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Plasticity in the Development of Handedness: Evidence From Normal Development and Early Asymmetric Brain Injury

ABSTRACT: *Previous research revealed that shifting patterns of hand preference in the first year of life are linked to infants' sensory-motor experiences as they learn to sit, creep, and walk. In this report, we examine whether new and different forms of locomotion and sensory-motor experiences similarly contribute to alter patterns of hand preference in early development. We examined the cases of three infants with unique developmental histories. Two infants adopted distinctive forms of locomotion in lieu of typical hands-and-knees crawling. One infant scooted using both hands and legs in a coupled fashion, while the other infant performed an asymmetrical, left-biased belly-crawl using only one arm to drag his body. The third infant suffered damage to his left-brain hemisphere shortly after birth and received intense physical therapy to his right arm as a result of it. We followed all three infants on a weekly basis and tracked changes in their reaching behavior, mode of locomotion, and postural achievements. The two infants with unique locomotor patterns displayed changes in hand preference that reciprocated the arm patterns that they used during locomotion. The infant who coupled his body for scooting began to reach bimanually, while the infant who adopted the left-biased belly-crawl developed a strong unimanual, right-hand, preference. The infant with left-hemisphere damage initially displayed a right-hand preference, then a temporary decline in preferred hand use as he began to cruise and walk, and ultimately resumed a right-hand preference in the 2nd year of life. This data is consistent with previous work showing that the development of hand preference in the 1st year of life is highly malleable and sensitive to a variety of new sensory-motor experiences.* © *2006 Wiley Periodicals, Inc.* Dev Psychobiol 48: 460–471, 2006.

Keywords: *hand preference; infants; posture; locomotion; brain damage*

INTRODUCTION

The search for the origins of human handedness and brain laterality has been on the mind of neuropsychologists and psychologists for centuries (Marshall & Magoun, 1998). Indeed, handedness is quite manifest in humans compared to other vertebrate species (Hellige, 1993; Warren, 1980). Moreover, 75–90% of the human population across many cultures prefers to use the right hand to achieve a wide number of tasks involving various levels of dexterity. Although several accounts have suggested that hand preference may be linked to sensory-motor experience (Corbetta & Thelen, 2002; Coryell & Michel, 1978; Nudo, Milliken, Jenkins, & Merzenich, 1996; Provins, 1997) or environmental influences (Harkins & Michel, 1988; Harkins & Uzgiris, 1991; Provins, 1997), the view that hand preference is mainly genetically rooted has strongly prevailed over many decades (Annett, 1985; Levy & Nagylaki, 1972; McManus, 1985).

Several lines of evidence support a genetic origin of handedness. First, a number of genetic models of

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handedness have been successful at predicting population biases in preferred hand use and these predicted population biases match the actual population distributions in handedness (Annett, 1985; Levy & Nagylaki, 1972; McManus, 1985). Handedness also seems to run in families (Annett, 1973). A child born from a family where one of the parents is left-handed has a greater chance of becoming left-handed than a child born from two right-handed parents (Chamberlain, 1929; McKeever, 2000). Finally, it appears that the predominant right bias that is typical of adult populations is already present early in life. For example, a strong preferred right hand bias has been documented in 7 to 11-months-old infants (Michel, Sheu, & Brumley, 2002) and a preferred right bias has even been identified earlier in development in the spontaneous head turn of newborns (Coryell, 1985; Michel, 1981). Together, these findings not only suggest that human handedness may be deeply rooted in our phylogenetic and ontogenetic heritage, but also that it can manifest itself very early in life.

Although genetic accounts of hand preference seem to do well in predicting trends in large populations, they fall short in explaining individual development. From a developmental perspective, strict genetic models would not only predict to find a population right bias from early in life, but would also predict the maintenance and strengthening of these early biases over developmental time. Longitudinal observations of the development of hand preference in young infants have not shown such steady developmental trends (Corbetta & Thelen, 1996, 1999; Fagard, 1998; Gesell & Ames, 1947). Rather, they revealed highly individually defined and fluctuating developmental trajectories, where infants were shifting from one to two or, from right to left hand use several times during early development before acquiring a stable preferred hand use. Why do those developmental fluctuations occur? Are they random, autonomous shifts in behavior or are they the product of concurrent developmental factors? And to what extent are those biases and fluctuations modulated by early experience?

Nonlinear, discontinuous patterns of development are better understood from a system-oriented perspective which is nonpredeterministic in nature. Unlike strict genetic models, systems views see the emergence and change in behavior as the product of multiple interacting factors, both endogenous and exogenous to the organism. Dynamic systems approaches, for instance, see the behavioral characteristics of an organism and the course of their formation through life as the product of continuous intertwined reorganizations between multiple biological, environmental, and experiential factors that change and evolve as infants and children grow (Thelen, 1995; Thelen & Smith, 1994, 1998). Similarly, the psychobiological systems view stresses the multi-directional exchanges between genes, behavior, and environment. While genes can influence behavior, environment, behavior, and experience can, in turn, affect gene expression. Therefore, multiple factors (genetic, neural, behavioral, and environmental) can mutually influence the course of behavioral ontogenesis during individual development (Gottlieb, 1992; Gottlieb, Wahlsten, & Lickliter, 1998).

The aim of this article is to understand the origins of the documented developmental fluctuations in hand preference that are occurring in early development, from a dynamic systems perspective. In a prior work (Corbetta & Thelen, 2002), we discovered an interesting relationship between the locomotor patterns that infants were developing at different points in time during their first year of life and the pattern of hand use that infants were adopting at those particular developmental times. These were longitudinal studies where infants were either asked to reach for an object at midline or to retrieve an object concealed in a box with a hinged lid. We simultaneously screened these infants' postural development over the weeks. We observed that early in development, prior to the emergence of hands-and-knees crawling, infants tended to display a preferred right bias for reaching (Corbetta & Thelen, 1999) and exhibited a stable division of hand roles when opening the lid of the box with one hand while retrieving the toy with the other hand (Corbetta & Thelen, 2002). After infants began to crawl on hands-and-knees, however, those preferred right biases in reaching and steady division of hand role in object retrieval dissipated. For the remainder of the first year, infants began using either hand for reaching and alternated hand roles for opening the box and retrieving the toy. In other words, after the onset of hands-and-knees crawling, it became impossible to continue to discern a preferred bias in hand use as these infants solved these particular tasks.

We observed another change in hand use a few months later, when infants began to perform their first independent steps. Infants began to couple their arms for reaching and for opening the lid of the box (Corbetta & Bojczyk, 2002). This interlimb coupling in reaching subsisted as long as infants were precarious walkers and held their arms in a high guard position to control their balance. Several weeks later, when infants became relatively more stable walkers and began to lower their arms along the sides of their body, they also returned to more one-handed, lateralized reaches, and began again to show a steadier division of hand roles in the object retrieval task (Corbetta, 2005).

Our interpretation was that novel emerging patterns of locomotion interacted dynamically with the organization of preferred hand use during these critical periods of motor skill learning (Corbetta, 2005). Infants had already established seemingly preferred patterns of hand use prior to the emergence of self-produced locomotion, but these patterns underwent successive alterations as new locomotor skills emerged. Interestingly, the form and direction that these hand pattern alterations underwent reflected the motor patterns practiced during locomotion. When infants began to crawl on hands-and-knees and began to alternate the use of their right and left arm to locomote, they also began to use the right and the left hand alternately during reaching and object retrieval (note that during reaching and object retrieval, infants were securely fastened in an infant seat; they were not crawling while reaching). Similarly, when infants began to perform their first independent steps and began to couple the activity of both arms to maintain balance, infants also began to couple their arm movements during reaching and object retrieval, even though there were no direct balance constraints associated to these later tasks (again, when reaching and retrieving the object from the box infants were fully supported in an infant seat). Finally, we noted that these mutual changes in reaching and locomotor patterning were individually defined. Infants who learned to walk quickly and gained balance control within a few weeks also demonstrated a short period of two-handedness in reaching, while infants who displayed a slower progression in walking over a longer period of time also displayed a longer period of two-handed reaching (Corbetta & Bojczyk, 2002). These observations led us to conclude that early developmental fluctuations in hand use were not occurring randomly, but were associated with the emergence of novel sensory-motor experiences as infants learned to crawl and walk. Likewise, these observations led us to conclude that early biases in hand use were not strongly determined, but were rather highly malleable as infants developed and practiced new sensory-motor skills.

One goal of this article is to extend those findings and ask whether other forms of locomotion that do not involve crawling on hands-and-knees or walking influence patterns of hand use in infancy. Infants can display various forms of crawling and reveal different patterns of developmental progressions prior to walking upright (Adolph, Vereijken, & Denny, 1998). Some infants may even skip the more common hands-and-knees crawling form and adopt alternative and unique ways of locomoting. Given that our prior studies revealed that preferred patterns of hand use seemed to reciprocate the particular forms of hand patterning practiced during locomotion; here, we ask if skipping hands-and-knees crawling all together or if adopting a unique form of locomotion could similarly alter the developmental progression of preferred hand use in reaching. Given those varied developmental scenarios, would infants maintain their original preferred biases? Or, would they show other organizational forms of hand use that would not involve an alternating pattern between hands? To address these questions, we present the longitudinal manual and locomotor data of two infants who developed unique patterns of locomotion before to walk; one maintained an asymmetrical belly crawling pattern over months prior to walking and the other one learned to scoot in a sitting posture for a while before beginning to crawl on hands-and-knees.

A second aim of this article is to begin to ask whether other forms of sensory-motor experiences, that are not necessarily locomotor in nature, can also affect the direction of hand preference in development. From a dynamic systems perspective, behavioral patterns in development do not form as the result of single factors, but rather are the product of multiple interacting influences that can occur at different points in time. We begin to address this issue by looking at a unique case study whose developmental history of early asymmetric brain damage and history of rehabilitation had a significant impact upon the development and direction of his preferred hand use.

METHOD

Participants

Three infant males, GD, GC, and LBL were observed weekly over several months. GC and GD were respectively part of a previous pilot and study on the effect of locomotion on infant bimanual coordination. GC was followed over 17 weeks from 6:3 to 10:2 months. GD was followed for 32 weeks from 8:0 to 15:1 months; however, for the purpose of this report, we only focus on GD's first 17 weeks. Both infants had no known prior history of illness or neurological disorder. The pilot work and study were approved by the Purdue University Institutional Review Board.

The 3rd infant, LBL, was recruited at 6 months of age as a regular research participant in a laboratory studying infant speech at Purdue University. During this visit, the researchers learned about his medical history. LBL was born full term through C-section and had an APGAR score of 8 at 1 min and 9 at 5 min of life. However, 8–10 hr after birth, LBL began displaying twitching movements in his right shoulder and right leg, which were indicative of seizures. He was immediately given Phenobarbital and an MRI scan performed 1 day after his birth, which revealed a large (~5–6 cm) area of high signal along the gyri in the left, mid, and posterior temporoparietal lobes. This high signal was compatible with an acute ischemic infarct (absence of blood supply) in the left middle cerebral artery territory. There was no presence of hemorrhage, mass, or midline shift between hemispheres. The reason for the acute ischemic infarct was not clear. There was no family history of strokes, clotting disorders, or seizures. Additional EEG, EKG, and blood panel analyses did not reveal further abnormal findings. The conclusions of the medical report was that LBL was at risk for epilepsy, developmental delays (especially in the areas of motor & speech development), and cerebral palsy. LBL remained on high doses of Phenobarbital up to 6 months of age. He began to receive intensive weekly physical and occupational therapy, especially to his right arm and right leg from the age of 5 weeks until 9 months. Then therapy sessions continued at a monthly rate until LBL was 11 months old.

The speech researchers who discovered LBL were interested in performing more in-depth and long-term screening of LBL's motor, cognitive, and speech development, and the parents consented. Our motor developmental laboratory and a cognitive laboratory at Purdue University joined forces with the speech researchers to screen LBL's progress. Once procedures were in place, it took 2 ½ months to obtain approval from the Purdue Institutional Review Board to follow this case. Our laboratory began to follow LBL's motor skills on a weekly basis from the age of 8:3 months until he was 15:1 months old, that is, over a 29 visit period, and then, we performed three hand preference screening sessions at 16:1, 17:2, and 21:0 months. Also, of notable importance for the purpose of this article, LBL was born from a family with a strong left-handedness history. The two biological parents, one brother, the maternal grandmother, and a maternal uncle were left-handed. Another brother of LBL was more ambidextrous.

Material

The reaching of all three infants was tested with a set of 12 small and large colorful, solid balls that were 5 cm and 13 cm in diameter, respectively. The small objects were easily graspable with one hand; the large objects required two hands to be held. During testing, the infants were securely fastened on a specially designed infant seat that was reclined 15 degrees from vertical and provided full trunk support, while allowing the arms and legs to move freely. Behavior was videotaped using two Sony High-8 Handicams placed approximately 45 degrees front-right and front-left of the infant. A Videonics MX-1 Digital Video Mixer (Focus Enhancement, Inc., Campbell, CA) was used to merge and synchronize the views from both cameras on one screen providing a simultaneous view of both arms at the same time. For LBL, video frame numbers were inserted during recording on the video image by the means of a Horita TRG-50 time code generator (Mission Viejo, CA). Also, for LBL only, we collected endpoint-reaching kinematics using a Flock of Birds (Ascension Technology Corp., Burlington, VT), which sampled movement at a rate of 120 Hz. A mini 8-mm marker was attached to the dorsal side of each wrist with Johnson's hypoallergenic, nonirritating soft cloth tape. The markers' wires were taped along the arms of the infant and behind the seat so as to prevent hindrance of the infant reach.

In addition, we tested LBL's hand preference toward the end of his 2nd year of life with a set of toys similar to the ones used by Corbetta and Thelen (1999). The toys included a set of small blocks that could be inserted into a cylinder through fitting holes in the lid, a few coins and a toy bank, a xylophone with a small mallet, a hammer and pegboards, a baby bottle to feed a puppy, and a telephone toy.

Design and Procedure

Each laboratory session included two different tasks: a reaching task and a postural/locomotor assessment.

Reaching Task. The procedure for GC and GD was identical to the one described in Corbetta and Bojczyk (2002). This study did not involve movement kinematics; it used only video recording. Once the infants were securely fastened in the infant seat, an experimenter sat in front of them and presented the small and large objects to them, one at a time, at midline and at shoulder height until the infant reached for, touched, and eventually grasped the toy. Infants were presented eight trials of each size. All trials always resulted in contact/grasp with the target. Size presentations were blocked and counterbalanced every week. Because the present report focuses on hand preference, we rely only on the results relating to the small objects which were more appropriate to assess changes in hand use.

We recorded movement kinematics with LBL. LBL was similarly tested with the same small and large objects at midline, but also with the small objects presented on the right and left side of his body to assess the reaching patterns of each hand separately. As was the case for GC and GD, objects were presented one at a time, at shoulder height. We collected five trials with the small objects presented at midline, five trials with the large objects at midline, five trials with the small objects presented on the right side, and five trials with the small objects presented on the left side. All 20 trials resulted in successful contact/grasp with the target. Object size and location of presentation (middle, right, or left) were blocked and counterbalanced every week. As for GC and GD, this report focuses only on the small object presentations.

Postural Screening. At the conclusion of each laboratory session, the postural behaviors of all three infants were assessed. The screening took place on the laboratory floor—a hard carpeted surface—and toys were used to entice the infants to perform any of the following behaviors depending on their level of body control: scooting, crawling, creeping, pulling up to stand, standing with or without support, cruising along chair furniture, walking with support, and independent walking.

LBL's Hand Preference Testing. Because of his history of left-brain lesion, LBL was followed up to 21 months to assess the direction of his hand preference. Testing took place on a table with an experimenter sitting on one side while facing LBL sitting on the other side of the table. Handedness was assessed by presenting the toys to LBL one at a time and in a random order. Toys (i.e., xylophone) and their tools (i.e., mallets) were always placed at LBL's midline and presented to him in a way to prevent biases in hand choice. The different tasks were repeated up to three times each or to the extent that LBL was cooperating.

Behavioral Coding and Data Analyses

Two coders analyzed independently the reaching behaviors of each infant. The reaches were coded as unimanual or bimanual, based on the number of arms activated in the direction of the toy prior to contact (Corbetta & Thelen, 1996). A reach was classified as unimanual, if the infant reached for the toy using only one arm while the opposite arm remained inactive, or, if the infant began to reach with the second arm after the first hand had already contacted the toy. Reaches were classified as bimanual when the infant extended both arms (with or without a delay) within the same time window in the direction of the toy. Reaches were also coded as right- or left-handed based on the hand that touched the object first. The frequencies of unimanual and bimanual reaches and right and left-handed reaches per week were then transformed into frequency indexes using the following formulas: $(B - U)/(B + U)$ and $(R - L)/(R + L)$. These formulas yielded an index that varied from $+1$ to -1, where $+1$ corresponded to uniquely bimanual or uniquely right-handed reaches, and -1 corresponded to uniquely one-handed or uniquely left-handed reaches. A value of 0 reflected an equal number of both responses and values in between expressed mixed responses ranging from greater bimanual or greater right-handed to greater unimanual or greater left-handed responses. Between coders' reliability for unimanual and bimanual, and left and right-handed reaches was consistently above 92.3% for all three infants.

For LBL's kinematic analysis, two coders first identified the frames corresponding to the start and the end of the reach from the video. These video frames were then entered into a custom made Matlab program (Mathworks, Inc., Natick, MA) that converted them into matching kinematic frames. The program also filtered the kinematic data using a 2nd order, no lag, Butterworth low-pass filter with a 6 Hz cut-off and computed the 3D endpoint resultant velocity using a three-points differentiation technique. Then, the program plotted the 3D resultant displacement and velocity profiles for each trial on the computer screen allowing the user to check the onset and offset values of the reach identified on the kinematics profiles against the video. Following a method described by Corbetta and Thelen (1995), the program allowed the user to adjust the frame of reach start so that it always corresponded to the velocity minima closest to the picked video value. Reach end was always defined as the 1st frame of hand-toy contact. Once the start and stop of the reach were selected, the program computed a number of dependent variables such as the average velocity of the reach, the maximum velocity peak, the time to maximum velocity peak normalized in percent, and the number of movement units based on differences between successive minimum and maximum velocity peaks that were greater than .5 cm/sec. Between coders' reliability was 88% and 89.1% for the frame of reach start and frame of hand/toy contact, respectively.

For LBL's later hand preference testing, coders identified which hand(s) (right, left, or both) was used to reach for the tool (i.e., hammer) or object (i.e., cube), and which hand was used to manipulate these objects in relation to their target (i.e., hammering or fitting the cube through the lid of the cylinder). Repeated measures were then transformed using the same formula as for reaching $(R - L)/(R + L)$. Reliability coding was 100% for the hand used for reaching and the hand used for manipulating the objects.

RESULTS

Change in Reaching Patterning as a Function of Emerging Forms of Locomotion

We saw in the introduction that infants who adopted alternate hands-and-knees crawling as a first form of self-produced locomotion also tended to alternate patterns of hand use in reaching over the same period (Corbetta & Thelen, 2002). Likewise, we saw that when infants began to walk upright and temporarily coupled their arms in high guard to maintain balance, they also temporarily coupled their arms during reaching over the same period until they gained better balance control (Corbetta & Bojczyk, 2002). Here, we ask whether infants who do not develop the more common form of hands-and-knees crawling, but adopt alternate and more unique forms of self-produced locomotion early in development, also show a change in reaching patterning that reciprocate the form of arm patterning practiced during locomotion.

Figures 1 and 2 present changes in patterns of hand use for reaching for small objects at midline for GD and GC, respectively, during the first 17 weeks of their visits to our laboratory. On both figures, the top graphs display the index rate of unimanual versus bimanual reaching, and the bottom graphs reflect the rate of right- versus left-handed use. The figures also indicate the weeks when a new motor milestone emerged.

Figure 1 shows that prior to becoming mobile, during his first seven visits to the laboratory, GD was reaching predominantly with one hand—his left hand. In Week 7, he started to become mobile by scooting his body forward while in a sitting position (see stick figure). He was able to move his body forward by rocking his trunk back and forth while flexing and pulling both legs in the horizontal plane. While doing so, GD held his arms in a symmetrical position. He continued to scoot like that until Week 14, at which point he shifted to hands-and-knees crawling. In Week 9, shortly after GD began coupling his legs, arms, and body to scoot, he also began coupling his arms when reaching for the small objects at midline (Fig. 1, top graph). The change in reaching patterning between Week 8 and 9 was significant (Fisher exact test, $p = .001$). The same week, he displayed a temporary decline in his left hand preference (Fig. 1, bottom graph). Interestingly, GD maintained this bimanual coupling for reaching until he began to crawl on hands-and-knees at Week 14. When crawling emerged, he returned to a one-handed reaching pattern (Fig. 1, top graph). Again, the change in reaching patterning and coupling between Week 13 and 14 was significant (Fisher exact test, $p = .002$).

GC (on Fig. 2) was a belly crawler. When he became mobile at Week 4, he was performing a lateral army crawling motion. As he was lying on his belly, he first moved his left elbow forward and then slightly shifted his weight over his left side to drag his body forward with his left elbow while pushing with his right leg. This asymmetric motion had the advantage to free his right arm, which he could use to reach for or grab objects in his surrounding. When tested in the infant seat, GC displayed primarily one-handed reaching patterns (see Fig. 2, top

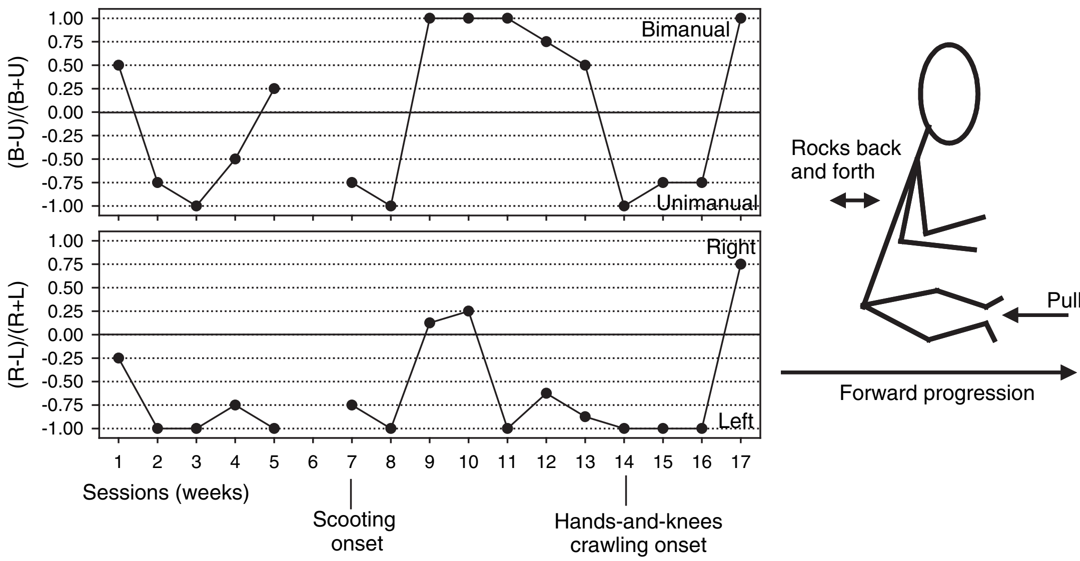

FIGURE 1 Index rate of bimanual versus unimanual responses (top graph) and index rate of right versus left responses (bottom graph) per session for infant GD when reaching for small objects at midline over a 17-week period. The stick figure represents the scooting motion that GD performed from Week 7 to Week 14.

graph), and his patterns became almost exclusively right-handed after he began to adopt this asymmetrical crawling mode of locomotion (Fig. 2, bottom graph). The change in preferred hand use that occurred between Week 2 and 4 when he began to crawl on his belly was significant (Fisher exact test, $p = .029$). Unlike hands-and-knees crawling infants who showed a disappearance in preferred hand use at this period of development (Corbetta & Thelen, 2002), GC developed a strong preferred hand use, presumably because he never used his two arms in an alternating fashion for crawling, but rather adopted a unique lateralized arm use to locomote.

Early Lateral Brain Injury and the Development of Hand Preference

The study of LBL was motivated by several questions. First, given the site of his left-hemisphere brain lesion

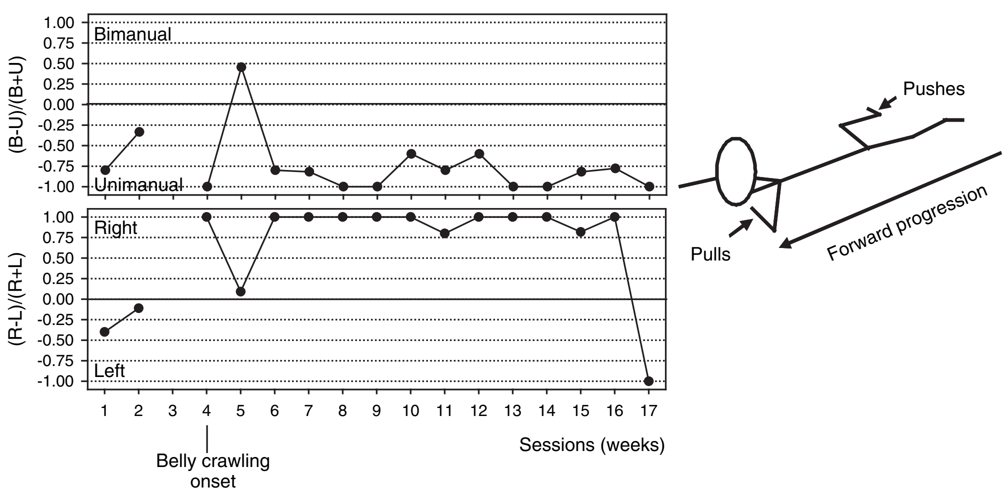

FIGURE 2 Index rate of bimanual versus unimanual responses (top graph) and index rate of right versus left responses (bottom graph) per session for infant GC when reaching for small objects at midline over a 17-week period. The stick figure represents the asymmetrical belly crawl that GC performed from Week 4.

(which assumingly would affect mainly his right arm) and the fact that he was born from a family with a strong left-handedness history, the question arose as to whether LBL would naturally develop a left hand preference. Second, given his early asymmetric brain injury, we wondered if LBL would compare to his peers and similarly display fluctuations in hand use as he would learn to crawl and walk. Finally, we were curious to assess whether LBL would show deficits in gross and fine motor control, and whether these deficits would be unilateral (right arm only) or bilateral.

Because it took a few months to obtain human subject approval to study LBL, we consulted the medical reports of his 3- and 6-month examinations in order to gain knowledge about his prior motor assessment history. The 3-month examination reported no obvious sign of hemiparesis. LBL had a moderate head control but was able to fix and follow objects passed midline. He was not reaching or batting at objects. At 6 months of age, LBL was reported to sit alone and able to reach for objects; however, it was noted that he tended to use his left hand more than his right and that he had no fisting on his right hand. LBL was described as a social and interactive infant, who was babbling, had normal muscle bulk and strength throughout the body, and was able to support his body weight with his legs.

When we began to see LBL at 8:3 months, we unexpectedly found that he displayed better control with his right than left arm for a few weeks. Hand differences in control were primarily revealed by the side object presentation conditions. Figure 3 that displays the rate of two-handed responses for side presentations, shows that on his first two visits to our laboratory, LBL was able to reach for the small objects presented to his right side with the right arm alone on most trials (black bars). However, when presented with a small object on his left side, he was always responding with two hands, that is, by crossing midline with his right arm as if he was trying to help his left arm (gray bars). This asymmetrical coactivation response for side presentations declined in the following weeks, which coincided with the time LBL began to crawl on hands-and-knees.

The kinematics recordings also revealed a weaker arm control in reaching during the early weeks compared to what would be produced by infants of his age. Figure 4A displays the average movement speed of the reach by week when the objects were presented on the sides. As shown, LBL's reaches were very slow at the beginning, then, as time passed, he was able to speed up gradually his movement. Figure 4B presents the average number of movement units performed when LBL was reaching for the small objects presented either on the right or left side. Likewise, this figure shows that the number of movement units during reaching was fairly high for both hands, especially during the first weeks of testing where LBL averaged three to four movement units per reach. For the purpose of comparison, previous longitudinal reaching studies on neurologically intact populations reported an average of one to two movement units per reach around that same age range (Thelen et al., 1993; von Hofsten, 1991). As time passed and as LBL increased movement speed, the number of movement units decreased gradually to attain a range close to normal of one to two movement units by Session 24 and beyond. There were no consistent differences between arm performances on these kinematics measures.

Hand preference was better assessed with the midline object presentations. Figure 5 displays the index rate of

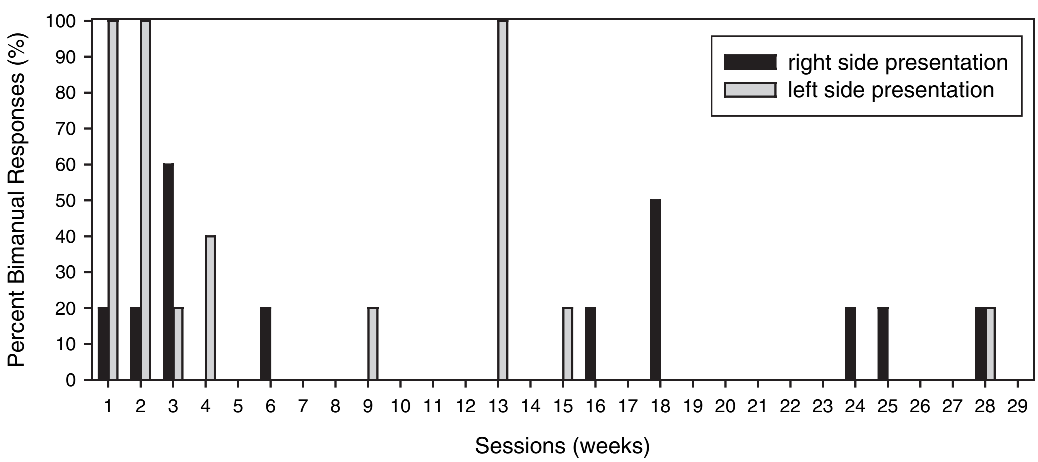

FIGURE 3 Percent of bimanual responses produced by infant LBL when small objects were presented either on his right or left side. When bars are missing, it indicates that during those weeks LBL produced only unimanual (right- or left-handed) responses ipsilateral to the side of the object presentation.

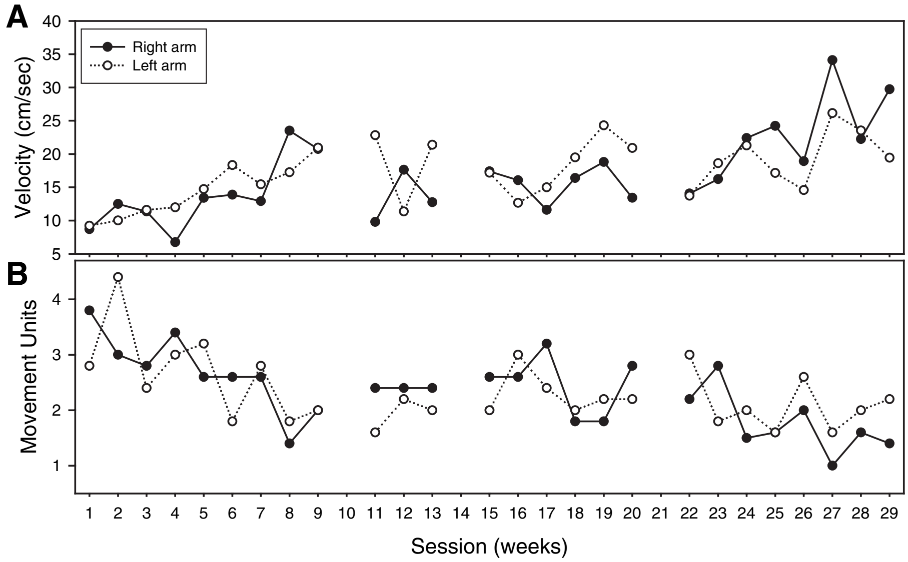

FIGURE 4 Average movement velocity (Graph A) and number of movement units (Graph B) for the right and left arm, respectively when infant LBL was reaching for small objects presented on his right versus left side.

right and left hand use when reaching for small objects at midline from Week 1 to Week 29. This figure also indicates the times at which LBL developed new motor milestones. Figure 5 shows that LBL's gross motor development was not delayed. He acquired all the typical motor milestones that are usually developed by most infants in the first year within the expected age range. Did his hand preference fluctuate as a function of these emerging skills? Figure 5 shows that during the first weeks of the study, when objects were presented at midline and LBL was given a choice in hand use, he preferred to use his right hand for reaching. This preference was consistent with the slight right hand advantage that was revealed by the side presentation conditions. Note, however, that for LBL, the emergence of hands-and-knees crawling on Week 3 did not have an immediate impact on the strength of his preferred hand use. His first significant drop in preferred hand use occurred a few weeks later, between Weeks 6 and 7 when he began cruising while standing along the furniture (Fisher exact test, $p = .048$). Then, from about Week 12 to Week 29, LBL did not display again a consistent strong right hand use for reaching.

His preferred right hand use returned and became clearly evident when we assessed his hand preference

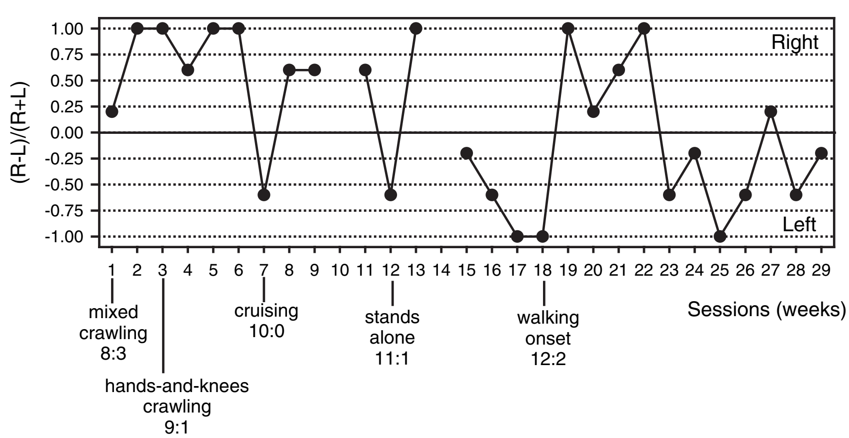

FIGURE 5 Index rate of right- versus left-handed responses for infant LBL when reaching for small objects at midline over the 29-week period of the study. The motor milestones that LBL developed over the course of the study are indicated on the figure with the age of onset.

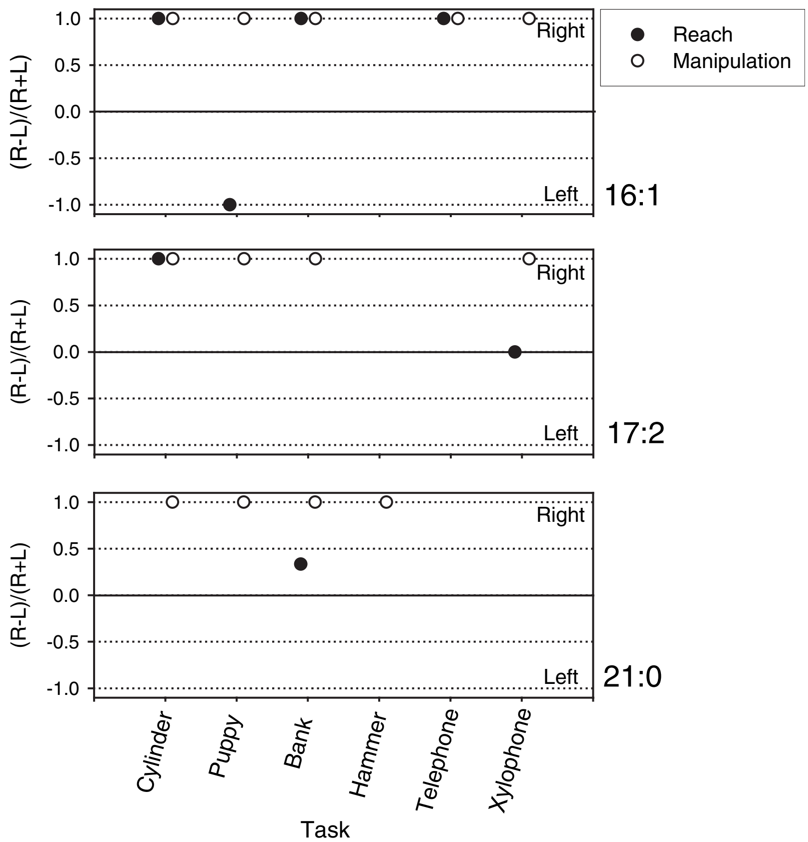

FIGURE 6 Hand preference index for infant LBL in his 2nd year of life as a function of task (reaching versus manipulating) and age of testing.

toward the end of his 2nd year of life. Figure 6 shows that at 16:1, 17:2, and 21:0 months, LBL strongly preferred to use his right hand for reaching for most objects and used his right hand exclusively to manipulate these objects when inserting a shape in the cylinder or a coin in a bank, when feeding the puppy, hammering the pegs, using the phone, or playing the xylophone.

DISCUSSION

The three case studies presented in this report confirmed early findings that hand preference is not a behavioral trait that remains strong or grows steadily over the first year of life. Instead, preferred hand use fluctuates widely between right and left over the weeks and months that are following the onset of voluntary reaching. These data are also consistent with our prior observations that such patterns of fluctuation in hand use are not happening randomly, but rather occur in concert with the postural and locomotor reorganizations that are taking place in the 1st year of life as infants learn to sit, crawl, stand, and walk (Corbetta & Bojczyk, 2002; Corbetta & Thelen, 1999, 2002). The case studies of GD and GC confirmed that it is the patterning of arm use practiced during locomotion that seems to transfer to reaching. GD and GC were studied because they developed unusual forms of locomotion in their first attempts to move in their environment, which gave us the opportunity to assess to which extent patterns of arm movements during reaching would reciprocate patterns of arm movement used during locomotion. We saw that GD, who coupled his limbs during scooting, also began to couple his arms when reaching for the duration he adopted this particular form of locomotion. On the other hand, GC who developed an asymmetrical form of belly crawling, in which he never coupled or alternated arm movements, developed and maintained a steady preferred hand use over the same period. Thus, changes in hand preference in the 1st year of life seem to be linked to the emergence and practice of novel sensory-motor experiences as infants acquire new motor skills.

The story of LBL revealed another aspect of the developmental plasticity of handedness. The study of LBL was particularly interesting because given the site of his brain lesion (left hemisphere, thus more likely to impair the right hand) and his strong family history of left-handedness, one could have easily predicted that LBL would have naturally become left-handed. Recall that LBL displayed twitching movements in his right arm and leg shortly after birth, and his 6-month examination reported no fisting in the right arm and a greater tendency to reach for objects with the left arm than the right. Yet, when LBL began his visits in our laboratory at 8:3 months, he displayed a right hand preference when reaching for small objects at midline, a greater motor proficiency with the right hand when reaching for objects presented on each side, and also displayed a clear and strong right hand preference later in his 2nd year of life when tested with a variety of assessment tasks. What might have triggered the development of this preferred right hand use? Here, we can only speculate about what might have driven the direction of this preference. When we reported our findings to LBL's family, the parents and grandmother immediately referred to the intense sessions of physical therapy that LBL received since the age of 5 weeks to his right arm and leg. Because LBL was at risk for delays in motor development and hemiparesis, the therapists focused primarily on the right side of his body. It is presumable that the sensory-motor stimulations provided to LBL's right arm may have contributed to rehabilitate that arm and helped strengthen its control compared to the left arm. Some research with adult stroke patients certainly supports the notion that rehabilitation therapy can help recover motor functions of the upper extremities, even in the case of hemiparesis (Luft et al., 2004; McCombe-Waller & Whitall, 2005). Note, however, that besides intense physical therapy, LBL still displayed a higher than expected number of movement units for his age in both arms, which denoted some difficulty in movement control. Other kinematics measures, which we did not present here for reason of parsimony, indicated that LBL was able to generate straight trajectories to the toy but had difficulty breaking his movement prior to attaining the target, especially when reaching for the small objects that required some level of movement accuracy. It appeared that the high occurrence of movement units in his reaching movements were the result of this difficulty to perform smooth movement decelerations. Consistent with this interpretation, additional analyses revealed long movement deceleration phases when LBL was reaching for small objects, whereas these decelerations phases were almost absent when LBL was reaching for the large objects. In fact, when accuracy demands were low, LBL tended to bat at the targets. Despite this early difficulty in deceleration, LBL's reaching ability improved over the time we followed him. By the end of the study, around Weeks 24–29, the number of movement units in his reaching movements neared a normal value of one to two and the duration of his deceleration phases began to resemble normal values as well.

In regard to his hand preference, LBL also displayed a decline in preferred hand use in the second half of his first year, similar to infants in previous reports (Corbetta & Thelen, 1999, 2002). This decline in preferred hand use occurred primarily in conjunction with the acquisition of the upright posture. Crawling on hands-and-knees did not quite have an immediate impact on the strength of LBL's preferred hand use as it has been the case of neurologically intact infants (Corbetta & Thelen, 1999, 2002). Here again, we can only speculate about this difference, but it could be possible that the intense exercises and stimulations that LBL received to his right arm have delayed the time at which hand preference responded to the pervasive motor reorganizations induced by the newly emerging locomotor skills.

In conclusion and in agreement with prior reports (Corbetta & Bojczyk, 2002; Corbetta & Thelen, 1999, 2002), the three case studies presented here support the view that hand preference in early development is highly subject to malleability and greatly sensitive to other concomitant developmental changes that are occurring during infants' motor development. Posture and locomotion may not be the only factors altering the development of early hand preference. Similar fluctuations in the strength of hand preference have been documented in relation to the emergence of infant babbling and subsequent milestones of language development (Bates, O'Connell, Vaid, Sledge, & Oakes, 1986; Ramsay, 1984, 1985). Clearly, patterns of hand use in early development interact with the development of other sensory-motor skills. The case of LBL even suggests that hand preference may shift to an impaired arm if given proper sensory-motor stimulation to rehabilitate that arm. From this work, however, one question remains. If hand preference in early development is so sensitive to sensory-motor experiences why does hand preference eventually settle into a preferred and stable lateralized pattern at a later age? In prior work, we have argued that hand preference may begin to show more stability around the 2nd or 3rd year of life because, by then, infants have achieved and overcome most of the important and novel motor transitions that are typical of early development such as learning to walk upright and learning to talk (Corbetta, 2005; Corbetta & Thelen, 2002). After infants have developed the basic requirements for these fundamental motor skills, they do not undergo any more sudden or drastic sensory-motor reorganizations in their development. Those skills, such as locomoting and talking, once they have emerged, continue to fine-tune and improve over time, but these improvements will not necessitate a complete recalibration of the system such as it occurs when infants are attempting to practice those skills for the first time, thus allowing hand preference to settle in a preferred direction. Clearly, further investigations will be needed to provide more support to this interpretation. But also, more investigations will be needed to understand which particular role early sensory-motor experience plays in the establishment of a predominant population right-bias.

NOTES

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