A Lateral Bias in the Neuropsychological Functioning of Human Infants

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Michel, GF. A lateral bias in the neuropsychological functioning of human infants. Developmental Neuropsychology. 1998; 14(4): 445-469.

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Abstract:

Using my published and unpublished research, a description of the development and functional significance of infant hand-use preferences is presented. Although the character of the infant's handedness will vary with the development of manual skill, the majority of infants maintain stable preferences throughout the 6- to 14-month age range. As with adult handedness, right-handedness predominates in infancy. Infants without stable hand-use preferences show delays, when compared to infants with stable hand-use preferences, in the development of several sensorimotor cognitive skills. Both maternal- and infant-generated experiences contribute to the development of handedness. Given evidence of limited interhemispheric communication during the 1st year, infant handedness can contribute to the development of the functional specialization of the cerebral hemispheres.

Article:

Examining the lateral bias in the neuropsychological functioning of humans usually means assessing the hemispheric specialization of certain cognitive skills (e.g., language). However, hand-use preferences represent sensorimotor skills that involve differences in functioning between the cerebral hemispheres; therefore, they also constitute a lateral bias in neuropsychological functioning. The clearly observable phenomena that identify hand-use preferences make the development of this sensorimotor form of lateralization relatively easier to study than other, less observable, lateralized functions (e.g., cognitive processing strategies, emotional feelings). Consequently, it is likely that knowledge of the origin and expression of manual preferences potentially can contribute to understanding the development of the lateralization of other neuropsychological functions. Also, because certain forms of bimanual coordination (including those influenced by handedness such as role differentiated bimanual manipulation) require effective callosal functioning (Jeeves, Silver, & Milne, 1988; Preilowski, 1972, 1975), examining the development of bimanually coordinated actions can contribute to knowledge about the development of interhemispheric communication. Thus, knowledge of the relation between developing hand-use preferences and developing bimanually coordinated skills can assist understanding of the more general issue of how the development of hemispheric specialization of function relates to the development of interhemispheric communication.

For the past 2 decades, my collaborators and I have been studying the development of manual skills during human infancy in pursuit of such understanding. We designed our research to address the following questions:

1. Do infants have hand-use preferences and how should they be assessed?
2. Do adult and infant hand-use preferences differ?
3. What are the functions of infant hand-use preferences?
4. How do infant hand-use preferences develop?
5. What does the study of the development of manual skills during infancy reveal about the development of hemispheric specialization of function and interhemispheric communication?

This article provides answers to these questions that are consistent with our published and unpublished research results, but no attempt will be made to provide a comprehensive review of the literature. Handedness is a complex phenomenon that has attracted the interest of many highly competent investigators. Although any review is not likely to please everyone, my collaborators and I hope that this article demonstrates the value of the programmatic research that we have conducted during the last 2 decades.

ASSESSING INFANT HAND-USE PREFERENCES

Although developmental research depends on good descriptive information, describing handedness, even that of adults, creates several problems. It is not clear whether hand-use preference should be identified via statistical or nonstatistical measures of actual performance, by self-reports of performance acquired via questionnaire, or by self-assignment (Bryden & Steenhuis, 1991). This has lead to the accumulation of a variety of descriptive methods for adults. However, despite all the variety, most research on adult handedness (particularly that associated with the study of hemispheric specialization) is conducted with descriptions based on self-assignment or questionnaire acquired information. Too often this information is then used to separate individuals into two classes: right-handed and not right-handed. Also, it is not clear how well such information describes actual hand-use preference as measured by frequency or pattern of use (Steenhuis & Bryden, 1989). Indeed, depending on the size of the questionnaire and the statistical procedures used to examine the responses, controversy has arisen about whether there are one, two, three, or possibly more types of lateral bias in the hand-use of adults (Annett, 1970; Healey, Liederman, & Geschwind, 1986; Peters & Murphy, 1992). Unfortunately, descriptions based on performance measures have not yet resolved these issues (Annett, 1985; Bishop, 1990).

Given the controversies concerning adult handedness, it is perhaps not surprising that there is controversy about infant handedness, despite the use of performance measures to describe infant hand-use preferences. It is often assumed that infants, preferences are too variable across assessment conditions and unstable across age to be assessed reliably or to provide accurate predictions about adult handedness status (cf. Michel, 1983). Some modern research does report frequent fluctuation (instability) of infant hand-use preference with age (Carlson & Harris, 1985). However, other research reveals stability of preference during the same age period (Michel & Harkins, 1986). Of course, the appearance of stability or instability of preference may depend on the means by which hand-use preference is assessed. Even adult hand-use preferences can appear variable according to the demand characteristics of the tasks used for assessment (Bryden & Steenhuis, 1991; Flowers, 1975).

Handedness is particularly difficult to assess in infants because it is manifested according to the level of the infant's manual ability. The extensive changes in manual skills that occur during infancy require that hand-use preferences be assessed with different skills (e.g., reaching, manipulation), in different situations (e.g., familiar and unfamiliar tasks, tool use and tool construction), with different object properties (single vs. multiple objects, with or without moveable or removable parts, with or without distinctive features or effects such as sounds, colors, and textures), and by different measures (e.g., initial use, frequency of use, level of skill achieved). Currently, most studies of infant hand-use preferences use assessment procedures that are idiosyncratic to the researcher's interests. Therefore, little comparability across studies is likely.

In our work on infants, we tried to provide a statistically reliable assessment of hand-use preference based on the presentation of at least 20 objects possessing different properties, and for each of which, several performance measures (reaching for and retrieving of objects and either unimanual or bimanual object manipulation) could be extracted (Michel, Ovrut, & Harkins, 1985). This assessment procedure allowed identification of two types of infants: those with preference measures that were unlikely to occur by chance and those whose preference score could have occurred by chance (i.e., those with and those without a hand-use preference) for each of the three manual actions. In addition, the assessment measure and the distinction between infants with right versus left hand-use preferences was validated by comparison with the infant's performance in a semistructured block play situation. The assessment procedure exhibited good test—retest reliability and demonstrated longitudinal stability provided that the performance measure was adjusted to reflect the changing status of the infant's developing manual skills.

Figure 1 shows that a hand-use preference predominates at all ages for reaching and unimanual manipulation activities but not for bimanual manipulation until 12 and 13 months of age. A hand-use preference for bimanual manipulation requires a role differentiated activity in which the "preferred" hand investigates or examines the object (e.g., fingering, patting) while the "nonpreferred" hand supports the ac tions of the preferred hand (e.g., holds, reorients). The majority of infants exhibit a right-hand preference for bimanual manipulation at 12 and 13 months of age. In contrast, a right-hand preference for reaching predominates at all ages except 13 months, and the right hand-use for unimanual actions predominates at all ages except 7 months. Whereas the difference in percentage of infants with right versus left preferences for reaching are not significantly different at 10, 11, and 13 months of age, the difference is significant for unimanual manipulation at those ages. An infant that exhibited a right preference for reaching at 7 to 9 months old might not exhibit a right preference at 10, 11, or 13 months old, although that infant would exhibit a right preference for unimanual manipulation at those ages. The right preference would not be exhibited in bimanual manipulation until 12 to 13 months of age. Obviously, assessments that fail to separate these three types of manual actions would provide a confusing pattern of infant handedness during the 9- to 13-month period. Although the original study was a cross-sectional design, a recent, unpublished, longitudinal study of 74 infants for the same age range confirms these results (Figure 2).

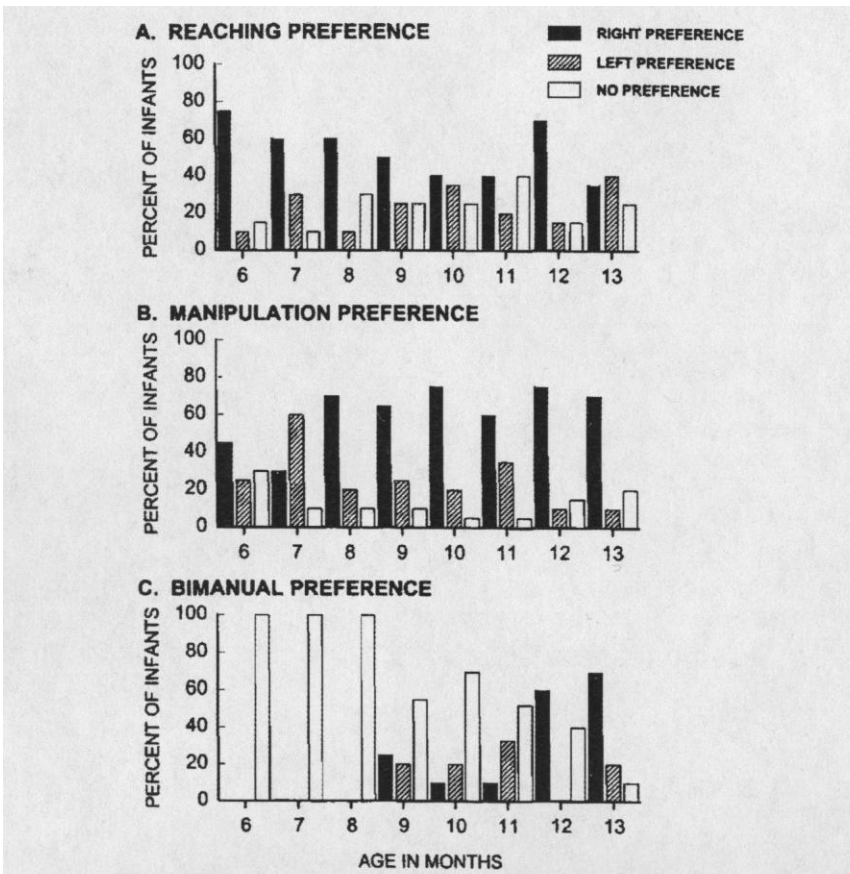

FIGURE 1 The percentage of infants exhibiting a right, left, or no hand-use preference when reaching for objects (A), manipulating them with one hand (B), or engaging in role differentiated bimanual manipulation at eight age groups during the period from 6 to 13 months postpartum.

The longitudinal study also show that tasks that elicit overpracticed skills or very novel skills may not yield longitudinally consistent or stable hand-use preferences for infants. Also, a longitudinally stable hand-use preference is less likely to be exhibited when a single task is used (e.g., the same type of toy is presented several

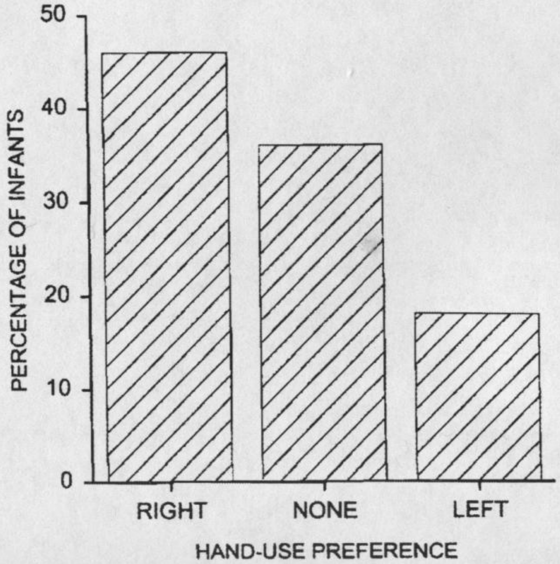

FIGURE 2 The percentage of infants (n = 74) who exhibited longitudinally stable right, left, and no hand-use preferences for both reaching and unimanual manipulation across four visits at 7, 9, 11, and 13 months of age.

times) or a single class or type of action is measured (e.g., reaching for objects). Thus, longitudinal investigation of infant hand-use preferences using either a few (4-5) or many (20-1-) presentations of the same object at each age and recording either the initial or most frequent reaches for the object at each presentation is unlikely to provide a reliable and valid assessment of the stability of preference across age.

For example, we observed that, although simple unimanual manipulations appear by 4 to 5 months of age, they do not reveal a hand-use preference until about 6 to 7 months of age. After 9 months of age, the infant may not exhibit a consistent hand-use preference for such simple unimanual manipulations (cf. Figure 1). Also, role differentiated bimanually coordinated skills appear as early as 7 months old (in fleeting, rather primitive forms; Kimmerle, Mick, & Michel, 1995); yet, infants do not exhibit a consistent hand-use preference until after 11 months old, when they occur more frequently and in a more robust manner.

In all of our work, we have assessed hand-use preferences by the frequency of use for specific manual skills. Based on this procedure, we conclude that a majority of infants will establish a hand-use preference early in the latter half of their 1st year, and they will maintain that preference throughout their 2nd year (Michel & Harkins, 1986). The factors responsible for maintaining the consistency of the preference, the relation of the infant preference to later handedness, and the factors responsible for the eventual establishment of a hand-use preference in the minority of infants that fail to exhibit a preference remain to be determined.

Recently, we have begun to develop a new assessment procedure for infant hand-use preferences. The quality of a manual action (i.e., skill) depends on finely timing and serially ordering sequences of the muscle contractions that comprise the action. Therefore, measures of hand-use preference that employ these assessments of manual skill potentially should reveal more about lateral biases in the state of the nervous system than do measures of preferred use (although preferred use must reflect differential skill to some degree). Consequently, the new hand-use preference assessment procedure for infants that we are devising measures differences between the hands in skill (timing and sequential order in the action) rather than in the acts accomplished by each hand or their frequency of use. We expect that such information will provide descriptions of the processes involved in the manifestation of hand-use preferences that will relate more directly to the neural processes underlying hemispheric specialization for cognitive functions.

ADULT AND INFANT HAND-USE PREFERENCES

To compare the characteristics of adult and infant hand-use preferences requires reliable and sophisticated descriptions of each. We chose Annett's (1985) description of adult handedness because it was built on a strong base of both questionnaire and performance-based data. According to Annett, human handedness possesses four characteristics:

1. For most people, the hands differ in both preferred use and skill.
2. The difference between hands varies continuously and not categorically among individuals.
3. The distribution of the differences is highly skewed in the population.
4. The bias in the population favors the right hand independently of cultural background or historical epoch.

Therefore, we can ask whether these same characteristics are present in the hand-use preferences of infants.

Our results show that infant hand-use preferences do exhibit the four adult characteristics (Figure 2). That is, the majority of infants have hand-use preferences that remain consistent throughout the period from 6 to 14 months old (about 18% with a significant left hand-use preference and 46% with a significant right hand-use preference). The distribution of the preference is continuously distributed among infants, and that distribution is skewed toward a right bias. However, in comparison with adults, the right bias is not as prevalent among infants, and there are fewer infants with distinct left or right preferences. Moreover, the specific characteristics of the preference (pattern of skill, domain of expression, dependency on contextual support, etc.) is not the same throughout development. The hand-use preference of the 6-month-old infant is qualitatively different (although similarly lateralized) from that of the 13-month-old infant. It is the character of the preference that changes, not necessarily the direction.

WHAT ARE THE FUNCTIONS OF HAND-USE PREFERENCES FOR INFANTS?

The question of function conceals two separable questions: What is the immediate consequence of the behavior, and what is the adaptive significance of the behavior? For most behavioral research, even with animals, the question of adaptive significance is the most difficult to answer (cf. Michel & Moore, 1995). Hence, handedness research usually examines whether the preference has immediate consequences. It has been demonstrated (e.g., Flowers, 1975; Todor & Doane, 1977) that the immediate consequences of adult handedness is the improved efficiency of performance of many manual actions and reduced decision time for the initiation and execution of manual actions (perhaps because the "choice-of-hand" step is eliminated in the information processing). Hand-use preferences may serve a similar function for infants.

The specific patterns of infant manual skill proliferate and become increasingly complex during the last half of the infant's 1st year. These complex patterns usually involve various forms of bimanual coordination including bimanual prehension and role differentiated bimanual manipulation of objects. Another aspect of this development is the ability to acquire and manage more than one object at a time (Kotwica & Michel, 1997). Early in development, after an object is grasped, presentations of additional objects will be ignored, or the grasped object will be dropped in retrieving additional objects. Subsequently in development, a grasped object will be stored (in the other hand or placed near the infant) so that additional objects may be acquired. This permits control of multiple objects and the assessment of their properties. Such management requires the coordination of both hands. By presenting four sets of objects with four distinct objects in each set to 38 seated infants (19 females) when they were 7, 9, 11, and 13 months old, we could entice them into acquiring and managing more than one object at a time. The manual actions used to manage (acquire and store) the objects were recorded on videotape and subjected to sequential analysis. The sequential organization of acquisitive skill varied with age, with more bimanual patterns emerging in older infants. Also, the 20 infants with stable hand-use preferences throughout this age period exhibited more sophisticated patterns than the 18 infants who exhibited nonstable hand-use preferences (Figure 3). Thus, a hand-use preference during infancy facilitates the acquisition of multiple objects that, in turn, permits experience with the cognitive skills of object comparison and the construction of object groups.

Bimanual prehension occurs more frequently during the last half of the 1st year and requires coordination of shoulder, arm, and wrist movements that involve participation of several neural systems (Massion, Paillard, Schultz, & Wiesendanger, 1983; Michel, 1991). Initially, bimanual coordination may derive from the intrinsic bilateral coactivation of homotopic muscles resulting in temporally and spatially synchronous movement patterns between the hands (cf. Goldfield & Michel, 1986b). Subsequently, bimanual reaching culminates in a role differentiated pattern of simultaneous complementary bimanual action or temporally sequenced complementary actions, likely involving functional development of the corpus callosum and supplementary motor cortex (cf. Diamond, 1991). Such role differentiation involves unique patterns of motor coordination and complementary specialization of directed attention to the two hands. Throughout the development of bimanual reaching, the infant's pattern of coordination appears to be influenced by the possession of a stable hand-use preference (Goldfield & Michel, 1986a; see also Figure 4).

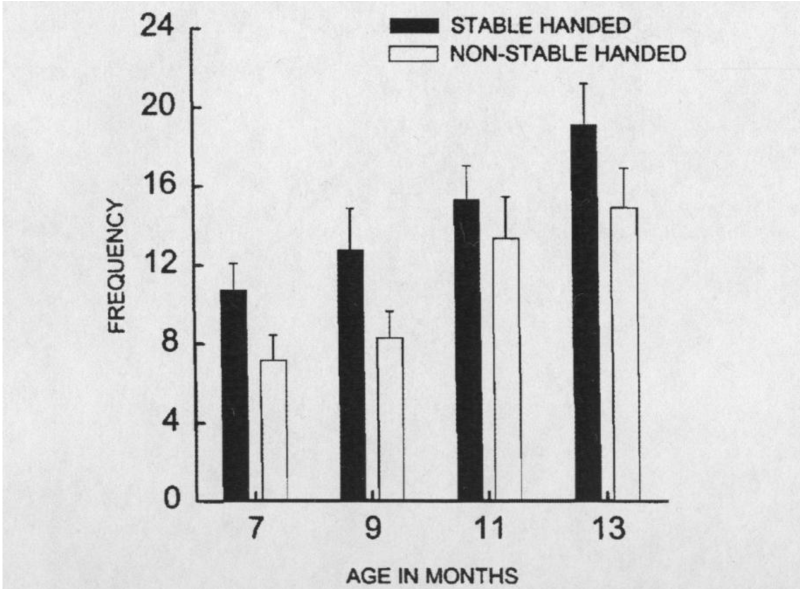

FIGURE 3 The mean frequency (standard error) of acts of object storage by infants with and without longitudinally stable hand-use preferences during the 7- to 13-month age period.

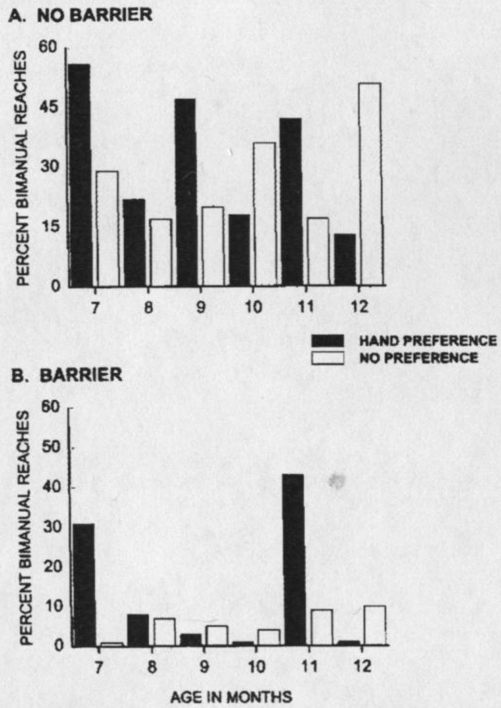

FIGURE 4 The percentage of simultaneous, complementary bimanual reaches exhibited by infants with or without a hand-use preference at six age periods when (A) there was no barrier blocking the trajectory of the hands or (B) when there was a barrier to the trajectory of one hand (the right hand for half of the trials and the left hand for the other half). Note that the barrier reduced the frequency of bimanual reaches despite the relatively minor alteration of trajectory required by the "obstructed" needed to maintain a bimanual reach. Also, although a hand-use preference permitted bimanual reaching in barrier conditions, it did so only at 7 and 11 months of age.

In a recent unpublished study (Michel & Lambrecht, 1997), bimanual reaching (for a "Nerf' soccer ball) was examined in 20 infants with stable right hand-use preferences at 7, 9, 11, and 13 months of age under three conditions: Both wrists wore 350g wrist weights, or only the left or only the right wrist wore the weight. Unlike the barrier condition, the weights required differential adjustment of the force of muscle contractions for each arm, rather than the trajectory (or pattern of muscle contraction), to maintain a bimanual reach. Frequency of unimanual and simultaneous bimanual reaches was recorded. In the condition with both wrists weighted, simultaneous bimanual reaches occurred less frequently than unimanual reaches until 11 months when they did not differ, and at 13 months, nearly all reaches were simultaneous bimanual (Figure 5). Weighting the left hand did not affect frequency of bimanual reaches (as compared to the both wrists weighted condition), although it did significantly increase the frequency of unimanual reaches at 7 months old. Weighting the right hand did not affect the frequency of bimanual or unimanual reaches at 7, 9, and 13 months old (as compared to the both weighted condition). However, at 11 months old, weighting the right hand decreased unimanual reaches and increased bimanual reaches (Figure 5). Thus, in infants with right hand-use preferences, differential perturbation (by a weight on the right wrist) of the force of contraction of right

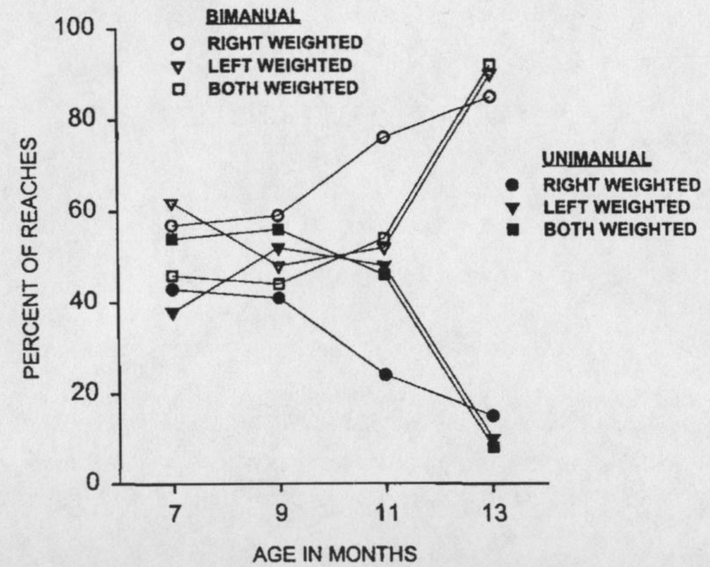

FIGURE 5 The mean percentage of bimanual and unimanual reaches for a "Nerf" soccer ball during the 7- to 13-month age period when the infant's right, left, or both wrists were weighted.

arm muscles during bimanual reaching does not disrupt bimanual reaching, whereas similar perturbation of the left hand sharply disrupts bimanual reaching.

Thus, infant handedness appears to affect certain bimanual skills: (a) Infants with longitudinally stable hand-use preferences can possess and manage objects more effectively than those without preferences and (b) infants with longitudinally stable hand-use preferences adjust to perturbation and obstacles in coordinating bimanual prehension differently than those without stable preferences.

It is likely that infants with stable hand-use preferences are creating sensorimotor experiences differently than those without stable preferences. These experiences likely contribute to the lateral bias in the functional organization of the cerebral hemispheres. Evidence from callosectomized monkeys and humans indicates that the corpus callosum is essential for the intermanual (interhemispheric) transfer of certain types of haptic (tactile) experience (Geffen, Nilsson, Quinn, & Teng, 1985a, 1985b; Trevarthen, 1978). Moreover, electrophysiological and behavioral evidence reveals that callosum function begins to appear after 7 months of age (Cernacek & Podivinski, 1971) and only achieves adult-like characteristics during the teen years (Galin, Johnstone, Nakell, & Herron, 1979; Salamy, 1978). If callosally mediated interhemispheric communication was absent or restricted during infancy, then certain forms of haptic experience would be confined to one hemisphere. The stable hand-use preferences prevalent during that age period are a likely means by which the two hemispheres could develop separate sensorimotor capabilities.

To test the extent of interhemispheric communication during infancy, a habituation and dishabituation procedure was used in a pilot study of the development of haptic discrimination in 12 infants at 7, 9, 11, and 13 months of age. The results showed that intermanual transfer of specific tactile experience of texture and shape does not occur before 11 months of age. All of the infants showed intermanual transfer of haptic temperature experiences (temperature information is conducted simultaneously to both cerebral hemispheres), even at 7 months of age. However, no infant exhibited intermanual transfer of either texture or shape information before 11 months of age.

Because most infants manifest hand-use preferences when playing with and exploring objects for at least 5 months before the age at which we obtained evidence of intermanual transfer of haptic experience (i.e., 11 months), it is likely that, for infants with stable hand-use preferences, one hemisphere receives haptic experiences that are different from, and not shared with, the other hemisphere. Trevarthen (1978) found that each hemisphere in a callosectomized baboon can establish separate sensorimotor skills, even when each has had access to the visual information about the use of both hands. Thus, the developmental elaboration of hemispheric specialization of function may depend, in part, on the early form of neural organization that restricts interhemispheric transfer of certain haptic experience. This restriction combines with the infant's hand-use preference to insure that the infant's spontaneous play with objects will provide each hemisphere with somewhat different capabilities for programming and controlling manual skills.

Unfortunately, such functional consequences of infant hand-use preferences do not specify the adaptive significance of handedness. The adaptive significance of any behavior is revealed by its effect on reproductive success (Hailman, 1982). If infant hand-use preferences are to be influenced by natural selection, it must be shown that these manual skills contribute to the development of skills and processes that affect reproductive success. Of course, the manufacture and use of tools are traits strongly tied to the evolution of humans (Oakley, 1972), and both a hand-use preference and the collaborative use of the hands are essential features of the manufacture and use of such artifacts. Moreover, these manual abilities are characteristics that may be linked to the evolution of language, another trait associated with the evolution of humans. The functional dynamics of hand-use and bimanual coordination share common features with those of motor speech control; therefore, these manual skills may have played an important role in both the evolution of language and tool construction (Bradshaw & Rogers, 1993).

In a comparative study of apes and humans, Vauclair (1993) reported that, in young apes, tool use tends to be performed unimanually, whereas human children almost always employ hand collaboration in tool use, even when the behaviors need not involve both hands (spooning food). Vauclair claimed that, although young apes may exhibit several forms of bimanual coordination, they do not exhibit a role differentiated bimanual coordination in which one hand delineates the frame of reference for the actions of the second hand (i.e., serial assemblage; Guiard, 1987). Moreover, he proposed that only this latter form of bimanual coordination implies asymmetric neuropsychological organization. However, several observers have reported role differentiated bimanual coordination among captive and wild chimpanzee adults (Hopkins & Rabinowitz, 1997) when acquiring food. A developmental study of wild chimpanzees' use of stones to crack nuts revealed that role differentiated bimanual coordination begins at about 11/2 years of age but does not become functionally successful until 31/2 years of age (Inove-Makamura & Matsuzawa, in press). Of course, as other articles in this volume demonstrate, attempts to discover the adaptive significance of the development of bimanual coordination in humans is greatly improved by careful and systematic comparative investigations of other apes. Although bimanual role differentiated manipulation has been observed in a majority of 1-year-old human infants (Kimmerle, 1991), until recently there had been no systematic examination of the development of this behavior during the infant's I st year. We video recorded the manual actions of 24 infants (12 males) at 7, 9, 11, and 13 months old to identify the relation of role differentiated bimanual skill to other bimanual skills (Kimmerle, Kotwica, & Michel, 1998). Frequency and duration was measured for 10 categories of bimanual actions exhibited during play with three single-part and three two-part toys.

Bimanual role differentiated actions were observed in 67% of the 7-month-old infants indicating an ability for intermanual coordination requiring the integration and sequencing of two separate motor acts. However, at this early age, role differentiated actions were relatively brief and represented a very small percentage of the total manual repertoire (4%), with unimanual (57%) and nondifferentiated bimanual (40%) actions making up the remainder (Figure 6). Also, they are uninfluenced by the characteristics of the toys (Kimmerle et al., 1995).

At first, the infants exhibit no hand-use preference for this pattern of manipulation, but they do exhibit a hand-use preference for prehension at 7 and 9 months old (and even as young as 4 months old). By 11 months old, role differentiated bimanual manipulation is occurring in frequency and duration more comparable to **that** of many unimanual actions. Also, at this age, a hand-use preference in role differentiated bimanual coordination begins to appear. By 13 months old, role differentiated bimanual actions are exhibited by all infants and a hand-use preference is well established (Figure 1). Moreover, role differentiated bimanual actions are of longer duration at this age, and they constitute an important aspect of the infant's

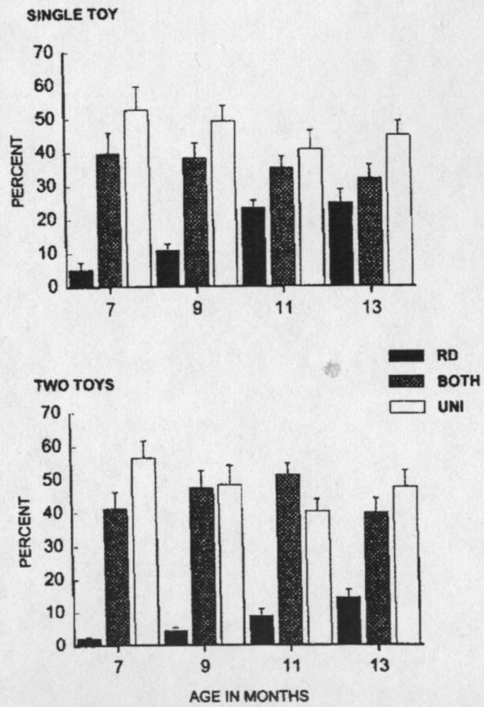

FIGURE 6 Mean percentage of role differentiated bimanual (RD), nondifferentiated bimanual (BOTH), and unimanual (UNI) manipulatory actions when playing with single toys or two toys at a time during the age period of 7 to 13 months old.

manual repertoire (Kimmerle et al., 1998). Thus, by 13 months old, role differentiated bimanual manipulation begins to expand in toy play, and it exhibits a distinct hand-use preference (Michel et al., 1985).

If role differentiated bimanual coordination is important for the development of tool use and construction, then there may be a natural selective advantage for role differentiated bimanual coordination. To the degree that hand-use preferences affect the development and organization of such coordination, there might be a selection pressure for handedness. However, this does not account for the right bias in the distribution of handedness (cf. Annett, 1995; Michel, 1995).

We have shown that concordance of hand-use preference greatly facilitates the imitative acquisition of manual skills in adults (Michel & Harkins, 1985). Left- and right-handed adult observers were shown (without verbal commentary) how to tie three different knots by either left- or right-handed teachers. Observational learning was significantly facilitated when observer and teacher were concordant for handedness (with no difference between left- or right-handed concordance) as compared to when they were discordant for handedness (Figure 7). It is likely that the transmission of manual skills among early hominid species relied primarily on observational learning without verbal mediation (Falk, 1980; Frost, 1980; Lieberman, 1975). Therefore, any characteristic that interfered with the nonverbal transmission of manual skill would be disadvantageous to both observer and demonstrator.

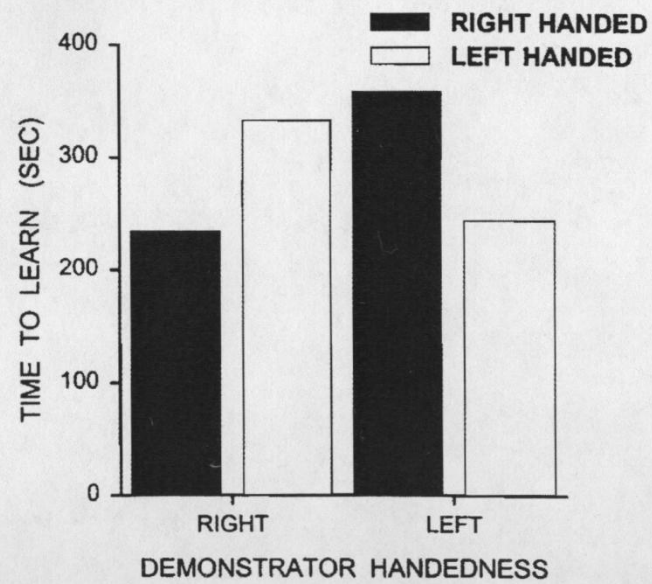

FIGURE 7 Mean time to learn how to tie knots for right- and left-handed adults when the knot-tying demonstrator was either right- or left-handed.

Of course, a disadvantage for discordance raises the question of why any individuals are discordant. Although some have argued that left-handedness arises from pathological conditions (Bakan, 1971; Satz, 1972), there is little evidence to support this notion (Bishop, 1990). Instead, handedness appears to be a polymorphic trait (Annett, 1995). That suggests that the minority or heterozygous types or both may have associated characteristics that are relatively more advantageous than the disadvantages derived from potential discordance. There is some evidence that left- or mixed-handed individuals have a greater proficiency for spatial orientation skills (Mebert & Michel, 1980) or other cognitive abilities (Annett, 1995).

Interestingly, discordance of handedness between parent and infant also affects the pattern of parent—child object play (Michel, 1992). Twenty-eight mother—infant pairs were videotaped while playing with toys while the infants sat on their mother's lap when the infants were 7, 9, and 11 months old. All mothers were right-handed, and half of the infants had stable left hand-use preferences and half had stable right hand-use preferences. Although the play was analyzed for five types of situations that would bias the infant's hand-use, the mother's hand-use was the dominant influence on infant's hand-use. Infants increased their matching of their mother's hand-use during the 7- to 11-month age period. Mothers did not adjust their hand-use, or the biasing patterns of their toy play, to the preference of their left-handed infants, and this may have accounted for the less-frequent use of the preferred hand by left-handed (as compared to right-handed infants) as they reached 11 months old. Infants match and imitate the manual actions (Uzgiris, Benson, Kruper, & Vanek, 1989) and hand-use (Harkins & Uzgiris, 1991) of their mothers. Therefore, an infant whose handedness is concordant with that of the mother is likely not only to have his or her handedness strengthened but is also likely to acquire various gestural and manipulative skills at an earlier age.

In a recent study (Mundale & Michel, 1997), the effect of the mother's handedness on her toy play with her infant was examined. Thirty-six mothers were divided according to their hand preference scores (as measured by the Briggs & Nebes, 1976, version of Annett's questionnaire) into right-handed (scores greater than 16 of a possible 24), left-handed (scores less than —16 of a possible —24), and no preference (scores between +16 and —16) groups (12 in each group). The mother's play with her infant was videotaped during three 20-min visits when the infant was 7, 9, and 11 months of age.

Figure 8 shows that the right-handed mothers used their right hands significantly more often for placing toys; activating movable parts of the toy (kinetic play); moving the toys about; touching the infant; and placing the toy in the infant's hand, deliberately maneuvering the infant's hand to engage it in play with the toy, or both.

Left-handed mothers were not a mirror reversal of the right-handed mothers. Left-handed mothers used their left hand to place the toys, move them, and maneuver the infant's hand, but they used their right hand for bimanual manipulation of the toy. Mothers without a preference used their hands

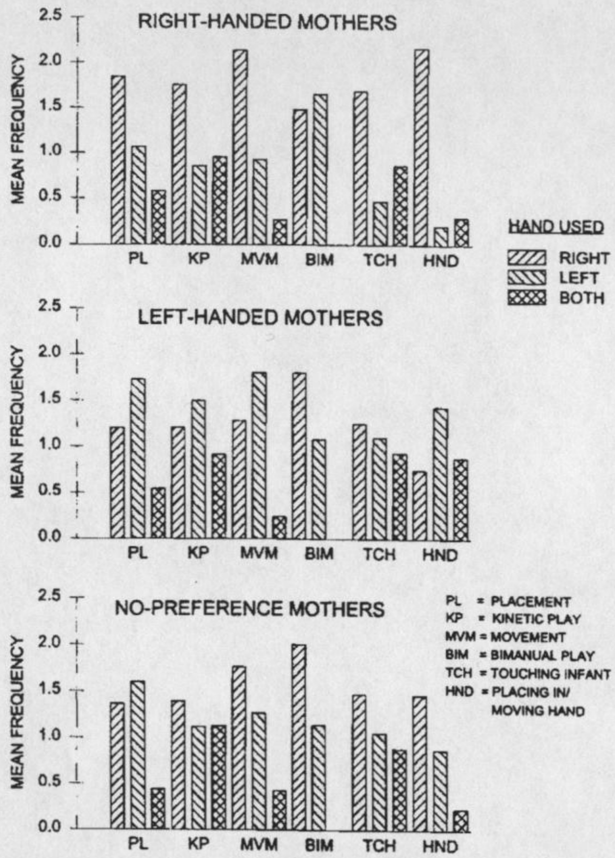

FIGURE 8 Mean frequency of right, left, and both hand-use for six manual actions by right-handed, left-handed, and no preference mothers when playing with their babies during the period from 7 to 11 months of age.

in ways more similar to that of right-handed mothers, except for bimanual manipulation of the toy. This study demonstrates that the influence of maternal handedness on the development of handedness will not be easily gaged. The influence of concordance versus discordance of mother—infant handedness on infant matching or imitative manual play will require rather large-scale, longitudinal, systematic observational study.

The archeological record shows that tools requiring complex object manipulation for their construction appeared before art and symbols (Bradshaw & Rogers, 1993). Handedness and role differentiated bimanual coordination were important factors in the tool-working abilities of early hominids (Falk, 1980; Frost, 1980; Toth, 1985). Moreover, Bates, Camaioni and Volterra (1975) showed that individual differences in the rate of development of the use of objects as tools and in combinatorial play predicts the rate of gestural and verbal communication in children. Therefore, it is possible that the development of sensorimotor processes involved in hand-use preferences and role differentiated bimanual coordination may play a role in both the evolution and acquisition of language. Both the capacity for communication and the use of tools involve the ability to understand means—end relations and the use of some intermediary means to acquire a goal. Concordance of hand-use preference between mother and child would facilitate the acquisition of communicative gestures and manipulative skills. Similar concordance would facilitate the acquisition of tool use and tool construction skills necessary for adult survival.

A selection pressure against discordance of handedness among individuals would mean that any bias in lateral asymmetry early in development, which might affect the bias in handedness, could become the developmental precursor favoring the establishment of the observed population bias in handedness distribution. Again, the evidence for the adaptive significance of handedness supports the notion of an advantage for a population bias but not for the right bias. Of course, the direction of the bias (in this case a right preference) may be an epiphenomenon of developmental processes that are neutral to natural selection or are, at best, an exaptation (Gould & Vrba, 1982).

HOW DO INFANT HAND-USE PREFERENCES DEVELOP?

As with the development of most psychological characteristics, the study of infant hand-use preferences has been affected by the nature—nurture controversy (Michel, 1983). Nevertheless, it is possible to engage in developmental research without dichotomizing psychology and biology (Michel & Moore, 1995). I have focused on the contribution of self-generated experiences and maternal influences on the development of infant hand-use preferences. Early developmental features of the infant often provide the conditions that alter the experiences of the individual. These experiences, in turn, can affect the subsequent course of development. Therefore, my research sought developmental precursors that would bias the infant's manual experiences. Also, I adopted an orientation of "development from" rather than "development to" in examining handedness so as to facilitate the discovery of subtle and unusual developmental precursors that could be formally distinct from that of differential hand-use. Adoption of a development from orientation allows the search for the developmental origins of handedness to extend beyond just seeking early indications of differential hand-use. Thus, the contribution of prenatal and neonatal postural asymmetries to the development of preferred hand-use could be considered.

Neonates exhibit only a few different postures when supine, prone, seated, or carried (Casaer, 1979) that represent continuation of patterns of behavior relevant to intrauterine conditions (Prechtl, 1982). These postures affect interaction with objects (Bullinger, 1983; Jouen, 1984; Rochat & Bullinger, 1994) and caregivers (Ginsburg, Fling, Hope, Musgrove, & Andrews, 1979). Several of the postures exhibit lateral asymmetries, and they provide asymmetries of visual, proprioceptive, and even corollary discharge experiences for the manual actions of the young infant.

Most neonates prefer to turn the head to one side when supine (Figure 9), usually the right (Michel, 1981). The neonate's preference is maintained for about 8 to 10 weeks after birth and results in both differential hand regard and arm movements (Figure 10; Michel, 1987). These experiences can produce asymmetries of kinesthetic, proprioceptive, visuospatial, auditory, and motor map registers in the nervous system (cf. Michel, 1988, 1991). These asymmetries, in turn, can bias use of one hand over the other for successful prehension (Michel, 1988, 1991). Indeed, infants with a leftward head-orientation preference during their first 2 months, preferred to use their left hand to obtain objects during the subsequent 12- to 74-week period (Figure 11; Michel & Harkins, 1986). In contrast, infants with a rightward head-orientation preference preferred to use their right hand. Thus, the direction of neonatal head-orientation preference predicts hand-use preference for obtaining objects throughout the first 18 months after birth.

Prehension of objects and hand-to-mouth actions precede the occurrence of object manipulatory actions. Because a hand-use preference for prehension precedes

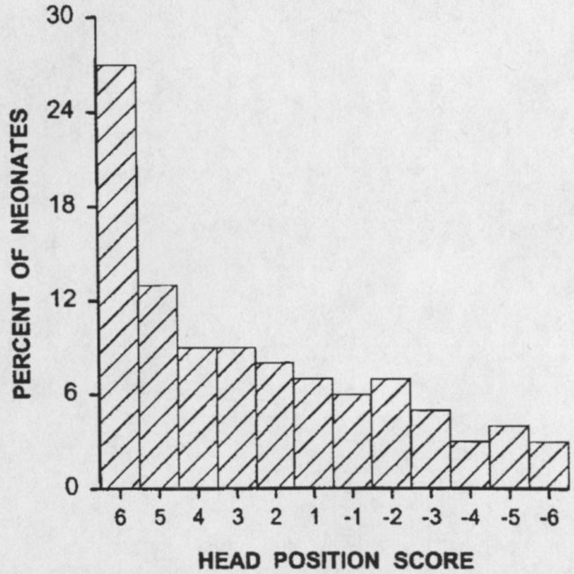

FIGURE 9 Distribution of neonatal ($n = 150$) head-orientation preferences assessed twice during the period from 13 to 48 hr after birth. Positive scores indicate a rightward, and negative scores a leftward, orientation with larger numbers indicating a more reliable orientation.

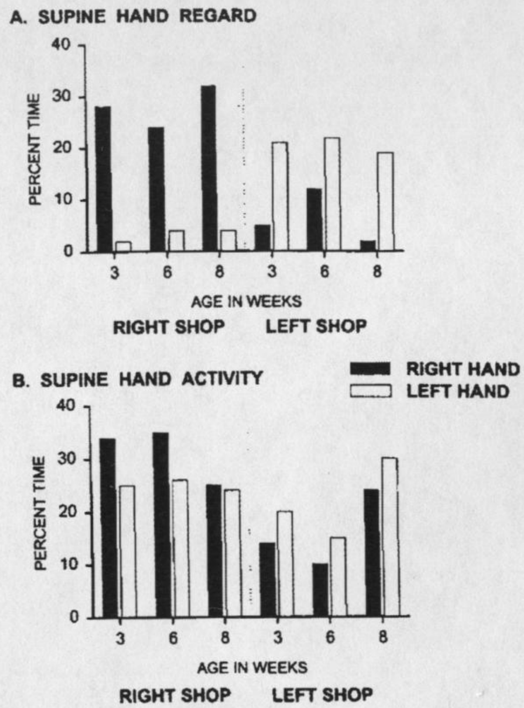

FIGURE 10 Percentage time that the right hand and the left hand are visually regarded (A) or active (B) for infants with right or left supine head-orientation preferences (SHOP) during their first 2 months postpartum.

both bimanual object manipulation and intermanual object transfer (using the month), the preferred hand can obtain more objects and engage in more unimanual manipulation and manually coordinated oral and visual inspection of them than can the nonpreferred hand. This difference in experience could promote skill differences in unimanual object manipulation and subsequently the development of different manipulation patterns for right- and left-hand performance during role differentiated bimanual manipulation.

Thus, prehension facilitates exploration of objects and the acquisition and practice of manual skill. Asymmetry of prehension yields asymmetry of unimanual manipulation that, in turn, can yield an asymmetry of bimanual manipulation. All of these asymmetries of action and experience can eventuate in asymmetry of skill. Of course, not all such asymmetries will favor the preferred hand. Also, because no step in this developmental sequence is obligatory, events and conditions that disrupt the sequence can alter both the eventual pattern of the individual's handedness and its relation to other forms of hemispheric specialization of function. Nevertheless, the normal spontaneous postures and movements of the neonate can be important con-

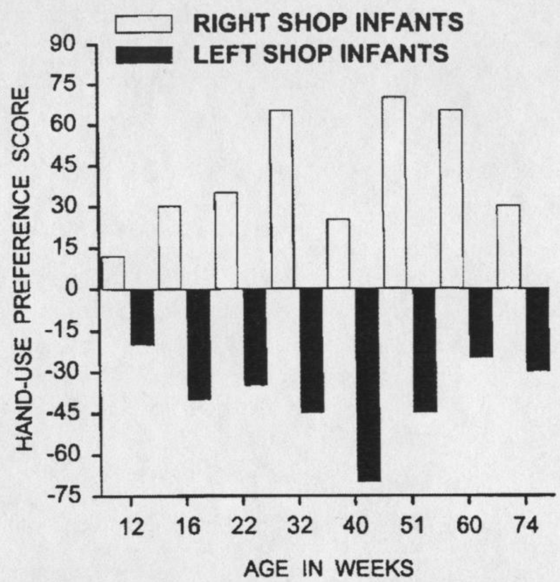

FIGURE 11 Mean hand-use preference scores when obtaining objects during the period from 12 to 74 weeks of age for those infants who had consistent right or left supine head-orientation preferences (SHOP) during their first 2 months postpartum. Positive scores indicate right hand-use, and negative scores indicate left hand-use.

tributors to the development of neuromotor asymmetries, with potentially long-term consequences for the neuropsychological character of the individual.

Our research evidence is consistent with the hypothesis that early head-orientation preferences contribute to the development of infant handedness by inducing laterally asymmetric sensorimotor experiences that, in a majority of infants, will produce a right preference in hand-use. An early leftward head-orientation preference in a minority of infants is associated with a left-hand bias in sensorimotor experience and a later left hand-use preference. There is no evidence in our research that the early postural asymmetry and the subsequent hand-use preference are different manifestations of the same, developmentally invariant, hemispheric asymmetry, although others have argued otherwise (cf. Kinsbourne & Hiscock, 1983).

Of course, nothing in this account contradicts the value of constructing genetic models of handedness. However, developmental research in mammals has demonstrated the value of "unpacking" genetic models to examine the separate influences of intrinsic genetic, extrinsic genetic, self-generated experiential, and maternal effects (Atchley & Hall, 1989; Michel & Moore, 1995). Our research should encourage more investigations of the contribution of self- and maternally generated experiences to the development of hemispheric specialization of function and interhemispheric communication.

WHAT DOES THE STUDY OF THE DEVELOPMENT OF INFANT MANUAL SKILLS REVEAL ABOUT THE DEVELOPMENT OF HEMISPHERIC SPECIALIZATION OF FUNCTION AND INTERHEMISPHERIC COMMUNICATION?

Infant hand-use preferences are aspects of hemispheric specialization of function. Differences in the manipulatory actions between the hands, as induced by postural asymmetries and prehensive hand-use preferences, will result in hemispheric differences in the structural organization of primary and secondary sensory and motor cortices, supplementary motor areas, prefrontal areas, basal ganglia, thalamic nuclei, cerebellar nuclei, and so forth (Massion et al., 1983; Spinelli & Jensen, 1982). Indeed, spinal organization is also likely to be affected. Therefore, the value of using research on handedness to study hemispheric specialization is not dependent on identifying some relation between handedness and cerebral lateralization of speech. This conclusion becomes especially important as modern research on the exact nature of speech lateralization reveals that it is murkier than conventional wisdom would have us believe (Bates, 1993).

Also, certain haptic experiences acquired during the manipulation of objects are not shared, via either corpus callosum or bilateral projection, between hemispheres before 10 to 12 months of age. This means that the experiences obtained by each hand about some of the tactile properties of objects will be unavailable to the other hand (hemisphere) for much of the infant's 1st year. Moreover, a hand-use preference during the 1st year will lead to differences in extent and type of manual sensorimotor skills acquired and promoted by each hemisphere. The contribution of those differences to interhemispheric communication and the functional organization of the callosum and hemispheric specialization for other functions remain to be determined.

CONCLUSIONS

During the first 18 months, normal infants with stable hand-use preferences manifest more sophisticated manual skills than normal infants without stable hand-use preferences. Hand-use preferences affect the infant's ability to acquire and possess objects, coordinate both bimanual reaching and role-differentiated bimanual manipulation of objects, and imitate the manual skills of the mother during mutual play. Differences between infants with left versus right hand-use preferences are few and minor. Right-hand bias in the population may be at best an exaptation. It may come under the influence of natural selection, but at present, there does not appear to be any evidence that it was either created or is maintained by selective forces. Also, there is no evidence that handedness is a derivative of selective pressures for cerebral hemispheric lateralization for language processes.

Nevertheless, infant hand-use preferences do reveal aspects of the status of both cognitive and neural development. The development of hand-use preferences also contribute to the developmental changes in cognitive and neural status as these are reflected in the condition of the neural systems involved in manual skills. A hand-use preference that affects the active manipulation of objects and the patterns of manual imitation of adults will create alterations in the neural medium involved in these actions. These media depend on such experience for their sculpting and organization (Quartz & Sejnowski, 1994). Moreover, callosal functioning is rather primitive during the infant's first 10 to 12 months. This allows the experiences generated by a hand-use preference to affect the organization of several components of each hemisphere in relative isolation from the other. As yet, we have no information as to how such differentiation affects the pattern of interhemispheric communication established once the callosum becomes fully functional.

The patterns of infant hand-use preferences and bimanual coordination reveal important aspects of neural functioning and pose special problems for theories of both motor control and cognitive functioning. They are not only important instances of a lateral bias in the neuropsychological functioning of infants but also perhaps the developmental precursors of the lateral biases of child and adult neuropsychological functioning.

ACKNOWLEDGMENTS

The research described in this article was supported by grants from the National Institute of Mental Health (1R0 MH 35528), the National Institute of Child Health and Human Development (1R01 HD 16107 & HD 22399) and the DePaul University Research Council.

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