious and seems trivial: If asymmetry persisted and became so widespread in the biological world it must have been highly adaptive—essential for the very existence of organisms. Selective pressure hence acts in favor of asymmetry independent of the level of biological organization. The main problem, however, is still unsolved: What makes asymmetry so important for adaptation?

We can suggest a highly speculative, but reasonable and testable, hypothesis. It seems from the laws of biomechanics that no propelling or aim-directed movement in bilateral organisms is possible under conditions of absolute asymmetry. One side always has to take the lead. It may be for this reason that mirror isomery (asymmetry) is so persistent and crosses all biological classes and orders. This “lead-side hypothesis” does not explain why or how this or that side of the bilateral organism assumes its dominant status. It seems that in each particular class the biological system has its own original solution, because there is no evident advantage for right or left dominance in particular.

MacNeilage et al. state that in the case of the highest organisms, especially primates, neural mechanisms no doubt became involved in the evolution of lateralization as the authors state. However, a retrospective review of the quantitative data on comparative brain morphology shows that there is no simple and direct correlation between the progressive evolution of the neocortex and the degree of left/right asymmetry of the hemispheres or of local regions such as the inferior parietal lobe or planum temporale.

I have analyzed and computed some data on the asymmetry of the whole hemispheres and the inferior parietal lobe in a comparative series of primates (Blinkov & Glezer 1968). The parietal region is one of the most likely “candidates” to reflect the left-hemisphere dominance in humans morphologically because of its intimate relation to acquired skills. Our data are based on measurements of serial sections through the whole brain and reflect dimensions not only of macroscopic structure but also of precise cytoarchitectonic regions (Figure 1). An index of asymmetry (A) was computed using the formula:  $(R - L)/(R + L) \times 100$ . R is the area of the surface of the right hemisphere or right cytoarchitectonic region; L is that of the left. A positive index indicates morphological dominance of the right hemisphere, a negative one left dominance. Figure 1 shows that in both cases (i.e., complete hemispheric asymmetry and asymme-

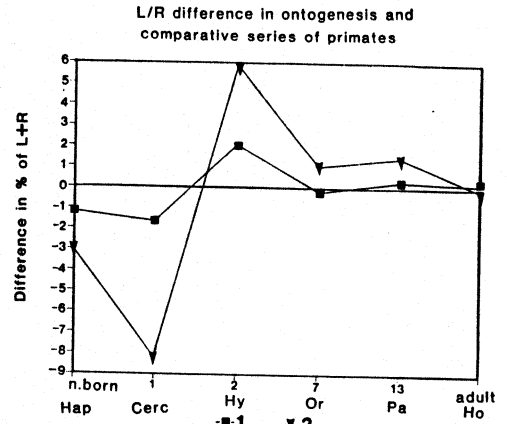


Figure 2 (Glezer). Graph showing right/left difference in the size of the entire hemisphere in human postnatal ontogenesis and in a comparative series of primates. X-axis: Age in years and primate species. Labels of the species are the same as in Figure 1. Note the decrease of morphological asymmetry with age and with ascent in the primate series.

try of the inferior parietal region) degree of the asymmetry decreases in an ascending primate series. It is of interest that in the lower part of the series the index is negative, in the middle part it becomes positive, and then it decreases almost to zero in apes, and especially in humans. We computed the same index for postnatal growth of the left and right hemispheres in humans (Figure 2) and here the same tendency was found, namely, morphological asymmetry decreases with age.

Thus, these indices computed from the data of different authors (Blinkov 1955; Filimonov 1949; Glezer 1958; Kononova 1962) show that in primate evolution morphological and functional asymmetry are not directly correlated phenomena. Perhaps this is why the morphological evidence for the neural basis of the asymmetry is so vague and variable, which can be seen from Table 9 of the target article. Our index also shows that in primate evolution and ontogenesis the actual quantitative morphological asymmetry diminishes, reaching zero in humans, where we might expect the greatest asymmetry. This decrease may be a reflection of the development of qualitative morphological and functional asymmetry.

We conjecture that in the evolution of the brain there are two opposite tendencies: The first promotes hemispheric asymmetry and specialization. At early stages of primate evolution this tendency would be strong enough to be measurable morphologically (in lower primates). At later stages of evolution there emerges a second tendency: A decrease in morphological asymmetry and an increase in functional asymmetry as a result of intensive development of interhemispheric communication. If we consult the old but often verified calloso-bulbar index of Anthony (1951), we can easily demonstrate that a decrease in morphological asymmetry in an ascending primate comparative series parallels the growth of the corpus callosum, the largest interhemispheric neocortical commissure. Other factors may also play a role in this tendency to decrease the morphological asymmetry, such as an increase of ipsilateral connections in evolution that can be demonstrated at almost all levels of the brain. Thus, in both the motor (pyramidal tract) and sensory system (optic nerve, trigeminal nerve) the number of ipsilateral (noncrossed) connections increases in an ascending comparative series of mammals (Blinkov & Glezer 1968). This tendency to equalize the left/right masses of the brain in evolution does not mean that qualitative asymmetry in the differentiation of the hemispheres did not occur. We can conclude that the question of the morphological basis of functional hand/speech asymmetry

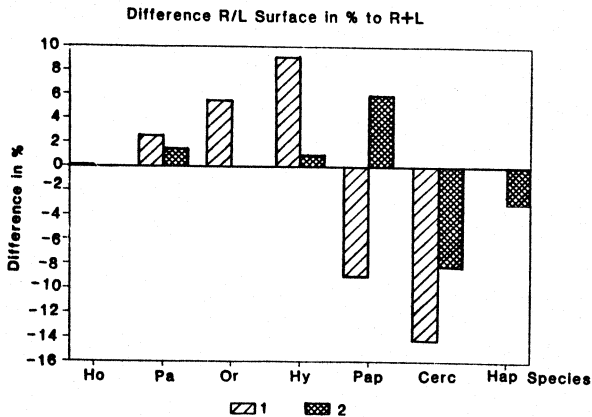


Figure 1 (Glezer). Graph showing right/left differences in the size of the hemisphere as a whole and of the inferior parietal region in a comparative series of primates. X-axis: Primate species as follows: Ho-Homo sapiens, Pa-Pan troglodytes, Or-Simia satyrus, Hy-Hylobates, sp., Pap-Papio hamadryas, Cerc-Cercopithecus sp., Hap-Hapale jacchus. Y-axis: Difference in % between surfaces in right and left hemispheres. 1-inferior parietal region; 2-entire hemisphere.

in humans and its phylogenesis is not as simple as one might expect.

Finally I would like to focus on the empirical existence of left-handed preference for reaching and right-handed manipulation in experimental animals. From MacNeilage et al.'s Table 2 it follows that 64 out of 127 monkeys in early testing and 44 out of 111 in late testing had no left/right preference at all. The number that had left preference in late testing is equal to the number with right preference. In one of the most crucial tables, Table 3 (based on Beck and Barton's data), only 35% of all animals used the left hand while performing simple reaching. At the same time, while performing combinations of reach and manipulation 99% used their left hand and only 56% used their right for manipulation.

It seems to me that these data say more about functional equivalences than about functional preferences in handedness. I would also like to mention that my own unpublished data on conditioning in baboons (*Papio papio* and *Papio hamadryas*) showed no specific hand preference in manipulation or simple reaching.

In my experiments, the animals had to differentiate two movements: Pulling a lever (1) with a finger and then (2) with the entire hand. The first of the movements includes reaching and manipulation. After quite a long period all animals performed the movements with minimal mistakes, although the time required to perform this kind of motor differentiation was very long (about two months). We especially looked for left/right preference and failed to find any.

I do feel that the authors of this very interesting target article have presented an extremely fascinating hypothesis about the evolution of handedness in humans. It is unfortunate that morphological and physiological data cannot be so easily accommodated as to confirm this hypothesis.

## Two hemispheres: One reaching hand

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Continuity in the form and function of different organs is one of the major criteria for organizing several species within a single order. For this reason, the demonstration by MacNeilage et al. that there are consistent and similar asymmetries in the hand preferences of several nonhuman primate species is particularly important. The results of their extensive reanalysis of the older data appear to have undercut almost completely the widely held belief that human beings are the only primate species showing population-level asymmetries in hand preference. Indeed, the preferences they have uncovered (reaching with the left hand, manipulating objects with the right) suggest an underlying asymmetry in brain organization that is not dissimilar to the human pattern.

The irony is, of course, that whereas the pattern of hemispheric organization reflected by the hand preference data may be similar to that of human beings, the hand preferences themselves differ in one enormous respect from those normally observed in human populations. Monkeys may reach for objects with the left hand and open containers with the right, but humans typically perform both tasks with the right hand. In acknowledging this apparent break in phylogenetic continuity, MacNeilage et al. suggest that humans have become so adept at manipulating their environment and so skilled in bimanual coordination that the right hand now predominates over the left even in visually guided reaching. Although this may be so, it is important to know whether and how the two hemispheres interact in controlling the right hand in human beings, and

whether there are any situations in which the left hand might be preferred.

In addressing these questions, MacNeilage et al. make much of the work of Guiard, Diaz, and Beaubaton (1983) in which a group of eight right-handers apparently produced smaller constant errors when using their left rather than their right hand to point to one of two small visual targets. Both Guiard et al. and MacNeilage et al. have assumed that the aimed pointing movement was ballistic because the subjects could not see their hand as it moved toward the target. This assumption is probably false, because information derived from proprioception and/or efference copy can be used to correct the trajectory of an unseen hand (Goodale, Pelisson & Prablanc 1986). In any case, the variable error in the Guiard et al. (1983) study appeared to be smaller when the right hand, not the left, was used to point to the target, even though movements with the right hand tended to be faster than those made with the left. Perhaps the greater speed of the right-handed reaches resulted in a systematic error in pointing and thus in a larger constant error. Whatever the results of this study might mean, it is clear that in most situations right-handed humans prefer to reach with their right hand when given an opportunity to use either. Indeed, even when right-handers are asked to use their left hand to point to small visual targets in situations where they can see their hand (just as the monkeys could in the studies reviewed by MacNeilage et al.), they have been found to make larger absolute errors with that hand than with their preferred hand (Fisk & Goodale 1985; Fisk, Goodale, Routhier & Davidson 1986).

What has happened then to the control of visually guided reaching in humans to make it so different from that seen in monkeys? It could be that as our hominid ancestors began to exploit ecological niches more similar to those of present-day hunter-gatherer societies, the increasing demands for accuracy and speed of limb movement, coupled with the need to coordinate that movement with the activity of other parts of the body, placed more and more emphasis on temporal as well as spatial precision in motor programming of visually guided reaching and throwing. If this was the case, then it is easier to understand why the hand contralateral to the left hemisphere has come to be preferred in situations where such constraints are operating. As MacNeilage et al. point out, there is a good deal of evidence to suggest that the left hemisphere plays a special role in the sequential organization of complex motor behaviour, such as articulation, nonverbal oral movements, and manual movements (Kimura 1982; Kimura and Archibald 1974). Indeed, speech may be only one example of a variety of "voluntary" motor behaviours in which the left hemisphere is particularly important for the timing and/or sequencing of the different movements involved. Rapid and accurate reaching movements presumably also require the participation of this left-hemisphere system in most phases of the movement control.

Support for this hypothesis is provided by some recent experiments in our laboratory in which we observed interesting temporal differences in reaches made with the right and left hands (Fisk & Goodale 1985). Not surprisingly, the latency of the limb movement was found to be quite a bit shorter for right-handed reaches than for left-handed ones. What was surprising was the fact that the latency of the saccadic eye movement preceding the limb movement was also shorter for right-handed reaches. This suggests (1) that mechanisms in the left hemisphere may be involved in the temporal organization of reaching movements and that the musculature controlling the right hand, by virtue of its more direct connections with this hemisphere, may be more efficiently programmed by these mechanisms than the left, and (2) that the temporal advantage conferred on right-handed reaches by programming in the left hemisphere might extend to the eye movements preceding the limb movement itself. Although the trajectories of the eye

movements are undoubtedly programmed elsewhere in the central nervous system, their onset may nevertheless be determined by a lateralized programming system in the left hemisphere. The synchrony between eye and limb movements ensures that at the end of the first saccade, the limb will be in approximately the same position with respect to the target in both left- and right-handed reaches. Any new information provided by foveal or parafoveal vision about the location of the target that might be used to modify the trajectory of the moving limb will, accordingly, be available at the same point in the trajectory of the left and right limb (Goodale, Pelisson & Prablanc 1986).

In summary then, the sequential organization of visually guided reaching (which involves movements of a number of different effector systems, including the hand, eyes, and head) may, like many other complex activities such as speech, depend in part on mechanisms lateralized to the left hemisphere. This is not to say, however, that visuospatial information derived from specialized mechanisms in the right hemisphere may not also be used in the programming of such movements. Very recently, we looked at visually guided reaching in a group of neurological patients with unilateral lesions (Goodale, Cohen, Fisk & Routhier 1985). In each case, we limited our analysis to the hand ipsilateral to the lesion to avoid the problem of interpreting hemiparesis. Although the kinematics of reaches made by patients with right-hemisphere lesions did not differ from those of the control subjects, reaching movements made by patients with left-hemisphere lesions showed a marked disruption in organization and were characterized by a lower peak velocity and a very prolonged deceleration phase. This pattern of deficits is again consistent with the suggestion that the left hemisphere plays a special role in the selection and/or timing of a complex movement, ensuring that all of the individual components are correctly orchestrated in an integrated sequence of behaviour. The patients with right-hemisphere damage also showed a clear deficit, however. They took much longer than control subjects to initiate a reach, even though once they got going, their reach appeared quite normal. Since the spatial location of the target varied from trial to trial, this observation is not too surprising. This hemisphere has been implicated in visuospatial processing in a large number of human studies, and the work of MacNeilage et al. suggests that this may be a relatively ancient arrangement in primate phylogeny.

Thus, the efficient visually guided reaching observed in humans would appear to depend on mechanisms in both hemispheres – one involved in timing and/or sequencing, the other in visuospatial processing. It is the demand for precision in timing, however, that appears to have shifted the hand preference from the left in monkeys to the right in humans, even though the underlying asymmetry in hemispheric organization suggested by the meta-analysis of MacNeilage et al. remains unchanged.

## Precursors to what? Theory is lacking for handedness in humans

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I cannot follow MacNeilage et al. in their hypothesized natural history of handedness. Their position, I believe, suffers from insufficient caution in the handling of published data, vagueness in the definition of handedness, and an atheoretical approach to the subject.

It is not that surprising that the body of data MacNeilage et al. gather together, which emanates from a wide range of specialists – ethologists, neuroscientists, and behavioural scientists – seems rather disorderly. Unfortunately, however, MacNeilage et al.'s review tends to reflect this and appears somewhat desultory, the reviewers being forced, in most instances, to recognize that a supposedly relevant study in fact provides no usable information.

MacNeilage et al. are not responsible for the heterogeneity of the literature on handedness, but the way they interpret the data seems questionable. First, I think they generally overlook the "file drawer problem" (Rosenthal 1979), particularly when considering that the published results suggest right-hand preference for manipulation in nonhuman primates: Suppose that just a few studies yielding opposite results have been filed away, and the suggestion disappears. Such a supposition may not be entirely gratuitous, because an investigator faced by chance with left-hand preference for manipulation in monkeys or apes will be apt to doubt the validity of a finding unlikely to represent a precursor to what is observed in man. Second, when they argue that investigators might have disclosed handedness in Old World monkeys had they used older subjects, or had they been more concerned with task difficulty and practice, I suspect that MacNeilage et al. are falling into the fallacy of interpreting null results.

The definition MacNeilage et al. give of the crucial handedness notion is seemingly cautious, but vague. The trouble is that it fails to distinguish between the *between-subject* and the *between-hand within-subject* senses of handedness, as is the case with the current notion. Accordingly, they use the word interchangeably, either in the former sense, as in the beginning of their Introduction, or in the latter sense, as in the phrase "left-handedness for reaching," which may apply to right-handed individuals. This confusion is unfortunate, as the authors provide no grounds for eliminating the possibility that, in primate evolution, manual specialization (leading to handedness in the within-subject sense) emerged before the direction of asymmetry became biased at a population level.

Apart from the specifics of the target article, I feel that MacNeilage et al.'s very *approach* to the problem is questionable in two closely related respects. First, they seem to adhere to the naive reductionist belief that one can dissipate the clouds that darken human handedness by merely describing its development (through either phylogenesis or ontogenesis). In fact, the target article confirms that there is less, rather than more, clarity in the handedness of nonhuman primates than of human ones. More generally, I wonder whether any valid research on the precursors of any human trait may be undertaken before a minimal number of theoretical assumptions delineating the trait in question are first formulated. Second, MacNeilage et al.'s approach seems to rely on the classical inductivist belief that scientific knowledge may spontaneously emerge from the mere recording of theoretically neutral facts. As emphasized by Popper (1935), there is no logically controllable pathway leading from the evidence to the concept: Scientific discovery consists of provisional agreement between empirical observations and predictions derived deductively from a priori hypotheses.

Thus, I regret that MacNeilage et al., before examining whether any precursors to human handedness exist in primates, have not overtly decided what handedness means in man, who presumably exhibits the phenomenon in a canonical form. MacNeilage et al. assume "hemispheric specialization for manual function" in man (sect. 7.5, para. 3), but, rather curiously, no manual specialization proper: they state simply that the preferred hand has the responsibility to cope with the most demanding manipulative acts. Unfortunately, this traditional view of within-subject handedness appears to be inadequate for an understanding of lateral preferences in skilled bimanual activities such as playing the violin or swinging a golf club (Oldfield

1969). In many instances, right-handers manifest prototypic lateral preferences, and yet the manipulative demands are extremely high in either component of the bimanual task.

In fact, MacNeilage et al. doubt that "the principles of manual control" differ between man and other primates (sect. 1, para. 2). I wish to suggest that, contrary to this opinion, there are at least three fundamental principles that conspicuously characterize human bimanual gestures (Guiard 1986b; 1986c). These principles are:

1. *Intermanual temporal and spatial metric contrast*: In bimanual tasks, the role spontaneously assigned to the right hand requires, not necessarily more skills, but, typically, motion obeying a *finer metric* (i.e., a finer temporal resolution but shorter movement times, a finer spatial resolution but smaller amplitudes).

2. *Left-hand precedence*: It is typically the left hand that starts a bimanual gesture, the right being recruited with a delay.

3. *Right-to-left spatial reference*: Motion of the right hand typically finds its vital spatial references in the results of motion of the left hand.

These three principles suggest that man has invented a truly original strategy in the use of his two hands, consisting of a hierarchical approach to manipulation problems, such that one hand systematically intervenes at a relatively *macrometric* level and the other at a relatively *micrometric* level. To condense this view into a minimal model, I have suggested that in humans the two hands cooperate with one another in the way a couple of serially assembled motors (representing a hierarchical system) do. More specifically, the roles man assigns to his left and right hands can be assimilated to those played, in a two-link kinematic chain, by the proximal and distal elements, respectively (Guiard 1986b; 1986c).

Forthcoming experiments will determine whether this metaphorical model is viable and heuristic, as tentatively suggested by the results of studies bearing on lateral preferences (Guiard, in preparation) and performance asymmetries (Guiard 1986a) in the manipulation of bimanual tools by right-handers. But what seems to me to be unquestionable is that one must be more committed theoretically than MacNeilage et al. are in order to study human and nonhuman handedness with some chance of success.

## Does a hand preference indicate a hemispheric specialization?

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Human primates derive pleasure from discovering precursors of their own characteristics in nonhuman primates. MacNeilage et al. provide the opportunity for discovering a precursor of hemispheric specialization. More correctly, they report act-specific hand preferences. Of the various issues raised in their target article, the relationship between hand preference and hemispheric specialization is the one I wish to comment on. Is it indeed true that the two types of hand preferences, given they exist, constitute indirect evidence for two types of functional hemispheric specialization?

The concept of functional hemispheric specialization refers to superior (or exclusive) capabilities of one hemisphere in certain functions called for by certain tasks. The concept relates to performance characteristics, not to preferences. Second, it relates to central (cortical) control of performance, and only indirectly to performance characteristics actually observed. Inferring hemispheric specialization from hand preference data thus involves two steps, each of which can lead to an error. The

first step is to replace "preference of the right/left hand" by "superiority of the right/left hand;" the second step is to replace "superiority of the right/left hand" by "superiority of the left/right hemisphere." The risks inherent in these two steps are acknowledged by the authors of the target article, but they nonetheless take the steps.

The very concept of "handedness" seems to contribute to confusion between hand preference and hand superiority because it fails to distinguish between these two phenomena. The concept seems to suggest that the hand that is superior in performing a certain task will be the one that is preferred. (In addition, treating handedness as a unitary concept suggests that the same hand is always both superior and preferred.) This view is simply wrong. The concordance of hand superiority and hand preference is notoriously low. The relation between these two phenomena is not straightforward.

The choice between hands seems to depend on more than their relative proficiency. This is acknowledged by Annett's theory (a comprehensive treatment is provided by Annett, 1985). In addition to proficiency differences, preference is assumed to depend on the location of a decision criterion on the continuum of proficiency differences, which can be influenced by other factors, such as social pressure. (The schema is similar to that of signal detection theory.) Thus, the nonpreferred hand may be superior to the preferred one.

Annett's theory is based on a unitary concept of skill. Generalizing the approach, one can conceive of a set of distributions for various tasks. For each distribution, one can define a criterion, the location of which is related to the population preferences observed for the task in question. With such a complex but more realistic scheme, the relationship between preference and superiority becomes quite complicated.

To give an example, it is likely that the various criteria are neither all the same nor constant across different situational contexts. This is obvious when bimanual tasks are compared with unimanual ones. The problem is that some apparently unimanual tasks may be "latently bimanual" ones. A task like reaching for a piece of food would be considered unimanual. But any shift of the center of gravity (as in stretching out one arm) requires a change of bodily support, in which the other arm may also be involved. The apparently unimanual reach may also be a latently bimanual task for the animal, because it may involve preparations for potential manipulations of the object grasped. Thus, the tendency toward a preference for left-handed reaching might be observed even with an inferiority of the left arm; only the "latent" involvement of the right arm would induce the corresponding right shift of the criterion that determines the preference rate.

It seems to be a well-established practice to take a manual superiority as an indicator of a hemispheric superiority. More specifically, superior hand proficiency on certain tasks is related to specialization of the contralateral hemisphere for certain functions invoked by the execution of these tasks. Although it is likely that hemispheric specialization contributes to hand differences in skill, the relationship may not be as straightforward as required by replacing "superiority of the right/left hand" by "superiority of the left/right hemisphere." Two kinds of data will suffice here to strengthen the view that such a simple substitution is likely to be incorrect.

The first kind of data is concerned with the output channels of the two hemispheres to the spinal motoneuron pools. As noted by Todor and Smiley (1985), relating skill differences between the hands to hemispheric specializations rests heavily on the fact that the majority of corticospinal fibers cross in the medulla oblongata. Differences between hands could, in principle, be due to more effective output channels of the one hemisphere as compared to the other – that is, to functionally low levels of motor control. Todor and Smiley review some data showing that the crossed fiber bundles from the left hemisphere are larger.



This corresponds to the majority of right handers. But a sizable percentage of right-handers, as determined by responses of relatives to retrospective questionnaires, is also found among atypical cases where the crossed fiber bundles from the right hemisphere are larger. Thus, there is no clear-cut association between the "strength" of at least one output channel and handedness.

The second kind of data is concerned with functionally higher levels of motor control. In right-handers almost all cases of apraxia are from lesions of the left hemisphere. Thus, given right-handedness, it is probably correct to ascribe superiority (or exclusiveness) for higher-level control of certain skills to the left hemisphere. As often seems to be the case, the reverse conclusion has a good chance to be wrong for left-handers. Faglioni and Basso (1985), for example, mention several cases of left-handers suffering apraxia after lesions of the left hemisphere rather than of the right.

The relationship between the superior hand and the hemisphere that is responsible for this superiority does not always follow the simple "contralaterality rule," at least in man; and even when this rule is valid for right-handers, it is usually not valid for left-handers. The relationship between hand superiority and hemispheric specialization poses a problem of inquiry, but there is no simple relation for inferring hemispheric specialization from hand superiority by the contralaterality rule. Ettlinger (1984) reviews some findings that indicate that the contralaterality rule would hold in monkeys, but that it need not do so.

### Which hand lost its cunning?

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I have problems with the behavioral data cited by MacNeilage et al., and most of my commentary focuses on these because it is hard to take theories seriously if one is uncertain about the data.

MacNeilage et al. are concerned to present "population level asymmetries," and in Figure 1 and Table 3, they feature data from Beck and Barton (1972) to illustrate such asymmetries. Figure 1 is at first glance convincing, but some of the strange numbers in Table 3 made me look more closely. There is something unbelievable about a 100% preference in behavioral studies, and in my effort to understand this and other numbers in Table 3, I reread Beck and Barton. The numbers were all there, but I found other numbers that made better sense. In addition to the 100% "left reach," Beck and Barton reported that 7 monkeys preferred their left hands in that task and the remaining 3 preferred their right hands. I hate to admit how much time I wasted trying to understand how 70% and 100% could both describe the same preference. The problem turned out to be in the way medians were used, and the problem was present for Figure 1 as well as for Table 3 (target article).

Each point in MacNeilage et al.'s Figure 1 represents median performance by each monkey on one task; it does not represent the frequency with which a monkey showed significantly biased performance on different tasks. (Significance was taken by Beck and Barton as  $p < .0027$ .) This use of medians can result in extreme values for monkeys that were very stereotyped in their behavior. If a monkey always took food with its left hand on 9 tasks and with its right hand on 8 tasks, it would have 100% left reach in Figure 1, even though it was reaching to the left on only 53% of the tasks. It would be represented as an extreme left-hander for food taking, whereas the more proper population statement would be that it was a consistent animal with respect to its preferences but that it took food with its left hand in some contexts and not in others. To test MacNeilage et al.'s hypoth-

esis, the graph should relate the percentages of the 17 reach tasks in which each animal preferred its left hand to the percentages of the 14 other tasks in which each animal preferred its right hand. The percentages appear in Table 1.

Evidently, fewer than half of the animals had a left-hand bias when reaching for food, and exactly half had a right-hand bias on the "other" tasks. If these data are graphed as in Figure 1, the points are centered pretty well about the 50% region on both axes rather than in the upper-right quadrant.

The percentages in MacNeilage et al.'s Table 3 refer to populations of repeated actions of a "median monkey." The numbers tell us about the frequency with which this monkey used its left or right hand for one act (task). When there are very high percentages in Table 3 for some of the acts, this presumably means that very stereotyped motor behavior patterns had appeared, as they often do in well-trained animals (and people). As in the data of their Figure 1, the basic information that MacNeilage et al. provide on Beck and Barton is on stereotypy rather than handedness.

There are other data in Beck and Barton that can be used as the basis for "population level" statistics on handedness as required by MacNeilage et al.: In 17 reach tasks, the number of monkeys preferring the left hand ranged from 1 to 8 (mdn = 5); the number preferring the right hand ranged from 0 to 5 (mdn = 2); and the number showing no preference ranged from 0 to 7 (mdn = 3). The mean percentage of monkeys preferring the left hand on reach tasks (averaged across 17 tasks) was 47.0. In the remaining 14 tasks, the number of monkeys preferring the right hand ranged from 3 to 8 (mdn = 6). From 0 to 5 of the monkeys had left-hand preferences for these tasks (mdn = 2.5). The number with no preferences ranged from 0 to 7 (mdn = 2). The mean percentage of monkeys preferring their right hands on the "other" tasks was 55.7. It should be kept in mind that the mean percentages are relative to the entire group of monkeys, including those with no preference as well as those with the opposite bias.

If one ignores the cases in which there was no significant hand preference, one can identify a small left-hand preference for reach; there was a small right-hand preference for "other" in this sample. To this extent, there is support for MacNeilage et al.'s contention. But this is hardly support for their view about general populations of acts and monkeys, nor is it clear that "ambidextrous" cases can be ignored. In most tasks there were some animals who showed no bias, and all animals showed no bias in some tasks. Beck and Barton's objective was to find lateral biases, and they succeeded. They then wanted to determine the consistency of the biases that had appeared, which may explain their odd use of medians. From the available data, I conclude that the performance of these 10 monkeys was not sufficiently consistent to be informative about the nature of

Table 1 (Jerison). *Reanalysis of Beck and Barton (1972) data*

Animal No.	Reach % left	Other % right
1	71	64
2	29	50
3	29	71
4	59	50
5	47	43
6	24	64
7	41	57
8	65	43
9	18	29
10	88	71



laterality in the species, beyond the evidence that when a preference for one hand appeared, it was likely to be strong.

These conclusions are relevant for the Itani et al. data presented by MacNeilage et al. in Table 1 of the target article. The problem is how to think about the different frequencies of left-hand, right-hand, and ambidextrous preferences. Their Table 1 hardly suggests selective advantages for biases one way or the other. Like the Beck & Barton (1972) data, the Itani et al. data suggest that handedness (including ambidexterity) is fairly evenly distributed among animals with respect to reaching for food. It was not clear that the effects of aging could be distinguished from the effects of practice, because several of the reports cited by MacNeilage et al. agree that these habits become stronger during prolonged testing. An increased stereotypy in food-gathering habits was to be expected as animals gained experience in Itani et al.'s artificial feeding setting.

Two sets of data reported by Itani et al. (1963) were not included in MacNeilage et al.'s Table 1. These reports were of data by Furuya of 37 left-handers, 38 right-handers, and 36 ambidextrous monkeys in a colony at Takakashi, and of data without counts by Kawai at Takasakiyama in which the right-handers were most frequent, followed by the ambidextrous, followed by the left-handers. Adding Furuya's data does not change the picture much for significance testing, but one might wish to track down Kawai's. They might change the statistical picture.

I didn't check all of the data cited in the target article, but there were more questionable statements. MacNeilage et al., not Subramoniam (1957), calculated the probability for left-handed insect catching by lorises, evidently assuming that all 8 animals had been observed in this activity and that there were no exceptions. Subramoniam mentioned one instance of a right-hand catch, and wrote, anecdotally, about "the loris," not 8 lorises. The "strong" left preferences in 12 galagos were balanced by equally strong right-hand preferences in 4 animals in the same study, with 9 animals in the middle ranges. When Rothe (1973) reported on hand preference in marmosets, the report on tests 2-7 (see MacNeilage et al.'s Table 6) includes the statement: "It is appropriate to draw attention to test 7, in which all of the subjects were ambidextrous" (p. 564). In answer to MacNeilage et al.'s query about "the apparent trend toward increasing right-hand preferences with practice" (sect. 7.2, para. 1) in Rothe's study, it evidently did not occur if test 7 was performed after tests 2-6. In summary, the behavioral evidence is not convincing.

I had no serious problems with the neurological data. Much more structural, as well as functional, asymmetry occurs in the vertebrate central nervous system than was suspected as recently as 20 years ago, and it is appropriate that MacNeilage et al. emphasize the changed view. There are still problems about interpreting the significance of the structural asymmetry, and not all of the literature can be accepted unquestioningly. There is an outright error in Falzi, Perrone and Vignolo (1982), for example, who reported asymmetry in 12 human brains, 9 of which had more surface area in Broca's area of the left hemisphere and 3 of which had a right-sided advantage. Their reported means and standard deviations are inconsistent with their own tabulated data, and if the data are right, they erred in reporting their statistical test as significant at the .05 level. It was not significant. There is a report (Scheibel, Paul, Fried, Forsythe, Tomiyasu, Wechsler, Kao, & Slotnick 1985) of hemispheric differences in dendritic branching in this part of the human brain, a conclusion that depends on a significant higher order interaction in an analysis of variance. Everybody is trying to demonstrate structural asymmetries, and these continue to be found, at least in statistical exercises. The Falzi et al. conclusion may be supported when larger samples become available, but one should wait for more evidence.

How should evolutionary biologists think about these behavioral and neurobiological data? One might begin with some

healthy skepticism, even when the reports are in refereed journals. The continuity issue is something of a red herring for neural evolution. Continuities in neural structure and function are identifiable at many levels (e.g., the structure of neurons, the chemistry of neurotransmitters, and the appearance of major nuclei and systems, such as tectal nuclei and the limbic system). But the detailed circuitry that controls behavior is usually developed by the interplay of genetic and environmental constraints. I cannot quote enough to provide a full flavor of the position, but I would recommend Warren's view. Beginning with a well documented example, he wrote: "Destruction of the ventromedial nucleus in the hypothalamus makes mammals fat and mean, no matter what their species-specific patterns of eating and fighting may be. By analogy [he concluded, and I agree], it seems reasonable to speculate that, although different functional lateralizations arose in different species to solve different problems in adaptation, all arose from the same sort of preadapted neural mechanism and all operate in basically very similar ways" (Warren 1980, p. 357).

There are very complex issues in the growth and development of neural control systems that make it difficult to accept simple models of natural selection to explain the phenotypes that occur. Normal neural development depends on a normal environment, both internal and external, within which nerves grow (and sometimes degenerate and die) and networks are established. Modeling the evolution of neural systems may be undertaken at that level of analysis (see Ebbesson 1984), and could specify how a preadapted neural mechanism, in Warren's sense, could have been established. It is assumed that these mechanisms are incorporated into actual neural control systems for species-typical phenotypic behavior patterns that arose under natural selection. The place of scenarios like MacNeilage et al.'s is to indicate the context in which they are incorporated.

I would discount such scenarios for handedness on the ground that the behavioral evidence is too weak. I would also criticize MacNeilage et al.'s scenario as being insufficiently demanding; the coordination they require could be handled by small neural structures without lateral specialization. One must assume more complex activity ("metafunctional capacities"?), such as the cognitive adaptations discussed by Hamilton and Vermeire (1982), to explain the investment in neural tissue. This is another kind of issue, the discussion of which may perhaps best be deferred for lack of good evidence.

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## Reaching for the brain

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The general concept that hand preference might provide a key to understanding cerebral organization can probably be dated to Bouillard in 1825. Observing that most people wrote, drew, painted, and fenced with the right hand, Bouillard suggested that the left hemisphere might control these acts via the fibres that were known to cross contralaterally from the brain to the limbs. If this was so, he asked, why shouldn't the left hemisphere control speech movements as well? One hundred sixty years later, the question of the relationship between manual specialization and cerebral organization is alive and well in this target article by MacNeilage et al. The authors have made some novel observations and done some ingenious synthesizing to lead them to their hypotheses regarding the basis and develop-

ment of handedness. From this they have made an inferential foray into the question of cerebral organization. Although we are intrigued by their analysis, we find some of their arguments wanting.

First, MacNeilage et al. make a good attempt to look at the relationship between handedness, language, and structural asymmetry. In the course of this discussion, they look for evidence that the control of speech and the control of fine manipulatory movements in the preferred hand are separable specializations in the brain. They find no conclusive evidence from anatomical studies (Table 9, target article) and then leave the issue. A problem they fail to consider is that the left-hemisphere specialization for the control of fine movements is associated with the hemisphere dominant for language rather than with the hemisphere contralateral to the preferred hand. Yakovlev and Rakic (1966) found that in 80% of right-handers there are more pyramidal tract fibers descending from *both* hemispheres to the right hand than there are to the left hand. This pattern of a right-side bias is also typical of the majority of left-handers, two-thirds of whom can be expected to have left speech representation. In addition, Milner, Taylor, and their colleagues (e.g., Milner 1976) have used the technique of individually anesthetizing the hemispheres with sodium amytal to confirm that language and praxic function are represented in the same hemisphere in left-handers. Given a dissociation between handedness and the control of praxis, we are left wondering what can be legitimately inferred about the brain from the study of hand preference.

It should also be noted that the special role of the speaking hemisphere in the control of praxic function is bilateral. We are hard pressed to see how this could arise from the development of hand preference. MacNeilage et al. suggest that the left hemisphere is specialized for bimanual coordination, but it would seem that the evidence favors a strong role for the supplementary motor cortex in bimanual coordination. For example, the surgical disconnection of the supplementary motor areas leads to severe deficits in the execution of certain forms of distinctive limb movements (Milner & Kolb 1985), possibly because both areas have bilateral control of both limbs and must therefore be able to "cooperate" in the execution of movement. This portion of cortex, however, is generally believed to be primitive phylogenetically (e.g., Pandya & Yuterian 1985) and thus would not seem the most likely place to look for neural correlates of the type of advanced manual specialization sought by MacNeilage et al.

If the left-hand preference predated the right, as MacNeilage et al. propose, then it seems reasonable to further suppose that some rudiment of this specialization would be found in species ancestral to primates. In addition, unless it is assumed that the left-hand specialization for visually guided movement was merely a random occurrence that somehow became a universal trait (which seems unlikely), there either must have been some selection pressure favoring the left limb, or the right hemisphere already had some specialization that led to the left-hand specialization. One possibility might be a preexisting neurochemical asymmetry, possibly related to posture, that favored the use of the left limb. The evidence of postural asymmetries in newborns would seem consistent with this idea, because the hemispheres are unlikely to play much of a role in such asymmetries in the newborn.

Finally, we have a concern about the kinds of behavioral observations in studies of hand preference in both human and nonhuman species. The possible responses the subjects can make are normally categorized a priori and described by words. This is problematic because the conceptual constraints imposed by the use of language to describe behavior may bias the observations themselves. In other words, an inference that a movement is manipulative, reaching, or postural is not based on a careful notation of movement [as it would be in the Eshkol-Wachman (1958) notation system, for example], or even on an

analysis of the kinetics of movement. Rather, it is based on a preconceived, subjective impression of what the behaviors might be. Such impressions may be insightful, but they are all too often wrong. To sell us on the hypotheses will require not only that the studies be done again, but also that the behavior be filmed and subjected to formal and explicit behavioral recording. Only then will we be convinced that the behavior of the left and right limbs is truly different in nonhuman species. (For an extensive discussion of the flaws in behavioral observation, see Jacobs et al., unpublished.)

## On the other hand . . .

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It is possible to explain the observations reviewed by MacNeilage et al. without resorting to any hypothesized differences between the functions of the left and right cerebral hemispheres of monkey and other subhuman primate populations. The resulting view appears to be simpler, albeit less exciting:

1. The handedness of monkeys is evident, at least in part, prior to any laboratory testing, although its genetic basis is open to question.
2. There is no overall population bias toward left- or right-handedness for single-component tasks.
3. Individuals have a low, but definite, tendency to use the same hand on different tasks if the task has only one component.
4. When the task has successive components, there is a superimposed tendency to switch hands between the components. This trend is most evident in more complicated tasks.

There is laboratory evidence that task repetition affects hand preference in monkeys (Lehman 1978; 1980a; Warren 1977b). That such laboratory testing is not itself the cause of the observed hand preference is suggested by evidence that the initial reach tends to predict a naive animal's overall preference over many hundreds of reaches (Lehman 1978; 1980a). More important, this effect is not the result of rewarding the first hand used, because the first reach is still predictive when it is not the first to recover a reward (Lehman 1980c). Evidence that the hand preference of offspring may be related to that of their mother (Brinkman, 1984a, quoted by MacNeilage et al.) also suggests that hand preference need not be the result of experimental manipulation. However, this correlation was not obtained in a previous study (Brooker, Lehman, Heimbuch & Kidd 1981).

Of greater relevance is the question of whether or not populations of monkeys tend to prefer one hand over the other. MacNeilage et al. cite evidence, most pointedly offered in Table 1, that monkeys prefer to use the left hand for simple reaching tasks. These data were selected by looking for studies in which there was an apparently significant asymmetry of hand preference in the population of animals being reported. This selection bias for degree of handedness leaves only the consistency of hand preferred between studies, rather than the degree of asymmetry over all studies, at issue. On a random basis, any such study would have a 50% chance of showing a bias for the right or the left hand. Thus, by restricting analysis to studies selected for asymmetry and choosing three, as in Table 1, chance alone dictates a  $1/2^3 \times 2 = 0.25$  probability that all three studies will demonstrate a preference for the same hand. It might be argued that the studies were not so selected. In this case, it is not valid to exclude other studies that do not show significant asymmetric preferences. If the 141 left- and 134 right-handed animals we have reported (Lehman 1978; 1980a; 1980c) from laboratory studies were grouped with the above, the overall results would not show a significant preference for left- or right-handedness.

That such conclusions should be based only on field studies seems dubious, because MacNeilage et al. heavily emphasize the left-sided preference for simple reaching found in the laboratory studies of Beck and Barton (1972), and they base their conclusions about right-hand preference for manipulation entirely on such laboratory data. It would appear that there is no definite evidence that populations of monkeys have a significant preference for the left, as compared to the right, hand on simple reaching tasks.

Although the tendencies are weak, monkeys do more frequently prefer the same hand for different one-step manual tasks than would be expected by chance alone. Studies reviewed in reaching this conclusion (Lehman 1980b) include those cited by MacNeilage et al. (Brookshire & Warren 1962; Cole 1957; Ettlinger 1961; Kounin 1938; Warren 1977). The study of Brooker et al. (1981) in a "field" situation also supports this conclusion. These findings are compatible with the notion that hemispheric specialization for handedness exists for individuals but is not consistent within populations (Lehman 1981).

However, when a task has multiple components, one might expect there to be some advantage to using different hands. Thus, the second hand could be brought into play prior to releasing the first. Furthermore, the first hand, maintaining its position, could in some instances make final recovery of food by the second hand more efficient. In the studies of multiple component tasks by Beck and Barton (1972), as well as those by Brookshire and Warren (1962), it is evident that monkeys often preferred to use different hands for the various manipulative (preparatory) and incentive (consummatory) components. However, the data of Beck and Barton and those of Brookshire and Warren indicate that when the same hand was preferred throughout a multiple-component task, this tended to be the hand preferred by that animal for most single-component tasks. Unlike the Beck and Barton study, and contrary to the proposal of MacNeilage et al. that the right hand is preferred for manipulation tasks, most of Brookshire and Warren's animals did not prefer the right over the left hand for manipulative task components.

Finally, it may be noted that 91 of 275 naive monkeys I have studied for handedness have been trained to make one of three visual discriminations between vertically arrayed shapes (Lehman, unpublished). Of these, 51 preferred the left hand to the right during the initial 600 trials whereas 50 preferred the left hand during the last 600 trials,<sup>1</sup> which led to and included performance at the criterion level of learning. More animals preferred the left to the right hand during visual discrimination. However, these results are not statistically different from chance, and consequently fail to confirm MacNeilage et al.'s hypothesis of a left-hand response preference during visual discrimination tasks.

MacNeilage et al. end their review by stating that their views are speculative. The data available are often inconsistent with their suggestion of a right-hand preference for manipulative activities and a left-hand preference during simple reaching tasks and visual discriminations, and they fail to confirm the authors' hypotheses at significant statistical levels.

#### NOTE

1. Fewer trials available for the 13 animals learning most quickly.

## Evolution of handedness

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The percentage of left-handedness in the modern population is estimated to be approximately 10% (Annett 1972; Hardyck & Petrionovich 1977). Estimations of left-handedness in the nine-

teenth century were more often reported to be in the range of 1–4% of the population (Cunningham 1902). These differences are unlikely to be the result of evolutionary changes (even by punctuated equilibrium!); rather, they are due to cultural influences and also to the methods used in determining handedness. Perhaps we also have not been using the most heuristic testing methods for studying handedness in nonhumans.

A few years ago I participated in a study of hand preference in more than 800 students in the 7th–10th grades of a school in the highlands of Papua, New Guinea (LeMay, Pim & Burch, in preparation). These students were, for the most part, the first in their families to attend school. The percentage of left-handedness was essentially the same as that in our own population, but the number of tasks reported performed by the nondominant hand, or by both hands, was much greater than in our society. As suggested in the target article, and in occasional past articles (Preilowski 1983), asymmetries of hand performance appear to be influenced by the complexity of the motor effort for the hand. The task most commonly performed with the nondominant hand by the New Guinea students was holding the arrow (when shooting with a bow and arrow), a task requiring little manipulative effort by the hand. Tasks requiring manual specialization, such as writing, were more often performed only by the dominant hand.

A statistical correlation has been noted in certain asymmetries of the cerebral hemispheres and handedness in some modern populations (Bear, Schiff, Saver, Greenberg & Freeman 1986; LeMay 1977). Brain asymmetries noted in nonhuman primates, and much less striking in New and Old World monkeys, tend to be in the same direction as those noted in humans (LeMay 1985). MacNeilage et al. point out in their target article that right-hand preferences have been found in nonhuman primates with more manipulative tasks. This is an interesting finding and points toward the direction suggested by Geschwind (1985), who wrote: "I would like to suggest that the capacity to carry out experimental studies on dominance in nonhuman species will have major implications for understanding of many of the highest functions in the human nervous system and for the characteristics of the human mind" (p. 271). There are animal studies suggesting that cerebral asymmetries in nonhuman primates may be an early manifestation in language development (Falk, Cheverud, Vannier & Conroy 1986; Heffner & Heffner 1984); the present target article, suggesting that the functional asymmetries noted in nonhuman primates may be a precursor to right- and left-handedness in modern humans, helps to confirm Geschwind's conjecture.

## Primate handedness should be considered – but not "reconsidered" at this point

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Although MacNeilage et al. state that "the term 'handedness' denotes a more or less uniform preference for one hand in a wide variety of activities" (sect. 2), they present data about manual preferences for a few specific acts in various animals. The title of the target article, "Primate handedness reconsidered," suggests that the authors wish to infer handedness as a characteristic of nonhuman primates. The case made is hardly compelling. Humans manifest substantial uniformity of manual preferences over a wide variety of manual acts, and the degree of consistent hand preference is greatest across acts requiring fine and complex motor control, particularly of the hands and fingers (see Healey, Liederman & Geschwind 1986). The hand preferences of humans appear to reflect asymmetries for the acquisition of complex manual skills. Thus, if one is seeking the "precursors"

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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



preference in the population. For some of their analyses (e.g., Box 1977), a bias in the population of responses in a task is identified rather than bias in the population of individuals doing the task. Of course, the bias in the distribution comprises individual preferences, but the relation between these two aspects of handedness must be identified for each study. Otherwise, very strong preferences in a minority of individuals can create the impression of a bias in overall distribution. Because the functional relation between these two aspects of handedness is unknown, they must be kept distinct.

One important consequence of MacNeilage et al.'s argument is that future investigations of nonhuman primate handedness may use greater methodological sophistication. MacNeilage et al. are quite persuasive in insisting that handedness should be assessed by appropriate criteria in more natural conditions, according to task demands and the age of the individual. Specific task characteristics could determine the bias in hand use. We found that if hand preferences of human infants are assessed with tasks that separately elicit manipulation and reaching, there is greater consistency of preference during the 6–13 months after birth than had been observed previously (Michel, Ovrut & Harkins 1985). Unlike data reported for monkeys, our finding was not that there were different hand preferences in human infants in these different manual skills. MacNeilage et al., however, argue that bimanual coordination is so important for human manual activity that the right-hand bias for that coordination has become powerful enough to supersede the left-hand bias for reaching.

We are uncertain why the predominance of bimanual coordination in humans should eliminate a left bias for reaching, because that bias would complement a right bias for bimanual manipulation and allow immediate action with the object – that is, a right bias in reaching requires that the obtained object first be transferred to the left hand before bimanual activities, with a right bias, can occur.

During infancy, a right bias for reaching precedes the appearance of bimanual manipulation by 4–6 months. When bimanual manipulation first appears, many infants switch their reaching preference to their formerly nonpreferred hand, apparently to facilitate using their preferred one for the more active role in bimanual manipulation. At later ages, they revert to using their preferred hand for reaching and engage in more cumbersome intermanual transfer of the obtained object before beginning bimanual manipulation. We therefore would conclude that bimanual manipulation is not the source of the right bias in human reaching. Rather, reaching and bimanual manipulation both reflect a bias toward the right hand. If there is a left bias for reaching in monkeys, then the transition to a right bias in human reaching remains to be explained.

MacNeilage et al. propose that the left bias for reaching and the right bias for manipulation, shown by some species of monkeys, mirror the underlying functional specialization of their cerebral hemispheres. The authors acknowledge that the evidence of this specialization is weak or nonexistent for monkeys, although such specialization does seem to be characteristic of humans. If hemispheric specialization is responsible for task differences in hand preferences in monkeys, shouldn't humans show the same pattern of hand bias as monkeys? Locating the precursor of human handedness in nonhuman primate hemispheric specialization requires an inexplicable shift of handedness in reaching during the evolution of humans and the acceptance of hemispheric specialization in monkeys. Unfortunately, no compelling evidence was provided for either the left-hand bias in reaching or hemispheric specialization in nonhuman primates, especially for visually guided movement.

Evolutionary precursors often have forms quite different from those of their descendants (e.g., jawbones in reptiles as precursors of earbones in mammals). Perhaps part of the problem in the search for precursors of the bias in human handedness is that

similarities in handedness or hemispheric specialization between humans and other primates have been sought. We (Michel & Harkins 1986) found that the direction of the infant's neonatal head orientation preference was a developmental precursor of later hand preference. Because the vast majority of neonatal infants prefer to orient their heads to the right (Michel 1981), there ought to be a right bias in later hand preference. The evolutionary precursor for the bias in human handedness might accordingly reside in the evolution of an influence of posture over hand use in nonhuman primates. Once posture was capable of affecting hand use, any laterally asymmetrical bias in posture would ensure bias in handedness.

The developmental association observed between human infant head orientation and hand preferences directs attention toward assessing the contribution of posture to primate hand use and handedness. If postural effects on hand use are considered a precursor of human handedness, then the human-specific bias in handedness distribution can be retained. As hominids evolved more complex social organizations and toolmaking abilities, shared handedness would have been advantageous for the transmission of manual skills through observational learning. Given a postural influence on hand use and the relative immaturity of human infants, a lateral asymmetry of neonatal posture may have evolved to bias handedness. Or perhaps there is an asymmetry in the neonatal posture of monkeys and apes that plays little role in their developing handedness because of their relative precocity. Such neonatal postural asymmetry would become evolutionarily significant in hominids as shared handedness became advantageous and neonatal immaturity became prevalent. The relation, if any, between an ontogenetic origin of the handedness bias in neonatal postural asymmetry and hemispheric specialization of function remains to be discovered.

The phenomenon of primate handedness deserves further investigation; MacNeilage et al. have provided some important conceptual and methodological requirements for such an investigation. The search for evolutionary precursors of both human handedness and hemispheric specialization deserves greater attention. However, constructing phylogenetic lineages from living species is fraught with pitfalls and requires careful use of certain conceptual and methodological tools (see Beer 1980; Hailman 1976). Also, attempts to identify the adaptive significance of behavior can result in plausible, but fallacious, accounts unless special precautions are undertaken (Gould & Lewontin 1978; Hailman 1982). Until primate handedness is assessed more appropriately and information is available about preferences during reaching and during unimanual and bimanual manipulation under natural conditions, it is premature to construct evolutionary lines of descent.

Have MacNeilage et al. identified a valid and plausible phylogenetic lineage and functional explanation for the evolution of the bias in human handedness? We think not. But we do think they have provided a convincing argument for a reconsideration of the study of primate handedness.

## Primate handedness: Reaching and grasping for straws?

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There has been a consensus for some time now among researchers that, unlike humans, nonhuman primates fail to show species-typical asymmetries of hand preference, or handedness, linked to hemispheric functional asymmetries. Hence, it has been common to ponder what peculiarities of human evolution-



ary' history led to the development of handedness and hemispheric lateralization (especially for language) as strongly linked, canalized biological processes (Levy 1977b).

MacNeilage et al. now challenge that consensus and traditional posing of the evolutionary problem. They argue that close inspection of published work in fact reveals a hitherto undetected consistency in patterns of handedness among non-human primates that can be linked to human hand and neural specializations. Challenging established opinion is a healthy process in science, and MacNeilage et al. are to be congratulated for their efforts. They fail, however, to build a persuasive case in favor of their view. As we will attempt to show, their case is weak on both empirical and theoretical grounds, but at the very least, their effort may cause investigators to suspect that the case on primate handedness is not closed.

Before proceeding, we must point to an apparent misunderstanding of the evolutionary process. Much of MacNeilage et al.'s impetus for their reanalysis seems to derive from their dissatisfaction with evolutionary accounts suggesting *de novo* evolution of traits (i.e., human hemisphere and hand specializations). Consequently, evolutionary scenarios that identify "precursors" or "preadaptations" to the traits in question are seen as more satisfying than the former, or, as they note in their conclusion, such scenarios have "the merit of suggesting a plausible adaptive sequence." (As an aside, the term "preadaptation" used by MacNeilage et al. might be better replaced by the less teleological "exaptation"; Gould and Vrba 1982.) Evolution being a conservative process, it does tend to produce new structures and functions by making the best of available existing materials; but this in no way precludes the emergence of novel structures or functions (the derivation of the mammalian middle ear being the classic example). We accordingly fail to see why an account of the evolution of a novel pattern of human hemispheric and manual asymmetry should be unsatisfactory in principle.

MacNeilage et al. review a large corpus of studies in an effort to show that nonhuman primates, from prosimians to apes, do show consistent asymmetries in hand preference, provided the data are examined appropriately. In particular, they argue that studies demonstrate a complementary functional specialization of the two hands, with the left specialized for visually guided reaching (or for later holding in bimanual activity), and the right specialized for postural control in prosimians and for manipulation in monkeys and hominoids. The evidence cited in support of these specializations, however, is for several reasons unconvincing.

First and foremost are data (not addressed by MacNeilage et al.) in each of the studies on the number of subjects exhibiting no hand preference on tasks. A quick calculation from the tables provided shows that more than 30% of the subjects from all studies combined had no hand preference for the tasks used. Similarly, from Table 2 of the Beck and Barton (1972) study it is evident that on average (across all tasks) 4 of the 10 subjects showed no hand preference. In some instances (Fragazy 1983; Itani 1957), the percentage of subjects without hand preference approaches 50% or more. Yet throughout the target article, MacNeilage et al. describe reported frequencies of hand preference as "population-level" phenomena. In the studies presented, hand preferences are, at best, characteristic of sample subpopulations; they are thus not at all comparable to population patterns of human handedness.

In examining that subpopulation of subjects exhibiting hand preferences, much is made of very little; indeed, it appears that only when data are grouped in certain questionable ways do statistically significant trends emerge. For example, consider the Japanese field studies and the laboratory studies by Ettlinger's group (Ettlinger 1961; Ettlinger & Moffett 1964; Gautrin & Ettlinger 1970; Milner 1970). Of the three Japanese studies cited (Itani 1957; Itani, Tokuda, Furuya, Kano & Shin

1963; Tokuda 1969), only one (Itani 1957) showed marginally significant differences in hand preference, and it is only by combining the results of the other two that statistically significant results emerge. What is the justification for combining the two, other than convenience? Given the methodological problems inherent in field studies of handedness described by Box (1977) and acknowledged by MacNeilage et al., it seems highly suspect in the absence of strong methodological justification to combine in this way data collected by different teams of investigators at different sites. Similarly, in the Ettlinger group studies, data are combined from a visual "expose and reach" task and from a tactile "expose and reach" task performed in the dark, yielding statistical differences in hand preference. It would seem, however, that MacNeilage et al.'s own hypothesis is inconsistent with such a combining of data: The visual task should favor the left hand, whereas the tactile task performed in the dark should favor the right hand (by drawing on the "fine somatic sensorimotor control" mechanisms that MacNeilage et al. conjecture evolved early among prosimian primates).

In several instances, MacNeilage et al. strain to interpret results (especially apparently contradictory ones) to fit their hypothesis. Thus as they display the panorama of evidence and counterevidence before the reader, their hypothesis about hand specializations seems to take on a chameleon-like quality, changing ever so slightly so as to account for all possible variations in the results. Consider the Beck and Barton (1972) study, for example, about which MacNeilage et al. observe that "the simplest reach task actually shows a right-hand preference" (sect. 2.1.3). Thus, MacNeilage et al. suggest that left-hand preferences increase with task difficulty and "are at their highest levels when both stabilization and *manipulation* are also required" (Section 2.1.3; emphasis ours). This blurs the originally proposed hypothesis of left- and right-hand specializations to a point where all data can be accounted for; or, put simply, the hypothesis cannot be disproved. The postulated trend for left-handedness among the Japanese macaques both in simple reaching for food and in catching thrown food (presumably more complex visuospatially than simple reaching), the bush baby's left-hand preference for retrieving proffered worms while in a vertical posture (but lack of such a preference while in a horizontal posture), and the right-hand preference shown by marmosets (Rothe 1973) on complex reach tasks – all of these are considered consistent with MacNeilage et al.'s model.

Before proceeding with a consideration of MacNeilage et al.'s evolutionary model of handedness, we wish to present handedness data from some of our recent work with chimpanzees (*Pan troglodytes*), which argue against consistent population-level hand-use asymmetries in our closest genetic relative. The first part of the research examined the spontaneous hand use in a semifree-ranging population of 27 chimpanzees (Marchant 1981; Marchant & Steklis, in preparation). Seven categories of hand use, comprising social (groom) and nonsocial (reach, feed, hold, carry, throw) activities, were recorded using a focal behavior sampling technique (Altmann 1974). In brief, population trends were determined by subjecting average differences between left- and right-hand use across subjects to paired *t*-tests, which yielded no significant differences for any behavior. For individual subjects, hand preference was determined by chi-square. In all, 14 (53%) of the chimpanzees showed consistent hand preferences between two or more behaviors, with 7 preferring the left and 7 the right hand for all behaviors; 8 (31%) switched hand preferences between behaviors, and 3 (12%) showed a preference in only a single behavior. Overall, there were 81 instances of statistically significant left- or right-hand preference for the various behaviors. Of these, 45 (55%) were preferences for the left.

Our behavioral category "reach" is comparable to MacNeilage et al.'s category "simple reach," and it most frequently showed significant subject hand preferences (see our Table 1).

Table 1 (Steklis and Marchant). Number of chimpanzees showing significant left, right, or no hand preference for six spontaneous behaviors

Behavior	Left	Right	Ambidextrous	N
Feed	9	4	13	26
Reach	11	10	5	26
Hold	4	1	21	26
Carry	7	4	15	26
Throw	4	5	17	26
Groom	2	1	23	26

However, only 11 (52%) of 21 subjects with a hand preference for reach preferred the left hand, a result not in accord with MacNeilage et al.'s model. Although these data reveal a complex pattern of individual and behavior-specific hand-use preferences, no overall, population-level hand-use pattern is discernible for any behavior.

A second part of the research consisted of administering a series of unimanual and bimanual tasks to a subgroup of five chimpanzees. These tasks were chosen because they are diagnostic of human handedness and cerebral dominance. The full results have been reported elsewhere (Marchant & Steklis 1986), but the general conclusions are in agreement with the majority of handedness research on nonhuman primates – that is, we failed to find evidence to support the existence of motor dominance, as reflected in patterns of hand use that were stable across tasks and individuals.

Finally, the evolutionary model of handedness and hemispheric specialization offered by MacNeilage et al. calls for some closer examination. The most troublesome aspect is the failure to articulate the relative adaptive advantages of particular manual and hemispheric specializations that appear and disappear at various stages of primate evolution. Consider MacNeilage et al.'s prosimian stage of primate evolution, for example. It is far from self-evident how a *Galago*-like or *Loris*-like primordial primate (both are quadrupedal, *not* bipedal as described by MacNeilage et al., with *Galago* a vertical clinger and leaper and *Loris* a slow climber) could feed relatively more efficiently (with reproductive consequences) if its left rather than its right upper limb (right hemisphere) were specialized for visually guided reaching while the contralateral limb served in postural support. For that matter, common sense suggests that a protoprosimian prone to capture prey on its left would see too many get away until there was none left! On the other hand, those unlucky few enticed to snatch with their right at some morsel in flight would soon fall from sight.

MacNeilage et al.'s model suggests that human-like asymmetries (i.e., left hemisphere specialization for bimanual tasks, right hemisphere specialization for body image and visuospatial tasks) had already evolved with the first monkey-like ancestors. But again, it is totally unclear in what sense such a particular configuration imparted a selective advantage to its possessor. Furthermore, extant monkeys do not show the cerebral morphological asymmetries found in apes and humans, suggesting that these evolved later in hominoids. We should also point out that although the human right hemisphere is relatively more involved with body image and visuospatial tasks than the left (as indicated, for example, by the relative severity of neglect syndromes after right rather than left hemisphere damage), this is apparently not the case in Old World monkeys (Mesulam 1984).

As MacNeilage et al. indicate, cerebral lateralization of function is more common among primates than has been previously

supposed. However, available evidence suggests that functional cerebral asymmetries described in nonhuman primates differ from those in humans, in that in the former the two hemispheres (like the two hands) are equipotential with regard to becoming specialized for particular tasks – that is, training may induce both cerebral dominance and handedness (see Steklis 1986). Thus, in some instances it has been experimentally demonstrated that the direction of cerebral asymmetry is contingent upon hand preference (e.g., Sutton, Trachy & Lindemann 1981).

In closing, we might add that proposals concerning the causal role of toolmaking in the evolution of human bimanual control mechanisms are still viable. Toth (1985) has shown that hominids by as early as 1.9 million years ago were already disproportionately right-handed toolmakers (57:43) and that their numbers in the population had increased relative to left handers (61:39) by around .4 million years ago. These figures suggest that the high modern population ratio of right-handers to left-handers took some time to evolve, perhaps because of increasing selection for cultural conformity.

## Why the left hand?

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Try as they might, MacNeilage et al. are unable to present unequivocal evidence for the existence of hand preferences in nonhuman primates because, quite simply, such data do not exist. For almost no species are the data perfectly consistent; for many species, the published reports do not provide enough detail for the authors to reanalyze the data in light of their hypotheses; and for many other species, a lack of naturalistic data prevents a convincing interpretation of the laboratory studies – or vice versa. Also of some concern is the fact that many of the data are interpretable only as population trends, with figures for individuals sorely lacking, whereas others concern so few individuals that generalization to a population is unwarranted. Despite all of this, I am convinced by the review that primate handedness is indeed an open question. In addition, I am convinced that future research can provide more definitive answers only by taking into account considerations of task differences and the functional differences that these imply.

The particular evolutionary explanation favored by MacNeilage et al. is interesting, but not without problems. If we are to believe their interpretation of the existing data, prosimians and monkeys most often show a left-hand preference in visually guided reaching. The most obvious question is, Why the left hand? The authors argue that arboreal reaching favors an asymmetry. Fine, but why couldn't an individual stabilize itself with the left hand and reach with the right on one occasion, and reverse the direction on another? Perhaps consistently choosing one direction is more efficient because each hand then becomes more skilled at its habitual function. Perhaps – but then why should most members of the species opt for an asymmetry in the same direction? Did Mother Nature flip a coin for the first primates and has everything subsequent thus resulted from a founder effect? Is there some asymmetry in primate morphology that might encourage the development of a left-hand preference during ontogeny? [See Corballis & Morgan: "On the Biological Basis of Human Laterality" *BBS* 1(2) 1978.] Might observational learning among species members play a role in this development? This seems to me to be an important question for all evolutionary hypotheses about handedness, not just MacNeilage et al.'s. I don't know that it is currently answerable, but at the very least it needs asking.

A second issue is the transition to humans. Humans most often show a right-hand preference for visually guided reaching (as for almost everything else). MacNeilage et al.'s hypothesis is that manipulation is a right-hand function (for all primates) and that for humans the manipulative function was so important that the right hand "took over" all kinds of other functions. Obviously crucial in such an account are data from the great apes, because they would seem to be in between monkeys and humans in terms of the importance of manipulative activities. As the authors recognize, these are the weakest data they review. Chimpanzees and orangutans engage in perhaps the most complex manipulative/constructional activities of any nonhuman primate (e.g., Reynolds 1983; Tomasello, Davis-Dasilva, Camak & Bard, in press; Wright 1972), and the data for these species are very sparse. What data there are suggest no hand preferences. *Cebus apella* is a highly manipulative New World monkey (Antinucci & Visalberghi 1986), but there are almost no data for this species either. Given this paucity of data, the specific hypothesis that the relative importance/prevalence of reaching and manipulative functions is decisive in the different handedness patterns among primate species cannot at this point be evaluated.

A final and related issue concerns the possibility that language, not manipulative function, is responsible for observed cerebral asymmetries in humans. I would like to believe with the authors that manipulative activities and the underlying cognitive processes are primary and, thus, that whatever hemispheric specialization language does show is derivative. But I do not think it helps their case to view "language" as a unitary structure/function. As a proponent of the view that what we call language is a conglomerate of cognitive, social, and sensorimotor skills (Tomasello, George, Kruger, Farrar & Evans 1985; cf. Bates 1979), I have problems understanding what is meant by statements such as "Language specialization is considered to be primarily in the left hemisphere." (sect 7.6, para. 3). Nearer to the truth, in my opinion, is something like Lieberman's (1983) hypothesis that specialized speech mechanisms are all that can legitimately be located in the so-called language centers in the left hemisphere of the human brain, and that all the other skills associated with producing cognitively meaningful symbols in appropriate social contexts are associated with a wide variety of other neural structures.

All of which is to say that I find the hypotheses of MacNeilage et al. interesting – even appealing – but I will await more definitive data, especially regarding the great apes, before passing judgment. Perhaps the greatest strength of this account is that it can be tested in a relatively straightforward manner.

## Visually guided reaching in adult baboons

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MacNeilage et al. suggest that simple reaching and grasping tasks provide good means of demonstrating left-hand use in nonhuman primates. The authors propose a series of conditions for the emergence of this left bias, among which are: (1) the need for the task to require visual control of the hand movement; (2) the use of adult subjects; (3) a nonstereotyped situation (the model for this being "a simple reaching in the field"); and (4) the use of a task that does not induce the choice of one or the other hand.

In order to test the MacNeilage et al. hypothesis of left-hand preference experimentally for visually guided movements, we recorded the behavior of a group of adult Guinea baboons ( $n =$

Table 1 (Vauclair and Fagot). *Distribution of preferential biases for adult baboons (Amb = ambidextrous)*

Subject	Present study		Previous study
	% Right	Bias	
Female	68.8	Right	Right
Female	52.8	Amb	Amb
Female	83.2	Right	Right
Female	77.3	Right	Amb
Female	31.9	Left	Amb
Female	15.5	Left	Left
Male	98.5	Right	Amb
Male	96.5	Right	Right
Male	100	Right	Right
Male	95.2	Right	Right
Male	45.5	Amb	Amb

11, average age: 7–8 years) living in a seminatural environment (an enclosure of 640 m<sup>2</sup>). We devised a simple task of food reaching by randomly scattering a mixture of wheat, barley, and broken corn grains on the ground of the enclosure; the monkeys could rapidly pick these up and bring them to their mouths. The main characteristics of this situation were the following: (1) The size and position of the target involved a constant visual orientation because the grains were distributed with different densities on a nonhomogeneous surface; (2) the task was novel, in the sense that the food was not part of the everyday diet of the monkeys; and (3) the food was always picked up unimanually and brought directly to the mouth (no intervention of a concurrent hand). Moreover, we controlled for the posture of the animal and the position of the object by counting only those reaches that were performed while the animals were seated and when the food was picked up in the midsagittal plane or by crossreaching. Finally, we were able to control for the baboons' manual preferences by comparing their distribution of left/right biases with data on spontaneous handedness gathered two years before the present study (Vauclair & Fagot, in press). The results for this pure reaching task (a minimum of 100 grasps/subject) are summarized in Table 1, along with the data obtained on this same group in the previous study.

Although our data indicate a larger proportion of right-handers than left-handers, this asymmetry is not statistically significant. In fact, neither set of results validates MacNeilage et al.'s theory; rather, our results conform to the pattern usually observed in nonhuman primates – namely, that no systematic bias exists towards the right or the left.

We feel that MacNeilage et al.'s model might be investigated not in adults but rather in young animals and, more precisely, in the first reaching attempts of infants. MacNeilage et al. have already commented on the changes in the strength of preference observed between infant, juvenile, and adult primates (we have shown this same effect in our study with baboons; Vauclair & Fagot, in press). But we also have evidence from our own observations: By the end of its first month, an infant baboon clearly used the left hand more than the right when it first reached for objects; it is interesting that this left preference was concurrent with the emergence of the precision grip. Such initial uses of the left hand have also been seen in a 15-week-old chimpanzee (Chorazyna 1976) prior to the establishment of a stabilized right preference, and they have also been reported for human infants (Gesell & Ames 1947; Seth 1973). In short, it might be more valuable to look at ontogeny than at phylogeny to verify some of the target article's interesting hypotheses.

## Or in the hand, or in the heart? Alternative routes to lateralization

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MacNeilage et al.'s examination of the evidence for primate handedness is extremely thorough, but I do not feel compelled to change the conclusion I drew at the end of the review from which they quote (Walker 1980): Human handedness is secondary to language (i.e., it is not inherited from earlier primate handedness). I have two reasons for not retracting this conclusion. First, despite the thoroughness with which their case is stated, it remains possible to doubt the authors' claim that there are population-level asymmetries of hand preference of some significance in nonhuman primates. Second, there are positive reasons for preferring the view that human handedness depends on language.

It does not seem to me that the evidence on primate handedness presented by MacNeilage et al. justifies their conclusion. For example, they cite a claim (LeGros Clark 1927) that one gorilla was observed to be strongly right-handed, and they add this to various other flimsy claims that gorillas are right-handed. In fact, the gorilla referred to by LeGros Clark was intensively domesticated at 15 Sloane Street, London for 2 years from 1918, with such success that his table manners were reported to be much admired: He always took afternoon tea, and coffee after dinner (Cunningham 1921). This animal might be cited as an example of primate behavioural plasticity, but surely not as evidence for population right-handedness. It is particularly striking that MacNeilage et al. give about the same amount of weight to Jane Goodall's quarter-century of observations of chimpanzees in the wild, which have revealed many pertinent examples of tool use and social skill, but no sign whatever of group handedness (e.g., Kummer & Goodall 1985). In the case of more empirical studies, the authors overinterpret a nonsignificant left-hand reaching preference found by Beck and Barton (1972).

I share MacNeilage et al.'s concern that an account should be given of the relation between human and other primate behaviours that is not in conflict with the theory of evolution. I do not believe, however, that this demands that all features of human psychology be directly traceable to traits present in other extant species of anthropoidea. It would not violate evolutionary theory if human handedness were derivative from language, rather than an adaptation directly affected by Mendelian selection. One reason for this assertion is that the variance associated with human hemispheric specialization for language functions is much smaller than the variance associated with handedness. Another reason is that the genes are usually left-right agnostic, and therefore any Mendelian selection can act only on sensitivity to somatic left-right gradients (Collins 1985; Morgan & Corballis 1978). As a counter-hypothesis that takes account of both these factors, I suggest that human handedness derives indirectly from a little remarked, but quite unequivocal, somatic asymmetry in primate (and indeed mammalian) innervation of the vocal apparatus:

1. The intrinsic muscles of the human larynx are innervated by the left and right recurrent laryngeal nerves, which branch off from the vagus.
2. The left branch arises from below the aorta, which it partly encircles, whereas the right begins below the subclavian artery.
3. Thus, taking into account individual variations, the left branch of the recurrent laryngeal nerve is considerably longer than the right and gives off more oesophageal branches.
4. The dependence of the voice on these nerves was established in the sixteenth century by Vesalius, using a pig.
5. The greater length and differing course of the left branch are held to be responsible for the finding that the left vocal cord is affected twice as frequently as the right in human laryngeal palsy (Greene 1980).

The foregoing might suggest to some that, given a degree of crossed-lateral control, there could be natural selection of left-hemisphere dominance for laryngeal control. It is at least equally plausible, however, that the shorter route to the larynx on the right side should provide an exclusively ontogenetic increase in the probability of left-hemisphere control of speech. Indeed, this could be deduced as a corollary of the theories presented under the heading of "The ordering of articulatory events" by Lenneberg (1967), who stressed the complexities of coordinating the very rapid and highly ordered muscular movements involved in vocalization. These complexities arise from innervation times being as long as, or longer than, the duration of some of the articulatory events they control, and from the differential innervation times needed by various parts of the vocal apparatus. The latter are largely due to the long innervation time required by the intrinsic laryngeal muscles, which may be two or three times longer than the innervation times required by the oral cavity. Either branch of the recurrent laryngeal nerve is capable of sustaining speech in adult patients, but it is arguable that problems of coordination would be most acute during fine timing operations when the left and right laryngeal muscles (in the case of the transverse arytenoid, different sides of the same muscle) require different central initiation times for their peripheral activation to be synchronous. In any event, crossed-lateral control in the corticobulbar tract may mean that left-hemisphere output reaches the larynx sooner than does output from the right; it is conceivable that this could supply a developmental impetus for left-hemisphere control of vocalisation in the human species as an aspect of the more general evolutionary factors that led articulate speech to arise from far more rudimentary forms of vocal expression (Walker 1986). Once the left hemisphere is dominant for speech, there are various ways in which hand preference could be probabilistically affected – either psychologically via the action-directing properties of inner speech or, more physiologically, by generalisation in the initiation of complex motor acts.

This alternative may be regarded as even more speculative than MacNeilage et al.'s own account, and they may find the details easy to dismiss (e.g., MacNeilage 1970). But my general point is that features shared by human ancestors and those of living primates could have been selectively important in the human line to the extent that humans and apes are distinctively different. We should not feel obliged to abandon evolutionary accounts if other primates do not share our trait of handedness. I agree with the authors, however, that there is a large theoretical gap in explanations of the relation between human and primate cerebral lateralization. If their empirical evidence becomes stronger then, in order to fill the gap, I will gladly shift my allegiance from an asymmetry within the primate heart to a difference between the primate hands.

## Primate handedness: Inadequate analysis, invalid conclusions

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MacNeilage et al. base their argument that monkeys and apes prefer to reach with the left and manipulate with the right hand primarily on their interpretation of handedness studies with *Macaca* spp. Their interpretation is inadequate and their conclusions are unsound because they neglect two salient facts: Many monkeys have no significant hand preference, and monkeys' preferences are inconsistent in time and over different tests. Consideration of these facts vitiates the authors' analyses of "Studies showing asymmetry of preference" (see sect. 2.1). **Japanese studies.** MacNeilage et al. claim Table 1 of the target article shows that monkeys prefer to reach with the left hand, in

spite of the fact that 62% of the sample had right or no preferences, and that the data are consistent with the hypothesis that right, left, and no preferences are equally frequent [ $\chi^2(2) = 5.56$ , N.S.].

Table 5 is presented in support of the statement that the number of monkeys with significant hand preferences increases with age. This claim is invalid. There is no significant difference in the proportion of animals with significant preferences between the youngest and oldest groups [ $\chi^2(1) = 1.04$ , N.S.].

Kawai (1967) and Tokuda (1969) tested hand preferences in the same set of 21 monkeys; 48% (10/21) had discordant preferences on the two tests. Tokuda noted that these animals yielded similar distributions of preferences on the two tests, in spite of the inconsistent behavior of almost half the subjects. This shows that population values may stay constant while individuals' preferences change drastically.

**Studies by Ettlenger's group.** MacNeilage et al. also construe the results of Ettlenger et al. in Table 2 as evidence for a left-hand preference in reaching by monkeys, even though 67 and 69% of the monkeys did not have a significant left preference in early and later testing. The case for predominant left preferences in these monkeys is further weakened by Ettlenger's (1961) observation that 45% (18/40) of his subjects had discrepant preferences on the early and later tests.

**The Beck and Barton study.** The thesis that monkeys reach with the left hand and manipulate with the right is apparently based largely upon MacNeilage et al.'s interpretation of Beck and Barton's (1972) group medians. The scores of individual subjects were examined to determine the extent to which the behavior of the monkeys conformed to the pattern postulated by MacNeilage et al. The data in my Tables 1 and 2 afford scant support for the authors' position. My Table 1 shows the number of right, left, or no preferences for each monkey, the percentage of right preferences, and the median percentage of right responses on all 14 manipulation tests. Three monkeys (5, 8, 9) preferred the right hand on less than half the tests, and used the right hand on fewer than 50% of all trials; two others (2 and 4) preferred the right hand on just half the manipulation tests. For the total sample of 10 monkeys, significant right preferences were seen on only 54% of the tests.

The monkeys' preferences on 17 reach tests are summarized in my Table 2. Six monkeys (2, 3, 5, 6, 7, and 9) preferred the right, rather than the left, hand on at least half the reach tests. The overall median scores show that monkeys 6 and 9 were right-handed, and that animals 2, 3, and 5 had median prefer-

Table 1 (Warren). *Preferences of Beck and Barton's (1972) monkeys on 14 manipulation tests*

Monkey	Significant preference			% Right preferences	Median % right responses
	Left	None	Right		
1	5	0	9	64	93
2	4	3	7	50	73
3	3	1	10	71	82
4	6	1	7	50	64
5	5	3	6	43	46
6	2	3	9	64	87
7	4	2	8	57	72
8	7	1	6	43	46
9	5	5	4	29	52
10	4	0	10	71	94
$\Sigma$	45	19	76		
%	32	14	54		

Table 2 (Warren). *Preferences of Beck and Barton's (1972) monkeys on 17 reach tests*

Monkey	Significant preference			% Left preferences	Median % left responses
	Left	None	Right		
1	12	4	1	71	92
2	5	7	5	29	54
3	5	5	7	29	45
4	10	5	2	59	71
5	8	8	1	47	53
6	4	5	8	24	40
7	7	6	4	41	62
8	11	5	1	65	90
9	3	5	9	18	38
10	15	2	0	88	85
$\Sigma$	80	52	38		
%	47	31	22		

ences within  $\pm 5\%$  of 50% and were therefore lacking a preference in reaching. Less than half (47%) of the tests revealed a significant preference for the left hand in reaching.

If MacNeilage et al. are right in their assertion that monkeys manipulate with the right hand and reach with the left, there should be a high positive correlation between right responses in manipulation and left responses in reaching. There is not. The rank order correlation is  $+.18$ ;  $.56$  is required for significance at the  $.05$  level of confidence.

**Deuel and Dunlop.** MacNeilage et al. fail to give adequate weight to an important aspect of Deuel and Dunlop's (1980) experiment. They observed 20 monkeys on three reach tests in a primate chair; they report a high degree of inconsistency in the preferences of individual monkeys; 30% of their subjects changed preferences between tests 1 and 2, and 45% between tests 2 and 3. Only 8 monkeys responded consistently on all three tests, and 3 of the 8 were consistently ambilateral (showed no preference).

From early infancy, humans manifest stable hand preferences that are consistent in diverse situations and in multiple manual activities. Monkeys do not. There is no compelling reason to regard "handedness" in monkeys as either homologous or analogous to handedness in humans.

## Authors' Response

### Primate predatory, postural, and prehensile proclivities and professional peer pressures: Postscripts

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As usual, peer commentaries present a mix of plaudits, complaints, and different perspectives. We will take up



the issues raised by the reviewers in the following order: (1) questions of data analysis; (2) new evidence provided by the commentators and by additional studies; (3) logical and empirical questions concerning the relations among handedness, manual ability, and hemispheric specialization; (4) the broad context of primate handedness, including other asymmetries in humans, nonhuman primates, and other animals; (5) criticisms of our overall approach and suggestions for alternative approaches. At the conclusion we restate our position on primate handedness in light of the commentaries and the earlier discussion.

Before we begin, let us mention one fact that readers should bear in mind as they consider these critiques and our responses to them. We wrote this review in the context of what we took to be, in general, a rather uncritical acceptance of the null hypothesis, represented by most of the references given at the beginning of the target article. Much of the consensus was based on secondary sources, and no single review included as many as one-third of the primary sources on the topic. In that context, we saw some merit in attempting an exhaustive review, and, in cases of uncertainty, we bent over backward to support the conclusion opposite to the currently fashionable one, hoping that this would eventually allow the dust to settle in the right place. We also saw, as do many of the commentators, some heuristic merit in attempting to give a comprehensive and testable account of the results.

**Data analysis: Is the evidence as we presented it?** Several commentators (Annett, Cicchetti, Corballis, Jerison, McKeever, Steklis & Marchant, Warren) criticize us for comparing numbers of left and right preferences, while disregarding animals (or tasks) with no preferences. Cicchetti's comments are the most constructive. For distributions of left, right, and null preferences, he recommends a series of five chi-square tests, proceeding systematically from a test for overall hand preferences to a test for left versus right preferences among those animals that do show a preference (the test we used). He also recommends a conservative correction for two cell tables (a correction not mentioned by Ferguson, 1981, or any of the several standard texts we consulted).

For our Table 2, Cicchetti's procedure leads to the same conclusions that we reached, though with a lower level of significance, due to the correction. For Table 1, on the other hand, we would have been blocked from further tests because, as Warren points out, the test for overall hand preferences is not significant. Here, given the paucity of data in an area that research has scarcely begun to explore, we are inclined to follow our noses and do the left-right tests anyway. When we apply Cicchetti's correction, we find significance levels slightly reduced from those we originally reported: For study A,  $\chi^2 L/R(1) = 3.67, .1 > p > .05$ ; for studies B and C combined,  $\chi^2 L/R(1) = 5.21, .05 > p > .02$ .

We take these to be interesting and suggestive results. For, as McKeever intimates, we need not expect that population biases will be as extreme as in the human population. Consistent preferences, within individual animals across some universe of functionally equivalent manual acts, may be of interest even in the absence of population bias (*pace Annett*), for they may reflect the emergence of "manual specialization . . . before the di-

rection of asymmetry became biased at a population level" (Guiard). Here, then, is one sound reason for disregarding animals that show no preference and for paying attention to those that do. At the same time, we should note that the conditions for establishing preferences have often been less than optimal. In instances of prolonged exposure to challenging situations (e.g., Beck & Barton 1972; Trevarthen 1978), animals without preference are not found. For example Warren's Tables 1 and 2 show that all animals had a significant preference for over 60% of the individual acts. One might argue that training artificially induces preferences, and presumably this is what Jerison has in mind when he characterizes the high median preferences on certain tasks in the Beck and Barton study as "stereotypy rather than handedness." However, if population biases are found in the absence of environmental biases, this argument loses its force.

In any event, both Guiard and Michel & Harkins correctly point out that although we adduced evidence for population biases, as well as for consistent preferences within individual animals and across small samples of animals even in the absence of a population bias, we did not distinguish among these types of evidence, as we should have done.

One consequence of this failure is that we confused McManus, who misinterpreted several of our *t*-tests. For example, he characterizes our *t*-tests of hand preferences in four lowland gorillas (Fischer, Meunier & White 1982) as an "inappropriate use of the *t*-test for assessing population lateralization." McManus takes our estimate of the variance of hand use in these gorillas to be an estimate of the population variance in laterality. However, we explicitly state that "four subjects are not enough to give a statistically significant hand preference asymmetry in the sample." Our estimate of variance was not for population laterality but for the infinite population of hand use acts for these four gorillas, sampled by Fischer et al., and our *t*-test was for the significance of the hand preferences displayed by these animals. No assumptions of the *t*-test have been violated, nor have we failed to recognize that the binomial and the *t*-test are here "asking different questions." (Quis custodiet ipsos custodes?)

A number of commentators criticize our analysis of the Beck and Barton study. What seemed the most trenchant criticisms came from Jerison and from Warren. They believe that the best way to analyze these data is to compute, for each animal, the percentage of reaching and manipulative acts on which the animal made more than 50% of its responses with one hand. Thus they collapse across acts within a monkey – treating each individual act as equally important – and find no significant group effects. The central point of our analysis, however, was that hand use may vary with task demands. Here we are handicapped by the problem that Tomasello notes: the lack of optimal data to test our hypothesis. Specifically, scores for individual monkeys on individual acts were not available. We were therefore obliged to fall back on the median preference levels within the group for individual acts, as reported in our Table 3. The table shows that there was a wide range of preference levels within the sets of reaching and manipulative acts, and that within each set, preference levels were related to the type of task. Left-hand preference levels increased with added task demands, and right-hand preferences increased for the



single finger manipulations where other task demands were low. Unlike Jerison and Warren (also Annett and McKeever, who fear sampling bias) we were struck by the evidence that at least one-half of a group of nonhuman primates could approximate a 100% preference level for the same hand on any subset of acts, let alone that the high preferences could be for a different hand on two functionally different task subsets. We do not see parallels to these levels in studies of groups of substantial size, with the exception of the study of Sanford, Guin, and Ward (1984).

We presented Figure 1 to show that these high preference levels for opposite hands were probably not being produced by different subsets of animals, and that they therefore represented population-level trends. An alternative way of confirming such a trend is to consider only instances of significant preferences for individual animals on single acts. From the data in Warren's Tables 1 and 2 (left-hand columns) we can determine, for each animal, the number of individual acts on which it behaved or did not behave as predicted by the hypothesis (left-reach, right-manipulate). We sum significant right preferences for manipulation (Table 1) and significant left preferences for reaching (Table 2), and we compare this value with the sum of the significant reverse preferences from the two tables. Nine out of ten animals have more significant preferences that fit the hypothesis (mean: 15.6) than significant preferences that do not (mean: 8.3). The difference is significant on a one-tailed matched pairs *t*-test, with  $t(9) = 3.10$ ,  $p < .01$ .

The stance taken by Jerison and Warren on the Beck and Barton results is a further example of the approach to this field that we criticize in the target article, one that eschews attention to the role of task differences in revealing manual laterality, either explicitly, as in these cases, or implicitly. Obviously, humans as a group and as individuals show, with some reliability, a wide spectrum of strengths of hand preference across individual acts. To analyze the data as Jerison and Warren have done is to deny the possibility that an analogous pattern in monkeys might have some significance. We believe that this insensitivity to the details of primate manual function is the main reason that the case we make for primate handedness is as weak as it is. However, in light of the above analysis it seems unrealistic to deny that there is a case to be made.

Jerison gives the impression that all of our data are suspect by saying "I didn't check all of the data" and noting that he found problems wherever he did look. In perhaps the most extreme example he suggests that we based a conclusion about eight lorises on one loris. He makes his case by citing the phrase "the loris" from the paper by Subramoniam (1957), wishing the reader to conclude that the definite article was used in the specific, not the generic, sense. We will provide the full context for our conclusion and let the reader judge. In her introduction, Subramoniam says, "The following is the result of an attempt to study the habits of eight specimens kept in captivity with as much simulation as possible of the natural arboreal environment" (p. 387). The full text of the section relevant to hand preferences is as follows: "Certain noteworthy characteristics were observed in the method of killing the insects and eating them. Whether the insect lay on the floor of the cage, or was placed on the

branches, or was proffered in the cage at the end of a pair of forceps, the loris never picked it with its mouth. The insect is first of all caught by both its hands if the victim is a big one, or by the left hand if the insect is a small one — always and consistently by the left hand. Only on one occasion the loris was found using the right hand to catch an insect, and at that time the left hand was gripping a support" (p. 388). The reader can now decide whether the author is talking about one loris (and one insect) or not.

Jerison notes that we omitted two "sets of data," reported by Itani, Tokuda, Furuya, Kano, and Shin (1963), that did not support the left-preference trend. These were omitted primarily because they were unpublished studies not accompanied by any description. We were also influenced by the failure to mention these results in two subsequent published field studies of Japanese macaques, including one by Tokuda, a co-author of the 1963 study, who did not mention these studies in his review of previous studies (Kawai 1967; Tokuda 1969). We hope that the completeness of our coverage of the published studies will reassure the reader against charges of selectivity. The commentators only added two published studies on handedness to those we described (Bressard & Bresson 1983; Brooker et al. 1981) and neither of these would have changed the picture we presented. In response to Walker's comments on selectivity, we included a reference to the acculturated gorilla John Daniel for the sake of completeness (prompted by a referee) and do not use this unfortunate animal to support our case. The paper Walker said we should have included (Kummer & Goodall 1985) does not contain anything about handedness.

There are two other points at which Jerison questions our interpretation of the data. He echoes our reservations about the significant right-hand preferences found in later testing of marmosets by Rothe (1973), but treats his reservations as a criticism of our stance. Like us, he mentioned his concern with statements by the author about the variability of the animals, despite the statistically significant result which was cited. We agree that a serial trend in tasks 2 through 7 is incomplete, if animals are ambidextrous on task 7. This is a more serious problem if, like Jerison, one treats all tasks as essentially the same rather than emphasizing, as we do, the importance of task differences. Jerison's final question concerns the study of Itani et al. (1963). He believes that the trend toward higher preferences in older animals in this study is not distinguishable from practice effects in the artificial feeding situation, although there is nothing to indicate that older animals received more practice than younger ones.

Like Jerison, Warren is unequivocally negative about the way we analyze the data, on the grounds that "many monkeys have no significant preference, and monkeys' preferences are inconsistent in time and over different tests." Despite the evidence we have cited to the contrary, and in disagreement with the evidence presented in the commentaries of Lehman and Vauclair & Fagot, Warren reiterates his claim (Warren 1977a; 1977b; 1980) that inconsistency is the only theoretically significant serial and intertask trend in monkey handedness research. He notes that the serial trend toward increasing preference with age in our Table 5 is not significant, but he does not comment on the data of Kruper, Boyle, and

Patton (1966) and Lehman (1978; 1980a) in which it is. In providing evidence of intertask inconsistency Warren combines cases in which there is a change from a significant preference in one hand to the other and cases in which change from preference to no preference and vice versa occurred within a set of tasks. The occurrence of the latter may be better regarded as related to strength of preference rather than to consistency. Quite different results are obtained depending on whether these two types of result are combined or considered separately. For example, Warren notes that 10 of 21 monkeys had "discordant preferences" on a reaching task (Tokuda 1969) and a catching task (Kawai 1967). However, 6 of the 8 animals that had significant hand preferences on both acts had the same preference. He also points out that in the Deuel and Dunlop study (1980) 30% of a group of 20 monkeys "changed preferences" between test 1 and test 2 of a group of three tests, and 45% changed preferences from test 2 to test 3. However, only 1 of the 20 animals changed from a significant preference for one hand to the other within the set of 3 tasks.

We would argue that Warren not only underestimates the consistency of monkey hand preferences, but, as we intimated earlier, he also overestimates the consistency of human preferences. He contends that "from early infancy, humans manifest stable hand preferences that are consistent in diverse situations and in multiple manual activities." It is well known that infant preferences can fluctuate considerably during the first year of life. In a review of research on early reaching Young, Segalowitz, Corter, and Trehub (1983) state: "Discontinuities, reversals and shifts in hand preference are suggested." It is quite likely that these shifts are principled (Michel & Harkins give one interesting example), but nevertheless the fact is that they occur. Relatively little has been done to test humans and monkeys under precisely comparable conditions. However, Harris and Carlson at Michigan State University (whose contribution is to appear in Continuing Commentary) have recently found that neither individual children (Carlson & Harris 1985) nor individual adults typically show anything close to a unanimous choice of one hand in reaching for objects in a simple reaching test of the kind used in many studies of monkeys (in which the target object is placed in one of three locations in front of the subject). As in monkeys (Cronholm, Grodsky & Behar 1963), the position of the object is a significant variable in determining which hand is used. In addition, as Bryden & Steenhuis point out, adults respond to a number of items in handedness questionnaires by indicating no preference. We would agree with Calvin that criteria such as those used by Warren lead to the premature rejection of the proposition that monkey handedness shares certain characteristics with human handedness.

To turn now to other commentators: Steklis & Marchant criticize us for pooling the results of studies which might be (e.g., the Japanese field studies) or are (e.g., the studies of Ettlinger and colleagues) dissimilar. This is not ideal. We pooled partly to increase sample size but, more particularly, because in both sets of studies all the published findings on a particular type of experimental paradigm showed the same trend.<sup>1</sup> Moreover, the use of visual pretraining trials in tactile discrimination tasks may go some way toward equating the two types of task, and so

may justify our pooling the Ettlinger studies. Of course, as Corballis and others point out, these and other steps, including formulation of a set of task categories, are post hoc and without independent justification. Like Kolb & Fantie we would prefer a better approach to behavioral classification. The work of Goodale may contain some valuable leads in this respect.

Corballis raises the issue of whether the relatively small number of statistically significant results we noted might not all be due to "biases in the immediate experimental environment." Although we cannot rule this out, it seems to be a better example of grasping for straws than the behaviors that Steklis & Marchant attribute to us under that heading.

Guiard and McManus both raise the problem of the file-drawer effect. We acknowledge this problem with respect to the null hypothesis (McManus), but note that peer commentary provides an avenue for the resurrection of such data. However, our analysis leads us to believe that much of the data on this topic that languishes in file drawers is in the right place for methodological reasons. Guiard suspects that the file drawer might also contain counterintuitive cases of left-hand preference for manipulation. If so, the trend should also apply to reaching, suggesting that the published trends for left-hand reaching are just the tip of the iceberg.

**New evidence: Human studies.** Several commentators consider further evidence from studies of humans that may bear on our hypotheses. Apart from the data of Guiard, Diaz, and Beaubaton (1983) that we cited in the target article, no data have been presented to show that the left hand of humans is better than the right at any aspect of reaching. Goodale presents data showing a right-hand advantage in adults. Nor is there any unimanual task that human right-handers, across cultures, prefer to do with their left hand. Evidently our proposed vestige of a left-hand reaching preference in humans is not confirmed. This leaves us with the less neat but not totally implausible conclusion that some special ability of the left hand possessed by some of our predecessors is no longer present.

Perhaps Goodale's suggestion that the demand for precision in timing shifted hand preference from the left in monkeys to the right in humans is the correct one, the result being that the right hand is now typically better than the left in all respects. As Goodale points out, this view is consistent with the possibility that a right-hemisphere visuospatial specialization is part of our prosimian heritage. Goodale's finding, from his work on patients, that "the efficient visually guided reaching observed in humans would appear to depend on mechanisms in both hemispheres" is important from our standpoint. In particular, the finding that right-hemisphere damage increases the latency of initiation of right-hand movements is consistent with our view that the right-hemisphere visuospatial specialization evolved primarily for off-line perceptuomotor organization (MacNeilage, in press a).

Two reasons for deriving this conclusion from the behavior of prosimians have been suggested:

First, once a stationary prey is sighted (and/or heard) movements of the predator into its vicinity are not dependent in a moment-to-moment manner on details of visual or auditory feedback from the prey. They are

dependent on the structure of the arboreal environment between the predator and the prey. Nevertheless, the fact that the reach will eventually be made with the left limb may give the right hemisphere the primary guiding role in this behavior. Second, and perhaps more important, once in the vicinity of the prey, the detailed "plan" for the forthcoming ballistic movement of the left arm is totally established off-line, that is, before the movement is made. Even computations underlying slower reaches for inanimate objects, more prominent in monkeys, may be primarily made in advance. The evolution in the right hemisphere of this off-line relation between perception and action, with the accompanying capacity for relative decoupling of the two, may be partially responsible for the fact that many aspects of right hemispheric specialization in humans, for both the extrapersonal and the intrapersonal world, now seem to be purely perceptual, and not related to action. The possibility that perceptual and motor functions could be decoupled may also have allowed the left limb reaching preference to drop out in hominids, perhaps under selection pressures favoring the manipulative capacity of the right limb, while retaining the right hemisphere perceptual specializations. [MacNeilage, in press a]

In response to the Michel & Harkins conclusion from human ontogenetic data that the evolution of bimanual coordination could not have eliminated a left-reaching preference, a clarification of our position is necessary (see also MacNeilage, in press a). We argue in the target article that the right-hand preference evolves "for foraging and processing food." The preference is for the right because a preexisting postural asymmetry makes (1) the right side more suitable for leading in whole-body interaction with the environment in foraging (e.g., bending branches, prying off dead bark, breaking off food objects against mechanical resistance) and (2) the right hand more adept at fine on-line sensorimotor control required for both foraging itself and bimanual coordination. We consider that the combination of these properties (sidedness and manipulative ability), not just the right-hand role in bimanual coordination, would tend to preempt the left-hand preference for reaching. We find the link between posture and handedness in infants noted by Michel & Harkins and by Kolb & Fantic very attractive. Whether handedness is an ontogenetic consequence of a potentiating effect of posture, as Michel & Harkins propose, or rather under independent genetic and epigenetic control is a question that genetic research will ultimately decide. In either event, the evolutionarily earlier postural asymmetry would probably be more evident than handedness in the earliest stages of infancy.

One of us (MacNeilage 1986) has shared the interest of Brésard & Bresson and Corballis in the possibility that the not infrequent reports of left-hand reaching preferences in early human infancy might be relevant to our evolutionary hypotheses. However, in an analysis of this question, Young et al. (1983) note that reports of left-hand preference are very much in the minority. Their conclusion that "the right upper limb seems preferred for directed activities, and the left for nondirected ones" (p. 30) (though counter to Warren's claimed homogeneity of preference in infants) does not appear to be consistent with our phylogenetic hypotheses. However, with some

modification of the hypothesis, it may be, as we will see later.

Several commentators make interesting observations on the possible importance to the understanding of hand use of additional variables that have not yet been satisfactorily considered in studies of primate handedness. Etlinger raises the plausible possibility that reaching preference might depend on "whether the animal is reaching to palpate, to retrieve, and/or to manipulate." He suggests that a common variable of reaching to palpate might account for the similar preference trends in the Japanese field studies and the studies of two-choice discrimination. Although this is possible, we feel that when animals are being fed routinely by experimenters the consistency of the food object rapidly becomes predictable to the animal, so that palpation would cease to play a role. The importance of whether or not the animal is reaching to manipulate is also emphasized by Bradshaw, Heuer, and Michel & Harkins. Bradshaw and Heuer suggest that left-hand reaching could be prompted by choice of the right hand for manipulation in a subsequent bimanual mode, and Michel & Harkins report that children seem to go through just such a phase. We would add our own suggestion – apropos of the Vauclair & Fagot finding (discussed later) – that the precision required in prehension might be an important variable. Finally, let us add that nobody, to our knowledge, has systematically studied bimanual coordination in primates in the most natural situation – that is, when the supporting hand holds an object to be manipulated in intrapersonal space. There may be a more invariant mode of operation in this condition than in cases of interaction with extrapersonal space, where postural contingencies may lead to more variability of hand preference.

**New findings on primate handedness.** Additional findings that have become known to us since we wrote the target article are summarized in Table 1. The positive findings provide additional support for our contention that handedness in nonhuman primates needs to be reexamined, but negative findings continue to accumulate.

Ward's group, who found the left-hand reaching preference in bush babies (Sanford, Guin & Ward 1984), continues to find left-hand reaching preferences in prosimians (Ward's contribution is to appear in Continuing Commentary). In work in progress they have found 24 lemurs with a left-hand preference and 7 with a right-hand preference. The breakdown of the results among 3 species is as follows: ruffed lemurs (*Varecia variegata*), 4 left, no right; ring-tailed lemurs (*Lemur catta*), 9 left, 3 right; black lemurs (*Lemur macaco*), 11 left, 4 right.

Moving next to monkeys, the most marked asymmetry in hand preference yet reported in nonhuman primates has been observed by Patricia Kuhl at the University of Washington (to appear in Continuing Commentary). She notes that all 30 monkeys (macaques, 3 species) she has tested on auditory discrimination tasks involving speech stimuli over the past 10 years have favored the right hand for the required response. Four particular aspects of this work should be noted: (1) The animals were young – 3 years of age and younger, (2) visual guidance of the hand was not possible, (3) the response key was located in the midline, and (4) the response complex – pressing, holding, and releasing – was of a manipulative type. We agree

Table 1 (Response). *Additional findings on primate handedness*

Left preference	No preference	Right preference
<b>Prosimians</b>		
Reaching; lemurs (Ward)		
<b>Monkeys</b>		
	Reaching and exploring; macaques (Brooker et al. 1981)	Auditory discrimination-key press; macaques (Kuhl)
Reaching; macaques (Deuel & Schaffer)	Various tasks; macaques (Deuel & Schaffer)	
	Lever pulling; baboons (Glezer)	
	Two-choice visual discrimination; macaques (Lehman)	
	Reaching; baboons (Vauclair & Fagot)	
<b>Apes</b>		
	Chimpanzees and orangutans (Brésard & Bresson)	Gorillas (Brésard & Bresson)
	Various activities; 4 species (Heestand 1986)	Locomotor initiation; 4 species (Heestand 1986)
	Reaching; chimpanzees (MacNeilage)	
	Various activities; chimpanzees (Steklis & Marchant)	

with Kuhl's (forthcoming) interpretation of these results as favorable to our hypotheses, but we also agree that, in this task, the possible role of a left-hemisphere specialization for auditory discrimination of certain types of sound must be considered.

Using the same tasks as Deuel and Dunlop (1980), Deuel & Schaffer present results from a study of 41 *Macaca fascicularis* monkeys. They take their findings to be counterevidence against our hypotheses in five out of six tasks. The only positive finding was a significant left-hand preference in a task requiring prehension of a moving food object. There may be three reasons why these results were not more consistent with our hypotheses. First, the primate chair is an unnatural postural situation for the animal, and this may have had a destabilizing effect on normal motor function. Second, the manipulative tasks were not very difficult – as compared,

for example, with the single-finger, recessed-hasop opening acts of the Beck and Barton study – and subjects had no more than 24 trials of practice on each task. Third, we would need to be convinced that the “wild-reared naive” monkeys were sufficiently adapted to laboratory conditions to behave in as natural a way as the conditions permit. One might ask how using the primate chair could interfere with preferences in the Deuel & Schaffer study, but not in the study of Kuhl (forthcoming), who also used the primate chair. The differences may be partly due to task experience. Whereas the animals studied by Deuel & Schaffer never had more than 24 trials on any task, Kuhl's animals had a two-hour training session every day for two years.

Deuel & Schaffer mention again the Deuel and Dunlop (1980) finding, cited in the target article, that a group of 15 animals showed opposite preferences on two simple reaching tasks, involving in one case the primate chair and in the other the Wisconsin General Testing Apparatus (WGTA). (Incidentally it was our analysis, not Deuel and Dunlop's, that led to the finding that the right-hand preference in the WGTA situation was statistically significant.) They argue that these opposite preferences are a function of the experimental situations “rather than . . . innate cerebral dominance.” We believe that the two conclusions are not mutually exclusive, and this dichotomy, if replicable, may be found to be due to differences in postural demands in the two situations.

Lehman reports an unpublished finding of the absence of a significant left-hand preference in a two-choice visual discrimination situation which appears to disconfirm the findings of Ettliger and his colleagues. A difference between this study and the studies of Ettliger et al. is that in this study the two stimuli were arranged vertically, not horizontally. It may be that this arrangement is less conducive to a lateral bias in response than when two stimuli are arranged horizontally.

Vauclair & Fagot present what appears to be a clear disconfirmation of our hypothesis that there is a left-hand reaching preference in monkeys. They found a 7:2 ratio of right- to left-hand preferences in 11 Guinea baboons (*Papio papio*) reaching for food in a field-like situation. This result, though not statistically significant, suggests to us that our claim for monkey left-hand reaching in field situations might be oversimplified. Either there are species differences in this behavior, or the detailed conditions of reaching might be important (or both). As to the experimental conditions, it should be noted that all data were gathered with animals in a sitting position, so that the other upper limb was not required for postural support. Moreover, the small size of the food objects (grains of wheat, barley, and broken corn) may have weighted the task in the direction of the supposedly more dextrous right hand. It is of interest that Harris & Carlson (to appear in Continuing Commentary) have found higher right-hand preferences in adult human right-handers when they are picking up objects that can be picked up with a “pincer” grip (thumb and forefinger juxtaposed on the object) than when picking up objects that require a whole-hand grip. Finally, Glezer reports a failure to find population-level hand preferences in baboons in a lever-pulling task, but gives no details.<sup>2</sup>

We turn now to findings on apes. Despite a good deal of new evidence, the question of handedness in the great

apes remains a confusing one. In a doctoral dissertation, Heestand (1986) studied hand preferences in 70 apes representing four species (*Gorilla gorilla*, *Pongo pygmaeus*, *Pan troglodytes*, and *Symphalangus syndactylus*) during various activities. The only category to show significant population-level hand preferences (in all species) was initiation of locomotion, in which both the upper and lower right limbs were favored. (Forsythe, in Ward's laboratory, found the same result in the group of four ruffed lemurs with a left-hand reaching preference.) Steklis & Marchant concur with the negative findings of Heestand in their study of various activities (not including locomotor initiation) in chimpanzees. In addition, one of us (MacNeilage, unpublished) found no population-level preference in a study of 591 reaches in a group of 51 chimpanzees in an open-field situation. In contrast to most other results, generally positive findings are reported by Brésard & Bresson, though without detail. They report that a group of 27 gorillas "appear to be mostly right-handed," citing two chi-square analyses for this result, both significant beyond the .001 level. They report a similar tendency in a small group of orangutans. In addition, they report a nonsignificant trend toward left-handedness in chimpanzees. Finally, although the development of handedness in other primates is of considerable interest, especially in comparison with human infant data, the two individual case studies reported by Brésard & Bresson are difficult to generalize.

McKeever, commenting without access to the new findings on the great apes, believes that our entire argument founders on the lack of evidence for handedness in great apes, since they are our closest relatives; Tomasello also stresses the importance of this relationship. It should be noted, however, that Napier (1962) considers the apes to be an evolutionary sidebranch of a tree linking monkey and man with respect to hand structure. He states, "Thus the extremely specialized form of the hand in the anthropoid apes can in no way be regarded as a stage in the sequence from tree shrew to man" (p. 59). And to our knowledge it has not been satisfactorily shown that apes have greater manual dexterity than monkeys. We nonetheless agree that a greater similarity between humans and great apes in manual laterality might have been expected.

**Handedness, manual ability, and hemispheric specialization.** A certain amount of discussion was focused on the relation among these three concepts. Ettliger and Heuer correctly chide us for not adequately coming to grips with the relation between preference and ability, which is not always as close as assumed, and they give some examples of problems and approaches to the relation. We agree that there eventually needs to be a theory of manual function consistent with both associations and dissociations of these variables. This is perhaps a more serious problem with nonhuman primates, where preferences are generally less strong, than it is with humans. However, we have no reason to doubt that the typical case is one in which preference is accompanied by greater ability, because variables leading to both are usually inextricably mixed in the history of the organism.

Heuer and Kolb & Fantie warn us against the assumption that hemispheric specialization for the preferred hand is always in the contralateral cortex. A few examples

of dissociation between handedness and contralateral praxic control do not lead us to share Kolb & Fantie's pessimism about the possibility of inference from hand preference to brain function. These exceptions are not inconsistent with the general proposition (Lindblom, MacNeilage & Studdert-Kennedy, in preparation) that the modal situation in evolutionary terms is for control of language, praxic functions, and bodily posture to be in the hemisphere contralateral to the preferred hand. The main exceptions to this are the two-thirds or so of left-handers who have left-hemisphere language. We suggest that many of these individuals have somehow "switched" hands for fine distal praxic functions (on which assessments of handedness are typically made) while retaining a strong tendency toward right-handedness with left-hemisphere control for manual function involving the rest of the body (implicating posture). Evidence for this possibility comes from the fact that in the factor analytic study of Healey, Liederman, and Geschwind (1986), left-handers made almost 30% right-hand responses on questions related to the "whole body" factor (items such as swinging an axe or baseball bat, carrying a suitcase, and doing a cartwheel). Perhaps visual-spatial considerations are more prominent in the manual praxis of these people than those with the normal contralateral relationship.

**The context for primate handedness: Other animals, other functions.** The nature of the phylogenetic context for any putative asymmetries in nonhuman primates is an obvious concern. Glezer and Calvin emphasize the point that, in Glezer's words, "mirror asymmetry in morpho-functional organization is a universal biological phenomenon." There may be various important reasons for these asymmetries. Closer to home, Glezer makes the interesting suggestion: "It seems from the laws of biomechanics that no propelling or aim-directed movement in bilateral organisms is possible under conditions of absolute symmetry" (cf. Annett). If this is so, then we would expect individuals of every species (including parrots, as both Brésard & Bresson and Corballis report) to display lateral preferences. As we have already noted in our remarks on Guiard's commentary, the discovery of systematic, genetically controlled individual differences in lateralization among primates would be of great interest, even in the absence of a population bias. However, our own case would be stronger if we could put the asymmetries we claim into a meaningful context of population-level asymmetries in phylogenetically related animals. Insofar as higher primates are right-handed for manipulation, hominids provide some context for the trend.

But what of the claim that the initial primate state is a left-hand/right-hemisphere reaching specialization and a right-side/left-hemisphere postural specialization? Bradshaw reviews several considerations relevant to this. 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



in nonprimate mammals, one perhaps shared by humans (Bryden 1982), with both specializations 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.

Brésard & Bresson and Corballis bring up the impressive evidence for left-footedness in parrots. We would like to interpret this as evidence for a right-sided (left-hemisphere) postural specialization. Manipulation and posture would therefore be dissociated because, unlike in primates, the right side never became free from the postural demands of whole-body support. As Brésard & Bresson note, the current evidence for the relation between footedness and left-hemispheric specialization for vocal communication is not at all straightforward.

The pattern of handedness that we suggest for non-human primates receives no direct support from neuropsychological studies of monkeys cited by us or by others, although no study specifically precludes the possibility of such a pattern. We know of no neuropsychological studies of great apes or prosimians which are germane to the question. However, the studies of neural asymmetries in monkeys summarized by Bradshaw suggest that the pattern may differ from that in humans. Results presented by Ettliger raise the possibility that hemispheric specialization is too global a concept, in the sense that specific structures in a hemisphere may be specialized, but others belonging to the same neural system may not. These complexities should not be swept under the rug.

The relation between functional and morphological asymmetries is not markedly clarified by the peer commentaries. LeMay points out that correlations between asymmetry patterns and handedness in humans have been established. Annett refers to Witelson's (1985a) findings of differences in corpus callosal dimensions between left- and right-handers. LeMay also notes the finding of Falk, Cheverud, Vannier, and Conroy (1986) that the left sylvian fissure is longer than the right in baboons, as it is in great apes and humans. However, Jerison criticizes the analysis of Falzi, Perrone, and Vignolo (1982), and Glezer presents the somewhat counterintuitive finding that size differences between the hemispheres decrease in an ascending primate series. The behavioral picture of primate handedness needs to be further clarified (as Guiard urges) before progress can be made in this area.

**General criticisms of our approach.** A common criticism of evolutionary scenarios concerns the plausibility of the proposed selection pressures. Annett and Steklis & Marchant are critical of the selection pressures we propose for the evolution of handedness. We recognize that there is an element of risk here and that ridiculous suggestions can be made. We agree with Steklis & Marchant that, a priori, arguments for either lateral bias or lack of it in prosimians seem equally plausible – in fact, we said as much in an earlier draft of the target article. However, we believe that the facts call for a selection pressure toward a lateral bias, and given the combined demands of manual predation and gravity in an arboreal habitat (both currently underestimated, in our opinion), a resultant lateral bias does not seem an unreasonable outcome.

Annett mistakenly believes that a lateralized gain in

reaching skill is necessarily accompanied by a "loss of skill" in locomotion which "would increase the risk of falling" in arboreal quadrupeds. We disagree that there is a necessary penalty, but we acknowledge that every adaptation reflects the resolution of many competing pressures. Annett also seems to misunderstand what we are saying about the ways in which our hypotheses are consistent with evolutionary theory. We do not believe that any animal without the hand preference we suggest would be at an adaptive disadvantage. A mirror image pattern would be equally adaptive in prosimians.

Annett and Steklis & Marchant also question our view of the possible course of evolution. Contrary to their conclusion, we do not wish to assert that "the evolution of a novel pattern of human hemispheric and manual asymmetry [is] unsatisfactory in principle." Clearly, as Annett remarks, "there must be some genes associated with unique human adaptations." The increase in brain/body ratio from the Australopithecines to *Homo sapiens* presumably reflects a massive increase in behavioral and cognitive capacity, much of the increase being in seemingly *de novo* adaptive functions for which precursors are forever lost in extinct hominids. We recognize, moreover, that as Michel & Harkins point out, evolutionary precursors often have forms quite different from their descendants. It was precisely this fact that spurred our interest in handedness and its neural underpinnings as a possible precursor to human linguistic capacity (Lindblom et al., in preparation). However, in the case of manual function a purely hominid course of evolution seems problematical, because partial freedom of the upper limbs from locomotor demands and their regular use in predation and feeding had already emerged in the primates some 40 million years before the earliest hominids. The pressures toward handedness may certainly have been greater on hominids than on monkeys and apes (e.g., the familiar tool use, and the increasing role of imitation, suggested by Michel & Harkins). And if it ultimately proves to be the case that a population bias of the kind we propose (or of some other kind) is present in monkeys, though weaker than in humans, this will doubtless be due to the increased pressures toward uniformity in humans. Nonetheless, it seems entirely reasonable, if not obligatory, to look for incipient biases in the lower primates on which the increased hominid selection pressures could have gone to work.

Jerison believes that "complex issues in the growth and development of neural control systems make it difficult to accept simple models of natural selection." He also discounts evolutionary "scenarios for handedness on the ground that the behavioral evidence is too weak." We certainly agree that the evidence is weak: A major purpose of our paper was precisely to reopen the issue and, by presenting a model of handedness function, to spur a more sophisticated approach to the gathering of evidence. As the evidence comes in, perhaps different and subtler models than ours will emerge. However, some model of function (that is, some evolutionary scenario) will ultimately be necessary. For, however complex a neural (or any other biological) structure may be, it has evolved by natural selection. Natural selection is the only account ever proposed – other than genetic drift – for the spread of a character through a population. The motive power behind the spread is necessarily a specific behavior



that increases an animal's adaptive fitness. That is why we are not drawn to proposals of "metafunctional capacities" such as Calvin's general sequencing specialization. Complex capacities that extend across many functions may well play a role in primate evolution. However, in our view, a metafunction must originate in the particular behaviors it comes to subsume.

Kolb & Fantie imply that the suggestion by us and by others that the left hemisphere is specialized for bimanual coordination is inconsistent with an important role of the supplementary motor area (SMA) for bimanual coordination [see also Goldberg: "Supplementary Motor Area Structure and Function: Review and Hypotheses" *BBS* 8(4) 1985]. We believe the evidence is consistent with the parietal cortex playing a crucial lateralized role for bimanual coordination in humans (see, for example, Kimura 1982) and both SMAs playing an important role in interhemispheric integration for bimanual coordination in monkeys and humans (see Brinkman 1984b; Laplane, Talairach, Meininger, Bancaud & Orgogozo 1977). We would not agree that the fact that the SMA is phylogenetically primitive rules out its participation in emergent functions. For example, we believe (Lindblom et al., in preparation) that the SMA can be assigned an important role in syllable production which is both new (if one considers speech) and old (if one considers the monkey lipsmack).

Kolb & Fantie find it difficult to understand how the special (bilateral) role of the speaking hemisphere in manual praxis could arise from the development of hand preference. We suggest that the initial left-hemisphere specialization for postural control is for bilateral control, and that control of the two hands and the two sides of the axial structures mediating speech are both built on this preadaptation.

Bryden & Steenhuis raise the question of the relationship between specializations in the two hemispheres, and credit us with their view that the relationship is noncausal. This is in contrast to the default view, according to which a second specialization is relegated to the hitherto unspecialized contralateral hemisphere. Our view is also causal, however. We believe that the left-hemisphere postural specialization developed together with the right-hemisphere visuospatial specialization as a unitary adaptive package for manual predation. We find the evidence that Bryden & Steenhuis cite for the noncausal relation unconvincing. The results of Bryden, Hécaen, and DeAgostini (1983) on the relation between left- and right-hemisphere lesions and aphasic and visuospatial deficits can be accounted for by language being more lateralized than visuospatial functions. In addition, contrary to the belief of these authors (and of Warren), a causal relation in phylogeny does not necessarily imply a positive correlation between strengths of left and right specializations in samples of the population.

**Alternative approaches to the explanation of human handedness.** No other attempts to account for handedness in nonhuman primates are presented by the commentators. But Annett, Guiard, and Walker offer three alternative views as to the origin of human handedness. Annett's view is that human handedness is a matter of chance plus a constant which weights the odds in favor of the left hemisphere in some people. She believes that

there are advantages to right-handedness in humans, although they are not sufficient to make it universal. Polymorphisms are in fact found in many characters of many species, of which the most obvious is sexual dimorphism. They may reflect "evolutionarily stable strategies" (Maynard Smith 1974; Maynard Smith & Price 1973), such that an advantage accrues to some percentage of a population for being different in some respect from other members of the population. [See also Maynard Smith: "Game Theory and the Evolution of Behavior" *BBS* 7(1) 1984.] The challenge for the evolutionary biologist is to understand the functional advantages that underlie such balanced polymorphisms. We have nothing to propose here (other than the well-known advantage that accrues to southpaws and switch hitters). We note, however, that an adequate account must rest on a correct understanding of function, that is, of why several forms take the form they do. Whatever the strength of Annett's theory in genetic terms, it has little to offer on this score.

Guiard presents a theory based entirely on bimanual coordination. This is accompanied by an undocumented claim that the proposed functional mode is specific to humans. Although the hypothesis is of interest (partly because it makes one wonder how nonhuman primates manage their bimanual coordination), we prefer discussions of the phylogenetic continuity of manual functions to embrace both unimanual and bimanual acts and to be based on phylogenetic evidence.

Although our primary interest is in language evolution, not the evolution of handedness, we do not have space here for a full discussion of Walker's hypothesis that a left-hemisphere vocal specialization preceded handedness due to a vocal onset time advantage arising from asymmetrical cranial nerve innervation of the larynx (see MacNeilage, in press b, or Lindblom et al., in preparation, for a full discussion). We agree that if language originated first, subsequent left-hemisphere control of praxis could easily be motivated, but we would suggest that the opposite sequence, with hand-mouth interactions giving a boost to articulatory capacities, is more plausible. We would make only two critical remarks here. First, Walker's proposal shares with Annett's the problem of having no implications for the precise form of the evolving behavior. Second, we know of no support for Lenneberg's (1967) idea that the brain has any problem in synchronizing output events via conduction pathways of different lengths.

**The reconsideration reconsidered.** Although our view of primate handedness does not receive massive affirmation from the peer commentators, neither does it receive disconfirmation, except for the claim of vestigial human left-hand reaching abilities. As Tomasello concludes, there is simply not enough information available to swing a conclusion one way or the other. Our main purpose will be served if this interchange leads to a more sophisticated consideration of this important question, and we are encouraged that some commentators expect this outcome. With the exception of our claim for human sinistral vestiges, we continue to stand by the original hypotheses, though we are probably underestimating species differences in taking this stance. In the light of the aforementioned finding of posture-related lateralities by Heestand (1986) and by Forsythe (unpublished), however,

and of some information on morphological asymmetries that we have recently obtained, we would now put more emphasis on the postural basis for manual function and would slightly elaborate our conception of monkey handedness.

Morphological evidence suggests that the well-known human tendency for both muscles and bones to be larger on the right side (Malina & Buschang 1984) even before birth (Pande & Singh 1971) is also observable in monkeys (Dhall & Singh 1977). The exceptions form an interesting pattern, however. The only exception to the pattern in monkeys is the left *pectoralis major*, which Dhall and Singh consider to be the most important muscle in forelimb suspension. The pattern suggests a specialization for below-branch feeding with a "strong" or "operative" right side interacting with the environment, in contrast to a preference for left reaches from a right-sided postural base in the tripod terrestrial condition. The larger left *pectoralis* is also observable in human fetuses (Pande & Singh 1971). This morphological continuity may be related to certain left-hand propensities in neonates noted by Young et al. (1983). These are summarized by MacNeilage (in press a):

They observed that "a left hand preference in suspension grasping seems evident. . ." (p. 26) in studies of infants in the range of 1-4 months. They also reported greater involvement of the left hand in instances involving palmar (versus digital) contact and use of a closed hand. These instances of left hand preference in behaviors which can be said to involve the power grip (Napier 1962), which is necessary for suspension grasping, form the bulk of the cases for which left hand preferences are exhibited in neonates, according to the review by Young et al. (1983).

In contrast, Young et al. concluded that "the right hand is preferred for more target-related activity whether the proximal hand-finger-wrist . . . or distal arm-shoulder musculature . . . is involved" (p. 27).

In human adults, the larger left *pectoralis major* is no longer observed, but the left femur becomes larger than the right (Von Bonin 1962). Perhaps as modern humans develop into terrestrial bipeds the left leg takes over the support function that the left arm provided in monkeys with at least partially arboreal habitats.

To summarize our current views on the role of posture in handedness, We propose that (with the exception of bimanual coordination in intrapersonal space):

Evolutionary developments in handedness across the primate order are embedded in developments in whole-body motor organization. The common element is an across-the-body pattern in which one upper limb is the prime mover, and depending on posture, one or more of the contralateral limbs is involved, with axial structures, in the support function. The conclusion that handedness developed in the context of whole-body action is not a surprising one when it is considered that the hands themselves evolved in that context. [MacNeilage in press a]

## NOTES

1. For this reason we plead innocent to Lehman's charge that we were selective in singling out field studies. Part of the problem here may be differing conceptions of what a field study is. Lehman describes the study of Brooker et al. (1981) as a field

study. In this study, as Brooker et al. describe it, 69 monkeys were "housed in a large rectangular room 7 ft high, 19 ft wide and 14 ft deep [and] were allowed access to a second room of identical size via a doorway" (p. 50). We suspect that when animals competing for food are as confined as they were in this study (and in Rothe's 1973 study) their pattern of hand choice may not be the same as when they are unconfined.

2. We also belatedly note the negative finding of Hörster and Ettlinger (1985) summarized by Ettlinger.

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