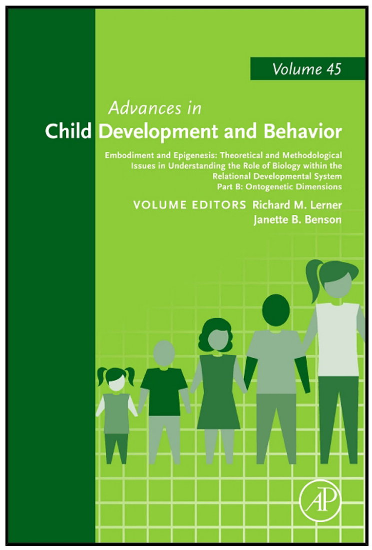

From Michel, G. F., Nelson, E. L., Babik, I., Campbell, J. M., & Marcinowski, E. C. (2013). Multiple Trajectories in the Developmental Psychobiology of Human Handedness. In R. M. Lerner & J. B. Benson (Eds.), *Embodiment and Epigenesis*: *Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System* Part B: Ontogenetic Dimensions. Elsevier Inc.: Academic Press, 227–260.
ISBN: 9780123979469

Academic Press

CHAPTER NINE

Multiple Trajectories in the Developmental Psychobiology of Human Handedness

George F. Michel*,[1], Eliza L. Nelson†, Iryna Babik*, Julie M. Campbell*, Emily C. Marcinowski*
*Psychology Department, University of North Carolina, Greensboro, NC, USA
†Psychology Department, Florida International University, Miami, FL, USA
[1]Corresponding author: E-mail: gfmichel@uncg.edu

Contents

Abstract

We show that handedness is a product of a multifaceted biosocial developmental process that begins prenatally and continues into adulthood. Although right-handedness predominates, handedness varies continuously across the population. Therefore, our phrase "multiple trajectories" refers to both differences in developmental pathways that can lead to *similarities* in handedness and similarities in pathways that can lead to *differences* in handedness. The task for the researcher is to identify how, when, and for what actions the trajectory of handedness development can be maintained or changed for an individual. Given the complexity of these developmental pathways, it is likely that the asymmetric sensorimotor activity that occurs during the development of handedness influences other hemispheric variations in neural processing. Indeed, researchers

Advances in Child Development and Behavior, Volume 45
ISSN 0065-2407, http://dx.doi.org/10.1016/B978-0-12-397946-9.00009-9

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

have investigated how handedness relates to cognitive, social, and emotional functioning because handedness represents *different patterns of hemispheric specialization*. Although the story of handedness development is not complete, it is well worth pursuing because it makes the development of brain–behavior relations more transparent, especially for hemispheric differences in function.

1. INTRODUCTION

For adult humans, handedness is a universal feature of their behavior and identity. Nearly all adults use one hand preferentially, and most often with more proficiency, on tasks requiring speed, precision, and skill. Most of these tasks involve tool use and although the "preferred" hand often may work alone (e.g., using a computer "mouse"), many tasks require both hands with one hand playing a supporting role (steadying or adjusting the position of the object) as the other hand engages in more precise actions with the object (e.g., dealing playing cards). This bimanual action is called role-differentiated bimanual manipulation (RDBM), and the preferred hand for unimanual tasks is most often the preferred hand for the precision actions in RDBM.

Both evidence from self-report questionnaires and unimanual proficiency tasks for which speed of execution and accuracy can be recorded (e.g., moving pegs from one row of holes to a second row) show that handedness is not a dichotomous or trichotomous trait but rather is continuously distributed across members of the population with a sharp skew toward right-handedness (Annett, 1985, 2002). Thus, there are two forms of bias in handedness: (1) that one hand is preferred over (or is more proficient than) the other and (2) that the right hand is typically the preferred, more proficient, hand. In both biases, the difference between right and left hand varies continuously across individuals both in preferred-use and proficiency.

Because there is no consensus about how to classify individuals along this continuum, studies differ in criteria for classification and hence, the proportion of "right-handed" individuals in any sample can vary from 80% to 97%. Although left-handedness varies with familial handedness and seems to "run in families", only 25–45% of the offspring of two left-handed parents are left-handed compared with less than 10% for two right-handed parents. These distributions "spoil" most genetic and social-learning models of handedness because the 10% proportion of left-handed offspring of two right-handed parents is too high and the proportion of left-handed offspring of two left-handed parents (35–45%) is too low (Annett, 1974, 1985). Left-handedness also appears to be more common in males than in females (Papadatou-Pastou,

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

Martin, Munafo, & Jones, 2008), which may reflect an influence of differences in gonadal hormones (Geschwind & Galaburda, 1985).

Although cultural groups vary in the proportion of self-identified right-handed adults, there is no predominantly left-handed cultural group or even one with more than 18% left-handedness (Annett, 2002; Marchant, McGrew, & Eibl-Eibesfeldt, 1995). Indeed, there is no historical evidence of anything other than predominantly right-handed cultural groups (Coren & Porac, 1977; Coren, Searleman, & Porac, 1982). Anthropological evidence suggests that the right-hand predominance appeared early in hominid evolution (Frost, 1980; Volpato et al., 2012). However, some have argued that the right shift in handedness distribution emerged with the great apes (Halpern, Guentuerkuen, Hopkins, & Rogers, 2005; Hopkins, 2006; MacNeilage, Studdert-Kennedy, & Lindblom, 1987, but see Cashmore, Uomini, & Chapelain, 2008; McGrew & Marchant, 1997; Papademetriou, Sheu, & Michel, 2005). Corballis (1997, 2009) proposed that there was a genetic mutation in hominid evolution (perhaps associated with the evolution of bipedal locomotion and/or affecting hemispheric specialization for language functions) that promoted preferential use of the right hand. Whatever the source, the right bias in human handedness is certainly a *species-typical* trait that likely has prevailed throughout human evolution (Falk, 1980; Frost, 1980; Spennemann, 1984; Toth, 1985; Volpato et al., 2012), although different cultures may have differentially enhanced or reduced its manifestation.

As an aspect of individual variability, handedness appears to be "related" to several other functional differences among individuals. An examination of the literature (more than 46,000 articles—PubMed search, June 2012) shows that "non-right-handedness" is associated with a host of psychological traits (e.g., autism, Attention Deficit-Hyperactivity Disorder (ADHD) developmental coordination disorder, schizophrenia and bipolar disorders, Down's syndrome, dyslexia, learning disabilities, stuttering, and sexual partner preferences) and medical conditions (e.g., congenital adrenal hyperplasia, arthritis and ulcers, recovery from brain damage, stature, and early menarche). Although most of the psychological traits involve developmental psychopathologies, there are some associations with left-handedness that are culturally admired and rewarded (e.g., athletic skills, cognitive–spatial abilities, and artistic talents). Nevertheless, many of the associations with left-handedness or non-right-handedness appear to be detrimental to the individual's reproductive success. Therefore, non-right-handedness should be under a natural selective pressure that would reduce its prevalence in the population. On the contrary, there is some evidence that the proportion of non-right-handedness

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

has remained constant in the population (Raymond, Pontier, Dufour, & Moller, 1996). Thus, both the predominance of right-handedness and the maintenance of a small proportion of left-handedness in human populations must be explained by any account of handedness development.

There are three reasons why reproductively detrimental phenotypes may continue as associations with non-right-handedness:

1. The associations are relatively new in human evolution and currently are in the process of elimination through natural selection. The end result would be the disappearance of non-right-handedness. This explanation is unlikely because there is no evidence that these associations are new or that there is a decline in the proportion of non-right-handers (Raymond et al., 1996);
2. The associations are only occasional pleiotropic consequences of the adaptively significant characteristics of humans and therefore may be manifested among a minority of individuals. A distinctly lateralized functional organization of the brain may have been an important development for the evolution of *Homo sapiens*, and one consequence of that is the occasional production of phenotypes that are atypical (Crow, 2002); and
3. The associations are a pleiotropic consequence of the adaptive significance of the polymorphism (or polyethism) in handedness. Left-handers or "mixed-handers" may be at an adaptive advantage (compared with right-handers) in some unique aspect of the human niche (e.g., as artist, architect, and athlete); hence, their proportion is maintained in the population. Left-handers appear in unusually higher proportions among occupations and activities typically involving visual–spatial skills (Mebert & Michel, 1980; Preti & Vellante, 2007; Raymond et al., 1996).

There is some evidence of the adaptive significance of both the predominance of right-handedness (Michel & Harkins, 1985) and the maintenance of the polyethism (Annett, 1995; Annett & Manning, 1989; Billiard, Faurie, & Raymond, 2005; Raymond et al., 1996). However, the adaptive significance of the polyethism has received little systematic investigation. Nevertheless, it is *both* the *right predominance* and the *maintenance of a minority* of left- and mixed-handed individuals that *must be accounted for* in any theory of the developmental *origins of handedness*.

Handedness is both an example of a lateralized functional asymmetry of the brain and it is "related" to other brain asymmetries of both anatomy and physiology (Annett, 2002; Bishop, 1990; Bradshaw & Rogers, 1993; Corballis, 2009; Crow, 2002; Halpern et al., 2005; Jones & Martin, 2010; Kinsbourne, 1997; Knecht et al., 2000; McManus, 2002; Steinmetz,

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

Volkmann, Jäncke, & Freund, 1991). Handedness (or even familial sinistrality; Carter-Saltzman, 1980; Isaacs, Barr, Nelson, & Devinsky, 2006; McKeever, 2000) seems to affect the manifestation of lateralized asymmetries in brain structural and functional organization, especially for language. Nevertheless, despite more than 50 years and tens of thousands of studies examining the relationship of handedness to psychological and medical problems, neuropsychological functioning, and neuroanatomy in adults, there are few solid results. In part, this is because most researchers have used measures of handedness that have no theoretical basis or empirical validation and the classification of individual handedness into separate subgroups is based on arbitrary criteria (Bishop, 1990). Measures of the development of handedness must use reliable and valid procedures and use classification techniques that are statistically defensible.

Although developmental research depends on good descriptive information, describing handedness, even in adults is somewhat problematic (Bishop, 1990; Provins & Cunliffe, 1972). There is no consensus about whether hand-use preferences should be identified via statistically evaluated measures of actual performance, self-reports of performance obtained via questionnaire, or self-assignment. Only actual performance measures can be employed with infants and young children.

Many studies of adults identify handedness by asking the participants or by noting their writing hand (Casasanto, 2009). Some more "sophisticated" studies categorize individual handedness according to a "screening" questionnaire (Willems, Hagoort, & Casasanto, 2010), and most use the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971) with arbitrarily defined scores creating the handedness groups (e.g., scores of 52–100 = right handed and −100 to +51 = not right handed). As do most questionnaires, the EHI primarily identifies the hand used for manipulating tools (e.g., toothbrush, knife, and spoon), most of which are culture bound (Perelle & Ehrman, 2005) or constrained to modern history (e.g., striking a match and using scissors), and the proper use of these tools (often involving control by the right hand) is taught in childhood. Therefore, the hand-use preference for these activities is confounded by how the individual was "taught" to use the tool. Of course, it is possible that in some cultures, parents unconsciously adjust their tool use "training" to relate to the young child's preference. However, it is likely tool use training will reflect cultural biases rather than the preferences of the child.

Responses on handedness questionnaires are poorly related to manual proficiency (Bishop, Ross, Daniels, & Bright, 1996; Bryden & Steenhuis, 1991; Cavill & Bryden, 2003; Flowers, 1975; Provins & Cunliffe, 1972;

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

Steenhuis & Bryden, 1989; Todor & Doane, 1977). Left-handers identified by questionnaire exhibit extreme heterogeneity in their manual skills (i.e., they report performing more tasks with their right hand than right-handers do with their left hand). Left-handers identified by hand proficiency are more homogeneous in their manual skills (Steenhuis & Bryden, 1989; Todor & Doane, 1978), and only those with high left-hand proficiency exhibit evidence of right hemisphere speech functions (Satz, Achenbach, & Fennell, 1967). Questionnaires, also, cannot distinguish between those with ambilateral scores who have high-level performance with both hands and the more common occurrence of those with low-level performance with both hands (Doane & Todor, 1978; Todor & Doane, 1977). Thus, determining handedness by questionnaire or even, as some have proposed, by writing hand is not sufficient to capture the variability of adult and child handedness.

The relatively weak association of handedness with cerebral asymmetry for speech control may be an artifact of particular operational definitions of handedness. "Handedness" is a self-identifying symbolic concept in children and adults. Although it must be tied to some aspect of brain functioning ("I am right-handed" may have neural mechanisms more in common with the self-identifying concept "I am an American"), the neural mechanism for a self-identifying construct may be quite different from the mechanisms controlling manual proficiency. The mechanisms controlling manual proficiency may be more closely related to the mechanisms controlling speech production. Therefore, it is difficult to justify using an identity or questionnaire measure of handedness as a way to understand the relation of handedness to other complex sensorimotor skills such as speech. These issues of classification and measurement are seldom addressed when examining the development of handedness.

Most questions about the development of handedness have focused on the right bias in its distribution in the population. When and in what form does the right bias in handedness appear? When the bias appears, is it stable or does it change in either direction or degree? If initially unstable, when does the right bias become stable? Does the development of handedness or its right bias follow the same course for all individuals, including males and females? What governs the course of handedness development?

1.1. When and in What Form Does the Right Bias in Handedness Appear?

Developmental studies of handedness begin in the first fetal trimester and extend into adulthood. By 9–10 weeks, fetuses exhibit independent limb movement. Ultrasound recording showed that 75% of 10-week fetuses

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

moved their right arm more frequently than their left and 13% moved their left arm more frequently (Hepper, McCartney, & Shannon, 1998). At 15 weeks, more fetuses had their right thumb in their mouth (Hepper, Shahidullah, & White, 1991). This right thumb bias was highly correlated with their handedness (as reported by parents) at 4 years (Hepper, Wells, & Lynch, 2005). Because this fetal manual asymmetry is related to childhood right-handedness, it was interpreted as reflecting early hemispheric specialization. Unfortunately, fetal lateralization of thumb sucking and arm movement was not independently confirmed by more systematic study (de Vries et al., 2001).

Although the developmental origin of handedness may begin in the uterus, it may not be related to differences in hand/arm movements or thumb sucking. Research frequently shows that the developmental origins of species-typical traits begin with nonintuitively obvious patterns quite distinct from the species-typical forms manifested later (Michel & Moore, 1995). Thus, the origins of handedness need not reside in the early differences in hand or limb use in utero but rather may reside in some other asymmetrical biases such as fetal posture and position.

The neonate's postural preference approximates its prenatal posture (Dunn, 1975). Intrauterine position is considered to be a major contributor to the organization of postnatal posture and "reflexes" (Caesar, 1979; Schulte, 1974). After the 16th week of pregnancy, the size, shape, and specific gravity of the fetus combine with the shape of the uterus and pelvic ring to restrict movement and position of the fetus in the uterus. The most prevalent uterine position is left vertex that places the fetus's head "down" and the left side "pressed" against the mother's backbone and pelvis (~85% of fetuses). This position constrains left arm movement and head turns directed toward the left. The maintenance of fetal posture throughout most of the latter half of pregnancy likely affects the elasticity of the skin and muscles as well as calibrates some general "set points" in the muscle spindle cells in the muscles of the arm and neck.

After delivery, gravity induces muscle stretch that violates spindle set points that initiate contractions that produce the characteristic neonatal postures and their similarity to fetal postures (Caesar, 1979). Subsequent recalibrations of spindle set points and greater supraspinal influence eventuate in a postural change and greater control relative to gravity (Coryell & Michel, 1978; Rönnqvist, Hopkins, van Emmerik, & de Groot, 1998).

The neonate's supine head orientation preference (HOP) is predicted by the fetal position in utero (Michel & Goodwin, 1979). Subsequently, the HOP is predictive of the early development of hand-use preferences for

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

certain manual actions (Michel, 1981; Michel & Harkins, 1986). HOP is likely a consequence of asymmetrically lateralized activation of neuromotor mechanisms at the level of brain stem nuclei, cerebellum, thalamus and basal ganglia (Rönnqvist et al., 1998) that have been established in utero and partly influenced by the fetus' position rather than simply a reflection of hemispheric specialization (Michel, 1983, 1988). As a consequence of the HOP, a neonate is more responsive to auditory and tactile stimulation of one ear and cheek, respectively, than the other (Turkewitz, 1977). Turkewitz (1977) proposed that the neonatal lateralized asymmetry of sensory and motor characteristics is an early predictor of later forms of other lateralized functions, including handedness. Michel (1981) reported that the HOP of 150 (81 males) neonates had a distribution of rightward to leftward preferences similar to those found for handedness in adults. Twenty (11 males) of these neonates were selected to have their hand-use preferences for prehension assessed at 12, 16, 22, 32, 40, 51, 60, and 78 weeks postpartum. Ten (5 males) had a neonatal rightward HOP and 10 had a leftward HOP. Their supine HOP was assessed more extensively at 3, 6, and 8 weeks postpartum. The correlation between their neonatal and post-neonatal HOP was significant, but 5 of the 20 infants changed their preference between assessments. Both the neonatal HOP and the post-neonatal HOP were predictive of infant hand-use preferences for prehension throughout the eight assessments, although the post-neonatal HOP was the more reliable predictor (Michel & Harkins, 1986).

HOP results in differential proprioceptive and visual experience of the hands and limbs that is important for the development of their visually guided control (Hein, 1980). Even relatively minor asymmetries in neuromotor action and visual experience of the left and right hands can produce differences in the cortical and subcortical mechanisms controlling motivated hand use (McFarland, 2009; Spinelli & Jensen, 1982). The direction of HOP also affects limb differences with the face-side hand/arm exhibiting more movement and grasping actions and availability for visual regard (Michel & Goodwin, 1979; Michel & Harkins, 1986). Neonates are reported to move their right arms more frequently and to take "swipes" at objects in their field of view. Also, objects placed in the hands during the first 2 months postpartum elicit a stronger grasp (Tan, Ors, Kurkcuoglu, & Kutlu, 1992) with longer duration of holding (Caplan & Kinsbourne, 1976). Because the neonate's HOP affects such limb differences, it is likely that these reported asymmetries are a consequence of the HOP (Michel, 1983). If we position the head opposite to the preferred HOP, the infant's hand and arm movements are shifted to the "new" face-side hand (Michel, 1981). Hence, the HOP seems to be affecting directly the bias in hand and arm movements (Rönnqvist et al., 1998).

By 8–10 weeks, the HOP has disappeared and the infant maintains a midline position for the head (Rönnqvist & Hopkins, 1998). Michel and Harkins (1986) found that the hand that was used initially for swiping at visually presented objects in the infant's midline at 12–16 weeks is the same hand that was on the face side during the earlier observed HOP. By 4 months, infants exhibit "directed reaching" toward objects but acquisition was unlikely. Again, the predominant hand for this reaching (left or right) is the face-side hand from the previous HOP. By 5–6 months, infants are able to acquire objects and they use the same hand that they used for directed reaching. Infants maintain this preference for acquiring objects for the next 12 months.

Thus, the development of handedness during infancy begins with an HOP that creates asymmetrical motor actions and hand regard. These asymmetrical "experiences" predict the hand that will be later used for reaching. It is likely that the HOP results in an asymmetry of visual–proprioceptive map of space because the face-side hand is moved more, creating more proprioceptive and corollary neural activity associated with that hand's position in visual space and its "felt" position relative to the body. Therefore, the face-side hand ought to have an advantage in reaching for objects located in space relative to the infant's body. That advantage concatenates into a greater probability of contacting the object, acquiring it, and building more extensive cortical–basal ganglia reentrant circuits for the "motivational" control of that arm (McFarland, 2009).

Unimanual (e.g., banging or shaking the object) and nondifferentiated bimanual actions become more frequent from 7 to 12 months postpartum (Kimmerle, Mick, & Michel, 1995). A hand-use preference for unimanual actions appears by 11 months, and that preference is predicted by their previously established hand-use preference for acquiring objects (Hinojosa, Sheu, & Michel, 2003). Furthermore, the hand-use preference for unimanual manipulation likely contributes to the hand-use preference in RDBM. As a result of the hand-use preference for acquiring objects and manipulating them, the preferred hand will have established many more "programs" or "schemas" (Michel, 1991) that can be employed with any object that affords RDBM.

Although infants exhibit RDBM as early as 7 months (Kimmerle et al., 1995), it is only a minor part of their repertoire (until 13 months) and seems to emerge entirely from the properties of the object, rather than from the coordinated actions by the infant. By 12–13 months, infants exhibit a hand-use preference for RDBM, and only at 13 months, do RDBM actions appear to be coordinated by the infant (Kimmerle, Ferre, Kotwica, & Michel, 2010). Thus, during the 6- to 14-month period, both unimanual actions and RDBM actions are only a small portion of the infant's manual repertoire and hand-use preferences in those actions appear only in the later months. Consequently, the action of acquiring objects is the only manual skill that is relatively constant in the manual repertoire and can show hand-use preferences during the 6- to 14-month age period. By 12–14 months, the strong hand-use preference for acquiring objects will appear to "weaken" as the infant more frequently uses the nonpreferred hand to acquire an object so as to engage more immediately in RDBM actions with the preferred hand (Michel, Ovrut, & Harkins, 1985).

By 18 months, infants are engaging primarily in RDBM and can solve many tasks that require an RDBM action (Nelson, Campbell, & Michel, 2013). A toddler's hand-use preference for RDBM is predicted by his/her hand-use preference for acquisition as infants. Moreover, a group of toddlers, who had no hand-use preference for acquiring objects as infants, developed a hand-use preference for RDBM during the period from 18 to 24 months (65% right handed and 30% left handed).

Using her peg-moving task, Annett (1985, p. 392) provided evidence that by 3–5 years of age, the distribution of skill differences between the hands was equivalent to that of adults. Hence, the same right shift in handedness skill shown by adults is apparent in preschool children. Although children may change their hand-use preference after 5 years of age, their subsequent pattern of handedness is likely to be different from that of children who do not change the pattern established during their first 5 years (Bryden & Steenhuis, 1991).

So, the right bias in hand-use preference can be observed quite early in infancy and may relate to the proficiency bias observed in preschool children's peg-moving skills. Infant hand-use preference likely derives from prenatally and neonatally established postural asymmetries that facilitate a bias in visually guided hand use. Those same postural asymmetries exhibit a continuous distribution (with a sharp right bias) that would account for the early development of left hand-use preference. The postural origin of handedness provides a developmental explanation for both the right bias in the distribution and the maintenance of left-handedness.

1.2. Is the Right Bias Stable or Does It Change in Either Direction or Degree? if Initially Unstable, When Does the Right Bias Become Stable?

Although it is conventionally assumed that the directional bias in handedness is stable only by 4–8 years of age (Dubois et al., 2009), improvements in skill and motor control continue during the preteen years. As in adults, left-handedness is more common in school-aged boys than in girls (Harris & Carlson, 1993). Cross-sectional studies show that right-handedness appears to increase with age (Gilbert & Wysocki, 1992; Iwasaki, Kaiho, & Iseki, 1995; Lansky, Feinstein, & Peterson, 1988) and may be explained by the following hypotheses:

1. Left-handedness may be correlated with lower survival, resulting in the decrease in left-handedness among older people (Coren, 1989; Halpern & Coren, 1991);
2. Social pressures against left-handedness have declined, so that younger people are less restricted and therefore show higher incidences of left-handedness (Brackenridge, 1981). Also, with increasing age, social contacts increase, which may increase the probability of switching toward right-handedness;
3. Society is right biased. Tools are made for right-handed individuals and, in time, this causes a shift toward dextrality in left-handed individuals (Porac & Coren, 1981);
4. Cerebral dominance development continues throughout life and causes the increase in right-handedness (Brown & Jaffe, 1975; Fleminger, Dalton, & Standage, 1977).

To distinguish among these hypotheses requires longitudinal studies that investigate the development of lateralization within individuals.

Many have argued that handedness in infancy is not a stable trait and that handedness cannot be reliably identified until the ages of 4–7 years (McManus et al., 1988) or somewhere between 6 and 10 years of age (Fennell, Satz, & Morris, 1983; Gesell & Ames, 1947). Infants are reported to change their preferences in hand use for reaching and manipulating objects, as well as their choice of one-handed versus two-handed strategies (Fagard & Lockman, 2005) across observation periods. Indeed, within-individual variability is a prominent characteristic of infant manual asymmetries (Corbetta & Thelen, 1999, 2002; Fagard, 1998; Piek, 2002; Thelen, Corbetta, & Spencer, 1996).

The consensus is that infant hand-use preferences are too variable across assessment procedures and unstable across age to be assessed reliably or to

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

provide accurate predictions about adult handedness status. "Infants initially use both hands indifferently (Corbetta & Thelen, 1999; Rönnqvist & Domellof, 2006), then preference for one hand becomes clear generally from 18 months of age on (Fagard & Marks, 2000) and is more and more pronounced during the following years (Ingram, 1975)" (Dubois et al., 2009, p. 414). Of course, even adult handedness can appear variable according to the demand characteristics of the tasks used for assessment (Doane & Todor, 1978; Provins & Cunliffe, 1972). Early in development, measurement of handedness can be influenced by choice of task, type of action measured, and the infant's comprehension of the task demands.

Because manual abilities change dramatically during infancy (Michel, 1988), research on the development of handedness during infancy has vacillated between two general notions: (1) infant handedness is ephemeral, is nonexistent, or fluctuates with state or transitions in the control of the limbs for locomotion and postural control (Corbetta & Thelen, 2002) and (2) infant handedness is a manifestation of an underlying inherent and constant asymmetry of the cerebral hemispheres (Kinsbourne, 1997; Witelson, 1990). The latter notion is difficult to empirically falsify, but the former notion can be empirically evaluated. Our current research, using a large sample of infants (n = 275) assessed monthly from 6 to 14 months, found that lateralized hand use for acquiring objects does not change in relation to transitions in the control of locomotion (Babik, Campbell, & Michel, in press for 2013). In contrast, the bimanual acquisition of objects does change in relation to changes in posture.

Variability in the type of handedness assessed and methodology (ages of assessment, frequency of assessments, and time between assessments) is likely to have contributed to the conventional notion that handedness is unreliable and unstable before 6–10 years of age (Ferre, Babik, & Michel, 2010; Schaafsma, Riedstra, Pfannkuche, Bouma, & Groothuis, 2009). Moreover, Michel (1991, 2002) argued that how the preference is defined can affect its apparent stability (Michel, Sheu, & Brumley, 2002). For example, defining a hand-use preference by a simple difference between hands (a "handedness index"; Ramsay, 1980) may show less stable preferences across assessment ages than a preference defined by statistical estimates of whether the inter manual differences are likely to have occurred by chance (Michel et al., 2002; Michel, Tyler, Ferre, & Sheu, 2006). Also, Ferre et al. (2010) found that four bimonthly longitudinal assessments during the period from 6 to 14 months of age show a different pattern of handedness development (no significant trend in hand-use preference) than nine monthly assessments

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

(a significant quadratic trend for right hand-use preference). Infant handedness reflects the consequences of an immature but rapidly developing nervous system and appears to be sensitive to various assessment procedures and conditions. Nevertheless, this does not mean that infant handedness is unreliable or even unstable or cannot be characterized.

Characterizing the pattern of handedness development during infancy is important because the cerebral hemispheres of the human brain control different functions, especially in adults, and handedness is both an example of such hemispheric asymmetry and associated with many other lateralized functions. Hemispheric specialization is expressed in side biases for information processing, and the control of actions in handedness is such a side bias with the left hemisphere controlling right-hand actions (Serrien, Ivry, & Swinnen, 2006; Volkmann, Schnitzler, Witte, & Freund, 1998). The right-biased distribution of handedness in the population resembles the distinct left hemisphere distribution of control of speech and other language functions. Because handedness is readily observable and can be assessed throughout most of the life span, Michel (1983, 1988, 2002) proposed that knowing how handedness develops could serve as a model for the investigation of the development of other forms of cerebral asymmetry, especially hemispheric control of speech functions.

Because the bias in distribution of right-handedness in the population has drawn the most interest, we can begin the search for the origins of the right bias in handedness by seeking similar biases in earlier forms of behavior. Longitudinal studies can show the path of development along with details of individual development. The data collected will have to be subjected to statistical modeling techniques that permit identification of the underlying trajectories and how these are influenced by changes in neurodevelopmental status, development of sexually differentiated characteristics, familial dynamics, differences in physical environmental contexts, and so on. Using too few assessments of an individual's handedness status early in development will not show how handedness comes to be related to so many psychological and medical phenotypic traits because those assessments can be readily affected by the infant's state and the conditions of the assessment.

We propose that object acquisition skills should be the focus of studies designed to assess the trajectory of the development of hand-use preferences during the period from 6 to 14 months of age. It is the most prevalent (and sufficiently challenging) manual skill in the infant's repertoire, and it becomes manifested after establishment of the skills of reaching for and contacting objects, and it is incorporated into all other manual skills

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

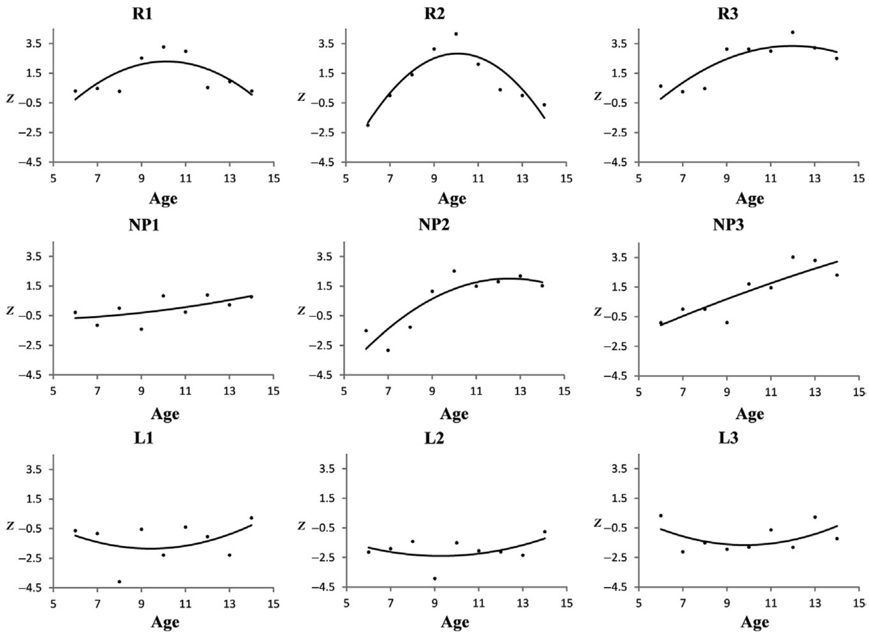

Figure 9.1 Observed developmental trajectories of handedness for three randomly selected infants from each of the three latent groups (top row—right-handers, middle—no preference, and bottom—left-handers) identified by group-based trajectory modeling.

involving object manipulation (tool use and the construction of objects). Because handedness in reaching and object contact relates to handedness in object acquisition (Michel & Harkins, 1986) and handedness in acquiring objects relates to handedness in object manipulation (Hinojosa et al., 2003), acquisition of objects is pivotal for the early development of handedness. We have found large individual differences (Fig. 9.1) in the trajectories of handedness for object acquisition (Ferre et al., 2010; Michel, Babik, Sheu, & Campbell, submitted), and nine monthly assessments permit identification of the nonlinear individual and group developmental trajectories.

Using a reliable and valid assessment procedure (Michel et al., 1985) capable of identifying significant differences ($p < 0.05$) in the use of each hand at each monthly assessment visit during the 6- to 14-month period (Michel et al., 2002), we assessed the longitudinal character of hand-use preference for 328 infants. Three types of developmental trajectories for acquiring objects were observed (Michel et al., submitted): those who manifest a stable right hand-use preference (about 38%), those who manifest a stable left hand-use preference (about 14%), and those (48%) who have a

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

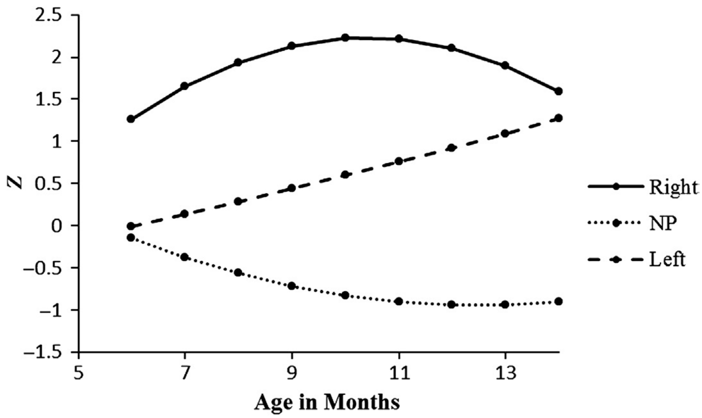

Figure 9.2 Estimated trajectories of handedness for the three groups defined by the latent class analysis (NP—no preference).

significant trend toward right-hand use (Fig. 9.2). Despite previous claims, right-handers and left-handers maintain their handedness for acquiring objects across 6–14 months and "no-preference" infants seem to be changing toward right-handedness. Thus, although there is variability across visits, these groups are distinguished by their hand preferences, which likely represent different patterns of neurobehavioral development.

Even during infancy, right hand-use preference is predominant over left hand-use preference. Yet, a substantial portion of infants do not manifest a consistent preference of hand use for acquiring objects. Therefore, additional longitudinal research is needed to determine whether right-biased fetuses, neonates, infants, or preschoolers become right-handed adults, whereas their left-biased counterparts become left-handed adults.

1.3. Does the Development of Handedness Follow the Same Course for All Individuals, Including Males and Females?

Previous research has reported that males and females may differ in their hemispheric specialization and handedness patterns (Annett, 1994; Jones & Martin, 2010; McManus, 2002). We discovered the typical sex difference (more non-right-handed males than females) in both the handedness assessment and in our validating block play task (Michel et al., 1985). A meta-analysis confirms that more males than females are likely to be left handed or ambilateral (Papadatou-Pastou et al., 2008). However, because there were no differences in proportions of males and females among the three groups identified by our analysis of the trajectories for hand-use preferences for acquiring objects for 328 infants, perhaps, the sex difference in handedness

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

emerges later in development. Currently, the origin of these sex differences is unknown.

It is important to remember that left-handedness is not the mirror image of right-handedness (Michel, 1998) but represents its own pattern of neurobehavioral organization (Jones & Martin, 2010; Knecht et al., 2000). Indeed, the reason researchers investigate the relation of handedness to people's cognitive, social, and emotional functioning is because handedness is thought to represent different *patterns of hemispheric specialization*. As noted earlier, it is the pattern of hemispheric specialization (not handedness, per se) that is believed to affect psychological functions.

1.4. So What Does It Mean for the Infant's Development if He/She Is Developing along a Right- or Left-Handed Trajectory?

Studies of children and adults (Casasanto, 2009; Casasanto & Henetz, 2011) suggest that left- and right-handed infants may be developing symbolic and abstract concepts differently. What, then, does that mean for the large proportion of infants who exhibit no hand-use preference? Does developing handedness status affect development of language abilities, object construction skills, tool-using skills, visual–spatial abilities, and executive functioning? Are the three patterns of developing handedness that we discovered associated with differences in the development of these abilities?

Kotwica, Ferre, and Michel (2008) found that infants without a hand-use preference were slower at developing the kind of object management skills that Bruner (1973) considered to be important in the development of symbolic abilities. If handedness is relevant for the development of tool-using skills, symbolic abilities, and so on, then infant handedness must play a fundamental role in the theories about, and empirical investigations of, infant cognitive, social, and emotional development.

1.5. What Governs the Course of Handedness Development?

Several explanations have been proposed to account for the course of handedness development. The developmental psychobiological explanation incorporates all of them within a general framework.

1.5.1. The Gene Explanation

Handedness may become related to so many psychological and medical phenotypes via gene-influenced hemispheric differences between right- and left-handers in neuroanatomy and neurophysiology, which, in turn, produce differences in cognitive and affective processing (McManus, 2002).

Family, twin, and adoption studies have provided evidence of a significant genetic association with handedness (Carter-Saltzman, 1980; Jones & Martin, 2010; Klar, 1996; McManus & Bryden, 1992; Medland et al., 2009; Neale, 1988; Sicotte, Woods, & Mazziotta, 1999; Van Agtmael, Forrest, & Williamson, 2002; Warren, Stern, Duggirila, Dyer, & Almasy, 2006; but see Laland, Kumm, Van Horn, & Feldman, 1995; Risch & Pringle, 1985, for alternative views). Even family history of sinistrality influences assessments of both individual handedness and hemispheric specialization (Annett, 2002; Corballis, 2009; McKeever, 2000).

The nature of the genetic association with handedness remains unknown. A segregation analysis of family data (Risch & Pringle, 1985) concluded that the data were consistent with a single-locus or a polygenic model of inheritance. Although several single-locus models of handedness exist (Annett, 1985; Klar, 1996), none fit all of the family and twin study data. Laland et al. (1995) presented a model of handedness that proposed that no distinct genetic variation underlies differences in handedness. Rather, variation in handedness is the result of a combination of cultural and developmental factors plus a small polygenic influence.

Of course, this does not mean that handedness is a learned or trained characteristic. Neale (1988) used biometrical genetic methods to analyze handedness data for monozygotic and dizygotic twins and found a significant common environment component and a heritable sex difference, with slightly more males likely to be left handed. Although there is no doubt that handedness represents a prevalent biologically significant characteristic, the genetic role in manifest handedness appears to be small, at best.

Despite the weak evidence for a genetic influence on handedness, its species-typical characteristic and relation to hemispheric specialization for language prompted searches for genetic distinctions between human and other primates that may relate to these lateralized asymmetries. Crow (1994, 2002), argued that the laterality gene is located in the Xq21.3/Yp11.2 region of homology on the X and Y chromosomes and suggested protocadherin XY as a likely candidate. Supporting evidence came from a study showing a higher concordance of handedness in siblings of the same sex than in opposite-sex siblings (Crow, 1994, 2002). McKeever (2000) and Corballis (1997, 2009; Corballis, Lee, McManus, & Crow, 1996) have suggested that the gene may be on the X chromosome alone. Indeed, Laval et al. (1998) reported that relative hand skill was associated to marker DXS990 on the X chromosome. However, a genome-wide search for the handedness gene failed to find an X-linkage but rather the region 2p11.2-12 on chromosome

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

2 was a likely candidate (Francks et al., 2002). Subsequent investigation narrowed the locus to the "leucine-rich repeat transmembrane neuronal 1" (LRRTM1) gene on chromosome 2p12, a maternally suppressed gene that appears to be associated paternally with handedness and schizophrenia (Francks et al., 2007). Because surveys of handedness have found a stronger maternal than paternal influence (Annett, 2002), it seems unlikely that LRRTM1 is the only gene involved in handedness and cerebral asymmetry. Linkage analyses have pointed to other regions of interest, including 17p11-q23 (Francks et al., 2003), 10q26 (Van Agtmael et al., 2002), and 12q21-23 (Warren et al., 2006). Inconsistencies among these reports might be because of differences in handedness definitions, differences in populations, or how the data were analyzed.

Gene explanations seek to account for the lower prevalence of left-handers as well as its familial association. The most prominent and parsimonious genealogical model posits that handedness is determined by a single gene with two alleles, one from each parent (Annett, 1978, 2002). The model assumes a relation between the left hemisphere control of speech and right-handedness. When the allele is present, the left hemisphere is biased to control speech and this increases the likelihood of right-handedness. When the allele is absent, then both the control of speech and handedness distribute randomly and independently. Oddly, it is not clear why the hemisphere controlling speech in the absence of the allele does not affect handedness, because it is the cerebral control of speech, when the allele is present, that supposedly creates the bias toward right-handedness. Either the allele biases handedness independently of its influence on left hemisphere control of speech (so that they can develop independently of one another when the allele is absent) or the allele prompts the development of left hemisphere control of speech, which in turn prompts the development of right-handedness. If the latter, then handedness and hemispheric control of speech should be more tightly associated, even in the absence of the allele, than the theory proposes. If the former, then how does the allele bias handedness development? Annett's model does not address these issues.

Because genes operate during the development of phenotypic traits within processes involving interactions with various environmental and experiential events (Michel, 2010), it is likely that hemispheric variations in the neurophysiology involved in cognitive and emotional phenotypes may be influenced by the asymmetric sensorimotor activity manifested during the development of handedness. Embodied cognition theory (which proposes that our actions in the world encode our cognitive processes) could account for how developing handedness skills might influence the development of cognitive and social/emotional differences between left- and right-handers (see below).

1.5.2. The Brain Explanation

Handedness and cerebral functional asymmetry are not unique to humans. Nevertheless, activities that are uniquely human (language) or are more highly developed in humans (manual skills) are linked to human cerebral asymmetries. Annett (2002) proposed that the genotypes underlying left-preference and no-preference individuals each represent a pattern of hemispheric development that may be different from that of strongly right-handed individuals. Handedness is associated in the adult brain with functional and anatomical hemispheric asymmetries in the speech perception/production and sensorimotor networks (Basso, 1992; Serrien et al., 2006). Moreover, both cerebral dominance for language and handedness are linked in their distributions, with a greater proportion of right hemisphere dominance for language found among left-handed people than among right-handed people (Corballis, 2009).

The brain explanation proposes that handedness reflects anatomical and physiological asymmetries in brain regions relevant for motor control (Kinsbourne, 1997; Witelson, 1990). Different stages of development in the manifestation of handedness are presumed to reflect different brain areas (e.g., fetal asymmetries reflect spinal and brain stem asymmetries). At the cortical level, specialization for programming finely timed sequentially organized movement patterns required for speech is employed for the control of the contralateral (preferred) hand. The apparent dissociation between handedness and cortical participation in speech control contradicts this hypothesis. However, the relation of handedness to cortical participation in speech control is clearer when proficiency measures of handedness are used.

Embodied cognition theory provides one developmental account for how psychological processes become instantiated in brain processes. Embodied cognition proposes that the processes of conceptualizing, language, and abstract reasoning comprise mental simulations of bodily experiences of actions on objects and interactions of the self with others (Anderson, 2003; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Barsalou, 2008; Beilock & Holt, 2007; Boulenger, Hauk, & Pulvermüller, 2009; Lakoff & Johnson, 1999; Oppenheimer, 2008). Accordingly, our comprehension of events, situations, or words involves an implicit mental simulation of our previous sensorimotor engagement with similar events, situations, or physical referents, using regions of the brain that support the perception and action for such engagement (Longcamp, Anton, Roth, & Velay, 2005; Willems et al., 2010; Willems & Hagoort, 2007; Willems, Toni, Hagoort, & Casasanto, 2009). Embodied cognition shares historical antecedents in the theories of intellectual development proposed by Baldwin (1895), Bruner (1973), and Piaget (1952), each of whom argued that symbolic cognitive processes derive from sensorimotor abilities developed during infancy and mediated through alterations in brain functioning.

Modern embodiment notions propose that mental simulations arise from correlations among bodily experiences (Lakoff & Johnson, 1999; see also Overton & Mueller, 2012) that create "mental metaphors." These mental metaphors incorporate a sensorimotor "source" domain (representing the structure of our actions) into a*conceptual* "target" domain that has a similar structure. This embodiment permits the ability involved in our judgments of "the *height* of people's excitement, the *depth* of their sadness, or the *breadth* of their compassion" (Lakoff & Johnson, 1999). Linguistic metaphors subsequently encode these mental metaphors. However, mental metaphors that lack linguistic metaphors (Murphy, 1996) also are derived from our engagement with the environment (e.g., our representations of *time* (Boroditsky, 2000, 2001), *number* (Dehaene, Bossini, & Giraux, 1993), *similarity* (Casasanto, 2008), *emotionally valenced* concepts (Casasanto & Dijkstra, 2010), *emotional attachment* (Williams & Bargh, 2008), and *power* (Schubert, 2005)).

If sensorimotor source domains constitute conceptual domains (e.g., abstract concepts), then, these concepts should be instantiated by the same neural structures involved in perception and action in the physical world. Indeed, participants who read action-related verbs (e.g., *kick*, *pick*, and *lick*) activate the effector-specific regions of premotor cortex that are activated when they move the effector associated with these verbs (Aziz-Zadeh et al., 2006; Boulenger et al., 2009; Gonzalez & Goodale, 2009; Willems & Hagoort, 2007). Casasanto and Dijkstra (2010) proposed that because action and emotion are intimately linked in our everyday experiences, abstract concepts carry either positive or negative *emotional valence* and this mediates their relation to action that also can have emotional valence (Maxwell & Davidson, 2007). In this way, such abstract concepts as intelligence, kindness, honesty, poverty, politeness, or ethics (which cannot directly engage our senses or be acted upon) can be embodied.

According to Casasanto (Casasanto & Henetz, 2011), beginning in infancy, people physically approach things typically identified as positive and withdraw from things typically identified as negative (Hane, Fox, Henderson,

& Marshall, 2008). Approach-related behavior is correlated with positive valenced experience and is lateralized to processes in the left frontal lobe, which controls the right side of the body, whereas avoidance-related behavior is correlated with negative valenced experiences and is lateralized to the right frontal lobe, which controls the left side of the body in right-handed individuals (Davidson, 1992). Actions performed with the right side of the body (e.g., contracting the muscles of the right hand or the right side of the face) reportedly create positive affect, whereas the same actions performed with the left side of the body create negative affect (Davidson, 1992; Schiff & Bassel, 1996).

Embodiment theory predicts that there should be differences between right- and left-handers in the left–right lateralization of positive/approach and negative/avoidance characteristics because the more proficient (preferred) hand acts more effectively on the environment. This greater sensorimotor proficiency has been shown to correlate with more positive evaluations of the objects of those interactions (Beilock & Holt, 2007; Oppenheimer, 2008). Thus, Casasanto and Chrysikou (2011) proposed that expertise in using our preferred hand implicitly associates positive/good emotions/good qualities with that side of our bodies and negative/bad emotions/bad qualities with the side we use less proficiently (the nonpreferred hand).

If concepts and word meanings are constituted by simulations of our own actions, then right- and left-handers, who consequently interact with their physical environments in systematically different ways, should form correspondingly different mental representations. Also, if thinking about actions involves mentally simulating the way we execute them, then actions that we perform with our preferred hand such as throwing a ball, turning a key, or writing should have different hemispheric representations in right- and left-handed individuals (Willems & Hagoort, 2007).

Comparison of premotor Functional Magnetic Resonance Imaging (fMRI) activation during a lexical decision task showed that the pattern of lateralization for manual-action verbs (e.g., grasp or throw) versus nonmanual-action verbs (e.g., kneel or giggle) was opposite in right- and left-handers (Willems et al., 2010). Imagining manual actions also is lateralized oppositely for left- versus right-handers (Willems et al., 2009). Moreover, left-handers are more likely than right-handers to associate *left* with positive ideas and *right* with negative ideas. Right- and left-handers tend to link good (positive emotional valence) things like intelligence, attractiveness, honesty, and kindness more strongly with the same side of space as their preferred hand. Thus, right- and left-handers

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

appear to engage in correspondingly different neurocognitive processing, even with highly abstract concepts, as a consequence of the emotional valence associated with the proficiency of their preferred hand (Casasanto, 2009).

If mental metaphors are created differently in right- and left-handers via a developmental history of asymmetrical sensorimotor experience by which their preferred hand acts on the environment, then the development of variations in abstract thinking in children should be linked to the pattern of their handedness development. Thus, there may be three "types" of neuro cognitive developmental trajectories, two representing those who develop strong right- or left-handedness early in infancy and one representing those who do not develop strong hand-use preferences during infancy. Because handedness continues to develop after 14 months of age (particularly for that proportion of infants without a hand-use preference), it is likely that these trajectories continue to shape subsequent development. Research on adults shows that most members of a group of "ambilaterals" manifest poor manual proficiency with either hand (Doane & Todor, 1978; Flowers, 1975). Hence, we might expect a different development of their conceptual ability and perhaps less distinct hemispheric specialization of function. In this way, notions about the embodied differences in cognitive processing among right-, left- and ambiguously handed individuals can be tested beginning with the early development of handedness.

It is likely that infants become motivated to reach for (i.e., approach) things that provide positive feedback (retrieved to the mouth and provides stimulation that is not too intense—e.g., sweet, soft, and round) and not to reach for things that provide negative feedback (retrieved to the mouth and provides intense stimulation—e.g., bitter, cottony, and spikey). This associates positive stimuli and approach behaviors with the preferred hand (mediated by the contralateral frontal lobe). Thus, hemispheric specialization for affective processing (and cognitive processing) could emerge from experienced "action–emotion" correlations, as right- and left-handers use their preferred hand for positive/approach behaviors. Different action tendencies in right- and left-handers could be both a cause and an effect of differently lateralized neural systems for affect, motivation, and cognitive processing.

1.5.3. The Social–Cultural Explanation

This explanation emphasizes the role of education, socialization, and cultural proscriptions in the development of handedness. Indeed, handedness is most obvious for actions that require special training and practice such as writing and utensil use. Also, the proportion of left-handers is much

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

reduced in cultures that discourage left-hand use for such actions. Even in "left-hand-tolerant" societies, left-handedness is less prevalent because of the predominance of "right-handed" artifacts.

Mother–child interaction is another social influence. Right-handed mothers prefer to cradle infants with their left arm (Donnot & Vauclair, 2007), whereas males have no preference (Damerose & Vauclair, 2002). Cradling by mothers induces asymmetrical sensory input and head and arm movements, potentially influencing development of lateralization. Although left-handed cradling may restrict right-arm movements, it supports an infant right HOP and the HOP modulates the side preference of adult cradling, but cradling does not modulate HOP (Bundy, 1979).

Harkins and Michel (1988) observed that infants of left-handed mothers were more likely to be left-handed (64% with significant left-hand use) than were infants of right-handed parents (0% left handed) and infants of left-handed fathers (0% left handed). Using Briggs and Nebes (1976) handedness questionnaire, Mundale (1992) created three groups of mothers with different handedness and observed differences in mothers' play with their infants during three bimonthly 7- to 11-month visits. Right-handed mothers used their right hands significantly more often for placing the toys in front of their infants, activating movable parts of the toy, moving the toy about, placing the toy in their infant's right hand, and deliberately maneuvering their infant's right hand to engage the toy in play. Left-handed mothers did use their left hand to place the toy in front of their infant, to move the toy, and to maneuver the infant's hand to engage the toy. However, left-handed mothers were not as strongly biased in these actions as right-handed mothers, and for most actions, they had a right-hand bias similar to right-handed mothers. Thus, left-handed mothers were not the mirror image of right-handed mothers in their interactions with their offspring. Mothers without a distinct hand-use preference used their hands in ways more similar to right-handed mothers than left-handed mothers. There are many potential caregiver influences on the development of handedness; however, Mundale's (1992) study shows that assessing the influence of maternal handedness on the development of infant handedness will require large-scale longitudinal study.

Porac, Coren, and Searleman (1986) found that social pressures within families increase right-handedness: males from right-handed parents were more likely to switch from left- to right-hand use than males with one or two left-handed parents. Also, Dawson (1974) reported that proportion of left-handedness is much lower (0.6–3.4%) among more conforming societies than among more permissive nonconforming societies (~11%).

These studies demonstrate how social situations may constrain the development of left-handedness.

1.5.4. The Developmental Psychobiological Explanation

Handedness is a complex character derived from biosocial processes during development. In behavioral–genetic research, the construct of endophenotype is used to denote complex developmental pathways that "channel" genotypes onto possible phenotypes. Developmental psychobiology provides research strategies that show the dynamic bidirectional relationships between the individual's biological processes and the individual's social and physical environment that make up these developmental pathways (Michel & Moore, 1995). The phrase "multiple trajectories" in this chapter title applies to both differences in the developmental pathways that can lead to similarities in handedness and similarities in developmental pathways that can lead to differences in handedness. The task for the researcher is to identify what factors during development contribute toward maintaining the consistency of the individual's trajectory and what factors contribute toward changing the trajectory.

If we consider development as a continuous process of individual–environment interactions, even individuals beginning with the same fertilized egg (identical twins) will necessarily be exposed to different interactions with *their* own environments (e.g., different cellular constituents as the zygote separates in twinning). This places each zygote in relation to each other and in a different relation to variation in the uterine environment. Continued interactions along this pathway can lead to divergences in the phenotypes of the twins and these likely account for the discordance on handedness in monozygotic twins. For twins, the developmental questions are the following: what factors support concordance and what factors support discordance in the developmental trajectories of their phenotypic characteristics.

After decades of research, we proposed a theory of handedness development during infancy (Michel, 2002) in which the trajectory of development is a complex cascade of contingencies involving prenatally influenced congenital postural asymmetries that feed into the establishment of early infant sensorimotor asymmetries of the use of the arms and hands with hand-use preferences reliably observed initially in acquiring objects and eventually in RDBM, construction skills, and tool use by the individual's second year postpartum (Fig. 9.3). Handedness for RDBM during the toddler period (18–30 months) likely relates to the development of handedness in skill differences that begin to appear in the preschool period. The asymmetries,

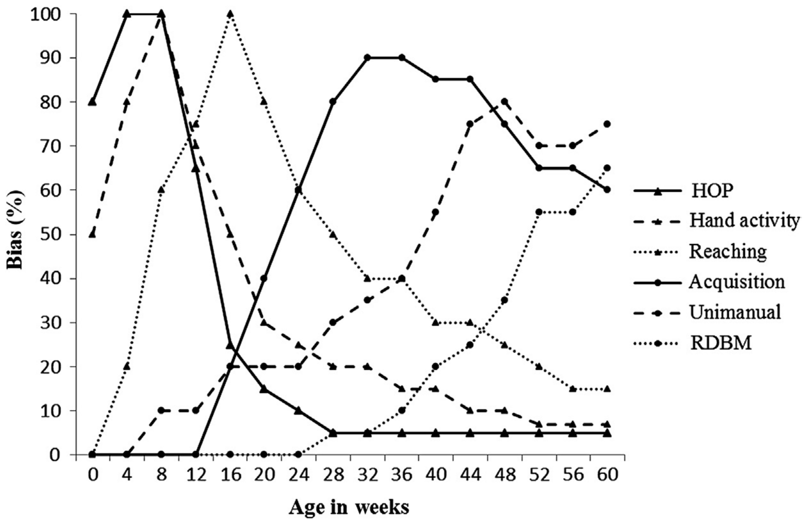

Figure 9.3 Dynamic character of the trajectory of handedness development during infancy.

throughout the trajectory, interact with the caregiver's handedness (a result of the caregiver's development within a specific cultural context) to further shape the individual's hand use such that by 18–24 months, most children have a hand-use preference across a range of unimanual and bimanual skills that will form the basis of all future hand actions. Our theory accounts for the predominance of right-handedness, the maintenance of a small proportion of left-handers, and the continuum of handedness across individuals.

Previously (Goldfield & Michel, 1986; Michel, 1998), we found that only infants with a stable hand-use preference for acquiring objects exhibit better coordination of their bimanual action reaching to obtain large objects when either hand is perturbed by a barrier or is slightly weighted. Thus, a hand-use preference was associated with the development of more effective bimanual control of the movement of the hands in space. Also, infants with a stable handedness manifest those manual skills that have been associated with the cognitive capabilities of "planning" sooner than those without a preference (Kotwica et al., 2008). Such results prompt examination of the relation of tool use and construction skills, design-copying skills, and notions of abstract concepts to the three types of handedness development we observed during infancy. With such knowledge, we may understand why uncommon patterns of handedness (left and ambilateral) are related to the development of uncommon psychological and medical phenotypes.

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

As the trajectories of handedness development are charted into the school-aged period, it may elucidate how preschool measures of design-copying skills manage to become excellent predictors of middle school mathematics, science, and reading achievement test scores (Cameron et al., 2012; Grissmer, Grimm, Aiyer, Murrah, & Steele, 2010). Although design-copying skills are conventionally interpreted as visual–spatial abilities, they may more appropriately represent visual–motor manual skills. As such, individuals with early hand-use preferences ought to exhibit better skills when copying designs than those without early hand-use preferences. If early handedness development is related to better design-copying skills of children, then the three patterns of infant handedness development may represent the three patterns of neurobehavioral development highly relevant for the development of scientific, reading, and math skills.

2. CONCLUSIONS

Handedness is a product of a multifaceted biosocial developmental process beginning prenatally and continuing well into adulthood. More information is needed on when, how, and for what actions the trajectory of handedness development may be maintained and changed. Although the story of handedness development is not complete, it is well worth pursuing because we can enrich our understanding of the development of handedness and brain–behavior relations, especially for hemispheric differences in function.

Given the complexity of developmental psychobiological pathways, it is likely that hemispheric variations in the neuroanatomy and neurophysiological processing involved in cognitive and emotional phenotypic expressions during development could be influenced by the asymmetric sensorimotor activity manifested during the development of handedness. Thus, those developmental processes that give rise to handedness also could give rise to the contrasting psychological and medical phenotypes often reported between left- and right-handers. There is much to be learned about the development of handedness, and that knowledge is likely to be a rich source of information about psychological development, in general.

ACKNOWLEDGMENTS

The work reported herein was supported by National Science Foundation grant DLS 0718045 and National Institutes of Health grant R01-HD 22399 to G. F. M. and National Institutes of Health/National Institute of Child Health and Human Development Training grant T32-HD007376 to E. L. N.

REFERENCES

Anderson, M. L. (2003). Embodied cognition: a field guide. *Artificial Intelligence*, *149*, 91–130.

Annett, M. (1974). Handedness in children of two left-handed parents. *British Journal of Psychology*, *65*, 129131.

Annett, M. (1978). Genetic and nongenetic influences on handedness. *Behavior Genetics*, *8*, 227–249.

Annett, M. (1985). *Left, right, hand, and brain: The right shift theory*. London: Erlbaum.

Annett, M. (1994). Handedness as a continuous variable with dextral shift: sex, generation, and family handedness in subgroups of left- and right-handers. *Behavior Genetics*, *24*, 51–63.

Annett, M. (1995). The right shift theory of a genetic balanced polymorphism for cerebral dominance and cognitive functioning. *Current Psychology of Cognition*, *14*(5), 427–480.

Annett, M. (2002). *Handedness and brain asymmetry: The right shift theory*. Hove, UK: Psychology Press.

Annett, M., & Manning, M. (1989). The disadvantages of dextrality for intelligence. *British Journal of Psychology*, *80*, 213–226.

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, *16*, 1818–1823.

Babik, I., Campbell, J. M., & Michel, G. F. (in press for 2013). Postural influences on the development of infant lateralized and symmetrical hand-use. *Child Development*.

Baldwin, J. M. (1895). *Mental development in the child and race*. New York: Macmillan.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, *59*, 617–645.

Basso, A. (1992). Prognostic factors in aphasia. *Aphasiology*, *6*, 337–348.

Beilock, S. L., & Holt, L. E. (2007). Embodied preference judgments: can likeability be driven by the motor system? *Psychological Science*, *18*, 51–57.

Billiard, S., Faurie, C., & Raymond, M. (2005). Maintenance of handedness polymorphism in humans: a frequency-dependent selection model. *Journal of Theoretical Biology*, *235*, 85–93.

Bishop, D. V. M. (1990). *Handedness and developmental disorder*. Philadelphia: L J. B. Lippincott.

Bishop, D. V., Ross, V. A., Daniels, M. S., & Bright, P. (1996). The measurement of hand preference: a validation study comparing three groups of right-handers. *British Journal of Psychology*, *87*(2), 269–285.

Boroditsky, L. (2000). Metaphoric structuring: understanding time through spatial metaphors. *Cognition*, *75*, 1–28.

Boroditsky, L. (2001). Does language shape thought? Mandarin and English speakers' conceptions of time. *Cognitive Psychology*, *43*, 1–22.

Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. *Cerebral Cortex*, *19*, 1905–1914.

Brackenridge, C. J. (1981). Secular variation in handedness over ninety years. *Neuropsychologia*, *19*, 459–462.

Bradshaw, J., & Rogers, L. (1993). *The evolution of lateral asymmetries, language, tool use, and intellect*. New York: Academic Press.

Briggs, G. H., & Nebes, R. (1976). Patterns of hand preference in a student population. *Cortex*, *11*, 230–238.

Brown, J. W., & Jaffe, J. (1975). Hypothesis on cerebral dominance. *Neuropsychologia*, *13*, 107–110.

Bruner, J. S. (1973). *Beyond the information given*. New York: W. W. Norton and Co.

Bryden, M., & Steenhuis, R. E. (1991). Issues in the assessment of handedness. In F. L. Kitterle (Ed.), *Cerebral laterality: Theory and research* (pp. 35–51). Hillsdale, NJ: Erlbaum Associates, Inc.

Bundy, R. S. (1979). Effects of infant head position on sides preference in adult handling. *Infant Behavior and Development*, *2*, 355–358.

Caesar, P. (1979). *Postural behavior in newborn infants*. Philadelphia: J. B. Lippincott.

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

Cameron, C. E., Brock, L. L., Murrah, W. M., Bell, L. H., Worzalla, S. L., Grissmer, D., et al. (2012). Fine motor skills and executive function both contribute to kindergarten achievement. *Child Development*, *83*, 1229–1244.

Caplan, P. J., & Kinsbourne, M. (1976). Baby drops the rattle: asymmetry of duration of grasp by infants. *Child Development*, *47*, 532–536.

Carter-Saltzman, L. (1980). Biological and sociocultural effects on handedness: comparison between biological and adoptive families. *Science*, *209*, 1263–1265.

Casasanto, D. (2008). Similarity and proximity: when does close in space mean close in mind? *Memory and Cognition*, *36*, 1047–1056.

Casasanto, D. (2009). Embodiment of abstract concepts: good and bad in right and left-handers. *Journal of Experimental Psychology: General*, *138*(3), 351–367.

Casasanto, D., & Chrysikou, E. G. (2011). When left is 'right': motor fluency shapes abstract concepts. *Psychological Science*, *22*, 419–422.

Casasanto, D., & Dijkstra, K. (2010). Motor action and emotional memory. *Cognition*, *115*, 179–185.

Casasanto, D., & Henetz, T. (2011). Handedness shapes children's abstract concepts. *Cognitive Science*, *36*, 1–14.

Cashmore, L., Uomini, N., & Chapelain, A. (2008). The evolution of handedness in humans and great apes: a review and current issues. *Journal of Anthropological Sciences*, *86*, 7–35.

Cavill, S., & Bryden, P. (2003). Development of handedness: comparison of questionnaire and performance-based measures of preference. *Brain and Cognition*, *53*, 149–151.

Corballis, M. C. (1997). The genetics and evolution of handedness. *Psychological Review*, *104*, 714–727.

Corballis, M. C. (2009). The evolution and genetics of cerebral asymmetry. *Philosophical Transitions of the Royal Society B*, *364*, 867–879.

Corballis, M. C., Lee, K., McManus, I. C., & Crow, T. J. (1996). Location of the handedness gene on the X and Y chromosomes. *American Journal of Medical Genetics, 67*(1), 50–52.

Corbetta, D., & Thelen, E. (1999). Lateral biases and fluctuations in infants' spontaneous arm movements and reaching. *Developmental Psychobiology*, *34*, 237–255.

Corbetta, D., & Thelen, E. (2002). Behavioral fluctuations and the development of manual asymmetries in infancy: contributions of the dynamic systems approach. In S. J. Segalowitz & I. Rapin (Eds.), *Handbook of neuropsychology*. New York: Elsevier.

Coren, S. (1989). Left handedness and accident risk. *American Journal of Public Health*, *79*, 1–2.

Coren, S., & Porac, C. (1977). Fifty centuries of right-handedness: the historical record. *Science*, *198*, 631–632.

Coren, S., Searleman, A., & Porac, C. (1982). The effects of specific birth stressors on four indexes of lateral preference. *Canadian Journal of Psychology*, *36*, 478–487.

Coryell, J. E., & Michel, G. F. (1978). How supine postural preferences of infants can contribute toward the development of handedness. *Infant Behavior and Development*, *1*, 245–257.

Crow, T. J. (1994). The case for an X–Y homologous determinant of cerebral asymmetry. *Cytogenetics and Cell Genetics*, *67*, 393–394.

Crow, T. J. (2002). Handedness, language lateralisation and anatomical asymmetry: relevance of protocadherinXY to hominid speciation and the aetiology of psychosis. *British Journal of Psychiatry*, *181*, 295–297.

Damerose, E., & Vauclair, J. (2002). Posture and laterality in human and nonhuman primates: asymmetries in maternal handling and the infant's early motor asymmetries. In L. J. Rogers & M. Andrew (Eds.), *Comparative vertebrate lateralization*. Cambridge: Cambridge University Press.

Davidson, R. J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, *20*, 125–151.

Dawson, J. L. M. (1974). Ecology, cultural pressures towards conformity and left handedness: a bio-social psychological approach. In J. L. M. Dawson & W. J. Lonner (Eds.), *Readings in cross-cultural psychology* (pp. 125–149). Hong Kong: Hong Kong University Press.

Embodiment and Epigenesis: Theoretical and Methodological Issues in Understanding the Role of Biology within the Relational Developmental System, First Edition, 2013, 227-260

de Vries, J. I. P., Wimmers, R. H., Ververs, I. A. P., Hopkins, B., Savelsbergh, G. J. P., & Van Geijn, H. P. (2001). Fetal handedness and head position preference: a developmental study. *Developmental Psychobiology*, *39*, 171–178.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, *122*, 371–396.

Doane, T., & Todor, J. I. (1978). Motor ability as a function of handedness. In D. M. Landers & R. W. Christina (Eds.), *Psychology of motor behavior and sport* (pp. 264–271). Champaign, IL: Human Kinetics.

Donnot, J., & Vauclair, J. (2007). Infant holding preferences in maternity hospitals: testing the hypothesis of the lateralized perception of emotions. *Developmental Neuropsychology*, *32*, 881–890.

Dubois, J., Hertz-Pannier, L., Cachia, A., Mangin, J. F., Le Bihan, D., & Dehaene-Lambertz, G. (2009). Structural asymmetries in infant language and sensori-motor networks. *Cerebral Cortex*, *19*, 414–423.

Dunn, P. M. (1975). Congenital postural deformities. *British Medical Bulletin*, *32*, 71–76.

Fagard, J. (1998). Changes in grasping skills and the emergence of bimanual coordination during the first year of life. *Clinics in Developmental Medicine*, *147*, 123–143.

Fagard, J., & Marks, A. (2000). Unimanual and bimanual tasks and the assessment of handedness in toddlers. *Developmental Science*, *3*, 137–147.

Fagard, J., & Lockman, J. J. (2005). The effect of task constraints on infants (bi)manual strategy for grasping and exploring objects. *Infant Behavior and Development*, *28*, 305–315.

Falk, D. (1980). Language, handedness and primate brains: did Australopithecines sign? *American Anthropologist*, *82*, 72–79.

Fennell, E., Satz, P., & Morris, R. (1983). The development of handedness and dichotic ear listening asymmetries in relation to school achievement: a longitudinal study. *Journal of Experimental Child Psychology*, *35*, 248–262.

Ferre, C. L., Babik, I., & Michel, G. F. (2010). Development of infant prehension handedness: a longitudinal analysis during the 6- to14-month age period. *Infant Behavior and Development*, *33*, 492–502.

Fleminger, J. J., Dalton, R., & Standage, K. F. (1977). Age as a factor in the handedness of adults. *Neuropsychologia*, *15*, 471–473.

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology*, *66*, 39–52.

Francks, C., DeLisi, L. E., Fisher, S. E., Laval, S. H., Rue, J. E., Stein, J. F., et al. (2003). Confirmatory evidence for linkage of relative hand skill to 2p.12-q11. *American Journal of Human Genetics*, *72*, 499–502.

Francks, C., Fisher, S. E., MacPhie, I. L., Richardson, A. J., Marlow, A. J., Stein, J. F., et al. (2002). A genomewide linkage screen for relative hand skill in sibling pairs. *American Journal of Human Genetics*, *70*, 800–805.

Francks, C., Maegawa, S., Laurén, J., Abrahams, B. S., Velayos-Baeza, A., Medland, S. E., et al. (2007). LRRTM1 on chromosome 2P12 is a maternally suppressed gene that is associated paternally with handedness and schizophrenia. *Molecular Psychiatry*, *12*, 1129–1139.

Frost, G. T. (1980). Tool behavior and the origins of laterality. *Journal of Human Evolution*, *9*, 447–459.

Geschwind, N., & Galaburda, A. M. (1985). Cerebral lateralization: biological mechanisms, associations, and pathology: II. A hypothesis and a program for research. *Archives of Neurology*, *42*, 521–552.

Gesell, A., & Ames, L. B. (1947). The development of handedness. *Journal of Genetic Psychology*, *70*, 155–175.

Gilbert, A. N., & Wysocki, C. J. (1992). Hand preference and age in the United States. *Neuropsychologia*, *30*, 601–608.

Goldfield, E. C., & Michel, G. F. (1986). Ontogeny of infant bimanual reaching during the first year. *Infant Behavior and Development*, *9*, 81–89.

Gonzalez, C. L. R., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, *47*, 3182–3189.

Grissmer, D., Grimm, K. J., Aiyer, S. M., Murrah, W. M., & Steele, J. S. (2010). Fine motor skills and early comprehension of the world: two school readiness indicators. *Developmental Psychology*, *46*, 1008–1017.

Halpern, D. F., & Coren, S. (1991). Handedness and lifespan. *New England Journal of Medicine*, *324*, 998.

Halpern, M. E., Guentuerkuen, O., Hopkins, W. D., & Rogers, L. J. (2005). Lateralization of the vertebrate brain: taking the side of model systems. *The Journal of Neuroscience*, *25*(45), 10351–10357.

Hane, A., Fox, N., Henderson, H., & Marshall, P. (2008). Behavioral reactivity and approach-withdrawal bias in infancy. *Developmental Psychology*, *44*, 1491–1496.

Harkins, D. A., & Michel, G. F. (1988). Evidence for a maternal influence on infant hand-use preferences. *Developmental Psychobiology*, *21*, 535–542.

Harris, L. J., & Carlson, D. F. (1993). Hand preference for visually-guided reaching in human infants and adults. In J. Ward (Ed.), *Current behavioral evidence of primate asymmetries* (pp. 285–305). New York: Springer-Verlag.

Hein, A. (1980). The development of visually guided behavior. In C. S. Harris (Ed.), *Visual coding and adaptability*. Hillsdale, NJ: Erlbaum.

Hepper, P. G., McCartney, G. R., & Shannon, E. A. (1998). Lateralised behavior in first trimester human fetuses. *Neuropsychologia*, *36*, 531–534.

Hepper, P. G., Shahidullah, S., & White, R. (1991). Handedness in the human fetus. *Neuropsychologia*, *29*, 1107–1111.

Hepper, P. G., Wells, D. L., & Lynch, C. (2005). Prenatal thumb sucking is related to postnatal handedness. *Neuropsychologia*, *43*, 313–315.

Hinojosa, T., Sheu, C.-F., & Michel, G. F. (2003). Infant hand-use preferences for grasping objects contributes to the development of a hand-use preference for manipulating objects. *Developmental Psychobiology*, *43*, 328–334.

Hopkins, W. D. (2006). Comparative and familial analysis of handedness in great apes. *Psychological Bulletin*, *132*, 538–559.

Ingram, D. (1975). Cerebral lateralization in young children. *Neuropsychologia*, *13*, 103–105.

Isaacs, K. L., Barr, W. B., Nelson, P. K., & Devinsky, O. (2006). Degree of handedness and cerebral dominance. *Neurology*, *66*, 1855–1858.

Iwasaki, S., Kaiho, T., & Iseki, K. (1995). Handedness trends across age in a Japanese sample of 2316. *Perceptual and Motor Skills*, *80*, 979–994.

Jones, G. V., & Martin, M. (2010). Language dominance, handedness and sex: recessive X-linkage theory and test. *Cortex*, *46*, 781–786.

Kimmerle, M., Ferre, C. L., Kotwica, K. A., & Michel, G. F. (2010). Development of role-differentiated bimanual manipulation during the infant's first year. *Developmental Psychobiology*, *52*, 168–180.

Kimmerle, M., Mick, L. A., & Michel, G. F. (1995). Bimanual role-differentiated toy play during infancy. *Infant Behavior and Development*, *18*, 299–308.

Kinsbourne, M. (1997). The development of lateralization. In H. W. Reese & M. D. Franzen (Eds.), *Biological and neuropsychological mechanisms: Life-span developmental psychology* (pp. 181–197). Mahwah, NJ: Lawrence Erlbaum Associates.

Klar, A. J. (1996). A single locus, RGHT, specifies preference for hand utilization in humans. *Cold Spring Harbor Symposia on Quantitative Biology*, *61*, 59–65.

Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, *123*, 2512–2518.

Kotwica, K. A., Ferre, C. L., & Michel, G. F. (2008). Relation of stable hand-use preferences to the development of skill for managing multiple objects from 7 to 13 months of age. *Developmental Psychobiology*, *50*, 519–529.

Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh: The embodied mind and its challenge to Western thought*. Chicago: University of Chicago Press.

Laland, K. N., Kumm, J., Van Horn, J. D., & Feldman, M. W. (1995). A gene-culture model of human handedness. *Behavioral Genetics*, *25*, 433–445.

Lansky, L. M., Feinstein, H., & Peterson, J. M. (1988). Demography of handedness in two samples of randomly selected adults. *Neuropsychologia*, *26*, 465–477.

Laval, S. H., Dann, J. C., Butler, R. J., Loftus, J., Rue, J., Leask, S. J., & Crow, T. J. (1998). Evidence for linkage to psychosis and cerebral asymmetry (relative hand skill) on the X chromosome. *American Journal of Medical Genetics: Neuropsychiatric Genetics*, *81*, 420–427.

Longcamp, M., Anton, J. L., Roth, M., & Velay, J. L. (2005). Premotor activations in response to visually presented single letters depend on the hand used to write: a study on left-handers. *Neuropsychologia*, *43*, 1801–1809.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences*, *10*, 247–303.

Marchant, L. F., McGrew, W. C., & Eibl-Eibesfeldt, I. (1995). Is human handedness universal? Ethological analyses from three traditional cultures. *Ethology*, *101*, 239–258.

Maxwell, J. S., & Davidson, R. J. (2007). Emotion as motion: asymmetries in approach and avoidant actions. *Psychological Science*, *18*, 1113–1119.

McFarland, K. (2009). Motor control: pyramidal, extrapyramidal, and limbic motor control. In G. G. Berntson & J. T. Cacioppo (Eds.), *Handbook of neuroscience for the behavioral sciences* (Vol. 1, pp. 431–453). Hoboken, NJ: Wiley.

McGrew, W. C., & Marchant, L. F. (1997). On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, *40*, 201–232.

McKeever, W. F. (2000). A new family handedness sample with findings consistent with X-linked transmission. *British Journal of Psychology*, *91*(1), 21–39.

McManus, C. (2002). *Right hand, left hand: The origins of asymmetry in brains, bodies, atoms, and cultures*. Cambridge, MA: Harvard University Press.

McManus, I. C., & Bryden, M. P. (1992). The genetics of handedness, cerebral dominance, and lateralization. In I. Rapin & S. J. Segalowitz (Eds.), *Handbook of neuropsychology* (Vol. 6, pp. 115–144). Amsterdam: Elsevier.

McManus, I. C., Sik, G., Cole, D. R., Mellon, A. F., Wong, J., & Kloss, J. (1988). The development of handedness in children. *British Journal of Developmental Psychology*, *6*(3), 257–273.

Mebert, C., & Michel, G. F. (1980). Handedness in artists. In J. Herron (Ed.), *Neuropsychology of left handedness* (pp. 273–280). New York: Academic Press.

Medland, S. E., Duffy, D. L., Wright, M. J., Geffen, G. M., Hay, D. A., Levy, F., & Boomsma, D. I. (2009). Genetic influences on handedness: data from 25,732 Australian and Dutch twin families. *Neuropsychologia*, *47*, 330–337.

Michel, G. F. (1981). Right-handedness: a consequence of infant supine head-orientation preference? *Science*, *212*, 685–687.

Michel, G. F. (1983). Development of hand-use preference during infancy. In G. Young, S. Segalowitz, C. Corter & S. Trehub (Eds.), *Manual specialization and the developing brain* (pp. 33–70). New York: Academic Press.

Michel, G. F. (1988). A neuropsychological perspective on infant sensorimotor development. In L. P. Lipsitt & C. K. Rovee-Collier (Eds.), *Advances in infancy research* (Vol. 5, pp. 1–37). Norwood, NJ: Ablex Pub. Corp.

Michel, G. F. (1991). Development of infant manual skills: motor programs, schemata, or dynamic systems. In J. Fagard & P. H. Wolff (Eds.), *The development of timing control and temporal organization in coordinated action* (pp. 175–199). NY: Elsevier.

Michel, G. F. (1998). A lateral bias in the neuropsychological functioning of human infants. *Developmental Neuropsychology*, *14*, 445–469.

Michel, G. F. (2002). Development of infant handedness. In D. J. Lewkowicz & R. Lickliter (Eds.), *Conceptions of development* (pp. 165–186). New York: Psychology Press.

Michel, G. F. (2010). The roles of environment, experience, and learning in behavioral development. In K. Hood, C. Halpern, G. Greenberg & R. Lerner (Eds.), *Handbook of developmental science, behavior and genetics* (pp. 123–165). Malden, MA: Wiley.

Michel, G. F., Babik, I., Sheu, C.-F., & Campbell, J. M. (submitted). Latent classes in the developmental trajectories of infant handedness. Developmental Psychology.

Michel, G. F., & Goodwin, R. (1979). Intrauterine birth position predicts newborn supine head position preferences. *Infant Behavior and Development*, *2*, 29–38.

Michel, G. F., & Harkins, D. S. (1985). Concordance of handedness between teacher and student facilitates learning manual skills. *Journal of Human Evolution*, *14*, 597–601.

Michel, G. F., & Harkins, D. A. (1986). Postural and lateral asymmetries in the ontogeny of handedness during infancy. *Developmental Psychobiology*, *19*, 247–258.

Michel, G. F., & Moore, C. L. (1995). *Developmental psychobiology: An interdisciplinary science*. Cambridge, MA: The MIT Press.

Michel, G. F., Ovrut, M. R., & Harkins, D. A. (1985). Hand-use preference for reaching and object manipulation in 6- through 13-month-old infants. *Genetic, Social, and General Psychology Monographs*, *111*, 409–427.

Michel, G. F., Sheu, C.-F., & Brumley, M. R. (2002). Evidence of a right-shift factor affecting infant hand-use preferences from 7 to 11 months of age as revealed by latent class analysis. *Developmental Psychobiology*, *40*, 1–13.

Michel, G. F., Tyler, A. N., Ferre, C., & Sheu, C.-F. (2006). The manifestation of infant hand-use preferences when reaching for objects during the seven- to thirteen-month age period. *Developmental Psychobiology*, *48*, 436–443.

Mundale, C. J. (1992). Influences of maternal handedness and behavior on infant hand use preferences. Unpublished Master's thesis. DePaul University: Psychology Department.

Murphy, G. (1996). On metaphoric representation. *Cognition*, *60*, 173–204.

Neale, M. C. (1988). Handedness in a sample of volunteer twins. *Behavior Genetics*, *18*, 69–79.

Nelson, E. L., Campbell, J. M., & Michel, G. F. (2013). Unimanual to bimanual: tracking the development of handedness from 6 to 24 months. Infant Behavior and Development, *36*, 181–188.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Oppenheimer, D. M. (2008). The secret life of fluency. *Trends in Cognitive Science*, *12*(6), 237–241.

Overton, W. F., & Mueller, U. (2012). Meta-theories, theories, and concepts in the study of development. In R. M. Lerner, M. A. Easterbrooks & J. Mistry (Eds.), & Irving B. Weiner (Editor-in-Chief). *Comprehensive handbook of psychology: Developmental psychology* (Vol. 6, pp. 19–58). New York: Wiley.

Papadatou-Pastou, M., Martin, M., Munafo, M., & Jones, G.V. (2008). Sex differences in left-handedness: a meta-analysis of 144 studies. *Psychological Bulletin*, *134*, 677–699.

Papademetriou, E., Sheu, C.-F., & Michel, G. F. (2005). A meta-analysis of primate hand preferences, particularly for reaching. *Journal of Comparative Psychology*, *119*(1), 33–48.

Perelle, I. B., & Ehrman, L. (2005). On the other hand. *Behavior Genetics*, *35*(3), 343–350.

Piaget, J. (1952). *The origins of intelligence in children*. New York: International Universities Press.

Piek, J. P. (2002). The role of variability in early motor development. *Infant Behavior and Development*, *25*, 452–465.

Porac, C., & Coren, S. (1981). *Lateral preferences and human behavior*. New York: Springer-Verlag.

Porac, C., Coren, S., & Serleman, A. (1986). Environmental factors in hand preference formation: evidence from attempts to switch the preferred hand. *Behavior Genetics*, *16*, 251–261.

Preti, A., & Vellante, M. (2007). Creativity and psychopathology: higher rates of psychosis proneness and nonright-handedness among creative artists compared to same age and gender peers. *Journal of Nervous & Mental Disease*, *195*, 837–845.

Provins, K. A., & Cunliffe, P. (1972). The reliability of some motor performance tests of handedness. *Neuropsychologia*, *10*, 199–206.

Ramsay, D. S. (1980). Onset of unimanual handedness in infants. *Infant Behavior and Development*, *3*, 377–385.

Raymond, M., Pontier, D., Dufour, A.-B., & Moller, A. P. (1996). Frequency-dependent maintenance of left handedness in humans. *Proceedings of the Royal Society of London B*, *22*, 1627–1633.

Risch, N., & Pringle, G. (1985). Segregation analysis of human hand preference. *Behavior Genetics*, *15*, 385–400.

Rönnqvist, L., & Domellof, E. (2006). Quantitative assessment of right and left reaching movements in infants: a longitudinal study from 6 to 36 months. *Developmental Psychology*, *48*, 444–459.

Rönnqvist, L., & Hopkins, B. (1998). Head position preference in the human newborn: a new look. *Child Development*, *69*, 13–23.

Rönnqvist, L., Hopkins, B., van Emmerik, R., & de Groot, L. (1998). Lateral biases in head turning and the Moro response in the human newborn: are they both vestibular in origin? *Developmental Psychobiology*, *33*, 339–349.

Satz, P., Achenbach, K., & Fennell, E. (1967). Correlations between assessed manual laterality and predicted speech laterality in a normal population. *Neuropsychologia*, *5*, 295–310.

Schaafsma, S. M., Riedstra, B. J., Pfannkuche, K. A., Bouma, A., & Groothuis, T. G. G. (2009). Epigenesis of behavioural lateralization in humans and other animals. *Philosophical Transactions of the Royal Society B*, *364*, 915–927.

Schiff, B. B., & Bassel, C. (1996). Effects of asymmetrical hemispheric activation on approach and withdrawal responses. *Neuropsychology*, *10*, 557–564.

Schubert, T. (2005). Your highness: vertical positions as perceptual symbols of power. *Journal of Personality and Social Psychology*, *89*, 1–21.

Schulte, F. J. (1974). The neurological development of the neonate. In J. A. Davis & J. Debbing (Eds.), *Scientific foundations of pediatrics*. Philadelphia: Saunders.

Serrien, D. J., Ivry, R. B., & Swinnen, S. P. (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews. Neuroscience*, *7*, 160–166.

Sicotte, N. L., Woods, R. P., & Mazziotta, J. P. (1999). Handedness in twins: a meta-analysis. *Laterality*, *4*, 265–286.

Spennemann, D. R. (1984). Handedness data on the human neolithic. *Neuropsychologia*, *22*, 613–615.

Spinelli, D. N., & Jensen, F. E. (1982). Plasticity, experience and resource allocation in motor cortex and hypothalamus. In C. D. Woody (Ed.), *Conditioning* (pp. 161–169). New York: Plenum.

Steenhuis, R. E., & Bryden, M. P. (1989). Different dimensions of hand preference that relate to skilled and unskilled activities. *Cortex*, *25*, 289–304.

Steinmetz, H., Volkmann, J., Jäncke, L., & Freund, H.-J. (1991). Anatomical left-right asymmetry of language-related temporal cortex is different in left- and right-handers. *Annals of Neurology*, *29*, 315–319.

Tan, U., Ors, R., Kurkcuoglu, M., & Kutlu, N. (1992). The lateralization of the grasp reflex in human newborns. *International Journal of Neuroscience*, *62*, 1–8.

Thelen, E., Corbetta, D., & Spencer, J. P. (1996). Development of reaching during the first year: role of movement speed. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 1059–1076.

Todor, J. I., & Doane, T. (1977). Handedness classification: preference versus proficiency. *Perceptual and Motor Skills*, *45*, 1041–1042.

Todor, J. I., & Doane, T. (1978). Handedness and hemispheric asymmetry in the control of the movement. *Journal of Motor Behavior*, *10*, 295–300.

Toth, N. (1985). Archeological evidence for preferential right-handedness in lower and middle Pleistocene and its possible implications. *Journal of Human Evolution*, *14*, 35–40.

Turkewitz, G. (1977). The development of lateral differences in the human infant. In S. Harnad, R. W. Doty, I. Goldstein, J. Jaynes & G. Krauthammer (Eds.), *Lateralization in the nervous system* (pp. 251–260). New York: Academic Press.

Van Agtmael, T., Forrest, S. M., & Williamson, R. (2002). Parametric and nonparametric linkage studies of several candidate regions for genes for human handedness. *European Journal of Human Genetics*, *10*, 623–630.

Volkmann, J., Schnitzler, A., Witte, O. W., & Freund, H.-J. (1998). Handedness and asymmetry of hand representation in human motor cortex. *Journal of Neurophysiology*, *79*, 2149–2154.

Volpato, V., Macchiarelli, R., Guatelli-Steinberg, D., Fiore, I., Bondioli, L., et al. (2012). Hand to mouth in a neandertal: right-handedness in Regourdou. *PLoS One*, 7(8), e43949. http://dx.doi.org/10.1371/journal.pone.0043949.

Warren, D. M., Stern, M., Duggirila, R., Dyer, T. D., & Almasy, L. (2006). Heritability and linkage analysis of hand, foot, and eye preference in Mexican Americans. *Laterality*, *11*, 508–524.

Willems, R. M., & Hagoort, P. (2007). Neural evidence for the interplay between language, gesture, and action: a review. *Brain Language*, *101*, 278–289.

Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: neural evidence from right- and lefthanders. *Psychological Science*, *21*(1), 67–74.

Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2009). Body-specific motor imagery of hand actions: neural evidence from right- and left-handers. *Frontiers in Human Neuroscience*, *3*(39), 1–9.

Williams, L. E., & Bargh, J. A. (2008). Keeping one's distance: the influence of spatial distance cues on affect and evaluation. *Psychological Science*, *19*, 302–308.

Witelson, S. F. (1990). Neuroanatomical basis of hemispheric functional specialization in the human brain: developmental factors. In I. Kostovic, S. Knezevic, H. M. Wisnioewski & G. J. Spilich (Eds.), *Neurodevelopment, aging, and cognition* (pp. 112–141). Boston, MA: Birkhauser.