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

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

**Predicting from the right shift theory**

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Among the commentaries on MacNeilage et al.'s (1987) target article and the authors' responses (1987; 1988) there are some statements which might mislead readers about the right shift (RS) theory of handedness (Annett 1972; 1985). The main source of ambiguity seems to be an oversimple interpretation of the theory along the lines that some people have RS and are right-handed and of those who do not, 50% will be left-handed; the 50% rule is then assumed to apply to left-handers for other asymmetries such as footedness. From the start, the RS theory was based on the displacement of a normal distribution to the right along the X-axis of a continuum of R-L skill, while those

lacking RS remained under a normal distribution with mean at 0. Overlap was always envisaged, since the shift needed to represent the congruity of hand preference data for humans and nonhumans was not great and bell-shaped distributions have long tails. Some people carrying the shift factor would be left-handed, on account of strong chance determinants of sinistrality; many not carrying the factor would be right-handed on account of the 50% rule, plus the effect of social pressures on those who were evenly balanced for skill. At first, there was no obvious way of estimating the extent of shift or size of the RS-proportion of the population. Successful application of the theory to the problem of the relationship between handedness and brainedness (Annett 1975), however, led to estimates of the parameters of the model that could then be used in the prediction of handedness in families (Annett 1978; 1979, and refined further in Annett 1985).

Figure 1 summarizes the current best estimate of the distribu-

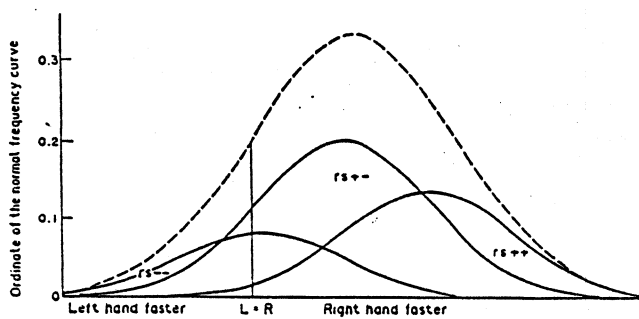


Figure 1 (Annett). Distributions of R - L skill assumed for the  $rs--$ ,  $rs+-$  and  $rs++$  genotypes when the frequency of the  $rs+$  gene is 0.57 and the extent of shift is 1.0z for  $rs+-$  and 2.0z for  $rs++$ .

tions and their overlap, on the assumption that there is a gene ( $rs+$ ) which shifts the distribution of chance differences in asymmetry by one standard deviation (1.0z) in single dose and 2.0z in double dose (the values deduced for males on an additive genetic model; the female shifts are put at 1.2z and 2.4z for  $rs+-$  and  $rs++$  genotypes respectively. See Chapter 16, Annett 1985). The overall distribution in the population can be expected to have a slight negative skew, but each genotype distribution is a true normal, with the same variance. With this assumption, it was possible to investigate the relations between handedness and brainedness, and also the genetics of handedness, with a table of the normal distribution function, a desk calculator, and an elementary knowledge of Mendelian genetics.

The success of this enterprise was demonstrated in the ability to account for all the family data available in 1978, and all studies published subsequently (Ashton 1982; McGee & Cozad 1980; Spiegler & Yeni-Komshian 1983; and new samples of my own. Table 16.7, Annett 1985). Fits of predicted and observed numbers of left-handed children in  $R \times R$ ,  $R \times L$  and  $L \times L$  families were excellent in all cases where the proportions depended on self-reported data for both generations; problems arose only in data which depended on indirect report of handedness by relatives, where the problem could be attributed mainly to slight underestimates of parental incidences. Relatively small errors in calculation of parental incidence of sinistrality are sufficient to throw the genetic predictions far off course; but given the correct ones, the model is equally successful with strict or generous criteria of parental sinistrality. (The actual incidences are used to infer the threshold, and hence the genotype proportions as shown in worked examples in the Appendices of Annett 1985). The distributions of handedness in twin pairs were also predicted (Table 16.11, Annett 1985). Walker's (1988, p. 732) remark that, "There are several difficulties in supporting a Mendelian account of lateralization," may apply to other attempts, but not to RS theory.

The application of the model to the calculation of proportions of left-handers carrying each genotype and the proportions of left-handers expected to be atypical for cerebral speech, is demonstrated in Table 1a, while Table 1b makes the corresponding calculations for right-handers. The first essential step is to estimate the relative sizes of the 3 genotype distributions. The incidence of the  $rs-$  gene could be 0.5, as suggested by Corballis (1987, p. 270), but there is no good reason to suppose it is. My estimate, 0.43, was derived from the proportion of cases of dysphasia associated with unilateral right sided lesions in 4 samples drawn from the general population (combining all cases irrespective of handedness gives 0.927 with right hemisphere speech, times 2 = 0.1854 gives the  $rs--$  proportion in the population and the square root gives the  $rs-$  gene frequency). This happens to agree with the figures derived by Trankell (1955) using a quite different method to estimate the frequency of a hypothesized recessive gene for left handedness which is

poorly expressed even in the recessive homozygote; Trankell showed that all the family series available at that time (Chamberlain 1928; Ramaley 1913; Rife 1940) gave estimates of the frequency of the recessive gene as between 0.40-0.43. Trankell's model is very similar to the RS theory if one acknowledges that left-handedness manifests in just under 50% of recessive homozygotes. A frequency of the  $rs-$  gene at 0.43 gives a frequency of the  $rs+$  gene as 0.57 and the genotype proportions shown in the first column of Table 1. Of course, the relative frequencies of alleles at the same locus can take any value between 0 and 1, and it is interesting that the  $rs+$  gene has risen so little above 0.5, for reasons to be considered later. Instead of Corballis's rough one quarter and one eighth rule, it would be nearer the mark to reckon with a one fifth and one tenth rule. For genetic predictions with large data, however, it is necessary to use precise estimates of genotype proportions.

The next value that must be known is the threshold or criterion of left handedness - where the continuum of R-L differences must be cut to divide left from right. As Heuer (1987, p. 277) remarks, the theory is like a signal detection model in this respect. This point is crucial to all predictions about brainedness or family transmission. There are no absolute answers to questions about left-handers; the reply must always begin with, "It depends on who you call left handed." For the calculations in Table 1a, the criterion or threshold is placed at -0.5z from the mean of the  $rs--$  distribution. Thus for the  $rs--$ , at this criterion, the normal distribution table tells us that there will be 0.695 of the distribution to the right of this value; for those to the left (our left-handers) we need  $1 - 0.6915$  or .3085; this tells us that about 31% of  $rs--$  are called left-handed. The proportion of  $rs+-$  called left-handed depends on the extent of shift, assumed here to be 1.0z. The threshold for left-handedness in the  $rs+-$  is thus at -1.5z (assuming identical thresholds for all genotypes), and the proportion is  $1 - 0.9332$ . For the  $rs++$  the threshold is at -2.5z and the proportion  $1 - 0.9938$ . To find the percentage of left-handers in the total population, each of the proportions has to be multiplied by the genotype proportions, as shown in the table. This gives an overall incidence of left handers in the population of about 9%.

The proportion of nonleft-brained speakers among these left-handers is estimated as that of the  $rs--$  divided by 2 (on the 50% rule which *does apply to the  $rs--$* ), and divided by the total incidence of left-handers. This shows that when the incidence of left-handedness in the population is about 9%, about 31% are expected to be right or bilateral for speech and 69% left-brained. The corresponding calculations for right-handers at the -0.5z threshold, in Table 1b, show that the proportion of right-brained speakers, 0.0657, is about 7% of the 91% of the population classified as right-handed.

Table 1c repeats the calculations for a threshold of left-handedness at +0.5z of the  $rs--$  distribution. The arithmetic is just as before, but care has to be taken in reversing the proportions under the normal distribution for a threshold on the "other" side of the  $rs--$  mean. Sixty-nine percent of  $rs--$  and some 30% of the total population are called left-handed on this criterion (as for a classification "nonright-handed"). But now the proportion of nonright-handers expected to be atypical for cerebral speech has fallen from 31% to about 21%. For right-handers, the proportion expected to be atypical has fallen from 7% to 4%. That is, as the criterion of sinistrality becomes more generous, the chances of finding a right-brained right-hander falls.

Inspection of the proportions of cases of atypical brainedness estimated in Table 1a compared to 1b, shows that for the strict criterion of sinistrality, there are about *twice as many right-brained speakers who are called right-handed as left-handed*. This important test of the theory was satisfied in the data for two series of World War II head injuries. Conrad (1949) found 11 right- and 7 left-handers, and Newcombe and Ratcliff (1973) found 19 right- and 8 left-handers with dysphasia and right

Table 1 (Annett). Predicting handedness and brainedness when gene frequencies are  $rs+ = 0.57$ ,  $rs- = 0.43$ , and when the extent of right shift is  $1.0z$  for  $rs+-$  genotypes and  $2.0z$  for  $rs++$  genotypes.

LEFT-HANDERS							
a. Predictions for threshold of sinistrality at $-0.5z$ of $rs--$ distribution							
Genotype	Proportion of genotype in population	Location of threshold (each distribution)	Proportion under normal curve to the left	=	Proportion called left-handed	Proportion of atypical brainedness	Proportion of all left-handers with atypical brainedness
$rs--$	0.1854	$-0.5z$	$1 - 0.6915$	=	0.0572	0.0286	0.3110
$rs+-$	0.4904	$-1.5z$	$1 - 0.9332$	=	0.0328		
$rs++$	0.3242	$-2.5z$	$1 - 0.9938$	=	<u>0.0020</u>		
					0.0920		
c. Predictions for threshold of sinistrality at $+0.5z$ of $rs--$ distribution							
$rs--$	0.1854	$+0.5z$	0.6915	=	0.1282	0.0641	0.2128
$rs+-$	0.4904	$-0.5z$	$1 - 0.6915$	=	0.1513		
$rs++$	0.3242	$-1.5z$	$1 - 0.9332$	=	<u>0.0217</u>		
					0.3012		
RIGHT-HANDERS							
b. Predictions for threshold of sinistrality at $-0.5z$ of the $rs--$ distribution							
Genotype	Proportion of genotype in population	Location of threshold (each distribution)	Proportion under normal curve to the right	=	Proportion called right-handed	Proportion of atypical brainedness	Proportion of all right-handers with atypical brainedness
$rs--$	0.1854	$-0.5z$	0.6915	=	0.1282	0.0641	0.0706
$rs+-$	0.4904	$-1.5z$	0.9332	=	0.4576		
$rs++$	0.3242	$-2.5z$	0.9938	=	<u>0.3222</u>		
					0.9080		
d. Predictions for threshold of sinistrality at $+0.5z$ of the $rs--$ distribution							
$rs--$	0.1854	$+0.5z$	$1 - 0.6915$	=	0.0572	0.0286	0.0409
$rs+-$	0.4904	$-0.5z$	0.6915	=	0.3391		
$rs++$	0.3242	$-1.5z$	0.9332	=	<u>0.3025</u>		
					0.6988		

unilateral lesions; sample incidences of sinistrality were 7–8%. On the more generous criteria of sinistrality in Table 1c and 1d, more of the atypical cases are called left-handed. In the population as a whole, twice as many right-brained speakers are now called left-handed as right-handed. In the clinical series of Hécaen and Ajuriaguerra (1964) and of Cloning and Quatember (1966), criteria of sinistrality were very generous, making it not surprising that no cases of right hemisphere speech in right-handers were found. Confusions about the relationships between handedness and brainedness are entirely attributable to changes in the criteria of sinistrality between series, and hence differing cuts in the distributions.

With regard to footedness, which Searleman (1980) suggests might be a better predictor of brain laterality than handedness and which MacNeillage et al. (1988, p. 743) believe offers a challenge to the RS theory, there are several points. First, Searleman's left-footed left-handers showed 33% left ear advantage (LEA) for dichotic listening, while the total sample of left-handed student volunteers (including left, mixed and right footers) were 20.5% LEA. These are almost exactly the proportions predicted in Table 1 for the stronger and weaker criteria of sinistrality; the RS theory does not predict 50% atypicality for left-handers except as a theoretical maximum at the left extreme

of the distribution of  $rs--$  when there is no overlap with the  $rs+-$  and  $rs++$  distributions.

The second main point is that the proportion of LEA in right-footed left-handers at 2.5% is indeed very small; it is smaller than would be predicted for right-handers (4–7% in Tables 1b, 1a, 1d). Searleman does not give the corresponding information for right-handers who are right- and left-footed in his sample, which would be needed to sustain the theory that footedness gives a better prediction of brainedness than handedness.

The third point concerns the question whether footedness is correlated with handedness, even in the atypical direction. In my sample of personally visited families of left-handed parents, the consistent left-handers were 85% left-footed, while weak left-handers (though writing with that hand) were only 32% left-footed. Recent studies (Chapman et al. 1987; Peters 1988) conclude that left-handers are about 50% left-footed; Searleman's sample gives 47% left-, and 66% left- plus mixed-footedness in left-handers. All these estimates are above the levels predicted on the calculations for the  $rs--$  in Table 1; hence footedness might be directly correlated with handedness in the accidents of brain asymmetry that generate the normal distribution of differences between the limbs; hence footedness might "go with" handedness more than 50% in the atypical case.

Searleman's (1980) data might have offered a challenge to the RS theory if the left-footed left-handers had included significantly more than 50% of individuals with LEA, but it would have been a challenge the theory was happy to accept as requiring a modification to the "unbiased in atypical cases" rule. The finding of significantly less than 50% LEA offers no challenge.

The RS theory has never made the overinclusive claim that, "Not only handedness but hemispheric specialization of *any* kind first evolved in hominids" (MacNeilage et al. 1988, p. 737). All that is necessary for the RS analysis is to say that the specializations of human braininess for speech probably evolved in hominids. Handedness seems to arise in all creatures built on a bilaterally symmetrical plan; the *slight* human species bias toward dexterity can be usefully interpreted as a byproduct of whatever induces left hemisphere speech. There is an enormous number of asymmetries in nature; who can say how many may turn out to be relevant to human asymmetries. The RS theory calls for only a very small nudge at some critical point in the path of epigenetic development. This is illustrated by a "Galton machine" built for me, in which ball bearings are dropped from a central point on a board and buffeted by nails set at equal intervals for several rows before dropping into vertical grooves to generate a normal distribution. If a small deflector is placed just to the left, below the point of release, this is sufficient to make the ball bearings fall into a normal distribution a little to the right of the first. Whatever supplies the nudge in human brain development must be operating on a developmental path evolved in vertebrate, mammalian, and primate ancestors. The null bias hypothesis of the RS theory offers a strong bench mark against which to test other hypotheses, and when other systematic asymmetries are found they will be exciting discoveries which need to be explained in their own right, not simply assimilated to the "bog" of left brain/right brain research of the last 20 years.

If there are significant species biases for handedness in non-human primates, I am glad I did not know about them at a time when they might have hindered the formulation of the RS theory. Otherwise I would not have undertaken my current research on the hypothesis, positively demanded by the genotype proportions (Table 1), of a human balanced polymorphism for the *rs+* gene with heterozygote advantage. The evidence that the frequency of the *rs+* gene has risen as high as required to give as many *rs+* genotypes as possible (maximum for a single locus is 50%) but not much further shows that the *rs+* gene must be "good for you" in a single dose but "bad for you" in a double dose. The question of what the disadvantages might be has been puzzling me since the genotype proportions were first deduced in 1977. The question cannot be tackled easily in undergraduates and other talented groups since these are almost certain to be selected for *rs+*. In large general samples of schoolchildren, deficits at the right extreme of the R-L distribution are now being demonstrated (Annett & Manning 1989).

## Human handedness reconsidered

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MacNeilage et al. (1987) propose some interesting hypotheses about the genesis of manual preference and hemispheric specialization in primates. Whereas I have no argument with the nonhuman studies that were reviewed or with the data suggesting a right hand/left hemisphere advantage for manipulative tasks in humans, I do believe that far too much was made of a single study (Guiard et al. 1983) reporting a human left hand advantage for manual aiming. In fact, the Guiard et al. (1983) study is an anomaly, perhaps for some of the reasons discussed

by Goodale (1987). In this commentary, I make the case that not only is MacNeilage et al.'s "proposed vestige of a left-hand reaching preference in humans" not confirmed (p. 292), but there is considerable evidence indicating right hand superiority for reaching. This right hand advantage is most pronounced in situations requiring a high degree of spatial and temporal precision.

The first evidence on this issue was provided by R. S. Woodworth (1899) in his doctoral work. Using a one-dimensional manual aiming task, Woodworth found that when subjects had visual information available to them (eyes open), right hand movements were more precise than left hand movements except when subjects were moving very slowly. In no-vision conditions (eyes closed), right hand movements were more accurate than left hand movements regardless of movement speed. Based on his results, Woodworth (1899, p. 34) suggested that the "seat of this superiority of the right hand is probably in the motor centers." He went on to add that since "the right hand gives better results also when the eyes are closed, it would seem that the muscle, joint and skin sensations from the right arm are probably more delicate than those from the left" (Woodworth 1899, p. 34).

In recent years, Woodworth's general findings have been replicated by a number of investigators using variations of Fitts's (1954) aiming task in which movement time has been shown to increase linearly with accuracy demands (index of difficulty). In an experiment examining both right and left-handers, Flowers (1975) demonstrated that right-handers perform reciprocal aiming more quickly with their right hand than their left, particularly when the accuracy demands are high. Todor and Doane (1978) extended this finding by showing that hand differences are more dependent on target width than the amplitude of the movement (i.e., the smaller the target, the greater the differences in favour of the right hand). Since hand differences vary with accuracy demands and because he found no hand differences on a rapid finger-tapping task, Flowers (1975) suggested that hand advantages are related to the speed or proficiency of the right hand system in using feedback. This theoretical stance provided the impetus for a number of other studies, all of which showed right hand superiority in manual aiming.

Annett et al. (1979) filmed subjects performing a peg-board task in which both movement amplitude and target tolerance were manipulated. Whereas movement time differences favoured the right hand in all conditions, more pronounced advantages were found when the target tolerances were small. Based on the analysis of their film data, Annett et al. suggested that the left hand system is inferior at programming the small corrective movements near the target area. Although the theoretical explanation is different from the one proposed by Flowers, the data are similar.

Other relevant work includes experiments by Roy (1983), Todor and Cisnesos (1985), and Bradshaw et al. (1988), all of whom found right hand advantages for manual aiming. In the Roy (1983) study it was found that the right hand advantage is most pronounced when speed as opposed to accuracy is emphasized in the instructions. Bradshaw et al. (1988) found that for a complex aiming task the right hand was faster at programming the various submovements involved in the task. Finally, Todor and Cisnesos (1985) report kinematic data that, like Annett et al.'s data, indicate that right hand superiority in target aiming results from the ability of the right hand to make rapid or more efficient corrections late in a movement. It is typically assumed that any late corrections result from visual feedback monitoring (see Keele 1981 for review); Eric Roy and I (Roy & Elliott 1986), however, have shown that the right hand accuracy advantages exist whether or not visual information is available to guide an aiming movement. Moreover, since hand differences in accuracy are more pronounced for rapid than slow movements, regardless of vision condition, we (Roy & Elliott 1986; Roy &

Elliott 1989) have suggested that hand differences may reflect the greater right hand consistency in the timing of force application (see Peters 1980 and Todor & Smiley 1985).

Irrespective of one's theoretical stance, the evidence, with the exception of the Guiard et al. (1983) study, indicates right hand superiority in tasks requiring rapid/accurate reaching (see also Fisk & Goodale 1985; Honda 1982; 1984; and MacKenzie et al. 1988). This situation makes MacNeilage et al.'s evolutionary model of manual specialization less parsimonious.

If one examines the tasks in which left-sided limb advantages have been found in humans (e.g., Benton et al. 1978; Carnahan & Elliott 1987; Roy & MacKenzie 1978; Witelson 1974), what they appear to have in common is a spatial *memory* component. That is, subjects were required to match a felt shape (Witelson 1974) or orientation (Benton et al. 1978) to something seen or touched previously, or to reproduce/recognize a previous limb position (Carnahan & Elliott 1987; Roy & MacKenzie 1978). Although more holistic right hemisphere processing mechanisms may have time to play a role in these self-paced types of tasks, perhaps the primary constraint in manual aiming is the ability to rapidly program initial and corrective movements.

## It's all in the hands of the beholder: New data on free-ranging rhesus monkeys

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MacNeilage et al. (1987) have provided us with some food for thought regarding the relationship between handedness and hemispheric lateralization. We take issue with four aspects of the target article and components of the peer commentary. First, the data set on naturalistic observations is weak and overinterpreted. Second, there are no clear results on ontogeny even though there is a good deal of speculation. Third, because it is difficult to decompose a complex task into its particular motor components (i.e., given the task descriptions set out by MacNeilage et al.) and then to assign each component with some index of task difficulty, it is not possible to establish what handedness would mean in a functional sense. Fourth, no field-oriented behaviorists were invited to comment on the target article; this unfortunately leads to some incorrect statements. We begin by describing the necessary background information for our study and then present our results. We conclude by discussing our data in light of some of the proposed hypotheses set out in the target article.

Data were collected on a population of free-ranging rhesus macaques (*Macaca mulatta*) living on Cayo Santiago, a 15ha island situated off the coast of Puerto Rico. Our study has several advantages over those summarized by MacNeilage et al. and various commentators. First, our task is complex (see below) and requires no training. Second, we have obtained data on close to 300 individuals. Thus, for the first time, we will be able to talk about "population-level" results. Third, young animals, differing in age and experience with the task, can be carefully examined with large samples of individuals and repeated samples within each individual.

Every morning between 7:30 and 8:30, Cayo Santiago personnel place chow into the three metal dispensers (i.e., hog feeders) located around the island. To remove chow from a dispenser, an animal must push open and hold a lid. Animals typically inspect

several pieces with one hand while holding the lid open with the other. After making a decision, they remove one or several pieces of chow and either eat at the dispenser or leave with their cheek pouches filled and eat elsewhere. Although we concentrate here on those who lift, we should point out that some individuals, adults as well as juveniles and yearlings, never lift lids; rather, such animals are opportunists, grabbing chow when lids are open, taking chow which has been scattered around the dispenser, and/or threatening lower ranking animals into dropping chow from their hands.

Using an opportunistic sampling technique, we recorded all observations of lid lifting. Data were collected on animals of all ages, both male and female, and from five of the seven rhesus monkey groups on Cayo Santiago. In general, there were four ways in which animals could obtain chow from the dispensers: (i) Lift the lid with the left hand, hold it with the left, and obtain chow with the right {LLHL}; (ii) Lift with the left, hold with the right, and obtain chow with the left {LLHR}; (iii) Lift with the right, hold with the left, and obtain chow with the right {LRHL}; (iv) Lift with the right, hold with the right, and obtain chow with the left {LRHR}. A few animals deviated from these techniques (e.g., lifting the lid with both hands simultaneously, with the head, or with the feet). Samples sizes, however, were too small to include in these analyses.

There were two major data sets. First we examined a single case of lid lifting for each individual observed. In situations where individuals lifted more than once, we included only the first observation. Second, we looked at the variability within individuals for all of those who were recorded five or more times. We considered individuals to have a strong preference for a particular technique if it was used in more than 50% of all observations.

For data set one, 277 individuals were sampled. Figure 1 shows a breakdown of the major components of the task (i.e., *lifting* the lid and *holding* the lid). Overall, and across age classes, individuals more frequently lifted with the left hand, held the hopper lid open with the right hand, and manipulated chow with the left. The proportion of all subjects using each technique was: LLHL = 14%, LLHR = 50%, LRHL = 23% and LRHR = 13%. Most individuals used LLHR (chi square = 98.7,

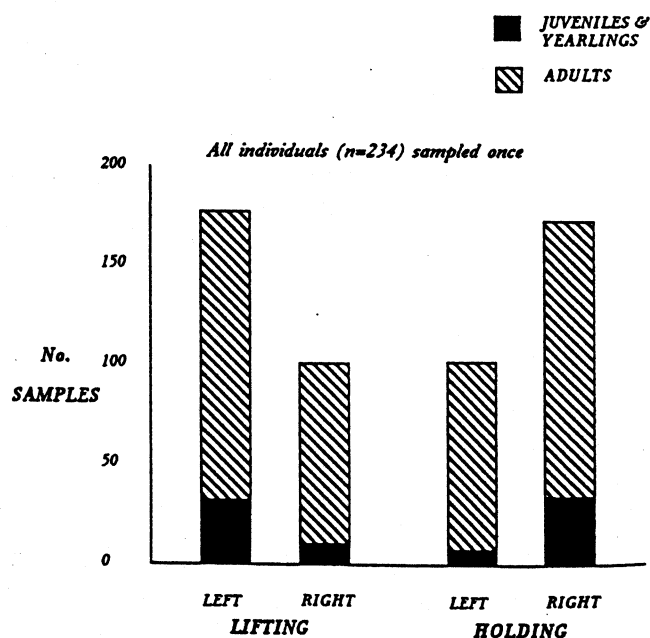
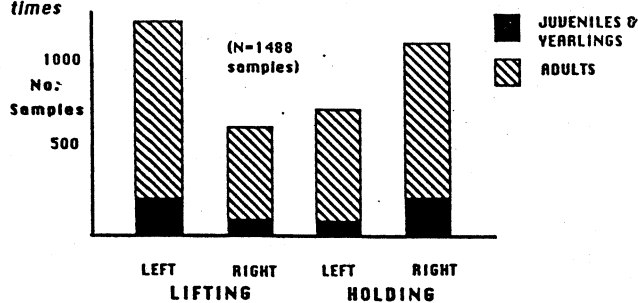


Figure 1 (Hauser et al.). Proportion of individuals using the right or left hand to lift and hold the hopper's lid. Analyses were carried out on data set one ( $n = 277$  individuals) where only one lift and hold sample was considered.

2a. All observations from individuals sampled >= 5 times



2b. First 5 observations from individuals sampled >= 5 times

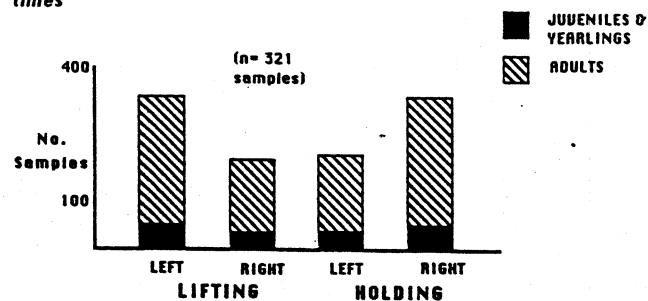


Figure 2 (Hauser et al.). Proportion of individuals using the right or left hand to lift and hold the hopper's lid. Analyses were carried out on data set two (n = 130 individuals) where an individual was only considered if he/she lifted and held the hopper's lid on five separate occasions.

df = 3, p < .01). Dividing this data set into adults and juveniles produced the same results. (Contrary to MacNeilage et al.'s statement that macaques are classified as juveniles up to the age of six years, rhesus macaque females reproduce at four years and males at five years.) Specifically, for 234 adults: LLHL = 14%, LLHR = 47%, LRHL = 26%, LRHR = 13%; for 43 juveniles and yearlings: LLHL = 9%, LLHR = 65%, LRHL = 12%, LRHR = 14%. Both adults and juveniles and yearlings preferentially used LLHR (chi square on adults = 69.5, p < .01; chi square on juveniles and yearlings = 37.1, p < .01). This suggests that hand preferences have crystallized at a young age (between one and four years).

Concerning hand preferences within data set two (n = 1488 samples), Figure 2 shows that most individuals lifted the lid with their left hand, held it open with the right, and manipulated chow with the left. Because some individuals lifted much more than others (max = 116, min = 5), however, we reran these analyses and only looked at the first five records for each individual. With a total of 321 samples, the results were the same as in the larger sample.

For data set two (n = 130 individuals), most individuals showed a clear and consistent use of one technique over repeated trials. Specifically, 6% used LLHL, 51% LLHR, 27% LRHL, 8% LRHR (chi square = 74.1, df = 3, p < .01) and 8% showed no preference at all. With regard to adults, 7% used LLHL, 50% LLHR, 26% LRHL, 8.5% (chi square = 60.8, df = 3, p < .01), and 8.5% did not exhibit any preference. Juveniles did not use LLHL or LRHR, but used LLHR 62% of the time, LRHL 31%, and showed no asymmetry on 7% of all observations.

Out of 130 individuals sampled in data set two, 91% used one technique more than 50% of the time; the mean preference strength was 85.7% (SD = 15.0, N = 119, Range: 51-100) and 33% of all individuals selected one technique 100% of the time. Dividing these data into age classes, 92% of all adults used one

technique over 50% of the time (X = 85.6%, SD = 15.0, N = 107, Range: 51-100) and 32% of the adults showing such biases used one technique 100% of the time. In comparison, 92% of all juveniles and yearlings (X = 88.6%, SD = 15.3, N = 12, Range: 54-100) used one technique over 50% of the time, and 42% used one technique 100% of the time. The two yearlings who were sampled repeatedly showed no evidence of variability in the use of lid lifting techniques (100% LRHR, N = 15 and 100% LLHR, n = 7).

Our results on free-ranging rhesus macaques can be summarized as follows. First, we have shown, on a population level, extremely strong evidence of asymmetry in hand use, both for the overall task and for its components; such hand asymmetries were extremely stable over repeated trials of the same task. In a recent paper by Rawlins (in press), evidence for consistent between-task hand preferences was reported in one rhesus group (n = 45) on Cayo Santiago. As Rawlins states, "if an animal used the left hand to pull leaves from a tree and braced with the right, it would raise chow hopper lids with the right and forage with the left." In addition, there was evidence that one genealogy was right hand dominant. Second, at least by the age of one year, there is no developmental modification of hand preferences (see also Rawlins, in press).

What do such data tell us about the debate on nonhuman primate handedness? MacNeilage et al. wish to break down tasks into their components and then assign "scores" to each task based on complexity. For purposes of comparison with the target article, let us look carefully at the lid lifting task for a hypothetical monkey, Sam, who is walking toward the chow dispenser.

- (1a) Sam sits in front of hopper before lifting. . . .
- .. 2) Sam reaches for
- (1b) Sam stops walking and dispenser lid. . . 3) Sam grasps stands in front of hopper . . . lid
- 4) Sam lifts lid . . . 5) Sam supports lid and, . . . 6a) picks one piece of chow
- .. 6b) picks several pieces of chow and puts them in cheek pouches
- .. 6c) sifts through pile of chow and then picks one or several pieces

With regard to the MacNeilage et al. view, steps 1a,b through 3 would be classified as "reaching" and to some extent "visually guided." Step 4 is a form of "manipulation" and step 5 is "stabilization." Steps 6a-c are all mixed motor acts, including reaching, manipulation, and visually guided movement. It is unclear to us which component of the lid lifting technique (i.e., the suite of motor patterns involved) is the most complex and can be used to determine handedness. As a result, we do not feel that the pattern of hand preferences discussed here or elsewhere can be directly compared to the pattern exhibited by humans.

One of the problems with the research summarized in the target article is that there is no objective measure of how difficult one task is compared with others. Task difficulty must be evaluated in the context of the species' natural environment. For example, tasks involving moving objects which must be captured are likely to be less difficult for the insectivorous bush baby than for the frugivorous/folivorous macaque. If this is a reasonable measure of task difficulty, then there is a great need for comparative studies, in which each species is examined under the same environmental conditions.

Even though we feel strongly about the caveats discussed in the previous paragraphs, our results can be considered to

support the MacNeilage-Studdert-Kennedy-Lindbloom hypothesis. That is, on a population level, there was a left-hand preference for reaching (i.e., for the lid), a right hand preference for stabilization, and bimanual coordination to obtain the chow. If manipulation of chow is seen as a single motor act, however, then the asymmetry observed (i.e., left hand preference) in our population goes against the prediction of MacNeilage et al. (i.e., right hand preference for manipulative tasks).

Although our developmental field data are certainly more substantive than those that have been presented in other studies, we feel that a more experimental approach is needed to address the ontogeny of hand preferences. For example, if one found evidence that experience affected hand preferences in a particular species, one might attempt to condition a group of individuals to use one hand consistently over the other. If innate predispositions were particularly strong for handedness, one might find that some individuals were simply incompetent at carrying out the task.

The functional advantage of handedness is still an open question and the evolutionary scenario proposed by MacNeilage et al. is as good (or bad) as any other Kiplingesque just so story. In reconstructing evolutionary scenarios we must make sure that our hypotheses can be rigorously tested: G. Isaac's (1978) work on the evolution of human foraging patterns, which is derived from archaeological data, is an excellent model. Although MacNeilage et al. claim that their "account" is "speculative but testable" they do not provide any tests. There are at least some possibilities for testing, however. For example, one could observe bush babies in their natural environment to determine which hand is preferred when holding onto trees and which for grabbing insects. Subsequently, place an individual in a cage where holding must be done with one hand and grabbing with the other. Are those individuals who are forced to hold with the "nonpreferred" hand less successful in capturing the insect?

In conclusion, further speculation on how the evolution of hemispheric lateralization relates to handedness should be put aside until we have more population-level data, a better understanding of what a complex task is, and what, if any, functional advantage might result from a particular hand preference.

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## Author's Response

### Primate handedness: The other theory, the other hand and the other attitude

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We respond to three commentators. In the first commentary, Annett clarifies and defends the precise statistical details of her Right Shift theory. As we see it, this is the main alternative to the postural origins theory of handedness evolution we outlined in an earlier response to continuing commentary (MacNeilage, Studdert-Kennedy & Lindblom, 1988r). The implicit claim of

Annett's commentary seems to be that the right shift theory is undamaged by the evidence of primate handedness that the commentator is familiar with. In the second commentary, Elliott reviews evidence regarding our initial claim of a vestigial advantage for the left hand in tasks requiring rapid accurate reaching in humans, concluding that a left hand advantage in humans can be observed only in tasks with a spatial memory component. In a third commentary, Hauser, Perry, Manson, Ball, Williams, Pearson, and Berard present valuable additional evidence for primate handedness, evidence consistent with our theory, but they conclude that our theory is no better than no theory at all.

We begin our response by noting a difficulty that some of the earlier continuing commentaries encountered. It is that positive evidence for population-level hand preferences in other primates is accumulating at such a rapid rate that those not sufficiently familiar with these developments whose commentaries depend on the contention that the evidence is weak, tend to end up with Commentaries having less force than they had expected. This is the position that Annett and Hauser et al. are in, in this round of commentaries. This is not only a problem for contributions to continuing commentary. More generally it is a problem for any theory of human evolution that depends on a minimization of prehomimid specializations. For example, with the support of his continuing belief that the evidence for primate handedness is "weak," Corballis (1989), one of the most critical commentators on our original review, has presented another of the most popular types of scenarios for human evolution, a one-step metafunctional scenario for evolution of a hominid-specific ability in the left hemisphere only, this one for "generativity" in *Homo erectus*.

In Table 1 we summarize most of the studies of hand preferences in other primates that have obtained significant positive findings. About two-thirds of the 30 findings (the starred items) have been added to our list since the 1987 review, but are not considered by Annett or Hauser et al. in their commentaries. There is strong evidence for left hand preferences, primarily for reaching, in several studies of Prosimians (see Ward 1991 for a summary). There is also some evidence of left hand preferences in higher primates in relatively simple reaching tasks (Box 1977; Ettlinger 1961; Itani 1957; Watanabe & Kawai 1990; Olson et al. 1990) though not in the great apes. In addition, there is evidence of high levels of left hand preferences in monkeys (King & Landau 1990; Fagot & Vauclair 1988a) and great apes (Fagot & Vauclair 1988b) in tasks that put relatively high demand on the use of visuospatial information.

Right hand preferences have been observed only in higher primates, more often for manipulative tasks than any other particular kind of task (Beck & Barton 1972; Hopkins et al. 1988; Kuhl 1988). In one case, better performance of the right hand *without* preference has been observed on a task requiring fine motor control (Preilowski 1979). Of particular interest is the study of Shafer (1987) in which, for the first time in other primates, a significant humanlike pattern consisting of a greater number of animals which preferred the right hand *for all acts* was observed.

These results (which are discussed in detail in MacNeilage, in press) are for the most part very consistent with

Table 1. Summary of studies showing functional asymmetries favoring the left or right upper limbs in nonhuman primates

Left upper limb	Right upper limb
<i>Prosimians</i>	<i>Monkeys</i>
Reaching etc. (Slender Lorises) Subramoniam 1957.	Expose & Reach: Visual & Tactile Discrimination-Later Trial Trend. (Rhesus) Ettlenger 1961. Milner 1969.
Reaching: Vertical versus Horizontal Posture. (Lesser Bush Babies) Sanford et al. 1984.	Various Acts (Later Trial Trend). (Rhesus) Warren 1977.
Moat Reaching. (Ruffed Lemurs) Forsythe et al. 1988.*	Manipulation In Multiact Situations. (Stumptail macaques) Beck & Barton 1972.
Reaching etc. (Ring-Tailed Lemurs) Milliken et al. 1989.*	Precise Finger Pressure Control. (Rhesus) Preilowski 1979.
Reaching. (Black Lemurs) Forsythe & Ward 1988.*	Hand-Mouth Interaction. (Baboons) Post et al. 1980*
Reaching. (Lemurs; 6 species) (N=194) Ward et al. 1990.*	Response Key Control: Auditory Discrimination Tasks. (Macaques) Kuhl, 1988.*
<i>Monkeys</i>	Suspended Reaching. (Squirrel Monkeys) King & Landau 1990.*
Reaches in Reach, Lift, Hold-While-Reaching Sequence. (Rhesus) Hauser et al. (Commentary)*.	<i>Monkeys &amp; Apes</i>
Reaching. (Marmosets) Box 1977.	Joystick Control: Computer Game. (Macaques & Chimpanzees) Hopkins et al. 1989.*
Reaching. (Japanese Macaques) Itani 1957.	<i>Apes</i>
Reaching. (Japanese Macaques) Watanabe & Kawai 1990.*	Initiation of Chest Beating. (Gorillas) Schaller 1963.
Expose & Reach: Visual & Tactile Discrimination-Early Trials. (Rhesus) Ettlenger 1961.	Reaching & Other Use (Gorillas) Fischer et al. 1982.
Prehension; Visual & Tactile Guidance (Rhesus) Fagot et al., in press.	Locomotor Initiation. (Siamangs & Gorillas) Heestand 1986*
Goldfish Catching. (Squirrel Monkeys) King & Landau 1990.*	All Categories: Naturally Occurring Behavior. (Gorillas) Shafer 1987.*
Adjusting Plexiglass Screen. (Baboons) Fagot & Vauclair 1988a.*	Bipedal Reach. (Gorillas) Olsons et al. 1990.*
<i>Apes</i>	
Reaching; (Gibbons) Olson et al. 1990.*	*These studies added after target article was written.
Adjusting Plexiglass Screen. (Gorillas) Fagot & Vauclair 1988b.*	

mates and with the decreasing importance of unimanual predation, the postural specialization may have evolved into a right-side (of the body) specialization for operations on the environment beyond simple prehension. Evidence for *postural* involvement includes posture-specificity of left hand preferences in prosimians (Sanford et al. 1984; Forsythe et al. 1988) and evidence of a locomotor initiation preference involving both right limbs in apes (Heestand 1986). Evidence that both right handedness and the left hemisphere location of the language specialization may have originated in a *postural* specialization includes Searleman's (1980) finding that human footedness (by definition a postural asymmetry) is more closely related to language lateralization than handedness, a finding recently replicated by Maki (1990).

**The other theory.** The current evidence is summarized here not only to bring readers up to date, but to show how inadequate the Right Shift theory of Annett has become as a theory of the evolution of handedness. We apologise for the oversimplified view of her two-allele model that we used in our earlier response. In addition, we do not wish to detract from Annett's accomplishments in presenting a general theory applying to patterns of human neurobehavioral lateralization. In the study of human lateralities, direction has been provided mainly by the attraction of some particular experimental technique. In that context, the conceptual scope of Annett's approach has been highly laudable.

Despite the merits of Annett's approach, however, it must be noted that the Right Shift theory has some serious problems in its application to both humans and other primates that the Postural Origins theory does not share. One problem is obvious on the basis of human results. While the right shift theory is based on the assumption that handedness is a unidimensional trait, it is now clear that this is not the case (Healey et al. 1986; Bryden & Steenhuis 1989). One particular departure from unidimensionality has postural implications. Many left handers and some right handers prefer the other hand for tasks loading on a factor describable in terms of the involvement of whole body postural control – tasks such as swinging a bat or an axe. (Healey et al. 1986; Bryden & Steenhuis 1989). Geschwind (1985) was sensitive to the existence of this dichotomy and had noted seven left handers who wrote on paper left handed but on a blackboard right handed. If handedness is not unidimensional then a single generalized shift/no shift dichotomy is an inadequate account of both within subject and between-subject hand preference patterns. A view of hand use preferences in which posture can be treated as an independent variable, however, fits easily within the postural origins theory (MacNeilage, in press).

Another major problem of the right shift theory in our opinion involves the motivation for the evolution of the +RS gene in the first place. According to Annett, the main function of the RS+ gene is to ensure that the production and perception of speech sounds are controlled in the same hemisphere (Annett 1985, p. 40). It has often been pointed out, however, that in most animal communication systems, including speech, sending and receiving are integral to each other, as the organism in some sense sends what it receives. Would there ever be any strong tendency for the development of one of these

the postural origins theory, as summarized in our 1988 response. According to this theory, a left-hand right-hemisphere perceptual-motor specialization for unimanual predation, complemented by a left hemisphere postural control specialization may have evolved in ancestral prosimians. Then with the change from a vertical clinging to a quadrupedal postural mode in higher pri-



functions in one hemisphere and the other in the other hemisphere? We think not, and Annett seems to agree with us when she states that even when the +rs gene is absent. "The inherent advantages of control from one side probably lead to the development of an efficient system on one side or the other." (p. 403). Although one in four humans is supposed to lack the +rs gene, we have never heard of a case in which the perception and production of speech were controlled in opposite hemispheres of the brain. We conclude that the motivation for the evolution of the +rs factor, as given by Annett, has probably never existed.

The problem with the right shift theory most germane to the present context results from the widespread evidence for two kinds of handedness in other primates. According to Annett, human right handedness evolved as an incidental effect of the evolution of the +rs gene to unify the hemispheric locus of speech perception and production. But there is now good evidence for the existence of human-like patterns of right hand preference in higher primates whose ancestors probably did not possess speech. And, more important in this context, there is good evidence of *left* hand preferences for other functions, which may have even preceded right hand preferences in evolution. A speech-based theory of the evolution of human right handedness does not even begin to provide an account of these hand preferences in other primates.

**The other hand.** In our initial review we took data from Guiard et al. (1983) that normal right handers perform rapid aimed movements with a smaller constant error when using the left than when using the right hand as evidence for a "residue of the spatiomotor specialization postulated in other primates." However, Goodale's convincing arguments (1987) led us to recant: "With the exception of our claim for human sinistral vestiges we continue to stand by the original hypotheses" (target article: response to commentators, p. 297). Elliott concurs with our revised view on the issue of human sinistral vestiges, and adds to the information provided by Goodale on right hand superiorities. He concludes that left hand advantages are only found in tasks with a spatial memory component and not in tasks in which anything like ballistic movements are the crucial acts.

While we have no quarrel with Elliott's arguments about right hand advantages and the role of a spatial memory component in left hand advantages, we are nevertheless inclined to reconsider our conclusion that the left upper limb in humans shows no residue of a spatiomotor specialization. Four sources of evidence leading us to this reversal will now be reviewed.

In a reaction time task in which four standing right-handed subjects were required to raise their hands from their sides, Lee (1980) studied three muscular components of the response complex, the ipsilateral biceps femoris, the anterior deltoid, and the contralateral biceps femoris. The mean overall reaction times and the reaction times for the three muscle components are shown in Table 2. While the left arm reaction times were not significantly shorter than the right, Lee observed a significant side-by-response effect ( $p < .005$ ) "reflecting shorter intervals between response components on the left than on the right side" (p. 191). Thus, in this task the

Table 2. Mean latencies, in milliseconds, of muscle activation and key release in a manual reaction time task

	Ipsilateral biceps	Anterior deltoid	Contralateral biceps	Reaction time
Right Arm Response	186	206	265	326
Left Arm Response	194	207	251	293

Source: Lee (1980)

actual execution time, measured from onset of observed muscle activity to key release, was over 40 ms shorter for the left limb. A particularly tight integration of motor response subcomponents might be a desirable property of a subsystem originally specialized for unimanual predation. In addition, the fact that this was observed in a task which required whole body postural control should not go unnoticed.

In a choice reaction time task in which subjects were given short notice as to which hand to respond with, Verfaellie et al. (1988) found that "reaction times for the left hand were faster than for the right hand (left = 475 msec; right = 493 msec;  $p < 0.01$ )" (p. 526). Verfaellie et al. interpret this in terms of "a right hemisphere superiority for intention" by which they mean "response readiness" (p. 529). But why would humans have such a specialization in the hemisphere not dominant for motor control, and why would it favor the contralateral hand? Such a result might be expected if the left hand/right hemisphere system had a history of preferred use for the rapidly organized responses sometimes required of a unimanual predator.

Watson and Kimura (1989) have recently shown that while the right hand is better than the left in dart throwing accuracy, the left is as good as the right in batting down approaching objects. This result is interpreted by Kimura and Watson, and by us, as showing that the left hand of right handers is not inferior to the right on a task that involves rapid on-line spatiomotor integration if demands for fine motor control of the distal musculature are not involved. Given the currently typical expectation that the right hand of right handers has an advantage in motor skill in general, the *lack* of an advantage in this task is a theoretical problem. But it is not a problem if the left hand/right hemisphere system has a residual capacity for quick whole-limb responses to objects suddenly appearing in extrapersonal space.

The three studies just described provide evidence of an unexpectedly great capacity of the left hand to make rapid *single* response. There is also some evidence of an advantage of the left hand in *continuous* high speed tasks, if the tasks involve a significant component of spatial judgment. Annett and Kilshaw (see Annett 1985, Ch. 17) have shown a significant advantage of the left hand over the right on a peg moving task (in which spatial precision is at a premium) in three of four types of comparison; when performance of the nonpreferred hands is compared in both males and females, and when preferred hands are compared in males. (In females, the right preferred hand has an advantage over the left preferred hand, but it is not

significant.) The result for the nonpreferred hand is particularly notable because it occurs in spite of the probability that left handers have a greater degree of bilateral praxic control than right handers (Kimura 1983; Simon & Sussman 1987) and that they might therefore be expected to do relatively better with their nonpreferred hand than right handers – if praxic control is all that is involved here.

This result can be contrasted with performance on simple tapping tasks in which spatial demands are at a minimum (e.g.; Peters & Durning 1979). On this task, the handedness groups were virtually identical for the preferred hand in both males and females, but the right hand was significantly faster than the left when it was the nonpreferred hand, as would be expected from the more bilateral praxic control of left handers suggested above. These results clearly suggest a positive contribution of the spatial capacities of the right hemisphere to the continuous motor control of the left hand in both right handers and left handed males.

These four findings suggest to us that the existence of specialized *spatiomotor* capacities for some types of phasic acts, and even perhaps some types of continuous acts in the human left hand/right hemisphere system should not be ruled out. Thus, in spite of Elliott's comments we have reverted to our original belief that a consideration of similarities in the left hand/right hemisphere motor control subsystem in humans and other primates may be rewarding.

**The other attitude.** Hauser et al. have the opposite attitude to ours about how to make progress in this area of research. They seem to believe that an explicitly atheoretical approach is preferable to ours. Not only do they believe (apparently without awareness of more recent findings) that our theory is simply a "just so story," no better than no theory at all, but they also propose an embargo on further speculation.

Here is our response to the four issues raised by these commentators in their introductory paragraphs. The first point was that the data on naturalistic observations in the target article were weak and overinterpreted. That is true. So were the data on experimental observations, as we noted in our Response; "We certainly agree that the evidence is weak." (p. 296): "In cases of uncertainty we bent over backward to support the conclusion opposite the currently fashionable one, hoping that this would eventually allow the dust to settle in the right place" (p. 290). As we noted earlier, however, the data, including naturalistic data (Watanabe & Kawai 1990; Shafer 1987), are getting stronger all the time, and the interpretations we have given them are looking better all the time.

The second point concerned the paucity of ontogenetic data. We are hardly to be blamed for that. Their absence did not weaken our position much, however, because it relied little on ontogenetic assumptions. In this category, our statement that macaques are classified as juveniles up to the age of 6 was criticized. We drew this statement from Napier & Napier (1985, Table 3, p. 59). These authors did not give the sources for their table, but we assume that their figures refer to wild populations. Hauser et al. give no sources for their own statement that rhesus macaque females reproduce at 4 years, males at 5 years. However, if the Hauser et al. data derive from

observations on the Cayo Santiago population, we may suspect that their lower figure is due to the enriched diet (regular chow in hog feeders) that the Cayo Santiago animals enjoy. An analogous reduction in the age of menarche for females in the Dobe !Kung (Namibian) population of hunter gatherers given access to the richer diet of colonial trading posts has been reported by Howell (1979).

The third point was about the lack of field primatologists among the commentators. If we had known of field primatologists who were interested in which hand other primates use, we would have invited them to comment. The editor of *BBS* presumably shared our problem in this regard.

The fourth issue Hauser et al. bring up is the need for a better task classification. We agree, but these commentators must first make sure they are up to the task. To describe the final act in their task as having a "manipulation" component seems to fit neither the technical treatments of this conception in the motor literature nor common sense. Hauser et al. describe the final phase of their task as follows. The animal either (a) "picks one piece of chow" or (b) "picks several pieces of chow and puts them in cheek pouches" or (c) "sifts through a pile of chow and then picks one or several pieces". Then Hauser et al. claim that: "Steps 7a-c are all mixed motoric acts, including reaching, *manipulation*, (emphasis ours) and visually guided movement." In all three tasks the animal picks up food and in each case this involves *reaching*. Only in 7c does any other manual operation on an object occur. In this case the animal "sifts." For us sifting is a visually guided motor search "to screen out the valuable or good" (this and further definitional statements come from Webster's 7th New Collegiate Dictionary (1971). Synonyms for sift might include "rummage" ("to engage in a haphazard search") or "scrabble" ("to scratch or claw about clumsily or frantically") but not "manipulate" ("to treat or operate with the hands or by mechanical means, esp. with skill"). We take "reaching" ("to touch or grasp by extending a part of the body [such as a hand])" to be the dominant component in the terminal phase of this task, *present in every instance of attaining food*, and it is no surprise to us that the dominant hand for this phase, as for the initial phase of reaching to grasp the lid, is the left hand. Neither is it a surprise that the next most favored pattern involves the right hand *for both acts*. The data tell us that the two phases evoke a common lateralized response as one would expect on theoretical grounds, and we take this as an instance in which theory informs methodology.

Hauser et al. have provided much stronger evidence for our claim of a left hand reaching preference in monkeys than they thought. It is of interest that this result is similar to the one obtained by Beck and Barton (1972), who also found relatively high levels of left hand reaching preferences in macaques performing tasks in which other acts were also required.

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