<u>Ontogenetic considerations in the phylogenetic history and adaptive significance of the bias in human</u> <u>handedness</u>

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Article:

Previous amounts 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 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 descendents (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.