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## Ontogenetic constraints on the evolution of right-handedness

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**Abstract:** Ontogenetic factors constrain the evolution of species-typical traits. Because human infants are born "prematurely" relative to other primates, the development of handedness during infancy can reveal important ontogenetic influences on handedness that may have contributed to the evolution of the human species-typical trait of a population-level right-hand dominance.

If left cerebral dominance for vocal communication evolved before right-handedness in humans and left-hemisphere dominance of speech (vocal communication) led to right dominance for hand use, then how can handedness become associated with vocalization? Corballis offers the very interesting solution that language evolved first as a manual and facial gesture system and vocalization was later incorporated into language gestures. Left-dominant vocal, manual, and facial gestures yielded right-handedness. However, when attempting to provide an evolutionary account for the occurrence of a species-typical trait, explanations of the development of the trait are often either ignored or simplified. Yet, how the trait develops constrains the optimality of the trait's adaptive character and can reveal much about the sequence of the emergence and transformation of the trait during phylogeny (Michel & Moore 1995).

A peculiarity about handedness is that although there are only two hands, the trait is not categorical. Instead, the trait distributes continuously among individuals in a manner similar to height. However, because there are two hands, we can take the equivalent use or preference for each hand as a zero-point when examining the distribution of handedness. Unlike those species for whom there is a forelimb preference of use, the distribution for humans shows that there are significantly more individuals whose handedness scores exhibit a right preference than those who exhibit a left preference. Hence, the species-typical aspect of human handedness is the population bias in distribution that favors right-handedness (although chimps may show a population bias toward right-handedness that may reflect confounding in the research designs, as Corballis notes). Unfortunately, the exact proportion of right-handed individuals depends on the criteria used to define right- and left-hand use preferences. This dependency has plagued studies that have examined the relation of handedness to other functions, or neural anatomy (Bryden & Steenhuis 1991). The proportions of right-handers can vary from 95% to 65% (depending on criteria) and the remainder is usually defined as "non-right-handed," reflecting the fact that they are a much more heterogeneous group.

In my own work on the development of handedness during infancy, I have chosen to use probability estimates to categorize the distribution into three groups: right-, left-, and undetermined-handedness (Michel 1998). With these categories, about 45% to 52% of infants during their first year had reliable ( $p < .05$ ) right-hand use preferences (the variation depends on whether the preference is based on reaching or object manipulation), 13% to 18% had reliable left-hand use preferences, and 30% to 42% exhibited hand use that could not be reliably categorized (undetermined-handedness) (Michel et al. 2003). Latent class analysis revealed that there is a group of infants whose development seems to reflect the influence of a hidden variable that is biasing them toward a right preference (Michel et al. 2001). However, the proportion of such infants varies from 32% to 61% depending on the criteria used to define their hand-use preference. The results do confirm that even during infancy, there is a right bias in the distribution of handedness.

Previously, I had shown that the right bias in hand-use preference when reaching for objects during the first 18 months was predictable from the direction of the infant's preference for orienting his/her head to one side when supine or when inclined in a seated position. Approximately 63% of neonates exhibit a significant preference for orienting the head to the right during their first two months postpartum (Michel 1981). Infants with a distinct early preference for orienting the head to the left manifested a left-hand use preference when reaching for objects beginning at four to five months postpartum, and those with a distinct preference for orienting the head to the right manifested a right-hand use preference (Michel & Harkins 1986). Because tactile perception of texture and shape is not transferred between the hands (and presumably the cerebral hemispheres) until about 11 months postpartum (Michel 2003), the hand preference for acquiring objects will provide one hemisphere with sensorimotor experiences for about six to seven months that are not shared between hemispheres. This raises interesting questions about the consequences of such experience on the cerebral circuits underlying the manual-facial gestural system upon which Corballis wants to base language.

The evolution of an upright, two-limb, locomotion strategy had such profound effects on the female pelvic skeletal structure that humans seem to be born some two to three months earlier than would be estimated from the general characteristics affecting primate gestation lengths. Consequently, unlike the chimpanzee, the human mother must carry her infant for several months postpartum as she locomotes. And when the mother is not carrying the infant, it is frequently deposited in a supine position. This permits the opportunity for brain-stem asymmetries influencing head orientation (which occur prenatally in other primates) to contribute to the development of lateral asymmetries in infant cortical neural circuits either directly or via their influence on arm movements and self-induced events in the visual field (e.g., hand regard).

The infant manifests a handedness pattern that is very similar to that of the adult, and the infant handedness may be a consequence of a preferred head position. That preferred head position may reflect simple lateral asymmetries in brain-stem development that increase their influence on cortical development because the human infant is typically born "prematurely" for a primate of its type. Elucidating the relation between manual-facial gestures (and language/speech) and right-handedness will require much more sophisticated research on the development of handedness (especially during infancy) and the development of infant vocalizations, manual and facial gestures, and their relation to the neural circuits that contribute to their expression and ontogeny. Corballis's theory has set an important task for developmental psychobiological research.