Examining the Development of Handedness in Rhesus Monkey and Human Infants Using Behavioral and Kinematic Measures

EXAMINING THE DEVELOPMENT OF HANDEDNESS IN RHESUS MONKEY AND HUMAN INFANTS USING BEHAVIORAL AND KINEMATIC MEASURES

A Dissertation Presented

by

ELIZA L. NELSON

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Approved as to style and content by:

_____
Neil E. Berthier, Co-Chair

_____
Melinda A. Novak, Co-Chair

_____
Agnès Lacreuse, Member

_____
Duncan J. Irschick, Member

_____
Jerrold S. Meyer, Program Director
Neuroscience and Behavior Program

DEDICATION

For Thelma and Louise who taught me all the best monkey tricks.

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ABSTRACT

EXAMINING THE DEVELOPMENT OF HANDEDNESS IN RHESUS MONKEY AND HUMAN INFANTS USING BEHAVIORAL AND KINEMATIC MEASURES

SEPTEMBER 2010

ELIZA L. NELSON, B.S., BALDWIN-WALLACE COLLEGE

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Neil E. Berthier and Professor Melinda A. Novak

Handedness is a widely studied behavioral asymmetry that is commonly measured as a preference for using one hand over the other. Right hand preference in humans occurs at a ratio of 9:1, whereas left hand preference in rhesus monkeys has been estimated at 2:1. Despite differences in the direction and degree of hand preference, this dissertation investigated whether primates share common underlying factors for the development of handedness. Previous work in human infants has identified a predictive relationship between rightward supine head orientation and later right hand preference. Experiment 1 examined the relationship between neonatal head orientation and later hand use in rhesus monkey infants (N=16). A leftward supine head orientation bias was found that corresponded to greater left hand activity for hand-to-face movements while supine; however, neonatal head positioning did not predict later hand use preference for reaching or manipulation on a coordinated bimanual task. A supine posture is common for human infants, but not for rhesus monkey infants, indicating that differences in early posture experience may differentially shape the development of hand use preference.

Movement quality is an additional factor that may affect how the hands are used in addition to neonatal experience. 2-D and 3-D kinematic analyses were used to examine the quality of reaching movements in rhesus monkey infants (*N*=16), human infants (*N*=73) and human adults (*N*=12). In rhesus monkey infants, left hand reaches were characterized as ballistic as compared to right hand reaches independent of hand use preference (Experiment 2). Left hand ballistic reaching in rhesus monkeys may be a carryover from earlier primates that relied on very fast reaches to capture insect prey. Unlike monkey infants, reach quality was a function of hand preference in human infants (Experiment 3). By contrast, a right hand advantage for reaching was observed in human adults regardless of left or right hand preference (Experiment 4).

Differential hand experience due to hand preference in early infancy may in part be responsible for the hand preference effects on movement quality observed in human infants but not monkey infants. Motor control may become increasingly lateralized to the left hemisphere over human development leading to the right hand advantage for reaching observed in human adults, as well as over primate evolution leading to right hand use preferences in higher primates like chimpanzees. An underlying mechanism such as a right shift factor in humans and a left shift factor in rhesus monkeys may be a common basis for primate handedness. Environmental and experiential factors then differentially shape this mechanism, including species-typical development. Further work examining the ontogeny of hand preference and hemispheric specialization in various primate infants will lead to a greater understanding of how different factors interact in the development of hand use across primate species.

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CHAPTER 1

INTRODUCTION

Handedness is a widely studied behavioral asymmetry that is commonly measured as a preference for using one hand over the other. Hand use preference has been well characterized in adult humans with the majority of individuals favoring the right hand (Annett, 2002). A population-level right hand preference has also been reported for chimpanzees; however, a left hand preference has been found in other primate species including lemurs and rhesus monkeys (Papademetriou, Sheu & Michel, 2005). Phylogenetically, the chimpanzee is the closest primate relative to humans, having diverged from the human lineage approximately 6 million years ago. By contrast, lemurs are some of the oldest extant primates and split from the human line approximately 50 million years ago. Old world monkeys, a group of primates that includes the rhesus monkey, diverged approximately 25 million years ago (Goodman, Grossman & Wildman, 2005). Although the direction of hand bias has changed across the primate order, the fundamental question posed in this dissertation is whether primates share common underlying factors for handedness.

An understanding of the factors that contribute to the development of handedness requires examination of the ontogeny of hand use in both human and nonhuman primate infants. Although a number of factors might affect handedness, this thesis focused on two factors that can be readily measured across species: (1) neonatal biases that may induce later hand use asymmetries and (2) differences in the quality of arm and hand movements that may be related to how the hands are used.

A number of studies have examined neonatal behavior in human infants, but equivalent data in nonhuman primate infants are largely limited to infant chimpanzees (Bard, Hopkins & Fort, 1990; Fagot & Bard, 1995; Hopkins & Bard, 1993; 1995; 2000). Of particular interest is the finding that neonatal right supine head orientation bias predicts later right hand use preference in both human and chimpanzee infants (Hopkins & Bard, 2000; Michel, 1981). Additional work is needed in a species with a known leftward hand bias, such as the rhesus monkey, to determine whether handedness trajectories are similar across primates regardless of hand preference direction. In Experiment 1, supine head orientation bias was measured in 16 nursery-reared rhesus monkey neonates and compared with various measures of hand use preference and other neonatal behaviors (Chapter 2). Because rhesus monkeys are often models for child development, knowledge of the mechanisms of hand use preference is important for further understanding the origins of advanced motor and cognitive skills, such as planning for future movements and using tools.

A longstanding question is why hand use preference changed from left to right across primate phylogeny. A prevalent hypothesis for this change in hand preference direction is the postural origins theory (MacNeilage, Studdert-Kennedy & Lindblom 1987; MacNeilage, 2007). According to this theory, primate hand use preferences are a consequence of environmental demands on feeding strategy and posture. MacNeilage and colleagues proposed that a left hand/right hemispheric bias emerged for prey capture, given that the diet of some of the earliest primates was primarily insects. The left hand was characterized as ballistic in nature because movements to capture moving insects had to be fast. A complimentary role was suggested for the right hand/left hemisphere in

providing postural support while living in an arboreal environment. When primates became more terrestrial, the right hand was freed from postural control and became specialized for motor control, particularly manipulation. Changes in living environment were also accompanied by changes in diet, and increased skill for manipulation allowed primates to access foods that would otherwise be unobtainable. Examples include wild long-tailed macaques who have been reported to open nuts and oysters attached to rocks with various stone tools (Gumert, Kluck & Malaivijitnond, 2009) and chimpanzees who use a number of tools for extractive foraging including blades of grass and twigs to fish for termites and ants (McGrew, 2010).

Hemispheric specialization is a term used to describe particular functions that are lateralized to one side of the brain, such as the right hemisphere (left hand) bias for reaching and the left hemisphere (right hand) bias for manipulation suggested by the postural origins theory. Behavioral evidence from nonhuman primate studies examining hand use on different types of tasks has largely supported these proposed roles for the left and right sides of the brain. A strong left hand preference was reported in black and white ruffed lemurs reaching for food under postural challenge (Forsythe, Milliken, Stafford & Ward, 1988). Moreover, Hopkins and Russell (2004) reported a right hand advantage in chimpanzees such that the right hand was found to make fewer errors gripping a small food item compared to the left hand. Although differences have been found for quality of fine motor skill, one limitation of previous work is that there have been no similar studies examining the quality of reaching movements to determine if the properties of left hand reaching are different from that of right hand reaching.

The left hand use preference noted for rhesus monkeys was largely based on studies of reaching (Papademetriou et al., 2005), and may be a carryover effect from a left hand specialization for ballistic prey capture in earlier primates. In Experiment 2, quality of reaching was examined in developing rhesus monkey infants (*N*=16) using two-dimensional (2-D) motion capture analyses (Chapter 2). Data were collected from the left and right hands on separate trials. Individual hand use preferences were determined from a prior reaching task and included as a factor in the statistical analyses. I hypothesized that reach quality would differ by hand, and predicted that the left hand would have ballistic characteristics. Differences in reach quality could also be the result of hand preference, and I made an alternative prediction that the preferred hand would have greater motor control compared to the non-preferred hand. To the best of my knowledge, these data represent the first report of motion analysis for hand use in any infant nonhuman primate, and are also the first direct test of movement quality differences between the left and right hands as well as the preferred and non-preferred hands in a nonhuman primate species.

Patterns of hemispheric specialization in humans are similar to those proposed for nonhuman primates. In adults, motor control has often been attributed to the left hemisphere (right hand), whereas the right hemisphere (left hand) is thought to be dominant for spatial and proprioceptive information processing (for reviews, see Serrien, Ivry & Swinnen, 2006; Goble & Brown, 2008). In addition, speech is lateralized to the left hemisphere in the majority of adults (Provins, 1997). One of the most prevalent explanations of human handedness is the right shift (RS) theory, which suggests that the left hemispheric specialization for speech mediates right hand preference (Annett, 1985;

2002). According to the right shift theory, a single allele (RS) confers left cerebral dominance. Individuals that are RS+ have speech lateralized to the left hemisphere and develop a right hand preference. Individuals that are RS- develop both speech cerebral dominance and handedness by chance. Other genetic models for human handedness have incorporated similar ideas (McManus, 1985; Corballis, 2009; Crow, 2010).

The right shift theory raises important questions regarding the nature of the relationship between hemispheric specialization and hand use preference, and whether cerebral dominance develops dependently or independently of hand dominance. Hand preference in human infants has often been characterized as dynamic, due to fluctuations in hand use within individuals in longitudinal studies; however, a right bias predominates in infancy across measures (Gesell & Ames, 1947; Corbetta & Thelen, 1999; Chapter 3). Previous studies that have examined reaching quality in infants have not taken individual infants' hand use preferences under consideration (Morange-Majoux et al., 2000; Hopkins & Rönnqvist, 2002; Rönnqvist & Domellöf, 2006). Studies are needed that analyze hand movements both in terms of left versus right hands and preferred versus non-preferred hands in infancy to further understand the relationship between cerebral dominance and hand dominance in development.

In Experiment 3, quality of reaching was examined in human infants (N=73) using three-dimensional (3-D) motion capture analyses (Chapter 3). Infants were examined when they were 11-months, 14-months, or 17-months-of-age. Data were collected from the left and right hands on separate trials for two different reaching tasks. Individual hand use preferences were determined from play and included as a factor in the statistical analyses along with gender and age group. I hypothesized that reach quality

would vary with hand preference, and predicted that the preferred hand would have characteristics indicating greater motor control than the non-preferred hand. Then again, any differences in reach quality could be the result of inherent differences between the left and right hands. I made an alternative prediction that the right hand would have greater motor control than the left hand, suggesting a left hemispheric bias that matches prevailing ideas of a right hand/left hemispheric specialization for controlling movement in adults. These predictions are not necessarily mutually exclusive, because the preferred hand for most infants will be the right. Nevertheless, this study was the first to examine qualitative differences between the hands in infancy as a function of hand preference, hand specialization, or some combination of both. Another important contribution was to measure movement quality in infants over the second year of life for the first time.

Finally, a control group of adults (*N*=12) was tested on the human infant reaching tasks in Experiment 4 to compare hand, hand preference, and hand-by-hand preference interactions in individuals with stable hand use preferences as opposed to infants who may have fluid hand use preferences (Chapter 3). Equal numbers of left- and right-preferent adults were tested, and data were collected from both the preferred and non-preferred hands. Previous studies have shown that adults are more proficient with their preferred hand on tasks involving fine motor skill (Steenhuis & Bryden, 1999; Corey, Hurley & Foundas, 2001; Annett, 2002; Judge & Stirling, 2003). I predicted that the preferred hand would outperform the non-preferred hand on the grasping elements of each task. Although kinematic studies have compared the left and right arms in right-preferent adults, there are no equivalent data comparing arm movements in left-preferent adults (Sainburg & Kalakanis, 2000; Bagesteiro & Sainburg, 2002; Grosskopf & Kuhtz-

Buschbeck, 2006; Wang & Sainburg, 2007). Consequently, a major contribution of this study was to examine movement quality differences between arms in left-preferent adults, as they may show a different pattern of hemispheric specialization than their right-preferent counterparts. Overall, the same predictions were made for adults that were made for human infants, with one prediction specifying a preferred arm advantage and an alternative prediction specifying a right arm advantage for reach quality.

In general, lateralization offers a number of potential advantages for both the individual and the group. Localizing functions to a particular cerebral hemisphere could increase efficiency and reduce redundancy in information processing. Behavioral asymmetries such as hand use are also advantageous in that they allow for a predetermined response, further saving processing time, and may also allow for one side of the body to become increasingly more skillful (Vallortigara & Rogers, 2005; MacNeilage, 2007; Hopkins & Cantalupo, 2008). Finally, lateralization may be an evolutionary stable strategy when it occurs at the population-level (Vallortigara, 2006).

Kinematic analyses can be a tool for examining effects of hand, hand preference and hand-by-hand preference interactions on movement quality to further understand how and why the hands are used in human and nonhuman primates. Both movement quality as well as relationships between neonatal behavioral asymmetries and hand use may help shape a trajectory for handedness in rhesus monkey and human infants. Ultimately, handedness may arise from a multifaceted gene by environment interaction. By studying the ontogeny of handedness in two different primate models, rhesus monkey infants and human infants, I hope to contribute to a greater understanding of factors that may in part be responsible for primate handedness.

CHAPTER 2

HANDEDNESS IN RHESUS MONKEY INFANTS

Humans are widely considered to be right-handed, with at least 90% of the adult population preferring to use the right hand (Annett, 2002). A right hand use bias has also been reported for human infants (e.g., Michel, Ovrut & Harkins, 1985; Michel, Tyler, Ferre & Sheu, 2006); however, many questions remain regarding the developmental trajectory of handedness. The origins of hand preference may include other lateralized behaviors present early in life that precede hand use. One of the earliest behavioral asymmetries observed in human infants is a bias in neonatal head orientation. The majority of infants preferentially turn their head to the right while in a supine position, a phenomenon that has been well documented under both observational (e.g., Turkewitz, Gordon & Birch, 1965) and experimental (e.g., Coryell & Michel, 1978) conditions. Infants do not show this robust rightward head preference while prone, and supine head positioning does not correspond to prone head positioning (Michel & Goodwin, 1979). Strikingly, Michel (1981) reported that neonatal supine head orientation preference predicts later hand use preference for reaching.

An early head positioning bias may induce other biases. Coryell and Michel (1978) hypothesized that a head turning asymmetry could create asymmetric visual regard of one hand, thereby linking neonatal head bias to a preference for using the hand that was viewed more prior to the onset of reaching and manipulation. They observed awake human infants across the first 12 weeks of life, noting supine head preference and the presence of the left or right hand in the infant's visual field. Infants with a right

supine head bias viewed their right hand more and likewise infants with a left supine head bias viewed their left hand more. Furthermore, the amount of hand viewing experience corresponded to hand preference for reaching at 12 weeks of age. Michel and Harkins (1986) further demonstrated greater activity in the hand corresponding to the side of supine head bias. Infants with a right head bias moved their right hand more and infants with a left head bias moved their left hand more. In a study of spontaneous arm movements in supine neonates, van der Meer, van der Weel, and Lee (1995) found that infants tend to move the hand that they can see, further linking supine head positioning, visual regard, and hand activity.

Like human infants, evidence from chimpanzee infants also suggests that neonatal supine head orientation is an early predictor of hand preference. Hopkins and Bard (1995) noted the head position of nursery-reared infant chimpanzees *(Pan troglodytes)* during sleep over the first three months of life. A rightward bias was found when chimpanzees were resting in a supine position, but no bias was observed when chimpanzees were in a prone position. Hopkins and Bard (2000) extended this work by showing that neonatal right supine head orientation bias corresponded to juvenile right hand use preference on a bimanual task given to subjects when they were 2 to 5 years old. Neither hand activity nor visual hand regard while chimpanzees were supine was quantified. Nevertheless, the predictive relationship between neonatal supine head preference and later hand use preference in both human and chimpanzee infants suggests that the factors underlying a trajectory for handedness may be similar in humans and chimpanzees.

In contrast to the pattern of rightward bias observed in humans and chimpanzees, a left hand bias has been reported in evolutionarily older primate species such as lemurs

and rhesus monkeys (for review, see Papademetriou, Sheu & Michel, 2005). An outstanding question is whether head positioning and hand use preferences are related in nonhuman primates that show a leftward pattern of asymmetries. Although not developmental in nature, Nelson, O'Karma, Ruperti and Novak (2009) found a relationship between left head positioning and left hand preference during feeding in adult black and white ruffed lemurs *(Varecia variegata variegata)*. Westergaard, Byrne and Suomi (1998) failed to find a group-level head bias in capuchin monkey infants *(Cebus apella)*. However, head bias was measured only as the infant straddled the mother's back in a prone position. Capuchins showed a group-level left hand bias later in development, but direction of prone head orientation did not predict later direction of hand preference.

At present, there are no data on supine head orientation for any monkey species. Furthermore, head orientation has not been assessed experimentally in any nonhuman primate infant, as previous studies have only observed spontaneous head turning. An important contribution of the present study was to experimentally measure supine head turning in rhesus monkey infants *(Macaca mulatta)*, as well as to compare supine and prone head preferences in monkeys for the first time. Another contribution of this work was to determine whether neonatal head orientation preferences correspond to later hand use preferences in rhesus monkeys observed longitudinally from birth to late infancy.

Experiment 1: Neonatal Biases and Handedness Trajectory in Monkey Infants

Prone and supine head orientation biases were assessed when rhesus monkeys were neonates, and hand use was measured for three different activities: hand-to-face

contacts while supine, unimanual reaching to objects, and manipulation on a coordinated bimanual task. Data from neonatal developmental assessments that measured responses on both sides of the body were also examined. I expected to find a supine, but not prone, head orientation bias given previous work in human, chimpanzee, and capuchin infants. Furthermore, I predicted that any head bias would be leftward, based on previous reports of a left hand preference for rhesus monkeys. If rhesus monkey infants have a supine head bias, I expected to observe greater activity in the hand that could be directly observed by the infant (ipsilateral to the head turn) as measured by the number of hand-to-face contacts. Finally, if factors that underlie handedness are similar across primates despite differences in the direction of preference, I also predicted that head orientation bias would correspond to later hand use for reaching as well as hand use for manipulation.

Method

Subjects

Subjects were 16 healthy, full-term infant rhesus macaques *(Macaca mulatta)* housed at the Laboratory for Comparative Ethology (LCE), Eunice Kennedy Shriver National Institutes of Child Health and Human Development (NICHD) in Poolesville, Maryland. Subjects were born between May and August 2009, and there were equal numbers of males and females. Infants were surrogate peer-reared according to standard LCE procedures described by Ruppenthal (1979) and Shannon, Champoux, and Suomi (1998) as part of a larger protocol unrelated to the current study. Briefly, infants were separated from their mother 24 to 72 hours after birth. Infants were then placed in a

plastic incubator and given an inanimate fleece surrogate for the first 15 days of life. After this period, infants and their surrogates were moved to individual wire mesh cages. Social groups consisting of four infants were formed as early as 37 days of age. Infants continued to live in individual cages, but were now given 2 hours of peer contact per day with their social group.

Infants were bottle-fed by human caregivers until they were able to feed independently, which was typically around 1 week of age (Dettmer, personal communication). During bottle-feeding, infants were held in a vertical position with either the back facing the caregiver or in ventral-ventral contact with the caregiver, depending on individual preferences. Importantly, infants were not cradled in either a prone or supine position by the human caregivers during feeding. Infants received a 50:50 mixture of Similac (Ross Laboratories, Columbus, OH) and Primilac (Bio-Serv, Frenchtown, NJ) formulas from birth. Beginning at 1 month of age, infants were given unlimited monkey chow (Purina High Protein #5038) and water. Bottle weaning began at 4 months of age and at 6 months infants were eating only solid food. Infants were followed from birth to late infancy and tested individually on the measures described below. The following procedures were approved by the NICHD Animal Care and Use Committee.

Primate Neonatal Neurobehavioral Assessment (PNNA)

All monkeys were administered the Primate Neonatal Neurobehavioral Assessment (PNNA; Schneider, Champoux, & Moore, 2006, **Appendix A**) on days 7, 14, 21, and 30 by experimenters trained to 90% inter-rater agreement. The PNNA is a 20-

minute battery of developmental tests and includes items in four clusters: orientation, motor maturity, activity, and state control. Of particular interest to the current study were four components of the PNNA that measured responses on both sides of the body, as I were interested in whether one side of the body responded differentially to stimulation. These components were the palmar grasp, plantar grasp, tactile reflex, and orient to auditory.

For palmar grasp, an experimenter moved a finger down the monkey's hand starting at the wrist. Monkeys were given a 0 if no grasp was made, 1 if a weak grasp was made with the digits closed loosely, and 2 if a strong grasp was made with the digits closed tightly. Half scores were possible, and both the left and right hands were tested during each session. Plantar grasp was elicited by an experimenter moving a finger down the length of the monkey's foot starting at the heel. Plantar grasp was rated in the same manner as palmar grasp, and both feet were tested during each assessment.

To measure tactile reflex, an experimenter drew a capped pen down the midline of each of the monkey's limbs, starting from the shoulder or hip and proceeding down to the wrist or ankle. Monkeys were given a 0 for no jerk reflex response, 1 for a slight jerk reflex response, and 2 for a definite or exaggerated jerk reflex response with half scores possible. The left and right arms as well as the left and right legs were tested at each assessment. Finally, an experimenter swaddled the monkey vertically with one side facing the tester for the orient to auditory measure and then made smacking noises with his or her mouth. The sound was repeated with the monkey facing the other direction. The monkey's response was scored as 0 for no orient to the sound, 1 for a partial orient to

the sound, and 2 for a full orient with visual inspection to the sound with half scores possible.

Head Orientation Measures

Supine Head Orientation

Supine head orientation preference was assessed experimentally. The procedure was modified from an established protocol used with human infants (Michel, 1981). In this procedure, monkeys received four trials per test session, with one test session occurring on days 1, 3, 7, 14, 21, and 30 ± 1 day (six sessions total). The infant was placed supine in the experimenter's lap for the procedure (**Figure 2.1**). The experimenter gently restrained the infant throughout testing by placing his or her hand on the infant's chest. A camera was mounted overhead in view of the infant's chest and head, and all trials were videotaped.

At the start of a trial, the experimenter held the infant's head in a fixed position (left, midline, or right) for 15 seconds. For the left position, the infant's head was held such that the left ear was touching the testing surface. For the midline position, the infant's head was held even and parallel to the testing surface. For the right position, the infant's head was held such that the right ear was touching the testing surface. The head was released on a cue from a second experimenter and the infant's subsequent head movements were followed via videotape for 30 seconds. A timer was used to ensure standard timing across infants and test sessions. The first and last trials in each session were midline trials and the middle two trials were randomized left or right.

The infant's head position was scored from the videotape as left, midline, or right using a point sampling method with 3-second intervals, resulting in a total of ten data points per trial per infant. Head positions were operationally defined by the position of the chin in reference to the right angle created by the throat and shoulder. For a left head position, the chin had to be turned greater than 45° towards the infant's left shoulder. For a right head position, the chin had to be turned greater than 45° towards the infant's right shoulder. When the chin was turned less than 45° towards either shoulder, the position of the head was scored as midline. In total, 240 data points were collected per infant (40 per test day x 6 days).

Prone Head Orientation

Monkeys' natural head positioning during sleep and rest was also recorded. These observational data reflect the monkeys' prone head positioning preference, as rhesus infants do not sleep in a supine posture. The observational procedure was modified from a measure previously used with infant chimpanzees (Hopkins & Bard, 1995). Observations were taken on each infant for its first 30 days of life, allowing direct comparisons to the experimental measure of supine head orientation that also ended on day 30. Infants at the LCE are fed at 2-hour intervals from 0800 to 2000 for the first month of life for a total of 7 feedings per day. Experimenters noted the infant's head position (left, right, or midline) if the infant was resting or sleeping in a prone posture prior to feeding (**Figure 2.2**). The right side of the face touched the surface for a left head turn and the left side of the face touched the surface for a right head turn. Any other prone head position was scored as midline. If the infant was sleeping, but positioned on

its surrogate, the experimenter did not record head position. Likewise, head orientation was also not recorded if the infant was sleeping entirely on its left or right side (a rare occurrence) or if the infant was active prior to feeding. In total, 210 observations were collected on each infant (7 per day x 30 days).

Figure 2.1. 14-day-old infant making a left head turn while supine.

Figure 2.2. Infant making a right head turn while prone.

Hand Preference Measures

Supine Hand-to-Face Contacts

Hand use for hand-to-face movements during supine head orientation testing was examined from videotape. A hand-to-face contact was defined as any portion of the hand touching any portion of the face (**Figure 2.3**). Instances where a head movement resulted in the face coming into contact with a hand were excluded. Only movements during the observation period of each supine head trial where the monkey spontaneously oriented its head were analyzed. Hand-to-face contacts that occurred when the head was being held in a fixed position at the beginning of each trial were excluded. Hand-to-face contacts were scored in frequency of left, right, or bimanual hand use.

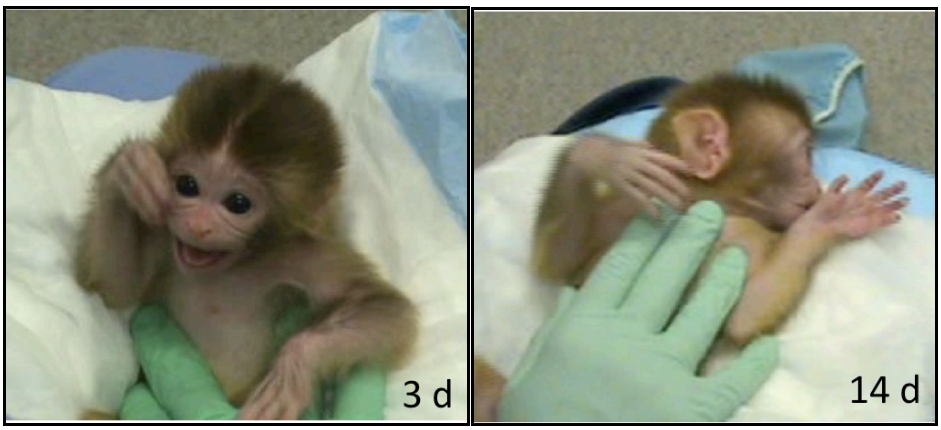

Figure 2.3. Left: 3-day-old infant touching its face with the right hand. Right: 14-day-old infant touching its face with the left hand.

Reaching to Objects

Hand use preferences for reaching to objects was examined when monkeys were between 14 and 44 days of age. This age was chosen because it corresponds to the onset of successful goal-directed reaching (i.e., ability to contact and grasp an object) in infant

rhesus monkeys. In this task, monkeys were held by an experimenter and presented with a toy object placed at the monkey's midline on a testing table (**Figure 2.4**). The toy was partially dipped in food (e.g., applesauce) to increase the monkey's motivation to reach for the object. Monkeys were given three to five trials per test day and were tested three times per week over this age range. All sessions were videotaped for later analysis. Only trials where the infant successful reached to and obtained the toy were scored for frequency of left, right or bimanual hand use.

Figure 2.4. 1-month-old infant reaching for a toy with the left hand.

Coordinated Bimanual TUBE Task

Monkeys were given the coordinated bimanual TUBE task (Hopkins, 1995; Bennett, Suomi & Hopkins, 2008) when they were 6 to 9 months of age (mean age=7.75 months). In this task, monkeys were given a single poly-vinyl-chloride (PVC) tube measuring approximately 23 cm in length and 2.5 cm in diameter containing peanut butter and banana mash. The food was smeared on the inside of one end of the tube, and the monkey was required to place one or more fingers inside the tube to retrieve the food.

The tube was presented through an opening in the monkey's enclosure at the monkey's midline **(Figure 2.5**). An experimenter held the opposite end of the tube, a modification to the original task because infants showed some difficulty in handling the tube without assistance. Nevertheless, monkeys still used one hand to retrieve the food and the opposite hand to stabilize the tube, creating a coordinated bimanual action. This task measured hand preference from frequency of hand use. Each entry into the tube where the hand was then brought to the mouth was scored as left or right. Hand entries that did not result in food being brought to the mouth were not scored. Monkeys were tested individually over two non-consecutive days. The first 15 responses in each session were counted, resulting in 30 data points per monkey on this measure. Hand use was scored in real-time by a second experimenter.

Figure 2.5. 7-month-old infant performing the TUBE task. The infant stabilized the tube with the left hand and used the right hand to retrieve the food.

Data Analysis

For the PNNA assessment, scores for the left and right sides of the body were summed separately for the palmar reflex, plantar reflex, arm tactile reflex, leg tactile

reflex, and orient to auditory. The minimum score a monkey could receive for each side of the body was 0 and the maximum score was 8. A difference score (DS) was computed by subtracting the left side total from the right side total, $DS=R-L$. Individual monkeys with a negative DS value were classified as having a greater response on the left side, monkeys with a positive DS value were classified as having a greater response on the right side, and monkeys with a DS value of 0 were classified as having an equal response on both sides. Chi-squared goodness-of-fit tests using exact probabilities (Radlow & Alf, 1975) were performed to assess whether DS distributions differed from an unbiased hypothetical distribution of 25% left bias, 25% right bias, and 50% no bias as defined by Annett (2006). Independent-samples t-tests were used to examine sex differences in DS values.

Head turn and hand use preferences were characterized with Laterality Indexes (LI). The LI was calculated by subtracting the number of left responses from the number of right responses and then dividing by the total number of left and right responses summed across all observations, $LI=R-L/R+L$. LI scores were calculated separately for each monkey on each measure (supine head orientation, prone head orientation, hand-to-face contacts, reaching, and the coordinated bimanual TUBE task). Scores range along a continuum of -1.00 (exclusively left responses) to 1.00 (exclusively right responses). One-sample t-tests with a test value of 0 were performed on LI scores to test for group-level biases. The absolute value of each LI score was computed to assess the degree of lateralization bias with numbers closer to 0 indicating weak lateralization and numbers closer to 1.00 indicating strong lateralization. Independent-samples t-tests were used to examine sex differences in the direction and degree of bias for LI scores. Pearson

correlations were used to determine whether the direction of bias was related across measures. Finally, LI scores for hand use were regressed onto LI scores for head orientation to determine whether neonatal head biases were predictive of later hand biases.

Results

PNNA

A Difference Score (DS) was computed for each of the target behaviors measured over the first month of life in the PNNA assessments. DS values for all of the behaviors are given in **Table 2.1**. Palmar grasp DS values ranged from -3.00 to 1.00 (M=-0.41, SD=1.11). Individually, 7 monkeys showed a greater palmar grasp response in the left hand, 5 monkeys showed a greater response in the right hand, and 4 monkeys were equally responsive in both hands. This distribution of palmar grasp scores did not differ from an unbiased distribution, χ^2=4.50, *df*=2, *P*>0.05. For plantar grasp, DS values ranged from -1.50 to 1.00 (M=-0.16, SD=0.70). The distribution of individual preferences was not lateralized, χ^2=2.38, *df*=2, *P*>0.05, with 6 infants showing a greater reflex response in the left foot, 5 infants showing a greater reflex response in the right foot, and 5 infants showing no difference between feet. Palmar grasp and plantar grasp DS values were not correlated, *r*=0.127, *P*>0.05.

Tactile reflex DS values for the arms ranged from -2.00 to 1.50 (M=-0.31, SD=0.79) and tactile reflex DS values for the legs ranged from -2.00 to 1.00 (M=-0.44, SD=0.89). A left bias was found for both tactile arm reflex, χ^2=8.50, *df*=2, *P*<0.05, and tactile leg reflex, χ^2=9.38, *df*=2, *P*<0.01. Individually, 9 monkeys showed a greater

response to left arm tactile stimulation, 3 monkeys showed a greater response to right arm tactile stimulation, and 4 monkeys had an equal response to tactile stimulation in both arms. Similarly, 9 monkeys showed a greater response to left leg tactile stimulation, 4 monkeys showed a greater response to right leg tactile stimulation, and 3 monkeys had an equal response to tactile stimulation in both legs. Arm and leg DS scores were not related however, r=0.194, P>0.05.

Table 2.1. Difference Score (DS) values by subject and sex for palmar grasp, plantar grasp, tactile arm response, tactile leg response, and orient to auditory components of the PNNA.

Subject	Palmar	Plantar	Arm	Leg	Auditory
Males					
ZH30	1.00	-0.50	1.50	0.00	1.00
ZH32	0.00	0.00	0.00	0.50	-1.00
ZH37	0.50	0.00	-0.50	-1.00	0.00
ZH39	0.00	0.00	-0.50	-2.00	0.00
ZH50	-0.50	-1.00	-0.50	0.00	2.00
ZH52	-3.00	-0.50	0.00	-0.50	0.00
ZH58	-1.50	-1.00	0.50	0.50	1.00
ZH60	-1.00	1.00	-0.50	0.00	0.00
Females					
ZH35	-1.00	-1.00	0.50	1.00	0.00
ZH36	0.00	0.00	-2.00	-0.50	-0.50
ZH38	-2.00	0.00	-1.00	-0.50	0.00
ZH43	1.00	0.50	0.00	-1.50	0.00
ZH48	0.50	-1.50	-1.00	-0.50	-0.50
ZH49	0.00	0.50	-1.00	0.50	0.00
ZH57	-1.00	0.50	-0.50	-1.00	0.00
ZH59	0.50	0.50	0.00	-2.00	1.50

Calculated with the formula $DS=R-L$, where DS=Difference Score, R=Total right side response, L=Total left side response. Positive values indicate a greater response on the right side, negative values indicate a greater response on the left side, and a score of 0 indicates equal responding on both sides of the body. PNNA=Primate Neonatal Neurobehavioral Assessment.

Orient to auditory DS values ranged from -1.00 to 2.00 (M=0.22, SD=0.77). This distribution of scores was not biased, χ^2=0.38, df=2, P>0.05, with 3 monkeys rated as

having a greater orient response to auditory stimuli presented on the left side, 4 monkeys rated as having a greater orient response to auditory stimuli presented on the right side, and 9 monkeys rated as orienting to auditory stimuli presented on both sides equally. Independent samples t-tests did not find sex differences for any of the target measures ($P>0.05$). Pearson correlations did not reveal any significant relationships between DS values ($P>0.05$).

Table 2.2. Head orientation biases by subject and sex for supine and prone postures.

Subject	Supine	Prone	Subject	Supine	Prone
Males			*Females*		
ZH30	-0.66	-0.11	ZH35	-0.01	-0.04
ZH32	-0.10	-0.11	ZH36	-0.15	-0.64
ZH37	-0.26	-0.49	ZH38	0.07	0.07
ZH39	-0.40	0.04	ZH43	-0.43	0.08
ZH50	-0.15	0.09	ZH48	-0.27	-0.07
ZH52	-0.19	-0.14	ZH49	-0.16	0.19
ZH58	0.37	0.22	ZH57	-0.11	-0.11
ZH60	-0.37	0.10	ZH59	-0.20	-0.17

Calculated with the formula $LI=R-L/R+L$, where LI = Laterality Index, R=Right response, L=Left response. Positive scores indicate a right bias and negative scores indicate a left bias.

Head Orientation

A Laterality Index (LI) was computed for each head orientation posture measured over the first month of life. Data for each head orientation measure are plotted in **Figure 2.6**. Supine head orientation LI scores across trials ranged from -0.66 to 0.37 (M=-0.19, SD=0.23, **Table 2.2**). A one-sample t-test revealed a population-level left bias for supine head orientation, $t(15)=-3.272$, $P<0.01$. Degree of supine head turning lateralization was measured by taking the absolute value of LI scores (ABS-LI). Supine ABS-LI scores ranged from 0.01 to 0.66 (M=0.24, SD=0.17). There was no difference between males

and females for either direction of supine head orientation bias, $t(14)=-0.529$, $P>0.05$, or degree of supine head orientation lateralization, $t(14)=1.759$, $P>0.05$.

Supine head orientation preferences were further examined by trial type to determine whether the initial 15-sec holding period influenced subsequent head positioning. For midline trials, LI scores ranged from -0.62 to 0.36 (M=-0.21, SD=0.25). A population-level left bias was found for head positioning following midline trials, $t(15)=-3.346$, $P<0.01$. On trials where the head was held in a leftward position and then released, LI scores ranged from -0.94 to 0.38 (M=-0.24, SD=0.37). A left head bias was also found for the group following left trials, $t(15)=-2.499$, $P<0.05$. On trials where the head was held in a rightward position and then released, LI scores ranged from -0.54 to 0.77 (M=-0.10, SD=0.37). Although the group mean was leftward, no head bias was found following right trials, $t(15)=-1.048$, $P>0.05$.

Prone head orientation LI scores ranged from -0.64 to 0.22 (M=-0.07, SD=0.23, **Table 2.2**). There was no population-level bias for prone head turning preference, $t(15)=-1.193$, $P>0.05$. Prone ABS-LI scores ranged from 0.04 to 0.64 (M=0.17, SD=0.17). There was no difference between males and females for direction of prone head orientation bias, $t(14)=0.308$, $P>0.05$, or degree of prone head orientation lateralization, $t(14)=-0.102$, $P>0.05$. Direction of head orientation bias was not correlated across the two head orientation postures, $r=0.188$, $P>0.05$.

Hand Preference

A Laterality Index (LI) was computed for each hand use measure. Data for each hand use task are plotted in **Figure 2.6**. For hand-to-face contacts, there were 831

unimanual movements (M=52, SD=18) and 51 bimanual movements (M=3, SD=3). Due to the small number of bimanual hand-to-face contacts, only unimanual hand-to-face movements were analyzed. LI scores for unimanual hand-to-face contacts ranged from -0.59 to 0.18 (M=-0.18, SD=0.24, **Table 2.3**). A one-sample t-test revealed a group-level left hand bias, $t(15)=-3.008$, $P<0.01$. The degree of lateralization for unimanual hand-to-face movements as determined by the absolute value of LI scores ranged from 0.02 to 0.59 (M=0.25, SD=0.17). Male and female infant monkeys did not differ on direction of hand use preference, $t(14)=-0.089$, $P>0.05$, or degree of hand use preference, $t(14)=0.562$, $P>0.05$, for unimanual hand-to-face contacts.

Hand use data for reaching were collected when monkeys were between 14 to 44 days of age. Monkeys were given 63 ± 3 trials on average, and successfully reached for and obtained the toy on 28 ± 10 trials on average. Of these successful reaches, 343 were unimanual responses (M=21, SD=7) and 106 were bimanual responses (M=7, SD=4). The onset of successful reaching was 23 ± 5 days. Due to the small number of bimanual reaches for each monkey, only unimanual reaches were analyzed. LI scores for unimanual reaching varied from -1.00 (exclusively left hand use) to 0.55 (moderate right hand use). Individual LI scores are given in **Table 2.3**. No bias was found at the group-level, $t(15)=-1.580$, $P>0.05$, M=-0.18, SD=0.47. The degree of lateralization for unimanual reaching varied from 0.00 to 1.00 (M=0.39, SD=0.30). No sex differences were found for direction of hand use preference for unimanual reaching, $t(14)=-0.589$, $P>0.05$, or degree of hand use preference for unimanual reaching, $t(14)=-0.456$, $P>0.05$. Hand use for unimanual reaching was not correlated with hand use for unimanual hand-to-face contacts, r=-0.081, $P>0.05$.

Hand use for the coordinated bimanual TUBE task was collected when monkeys were 6 to 9 months old. The average age was 233 ± 22 days. The hand retrieving the food from the tube was recorded as left or right. Hand use for the TUBE task showed the greatest range of any of the measures, with LI scores that varied from -1.00 to 0.80 (M=-0.02, SD=0.57, **Table 2.3**). There was no group-level hand bias for the TUBE task, $t(15)=-0.110$, $P>0.05$. The degree of hand preference lateralization for the TUBE task varied from 0.00 to 1.00 (M=0.45, SD=0.33). Males and females did not differ in direction of hand preference, $t(14)=-0.336$, $P>0.05$, or degree of hand preference, $t(14)=-0.775$, $P>0.05$, for the coordinated bimanual task. Hand use on the TUBE task was not correlated with hand use for unimanual neonatal hand-to-face movements, r=-0.214, $P>0.05$, or hand use for unimanual reaching at 1 month of age, r=-0.223, $P>0.05$.

Table 2.3. Hand use preferences by subject and sex for hand-to-face contacts, reaching, and the coordinated bimanual TUBE task.

Subject	HFace	Reach	TUBE	Subject	HFace	Reach	TUBE
Males				*Females*			
ZH30	-0.30	-0.67	0.33	ZH35	0.07	-0.31	0.80
ZH32	0.18	0.14	-0.93	ZH36	0.12	0.00	-0.40
ZH37	-0.35	-0.08	0.00	ZH38	-0.05	-1.00	0.80
ZH39	-0.28	-0.43	0.22	ZH43	-0.42	-0.44	0.00
ZH50	-0.20	-1.00	-0.41	ZH48	-0.56	0.55	-0.13
ZH52	-0.13	-0.18	0.74	ZH49	-0.02	-0.41	-1.00
ZH58	0.16	0.27	-0.40	ZH57	-0.24	0.28	-0.40
ZH60	-0.59	-0.08	-0.07	ZH59	-0.32	0.42	0.60

Calculated with the formula $LI=R-L/R+L$, where LI = Laterality Index, R=Right response, L=Left response. Positive scores indicate a right bias and negative scores indicate a left bias.

Does Direction of Head Bias Predict Direction of Hand Bias?

A linear regression analysis found that direction of supine head orientation bias predicted direction of hand use preference for hand-to-face contacts, $F(1,14)=11.450$,

$P<0.01$, $R^2=0.45$ (**Figure 2.7**). Supine head bias and hand-to-face movements were positively correlated, such that the greater the leftward supine head bias, the greater the left hand use bias for hand-to-face movements. Direction of supine head turning preference however did not predict direction of hand use preference for reaching at 1 month of age, $F(1,14)=0.519$, $P>0.05$, $R^2=0.04$, or hand use preference on the coordinated bimanual TUBE task at 6 to 9 months of age, $F(1,14)=0.200$, $P>0.05$, $R^2=0.01$. Direction of prone head orientation preference did not predict direction of hand preference for any of the hand use measures (hand-to-face contacts: $F(1,14)=0.051$, $P>0.05$, $R^2<0.01$; reaching: $F(1,14)=1.183$, $P>0.05$, $R^2=0.08$; coordinated bimanual TUBE task, $F(1,14)=0.069$, $P>0.05$, $R^2<0.01$).

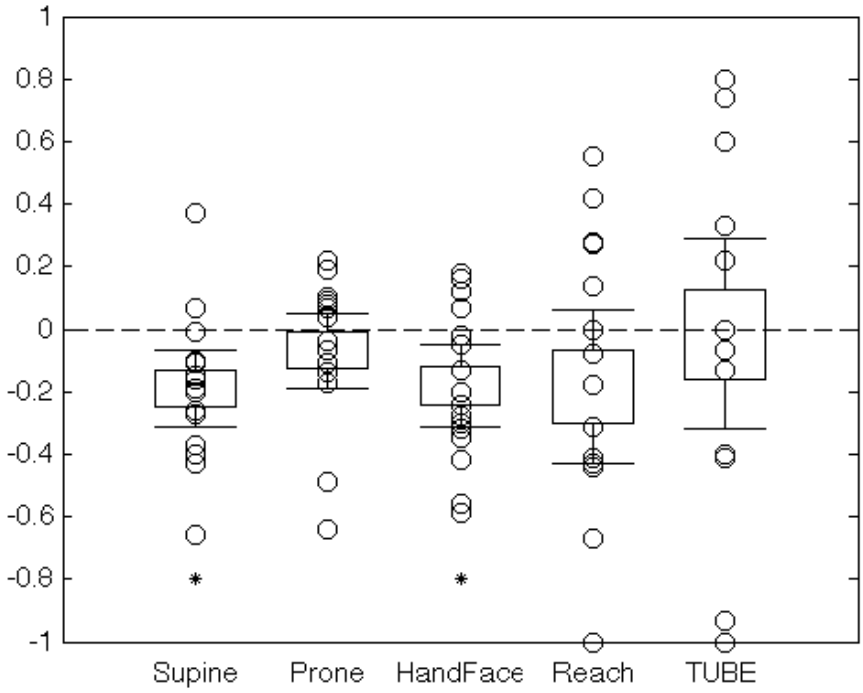

Figure 2.6. Distribution of Laterality Index (LI) scores for each head orientation and hand use measure. Boxes represent the group mean and standard error on each task. Whiskers signify 95% confidence intervals. Asterisks denote significant group-level biases as determined by one-sample t-tests with an alpha level of 0.05.

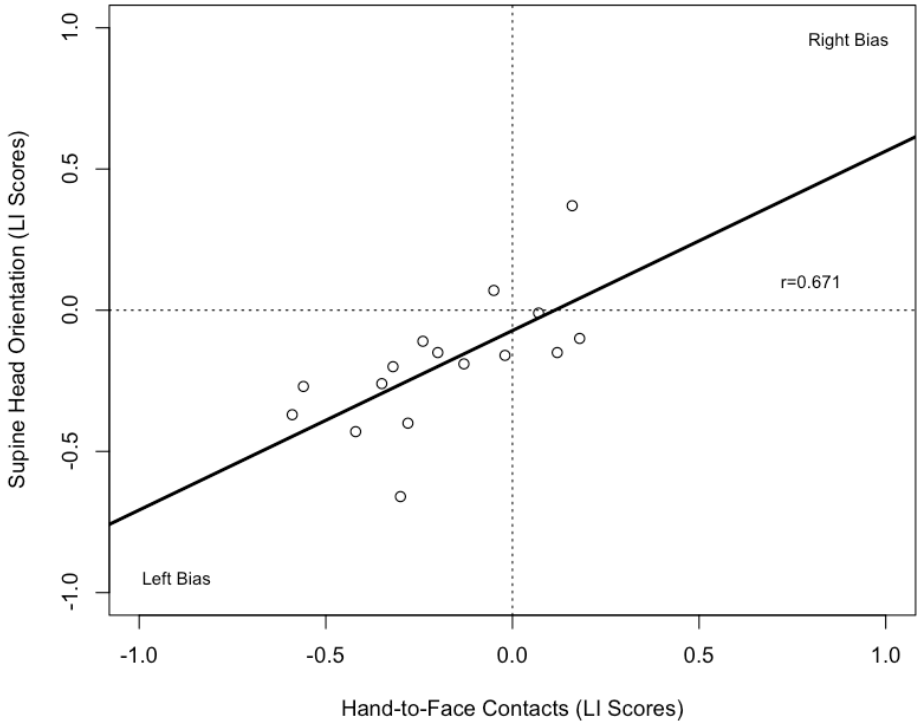

Figure 2.7. Supine head orientation preference corresponds to hand use preference for hand-to-face contacts. The greater the leftward head bias, the greater the left hand bias. LI scores were calculated by the formula *LI=R-L/R+L*, where LI=Laterality Index, R=Right response, L=Left response. Positive scores indicate a right bias and negative scores indicate a left bias.

Discussion

As predicted, the majority of rhesus monkey infants preferentially turned their heads to the left while supine, but did not exhibit head turning preferences while prone. Additional analyses of supine head orientation revealed that monkeys spontaneously oriented their heads to the left following a midline starting head position, and that monkeys maintained a left head orientation following a period of experimenter-induced left head positioning. Monkeys did not however maintain a right head turn following induced right head positioning. Furthermore, the left supine head positioning bias corresponded to a left hand preference for unimanual hand-to-face movements made

during supine head orientation testing. Thus, the left supine head bias may have resulted in greater activity in the left hand and possibly greater visual regard of the left hand. Nevertheless, supine head bias did not predict later hand preference as measured by unimanual reaching at 1 month of age or manipulation on a coordinated bimanual task at 6 to 9 months of age as previously reported in human and chimpanzee infants (Hopkins & Bard, 2000; Michel, 1981).

One possibility for the lack of correspondence between neonatal supine head orientation and later hand use may be that nursery-reared rhesus monkey infants do not spend time supine naturally. By comparison, the supine posture is spontaneous and part of the natural repertoire for human and chimpanzee infants. Any asymmetric hand experience that occurred during supine head testing for the rhesus infants such as the left hand bias observed for hand-to-face contacts may have been too limited to affect the development of hand preference. In addition, macaque infants develop at a rate that is approximately four times as fast as human infants (Gunderson & Sackett, 1984), further limiting the role of experience in influencing behavioral asymmetries. The onset of successful reaching in these monkeys was approximately 3 weeks of age, whereas the onset of successful reaching in human infants does not occur until 4 months of age (Berthier & Keen, 2006).

In addition to a left supine head bias and a left hand-to-face bias, the majority of infants also showed a greater response to tactile stimulation on the left side of the body (left arm and left leg) compared to the right side during the neonatal reflex assessments over the first month of life. No other asymmetries were found for the other neonatal developmental tests of interest. One possibility is that a left side bias is present early in

rhesus monkeys, but is not manifested in unimanual hand use until later in development after sufficient reaching experience. We did not find a group-level hand bias for reaching measured at 1 month of age; however, Westergaard, Champoux and Suomi (1997) reported a left hand preference for unimanual reaching in rhesus infants aged 4 to 11 months (mean age=6 months) and also found a left hand bias on the TUBE task in this same cohort of 19 infants. Our TUBE task data although largely age-matched to Westergaard et al. (1997) more closely mirror that of Bennett et al. (2008) who did not find a population-level bias for rhesus monkeys on the TUBE task in a much larger sample of 124 individuals approximately 3 to 6 years of age. There was also no correspondence between unimanual reaching and coordinated bimanual hand use in our sample of infant rhesus monkeys, a finding that has also been reported for chimpanzees (Hopkins & Bard, 2000). These data collectively suggest that the factors that underlie unimanual and bimanual patterns of hand use may differ, and that hand preference development may be discontinuous in rhesus monkeys.

A developmental trajectory for the leftward bias observed in rhesus monkeys may differ from that of humans and chimpanzees who show a rightward bias for a number of other reasons. First and foremost, the direction of bias differs and simply put, a leftward trajectory may be inherently different than a rightward trajectory. Second, population-level hand preference in rhesus monkeys is not as robust compared to humans. Papademetriou et al. (2005) reported 68% left hand use in a review of rhesus monkey studies, in contrast to the 85% or greater right hand use observed in adult humans (Annett, 2002). Therefore, we might expect that infant rhesus monkeys will not be as strongly lateralized or show the same degree of relatedness between behavioral

asymmetries. Third and finally, the differences observed between rhesus monkey infants and human infants may be due to prenatal, rather than postnatal, factors such as intrauterine positioning.

Human infants undergo a period of stable intrauterine positioning in the month preceding birth due to restrictions in mobility from increased size and the mother's anatomy, and the majority of infants are born in a left occiput anterior or left occiput transverse position with the right ear facing out (Previc, 1991). Furthermore, head position at birth corresponds to postnatal measures of supine head turning preference, but not prone head turning preference (Michel & Goodwin, 1979). Previc (1991) hypothesized that that the ear and vestibular system are differentially stimulated due to the asymmetry observed in the intrauterine positioning of the fetus during the last trimester and forces acting on these systems from the mother's bipedal posture, contributing to a postnatal right supine head positioning bias and a right ear advantage.

Very little is known about intrauterine positioning in macaque monkeys. The fetus tends to spend most of the pregnancy in a head-up position well into the third trimester and then changes to a head-down position. Ultimately, the majority of macaque infants are born head first and face-up (Goodlin & Sackett, 1983). Macaque monkeys are quadrupedal, so the forces derived from the mother's gait may be different from that of a human mother's gait; however, rhesus monkey mothers also spend time in other postures. We did not find evidence of an auditory side bias in our assessments of rhesus monkey neonates, but the orient to auditory measure may not have been sensitive to detecting superiority in one ear over the other. Future work examining fetal positioning in rhesus monkey fetuses and later postnatal behaviors in the same subjects would provide

important information for understanding how prenatal factors may contribute to behavioral asymmetries in rhesus monkeys.

Evidence of a leftward neonatal asymmetry in rhesus monkeys infants was found including a left supine head orientation bias, a left hand preference for hand-to-face movements, and a greater response to tactile stimulation on the left side of the body observed over the first month of life. Later assessments of hand use did not reveal population-level preferences or relationships to earlier behavioral asymmetries. The faster development of rhesus monkey infants compared to human infants may have limited the asymmetrical experience that could be in part responsible for linking early head positioning to later hand preference. Nevertheless, other factors may be involved in a trajectory for handedness, and similar patterns in behavior may not share the same underlying mechanisms across species. In addition, hand preference may not have been fully developed at 6 to 9 months of age, given reports of a left bias for adult monkeys.

Overall interpretations of these data are limited, as results may not extend to rhesus monkey infants raised under mother-reared captive or wild conditions. A left bias has also been reported for mother-infant carrying and infant nipple preference in mother-reared rhesus monkey infants (Tomaszycki, Cline, Griffin, Maestripieri & Hopkins, 1998). Rhesus monkey infants are held on the mother's ventral surface, resulting in a vertical position when the mother is stationary and a horizontal position when the mother is engaged in quadrupedal locomotion. There are no data on infant head orientation preferences during either nursing or mother-infant locomotion. Additional studies investigating the early posture of the infant in relationship to later hand use preference and maternal influence would contribute to our understanding of developmental

trajectories for asymmetries in rhesus monkeys, and whether patterns of laterality share common factors across primates.

Experiment 2: Movement Quality and Handedness Trajectory in Monkey Infants

In addition to neonatal asymmetries such as supine head orientation bias and hand use preference for hand-to-face contacts, the quality of arm movements may also play a role in shaping a trajectory for handedness in rhesus monkey infants. A leftward pattern of asymmetries has been reported for rhesus monkeys in both the neonatal data presented in Experiment 1 as well as previous studies of hand preference (Papademetriou et al., 2005). The possible origin of this left bias and speculation on how hand use preference may have evolved in primates has received a great deal of attention in the nonhuman primate literature.

In a landmark paper, MacNeilage, Studert-Kennedy and Lindblom (1987) outlined the postural origins theory of primate handedness. The postural origins theory proposed that hand use preferences in primates are related to feeding strategy and environmental postural demands. The theory is based on the finding that some of the earliest primates relied on capturing moving insect prey and lived in an arboreal environment. MacNeilage and colleagues suggested that a division of labor between the hands and corresponding brain hemispheres might have emerged, such that the left hand/right hemisphere became specialized for visually-guided reaching and the right hand/left hemisphere was used for postural support. Left hand reaching movements were ballistic, involving fast, uncorrected reaches to capture prey. As primates evolved, their environments and feeding strategies changed. Predation was no longer the main source of

food, and diets diversified to include things like leaves and fruits. Primates became more terrestrial, freeing the right hand from postural demands and allowing it to become specialized for manipulation (e.g., processing food that would otherwise be unobtainable such as cracking nuts and peeling fruit). Although the postural origins theory may not be able to explain the hand use preferences of every primate species, the broad ideas of a left hand preference for reaching and a right hand preference for manipulation have been largely supported by the research generated in the two decades since the original publication (MacNeilage, 2007).

Monkeys present an interesting case for the postural origins theory as a possible intermediate group between the left hand preference observed in prosimians such as lemurs and the right hand preference seen in chimpanzees. Papademetriou and colleagues (2005) recently performed a meta-analysis of primate hand use preference papers, noting that the majority of studies used reaching paradigms to measure hand use. Although there was some variability in hand use by task, overall a left hand preference was found for rhesus monkeys. One possibility is that rhesus monkeys maintained a left hand bias for reaching from prosimians, while also beginning to develop hand preferences for manipulative tasks. If this is indeed the case, left hand reaching in rhesus monkeys should have ballistic qualities. These qualities may include greater smoothness and faster peak speeds in left hand reaches as compared to right hand reaches, given that ballistic movements, once started, continue uncorrected to the target and are carried by their own momentum.

Reach quality can be assessed with motion capture analyses that track arm movements in either two-dimensional (2-D) or three-dimensional (3-D) space. Kinematic

data can be recreated from videotape by manually adding points of interest to each video frame. Data can also be collected in real-time from sensors worn by the subject. Kinematic analyses have previously been used to examine reaching in adult macaques (Roy, Paulignan, Farnè, Jouffrais & Boussaoud, 2000; Christel & Billard, 2002; Roy, Paulignan, Meunier & Boussaoud, 2002; Roy, Paulignan, Meunier & Boussaoud, 2006; Pizzimenti et al., 2007). In the majority of these studies, one hand was trained to perform the reaching task(s); consequently, subject numbers have been limited, ranging from 3 to 5 monkeys. There are no known studies comparing left and right arm movements within subjects, or studies comparing reaching movements of the preferred and non-preferred arms for rhesus monkeys. There are also no reports of reaching kinematics in any infant nonhuman primate. The current study was the first attempt to assess quality of reaching in the left and right arms while controlling for individual hand use preferences in a large cohort of infant rhesus monkeys.

Quality of reaching was explored with 2-D motion capture analyses. I hypothesized that there are kinematic differences between arms in infant rhesus monkeys. If these differences are the result of a specialization for reaching, I predicted that the left arm would have a faster average speed, higher peak speed, and a smoother reach compared to the right arm based on the postural origins theory (MacNeilage et al., 1987; MacNeilage, 2007). Alternatively, qualitative differences between the arms could also be a product of hand preference. If arm differences are the result of hand use preference, I predicted that the preferred arm would have a shorter duration and straighter reach to a target, indicating greater hand control, as compared to the non-preferred arm.

Method

Subjects

The rhesus monkey infants observed in Experiment 1 were tested in Experiment 2 (*N*=16) when they were approximately 4.5 months old (mean age = 138 ± 5 days). Monkeys were divided into hand preference groups based on hand use preferences for unimanual reaching at 1 month of age (see **Table 2.3**). Monkeys with at least 65% left hand use were classified as left-preferent. Because only 2 monkeys could be classified as right-preferent using the 65% hand use criterion, the remaining monkeys (right-preferent and ambi-preferent) were combined into a category designated as non-left-preferent to increase statistical power. The total number of monkeys in each hand preference group as well as the distribution of males and females in each group is given in **Table 2.4**. The following procedures were approved by the NICHD Animal Care and Use Committee.

Table 2.4. Distribution of hand preference groups for infant monkeys.

	Left	Non-Left
Males	3	5
Females	4	4
Total	*7*	*9*

Reaching Task

Quality of movement was assessed from a reaching task. To elicit reaching movements from the left and right hands on different trials, a small grape slice was presented on a stationary platform to the monkey's left or right side in line with the corresponding hand. The monkey's task was to reach to and pick up the food **(Figure 2.8**). An experimenter held the monkey in a fixed position that stabilized the trunk but allowed the arms to move freely for the duration of the test period. Monkeys were given

3 blocks of 5 trials in a single session and all sessions were videotaped for later analysis. The camcorder was positioned perpendicular to the monkey's arm and reaches were filmed at the level of the testing table. The location of the subject (left or right side of the camcorder) was alternated for each block of trials, with the starting configuration randomized across subjects.

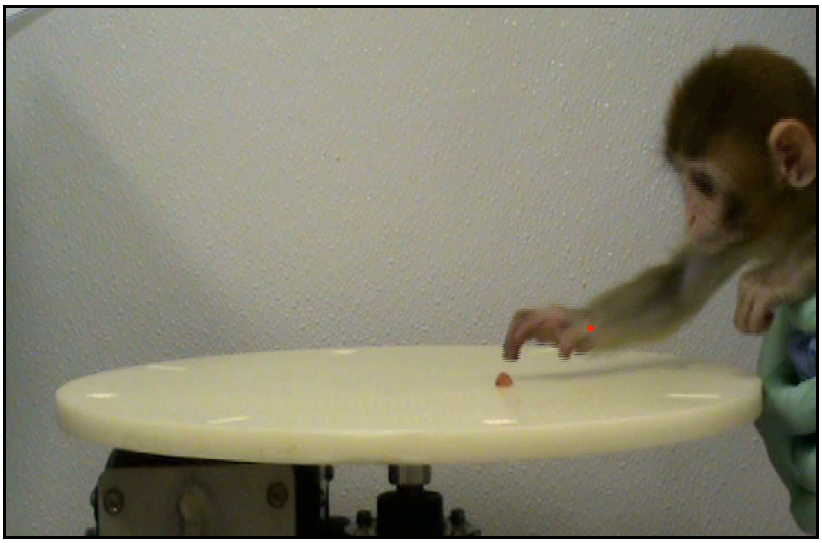

Figure 2.8. 4.5-month-old monkey infant reaching for grape with the right hand. Red dot denotes point added with MaxTRAQ Lite+ to track 2-D arm movements.

Kinematic Analysis

Reaching quality was examined with the 2-D motion analysis program MaxTRAQ Lite+ (Innovision Systems, Inc., Columbiaville, MI). A single point of interest on the radial portion of the monkey's wrist was manually digitized in a frame-by-frame analysis (30 frames per second) for unimanual movements where the infant successfully reached to and picked up the food (**Figure 2.8**). The inner wrist was chosen as a landmark because it was highly visible on the videotape regardless of which hand was used, and could be reliably identified in each video frame. The onset of the reach was

defined as the first frame of arm movement towards the food. The offset of the reach was defined as the first frame of hand contact with the food. After a reach had been digitized, the coordinate system was scaled using the known length of the testing platform. Data were excluded from analysis if the video was not suitable for reconstructing 2-D movements due to camera placement or zoom angle. The primary observer digitized all of the usable reaches and was blind to hand preference condition. Approximately 20% of the data were later reexamined for intra-rater reliability. The signed and unsigned differences between ratings for each dependent variable are given in **Table 2.5**.

Kinematic data were extracted with Matlab (The MathWorks, Inc., Natick, MA) using custom programs for the behavioral parameters of interest that were manually digitized with the motion capture software. Data were filtered at a frequency of 6 Hz with a 2nd order dual-pass Butterworth filter. A three-point differentiation technique was used to calculate speed (mm/s). The average speed was the mean speed of the frames during the reach, and the peak speed was the maximum speed of the reach. Other variables of interest including reach duration, straight-line distance, path length, and reach smoothness (number of movement units) were calculated with finite difference methods. Reach duration was the time in seconds between the onset and offset of the reach. Reach straightness was computed by the ratio of straight-line distance to path length, with values closer to 1 indicating straighter reach movements. Movement units were computed with an algorithm derived from von Hofsten (1991). A movement unit was composed of a significant acceleration (defined as having a minimum cumulative velocity of 200 mm/s and minimum cumulative velocity over reach time ratio of 500 mm/s^2) followed by a

similarly sized deceleration. To describe it visually, a movement unit consisted of a movement peak and the corresponding valley.

Table 2.5. Intra-rater reliability by dependent variable for monkey reach kinematics.

	Mean Signed Diff.	Mean Unsigned Diff.
Overall Reach		
Reach Average Speed (mm/s)	30.71	47.69
Reach Peak Speed (mm/s)	25.72	70.81
Reach Duration (s)	-0.04	0.13
Reach Smoothness (MUs)	-0.25	0.81
Reach Straightness (SLD/Path)	0.01	0.07
Early Reach		
Early Average Speed (mm/s)	7.77	85.09
Early Duration (s)	0.03	0.13
Early Straightness (SLD/Path)	0.03	0.06
Later Reach		
Later Average Speed (mm/s)	40.05	57.66
Later Duration (s)	-0.07	0.11
Later Straightness (SLD/Path)	0.00	0.06

Statistical Analysis

Linear mixed-effects models (Bates & Maechler, 2009) were used to examine the effects of hand (left or right), hand preference (hand recoded as preferred hand or non-preferred hand), and sex (male or female) on each dependent variable for the reaching task using the statistical program R (R Development Core Team, 2009). For the left-preferent group, the preferred hand was the left hand and the non-preferred hand was the right hand. For the non-left-preferent group, the preferred hand was the right hand and the non-preferred hand was the left hand. P-values were estimated from Monte Carlo simulations (Baayen, 2008).

Models used the following formula: *Dependent Variable ~ Hand * Hand Preference * Sex + SLD + (1|Subject)*. Straight-line distance (SLD) was used as a covariate to control for differences in arm sizes. Duration was an additional covariate in models for smoothness. Values three times the interquartile range (IQR) were excluded from analyses (**Table 2.6**). For the overall reach, the dependent variables included reach duration, reach average speed, reach peak speed, reach smoothness, and reach straightness. In addition, time to peak speed and percentage of the movement to peak speed were also examined to determine whether movements could be divided into early and later segments at the peak speed.

Preliminary analyses did not find any effects on time to peak speed or percentage of the movement to peak speed ($P>0.05$). Therefore, reaches were divided at the peak speed into two segments to further examine potential differences in movement quality between the left and right arms. Dependent variables for the portion of the reach preceding the peak speed included early reach duration, early reach average speed, early reach peak speed, and early reach straightness. Dependent variables for the portion of the reach following the peak speed included later reach duration, later reach average speed, later reach peak speed, and later reach straightness. Alpha was 0.05 for all tests.

Results and Discussion

In total, 181 reaches from 15 infant monkeys were examined. Data from one left-preferent female infant were ultimately excluded from kinematic analysis due to camera error. The average number of digitized reaches from each monkey was 12 ± 4. There were 75 left-handed reaches and 106 right-handed reaches. Results from the reaching task

are presented in **Table 2.7.** For the overall reach, the left hand was found to be significantly smoother than the right hand, as measured by a smaller number of movement units. There were no effects of hand on reach duration, reach average speed, reach peak speed, or reach straightness (P>0.05). There were no effects of hand preference on any of the parameters of the overall reach (P>0.05). There were also no sex differences for any of the overall reach dependent variables (P>0.05).

Table 2.6. Outliers for the reaching task identified as values three times the IQR.

Variable	Values Excluded	Total Observations
Overall Reach		
Reach Average Speed	>818 mm/s	174
Reach Peak Speed	>1486 mm/s	175
Reach Duration	>1.6 s	180
Reach Smoothness	None	181
Reach Straightness	<0.39	178
Early Reach		
Early Average Speed	>1272 mm/s	173
Early Duration	>0.90 s	179
Early Straightness	<0.44	149
Later Reach		
Later Average Speed	>818 mm/s	175
Later Duration	None	181
Later Straightness	<0.57	177

IQR=Interquartile Range.

Table 2.7. Results for the reaching task in monkeys.

Variable	*Effect*	*P-value*	*Means*
Overall Reach			
Smoothness (MUs)	Hand	0.010	Left=1.49, Right=1.93
Early Reach			
Peak Speed (mm/s)	Hand	0.036	Left=525, Right=428
Later Reach			
Average Speed (mm/s)	Hand	0.048	Left=274, Right =224

When reaches were divided into early and later segments at the peak speed, the left hand achieved higher early reach peak speeds compared to the right hand. The left hand was also faster than the right hand in the later part of the reach as measured by average speed. There were no other hand effects for either the early reach or the later reach ($P>0.05$). There were also no effects of hand preference on movement quality for the earlier or later portion of the reach ($P>0.05$). Finally, there were no differences between males and females for any of the dependent variables of the early or later segments of the reach ($P>0.05$).

These data suggest a left hand specialization for reaching in infant rhesus monkeys independent of hand preference. The left hand was found to be smoother for the overall reach, attained higher peak speeds in the early portion of the reach, and was faster on average in the later portion of the reach when compared to the right hand. These findings indicate that the movements of the left hand in rhesus monkeys can be characterized as ballistic, lending support to the postural origins theory of primate handedness in which a left hand preference in early primates was derived from ballistic prey capture (MacNeilage et al., 1987; MacNeilage, 2007). The postural origins theory was formulated from a review of studies on hand use frequency, and to the best of our knowledge, these are the first data to systematically explore kinematic differences in the quality of left and right hand reaching movements in nonhuman primates.

Although these data illustrate movement quality differences between the left and right hands, they cannot explain why the left hand became specialized for reaching as opposed to the right. One possibility is that preexisting hemispheric specialization may have shaped the development of hand preferences in primates. The right hemisphere

largely controls the left side of the body, and is generally associated with processing visual and spatial information in humans (for reviews, see Serrien, Ivry & Swinnen, 2006; Goble & Brown, 2008). The right hemisphere has also been implicated in spatial cognition in non-primate species such as birds and rats (Vallortigara & Rogers, 2005), as well as haptic tasks in rhesus monkeys and capuchins (Fagot, Drea & Wallen, 1991; Lacreuse & Fragaszy, 1996; 1999). A right hemisphere advantage for visual and spatial information may therefore have given rise to left hand use for visually-guided reaching. Having a hemispheric/hand specialization could be advantageous in that it may reduce redundancy and increase efficiency by consistently allocating resources for a particular task to the same hemisphere and allowing for one side of the body to become more skillful (Vallortigara & Rogers, 2005; Vallortigara, 2006; MacNeilage, 2007). Additional studies of hemispheric specialization in rhesus monkeys are needed, including greater examination of the role of the right hemisphere in processing visual and spatial information particularly as it pertains to reaching.

Analysis of reach quality in infant rhesus monkeys did not reveal any effects of hand preference when monkeys were divided into left and non-left (right and ambi combined) groups. In a follow-up analysis, reach data were re-examined using a three-group classification with 6 monkeys classified as left-preferent, 2 monkeys classified as right-preferent and 7 monkeys classified as ambi-preferent. There were no effects of hand preference group on any of the reaching variables. Additional work is needed with a larger sample size, particularly for the right-preferent group to validate these findings. These results do suggest however that there was no difference in dividing monkeys into two groups as compared to three groups for hand preference to examine reach quality.

One possibility is that hand preference does not affect reach quality in infant rhesus monkeys. In a study of squirrel monkeys (*N*=16) fishing for goldfish in either a bowl or a wading pool, significantly more left hand attempts were made than right hand attempts; however, there was no difference in the rate of successful capture between the preferred hand and the non-preferred hand (King & Landau, 1993). The authors attributed the left hand preference for fishing to the demands of the task, as fish capture required a fast, ballistic movement, visual guidance, and postural support from the side of the body contralateral to the arm used for reaching. Fishing is not in the normal behavioral repertoire for squirrel monkeys however. If fishing experience were extended beyond this set of studies, differences between the preferred and non-preferred hands may have emerged.

This interpretation can be extended to the rhesus monkey data, in that there may be differences between hands based on preference later in life, but not in infancy when hand preference may still be under development. Furthermore, early differences in movement quality could contribute to later hand use preference by creating a greater divergence between the abilities of each hand. Future work may want to examine reaching to both static and moving objects across development and in adult subjects to further understand the role of movement quality on handedness trajectory and potential changes in the relationship between the left and right hands as well as the preferred and non-preferred hands.

One limitation of the current study was that monkeys were classified using hand use preferences from 1 month of age, as data were not available for hand use preferences at 4.5 months of age when reach quality as examined. An attempt was made to examine

quality of reaching at 1 month, but video data were not suitable for 2-D motion capture analysis. Early hand use preference may not be indicative of later hand use preference if the development of handedness in rhesus monkeys is discontinuous, as suggested by the results of Experiment 1. No relationship was found between hand use preference for hand-to-face contacts over the first month of life, reaching at 1 month of age, or manipulation on a coordinated bimanual task at 6 to 9 months of age in this cohort of infant monkeys. Interestingly however, both the development of reaching and the development of handedness in human infants have been described as dynamic, undergoing change or fluctuation before stabilizing (Corbetta & Thelen, 1996; 1999; 2002; see Chapter 3). A trajectory for handedness in rhesus monkeys may also be dynamic, and under the influence of many factors, two of which may be early neonatal biases as measured in Experiment 1 and movement quality as measured in Experiment 2.

An additional limitation of this work was that reaching was sampled at a low frame rate (30 fps) with a single camcorder due to the video equipment that was available at the testing facility. Results should be interpreted with some caution due to possible error in digitizing reaches with this technique. A low frame rate could result in error calculating acceleration and error could also have occurred from the process of adding the marker manually to the same place on the monkey's wrist in each frame. To control for these possible sources of error, the raw reaching data were smoothed with a Butterworth filter, a common technique in studies of human reaching (e.g., Berthier & Keen, 2006). In addition, the same observer scored a subset of the reaches twice for intra-rater reliability. Future studies should consider using a single high-speed camcorder or multiple camcorders to re-create reaches in a 3-D space. Future work could also examine

the dynamics of the neuromuscular system for arm movements in monkeys, with particular regard to whether movement units represent separate motor commands or shifts in muscle properties such as muscle rest length (Jindrich & Full, 2002; Berthier, Rosenstein & Barto, 2005).

In summary, I want to emphasize that these data represent the first attempt to quantify reach quality in not only rhesus monkey infants, but also any nonhuman primate infant. Therefore, these results while preliminary may serve as the basis for future studies and hypotheses regarding the relationship between movement quality and hand use in primates.

CHAPTER 3

HANDEDNESS IN HUMAN INFANTS

A right hand use preference has been well established in adult humans (Annett, 2002) and has even been documented in human fetuses using real-time ultrasound at 10 weeks gestational age, the earliest time at which arm movements are observed (Hepper, McCartney & Shannon, 1998). Nevertheless, longitudinal infant studies have documented considerable variation in hand use over development, indicating a disparity between early reports of a right bias and the adult pattern of hand use preference (Gesell & Ames, 1947; Corbetta & Thelen, 1999). Many factors likely contribute to a trajectory for handedness in human infants, only some of which will be discussed here including prenatal and early postnatal biases as well as movement quality or the abilities of each hand.

Further examination of fetal arm movements confirmed a rightward pattern in early gestation, but preferences for later gestation arm movements may vary. McCartney and Hepper (1999) found a consistent right arm bias in a longitudinal study of fetuses observed from 12 to 27 weeks gestational age. de Vries and colleagues (2001) also observed a group-level right arm bias at 12 and 16 weeks gestation; however, a group-level left arm bias was seen in the same fetuses from 20 to 36 weeks gestation. In contrast, Myowa-Yamakoshi and Takeshita (2006) failed to find any bias in fetal arm movements observed from 19 to 35 weeks gestation.

Despite fluctuations in fetal arm preferences, hand biases observed in utero may be indicative of hand use preferences later in life. Hepper, Shahidullah and White (1991) examined thumb sucking in 274 fetuses using real-time ultrasound. Fetuses were

examined once at either 15 to 21 gestational weeks of age, 28 to 34 gestational weeks of age, or 36 gestational weeks of age to term. A group-level right thumb preference was found at every age. Furthermore, hand preference for fetal thumb sucking was found to predict hand use preference as measured by a modified Edinburgh Handedness Inventory in a follow-up study when participants were 10 to 12 years of age (Hepper, Wells & Lynch, 2005). All of the children that had preferred the right thumb as fetuses were classified as right-preferent as adolescents. In the children that preferred the left thumb as fetuses, two-thirds were classified as left-preferent and one-third was classified as right-preferent. Thus lateralized hand and arm movements have been documented prenatally, and show relationships with postnatal measures of hand use.

Following birth, differences in hand use in very young infants have been explored using holding time duration. In a study by Caplan and Kinsbourne (1976), infants ranging in age from 1.5 to 4 months old held a rattle longer in the right hand than the left when rattles were tested singly in each hand. Petrie and Peters (1980) replicated this finding in infants tested monthly over the first 4 months of life. Infants not only held a toy longer with the right hand, but also made a stronger grasp response with the right hand compared to the left as measured by a gripometer. Holding duration was also measured by Hawn and Harris (1983) in 2-month-old and 5-month-old infants. At both ages, the right hand outperformed the left hand in holding time length. By contrast, Yu-Yan, Cun-Ren and Ove (1983) found a left hand bias for unimanual holding in infants from 2 to 4.5 months of age whereas Strauss (1982) did not find a hand difference in unimanual holding for infants tested at the mean ages of 3.3 days or 2.4 months. Like fetal arm and

hand preferences, a right bias has been observed in the majority of early holding time studies.

The frequency of left and right hand use for reaching as well as for object manipulation has also been examined to determine when hand use preferences emerge in infancy. Longitudinal studies have documented considerable variation in hand use within individuals (Gesell & Ames, 1947; Corbetta & Thelen, 1999). Hand preference appears to be sensitive to sensory-motor development over the first years of life, particularly at major locomotor milestones such as the transitions to sitting, crawling, and walking (Corbetta & Bojczyk, 2002; Corbetta & Thelen, 2002; Corbetta, Williams, Snapp-Childs, 2006). Nevertheless, a group-level right hand bias for reaching to and manipulating toys has been found for infants from 6 months through 13 months of age (Michel, Ovrut & Harkins, 1985; Michel, Tyler, Ferre & Sheu, 2006). In addition, Hinojosa, Sheu and Michel (2003) showed an increase in the degree of lateralization from 7 to 11 months such that right hand bias increased in right-preferent infants, left hand bias increased in left-preferent infants, and infants with no preference at 7 months showed an increase in right hand use for unimanual actions at 11 months. There have been fewer studies of hand preference over the second year of life after the onset of walking. Interestingly, Geerts, Einspieler, Dibiasi, Garzarolli and Bos (2003) noted a strong right hand bias at 14 months, but a weakened right bias in the same infants tested again at 18 months of age. Therefore, the development of hand preference may be non-linear with periods of clear right hand preference.

In addition to the previous studies that measured frequency of hand use in infants for various tasks, two-dimensional (2-D) and three-dimensional (3-D) kinematic studies

have assessed quality of arm movements. Infants move their arms with and without an object present from an early age (i.e., pre-reaching), but successful goal-directed reaching where the hand grasps the object does not appear until about 16 weeks of age (Van der Fits & Hadders-Algra, 1998; Berthier & Keen, 2006). Lynch, Lee, Bhat and Galloway (2008) examined arm differences during pre-reaching in infants from 8 weeks old until reach onset using 3-D motion capture, but did not find a consistent difference between the left and right arms. In infants followed from 20 to 32 weeks of age using 2-D kinematics, Morange-Majoux, Peze and Bloch (2000) found a right hand advantage for reaching such that the right hand was straighter and had a shorter movement time than the left hand. Similarly, Hopkins and Rönnqvist (2002) found that the right hand was smoother than the left hand for unimanual reaching in infants 6 months of age using 3-D kinematics. Rönnqvist and Domellöf (2006) extended these findings to older infants. The right hand was smoother than the left hand at 9, 12 and 36 months of age. The right hand was also significantly straighter than the left hand at 9 and 12 months, but there was no difference between hands for straightness at 36 months.

Collectively, these data suggest that qualitative differences between the left and right hands emerge after the onset of reaching. However, it is not clear whether these arm differences are maintained, as there are no kinematic data comparing arm performance between 13 and 35 months of age. Previous longitudinal research has suggested that the development of reaching may be non-linear, meaning individual infants may improve, worsen, or remain stable over different periods (Corbetta & Thelen, 1996; 1999; Thelen, Corbetta & Spencer, 1996). In addition, reaching parameters are still changing beyond

the first year of life (Berthier & Keen, 2006). Additional studies are needed that examine reaching quality over the second year of life of infant development.

Experiment 3: Movement Quality and Handedness Trajectory in Human Infants

Many of the previous studies of infant hand use have focused on either differences in the frequency of left and right hand use or differences in the abilities of the left and right hands. If infant handedness changes dynamically in development, meaning that infants experience periods of both stability and instability in hand use, it is possible that the relationship between hand preference and hand ability may also fluctuate. On the other hand, either hand preference or hand proficiency could be driving handedness trajectory, and consequently influencing the other. Studies are needed that examine both what hand the infant prefers to use as well as the quality of the movements of each hand.

The purpose of the present study was to measure frequency of hand use during play as well as quality of hand use using 3-D kinematics at three different time points in development: 11 months, 14 months and 17 months. Two reaching tasks were chosen to examine movement quality that required different grasping movements, either a whole-hand grip to pick up a ball and fit it into a toy or a thumb to forefinger pincer grip to remove a small piece of food from a cup. The ability to make a pincer grip develops in infants from 10 to 18 months of age (Van der Fits, Otten, Klip, Van Eykern & Hadders-Algra, 1999). The younger age of 11 months was chosen when this ability is just starting to develop and the older age of 17 months was chosen when this ability is almost fully developed. I expected infants' performance on both tasks to improve with age. I also expected to see a group-level right hand preference for play at 11 and 14 months,

matching previous findings in these age groups. There are no known data on hand preference from 17-month-olds, although a right preference may also be expected given the general pattern of rightward biases observed across development.

Although kinematic differences have been found between arms for previous tasks involving reaching in infants, these studies did not take into account individual infants' hand use preferences. Previous findings may therefore be confounded with handedness. If differences in movement quality are the result of hand preference, I predicted that the preferred arm would have a shorter duration and straighter reach to a target, indicating greater hand control, as compared to the non-preferred arm. In addition, the preferred hand was predicted to be faster to grasp the ball and to remove the food from the cup. Alternatively, qualitative differences between the arms could be the result of a hemispheric specialization for reaching. If differences are the result of specialization, I predicted that the right arm would have a shorter duration, smoother reach, and straighter reach as compared to the left arm, matching previous infant studies that found a right arm advantage for reaching at various ages (Morange-Majoux et al., 2000; Hopkins & Rönnqvist, 2002; Rönnqvist & Domellöf, 2006) as well as reports of a left hemisphere specialization for motor control in adults (for reviews, see Serrien, Ivry & Swinnen, 2006; Goble & Brown, 2008).

Method

Participants

Local families were recruited for participation in this study, and all data were collected at the Child Study Center at the University of Massachusetts Amherst. Infant

names were acquired through public birth records or a commercial source. Parents first received a letter describing the study (**Appendix B**). They were then contacted by phone. A lab visit was scheduled within two weeks before or after the child's target age birthday. In total, 73 healthy, full-term infants participated in this study. There were 35 infants in the 11-month group (males=21; females=14). The average age was 11.2 months (336 ± 6.1 days). There were 18 infants in the 14-month group (males=10; females=8). The average age was 14.0 months (419 ± 8.3 days). There were 20 infants in the 17-month group (males=10; females=10). The average age was 16.9 months (508 ± 10.8 days). Infants received a token gift for participating.

Procedure

The University of Massachusetts Institutional Review Board (IRB) approved the following procedure. Infants were tested once when they were 11-, 14-, or 17-months-old. Before the study began, the primary investigator reviewed the informed consent form with the parents (**Appendix C**), described the study procedure, and explained the motion capture equipment. Parents were informed that testing was not in any way diagnostic. Infants were seated on a parent's lap at a table for the duration of the study. Parents were told not to assist their child. Sessions were recorded onto mini DVD-R discs using a Sony Handycam® DCR-DVD405 digital camcorder that was positioned behind the experimenter to record the infant's behavior.

The experiment consisted of three tasks. All infants received the tasks in the same order. In the first task, infants were presented with a series of five toys during a free-play period (**Figure 3.1**). The items consisted of a hard block, a toy hammer, a toy phone,

plastic stacking rings and an animal pop-up toy. Toys were selected for maximum manipulation on the basis of bright coloration, noise generation, and/or moveable parts. All toys were obtained from a local store. Each toy was presented individually at the infant's midline. A timer was started when the infant first contacted the toy, and the infant was then given 90 seconds of playtime with each toy. The purpose of this series of toys was to establish the infant's baseline hand preference during his or her natural play.

Figure 3.1. Toys used in the hand preference assessment.

The second experimental task assessed the infant's ability to reach to a ball and fit it into the top opening of a toy (**Figure 3.2**). The diameter of the opening was approximately 5 cm and the ball just fit through this opening. The toy itself measured approximately 17 cm in height. It was attached by industrial strength Velcro® to a painted wooden platform measuring 45.7 x 26.7 cm. Two circular wells were made 18.5 cm from the center point of the top opening to the center point of the outermost well on each side of the toy (the inner wells were not used). These wells served as the starting locations for the ball during the task. The starting location (left or right) was randomized across trials.

The experimenter first demonstrated the task for the infant by fitting the ball twice with each hand. A song played when the ball fell through the opening, which was an exciting auditory reinforcement for the infant. The infant was given 12 trials. If the infant used the contralateral hand or did not complete a trial, additional trials were given in an effort to collect sufficient data from each hand. Infants wore infrared markers to measure movement kinematics during this task.

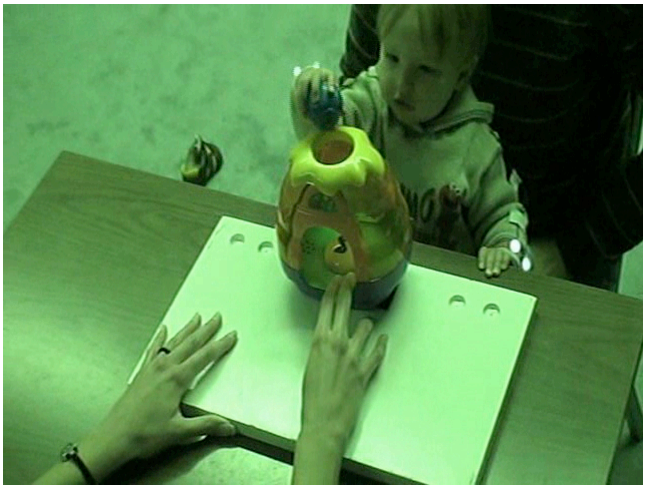

Figure 3.2. 14-month-old infant participating in the fitting task. The ball started from one of the outermost wells. The inner wells were used in piloting only.

In the third and final task, infants were presented with a small stationary cup and asked to retrieve a food item that had been placed inside (**Figure 3.3**). Parents chose either Gerber® Graduates® Fruit Puffs, Cheerios®, or Baby Goldfish® for their child depending on age and preference. These food items were similar in size. A clear 118 ml plastic cup was attached by industrial strength Velcro® to the opposite side of the wooden platform used in the previous task. The cup measured 5.5 cm in height and had an opening of 7 cm in diameter. The cup was affixed to either the left or right of the infant.

Although there was a middle location on the apparatus, it was not used during testing. Cup placement was randomized across 12 trials. A single food item was placed into the cup at the start of each trial and the infant was allowed as many tries as necessary to retrieve it. Infants were allowed to eat the food item between trials. Food was a strong motivator for this activity. As in the previous task, additional trials were given if needed in an effort to obtain sufficient data for each hand, and infants wore infrared markers to measure movement kinematics.

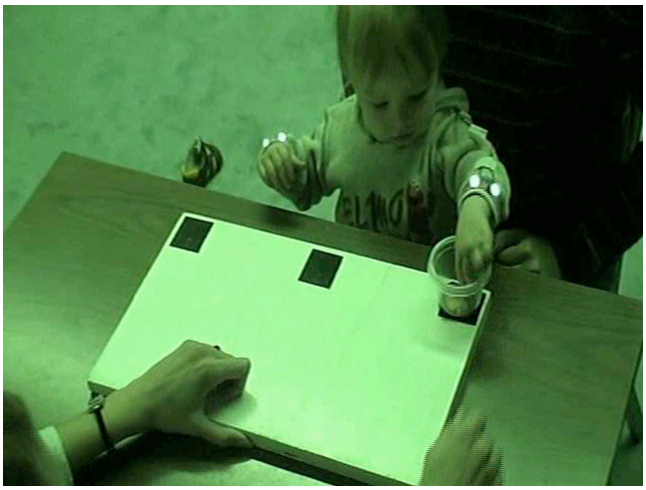

Figure 3.3. 14-month-old infant participating in the cup task. The cup was placed at either the left or right location. The middle location was created for piloting only.

Upon completion of the experimental tasks, the primary experimenter reviewed the video consent form with the parents (**Appendix D**). University protocol required that parents be asked if they would like the video recording of their child destroyed after the data has been analyzed. Data collection concluded with a short questionnaire on the infant's developmental history and previous experiences with the stimuli used in the experiment (**Appendix E**).

Behavioral Analysis

Video data were reviewed frame-by-frame at 30 frames per second using MPEG Streamclip (Squared 5) for all tasks. Hand preference was scored from the free-play period in 6-second intervals. The first time point was recorded when the infant initially reached for and contacted the toy. Manipulations were coded as unimanual, bimanual, or no action/unable to score. For an action to be considered unimanual, either one hand was manipulating the toy while the opposite hand was not contacting the toy, or one hand was manipulating the toy while the opposite hand worked in a complementary fashion (e.g., held the toy). The hand doing the manipulation was noted as left or right. If both hands were engaged in the same action, the behavior was coded as bimanual. This basic classification scheme yielded 75 data points per infant. Previous inter-rater reliability using percent agreement for this hand preference protocol was 89% (Nelson, 2007).

For the fitting task, the primary observer scored the following behaviors from videotape on trials where the infant picked up the ball with the ipsilateral hand and fit successfully. Reach time was defined as the first frame of reaching movement towards the ball to the first frame where the infant contacted the ball. Grip time was defined as the first frame where the infant contacted the ball to the first frame where the infant moved the ball off of the platform. Transport time was defined as the first frame where the infant moved the ball off of the platform to the frame where the midline of the ball passed through the opening of the toy. Trials where the infant picked up the ball and manipulated it in some manner before fitting, transferred the ball to the opposite hand, or did not fit successfully (e.g., overshot the opening of the toy) were not scored. A second observer scored 10% of the fitting data. Inter-rater reliability using a percent agreement score that

allowed for a difference of 5 frames between observers was 89% for reach onset, 98% for ball contact, 100% for ball lift, and 93% for ball fit. Kinematic data were computed for reach time and transport time (see below).

For the cup task, the primary observer scored the following behaviors from videotape on trials where the infant reached to the cup with the ipsilateral hand and successfully obtained the food item. Reach time was defined as the first frame of reaching movement towards the cup to the first frame where the infant's hand entered the cup. Grip time was defined as the first frame where the infant's hand entered the cup to the first frame where the infant's hand was entirely removed from the cup. If the infant made multiple attempts to retrieve the food item, only the successful attempt was scored. Reaches with the hand opposite to the cup and trials where the infant changed hands before retrieving the food were excluded. A second observer scored approximately 10% of the cup data. Inter-rater reliability using a percent agreement score that allowed for a difference of 5 frames between observers was 93% for reach onset, 98% for cup entry, and 99% for cup exit. Kinematic data were computed only for the infant's reach to the cup (see below).

Kinematic Analysis

During the two measures that assessed movement quality (fitting task and cup task), infants wore 2 or 4 infrared marker arrays on each wrist to record their motor movements. The 5 mm markers were embedded in Velcro® wristbands and operated with a tethered system. The markers were tracked by either a one or two camera VZ4000 Visualeyez™ real-time motion capture system (PhoeniX Technologies Incorporated,

Burnaby, B.C., Canada). Each camera had three sensor bars. Two cameras were used for infants that participated before May 2007, and the testing area was calibrated prior to data collection. In the two-camera setup, the cameras formed a right angle, with one camera parallel to the infant's chest and the second camera perpendicular to the infant's right side (**Figure 3.4A**). A single camera was used for infants that participated after May 2007 due to changes in lab personnel and equipment. In the one-camera setup, the camera was parallel to the infant's chest (**Figure 3.4B**).

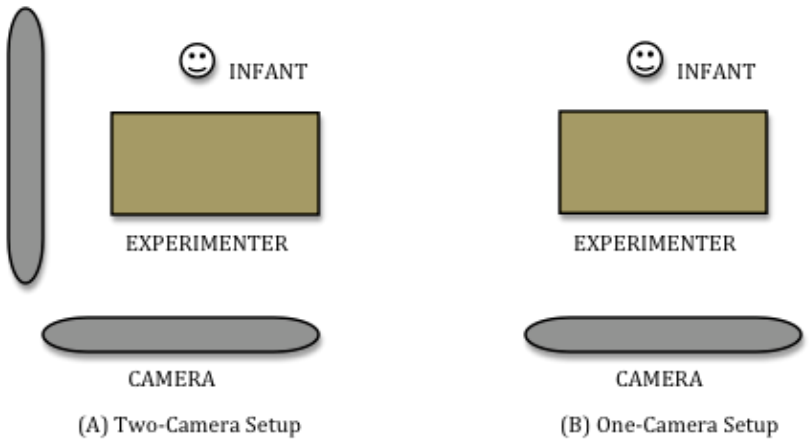

Figure 3.4. Diagram of two-camera (A) and one-camera (B) motion capture setup.

A second experimenter operated the motion capture system out of view of the infant. Motion capture was started and stopped by pressing a button on a computer. An audible beep signaled to the first experimenter that the system had been started and trials could begin. Kinematic data were captured continuously throughout each reaching task at 100 frames per second using VZ Soft™ V2.80 software (PhoeniX Technologies Incorporated, Burnaby, B.C., Canada). Kinematic and behavioral data were synchronized

by the NightShot® function on the camcorder, which recorded infrared light from the active markers as well as the infant's behavior.

Kinematic data were extracted with Matlab (The MathWorks, Inc., Natick, MA) using custom programs. Programs used the marker onset time and the behavioral parameters of interest. Data were processed from a single marker with valid data from the 2- or 4-marker array. Data were smoothed using a 4th order 4 Hz dual-pass Butterworth filter. A loss of up to 30 kinematic frames (approximately 10 video frames) or 1/3 of a second was interpolated with cubic spline interpolation. The onset of the reach was refined by an algorithm that searched for the minima velocity in a 30 kinematic frame window prior to the behaviorally coded start of the reach (see Corbetta & Thelen, 1996 for similar algorithm). A three-point differentiation technique was used to calculate speed (mm/s). The average speed was the mean speed of the frames during the reach, and the peak speed was the maximum speed of the reach.

Other variables of interest including reach duration, straight-line distance, path length, and reach smoothness (number of movement units) were calculated with finite difference methods. Reach duration was the time in seconds between the onset and offset of the reach. Reach straightness was computed by the ratio of straight-line distance to path length. Smoother reaches were indicated by values closer to 1, the typical adult straightness ratio for unobstructed reaches (Churchill, Hopkins, Rönnqvist & Vogt, 2000). Movement units were computed with an algorithm derived from von Hofsten (1991) and described previously in Chapter 2 of this thesis.

Statistical Analysis

Hand preference was characterized at both the group and individual levels. Analysis at the group level used a Laterality Index (LI) score. The LI was calculated for infants with at least 10 unimanual actions. The LI was computed by subtracting the number of left unimanual responses from the number of right unimanual responses and then dividing by the total number of unimanual responses, $LI=(R-L)/(R+L)$. Hand preference values on this index range from -1.00 to 1.00 with negative values interpreted as a left bias and positive values interpreted as a right bias. One-sample t-tests against a hypothetical mean of 0 were performed on LI scores for each age group. The absolute value of each LI score was computed to assess degree of lateralization bias with numbers closer to 0 indicating weak lateralization and numbers closer to 1 indicating strong lateralization. Two sample t-tests were used to examine sex differences in LI scores. Infants were classified at the individual level by percentage of hand use. Infants with at least 65% right hand use were considered right-preferent. Infants with at least 65% left hand use were considered left-preferent. All other infants were considered ambi-preferent.

Linear mixed-effects models (Bates & Maechler, 2009) were used to examine the effects of hand (left or right), hand preference (hand recoded as preferred hand or non-preferred hand), and gender (male or female) on each dependent variable for the reaching task using the statistical program R (R Development Core Team, 2009). P-values were estimated from Monte Carlo simulations (Baayen, 2008). Models used the following formula: *Dependent Variable ~ Hand * Hand Preference * Gender + SLD + (1|Subject)*. Straight-line distance (SLD) was used as a covariate to control for differences in arm

sizes. Duration was an additional covariate in models for smoothness. For models involving behavioral parameters, the formula was similar but did not include any covariate terms. Values three times the interquartile range (IQR) were excluded from analyses (**Table 3.1**).

Table 3.1. Outliers for the reach tasks identified as values three times the IQR.

	Variable	Values Excluded	Total Observations
Fitting Task			
	Reach Average Speed	>682 mm/s	170 (*N*=37)
	Reach Peak Speed	>1930 mm/s	169 (*N*=37)
	Reach Duration	>1960 ms	173 (*N*=37)
	Reach Smoothness	>10	170 (*N*=37)
	Reach Straightness	None	174 (*N*=37)
	Grip Ball	>121600 ms	173 (*N*=37)
	Transport Average Speed	>967 mm/s	131 (*N*=29)
	Transport Peak Speed	>2522 mm/s	129 (*N*=29)
	Transport Duration	None	135 (*N*=29)
	Transport Smoothness	>11	129 (*N*=28)
	Transport Straightness	None	135 (*N*=29)
Cup Task			
	Reach Average Speed	>633 mm/s	365 (*N*=56)
	Reach Peak Speed	>1363 mm/s	362 (*N*=55)
	Reach Duration	>2830 ms	371 (*N*=56)
	Reach Smoothness	>7	355 (*N*=55)
	Reach Straightness	None	375 (*N*=56)
	Grip Food	None	375 (*N*=56)

IQR=Interquartile Range; *N*=Number of participants.

For reaching to the ball and to the cup, dependent variables included reach duration (ms), reach average speed (mm/s), reach peak speed (mm/s), reach smoothness (number of movement units), and reach straightness (SLD/path). On the fitting task only, additional dependent variables included grip ball time (ms), transport duration (ms), transport average speed (mm/s), transport peak speed (mm/s), transport smoothness (number of movement units), and transport straightness (SLD/path) for the portion of the movement fitting the ball into the toy. On the cup task only, grip food time (ms) was also

examined. Finally, time to peak speed and percentage of the movement to peak speed were analyzed for each task.

Results

Hand Preference

Sufficient hand preference data were collected from all infants in the 11-month (*N*=35) and 14-month (*N*=18) age groups. One infant in the 17-month age group could not be separated from a toy brought in from home and his hand use play data were not included in the statistical analysis of hand preference (*N*=19). Laterality Index (LI) scores in 11-month-olds ranged from -0.48 to 1.00 (M=0.20, SD=0.31, **Figure 3.5**). A one-sample t-test found a population-level right hand bias, $t(34)= 3.720$, $P<0.001$. A two-samples t-test did not find a difference between males and females for direction of hand preference, $t(29.876)=-0.005$, $P>0.05$ (Males=0.20, Females=0.20). Degree of hand preference lateralization as determined by the absolute value of LI scores ranged from 0.00 (not lateralized) to 1.00 (strongly lateralized). The mean degree of lateralization for the 11-month-old group was 0.30 (SD=0.21). There was also no gender difference for degree of hand preference lateralization, $t(30.944)=-0.141$, $P>0.05$ (Males=0.30, Females=0.29). Individually, 3 infants were classified as left-preferent, 11 infants were classified as right-preferent, and 21 infants were classified as ambi-preferent.

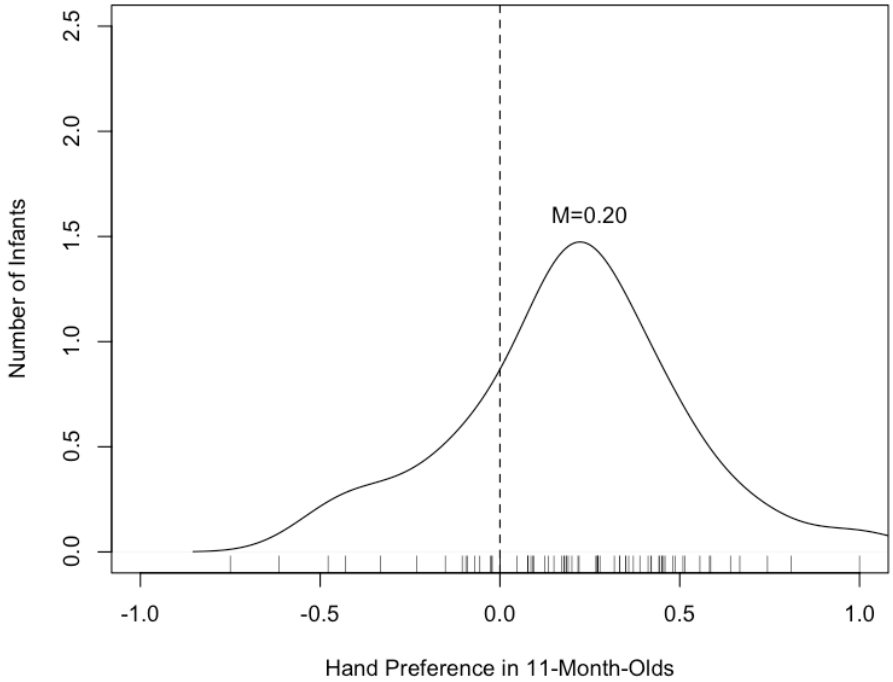

Figure 3.5. Hand preference distribution for 11-month-olds.

LI scores in 14-month-olds ranged from -0.09 to 0.81 (M=0.29, SD=0.25, **Figure 3.6**). A one-sample t-test revealed a population-level right hand bias, $t(17)=4.968$, $P<0.001$. Degree of hand preference lateralization ranged from 0.00 to 0.81 (M=0.31, SD=0.23). There was no gender difference for direction of hand preference, $t(15.888)=-0.575$, $P<0.05$ (Males=0.32, Females=0.26), or degree of hand preference lateralization, $t(15.939)=-0.888$, $P>0.05$, for 14-month-olds (Males=0.40, Females=0.26). At the individual level, 0 infants were classified as left-preferent, 10 infants were classified as right-preferent, and 8 infants were classified as ambi-preferent.

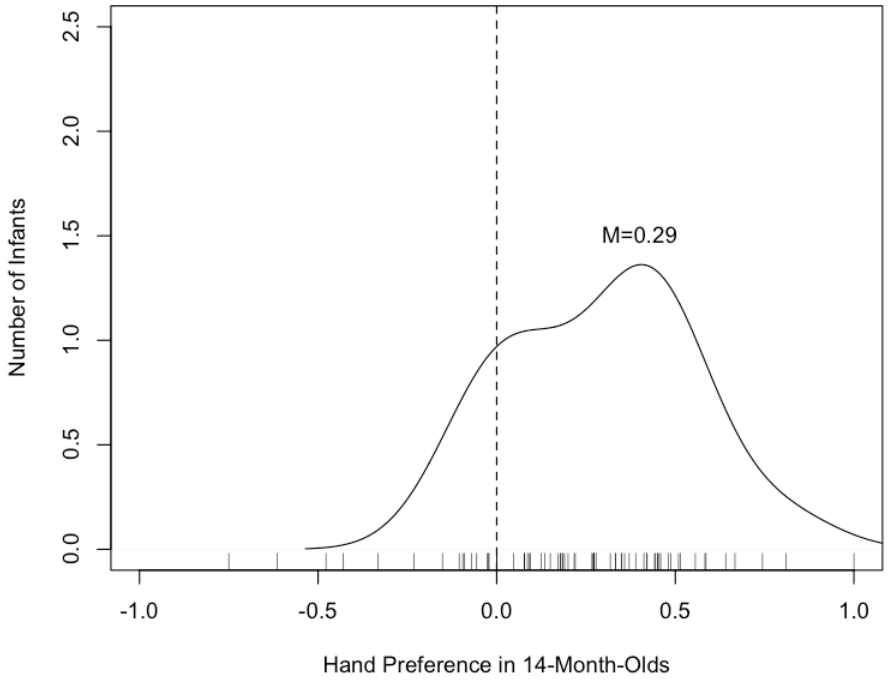

Figure 3.6. Hand preference distribution for 14-month-olds.

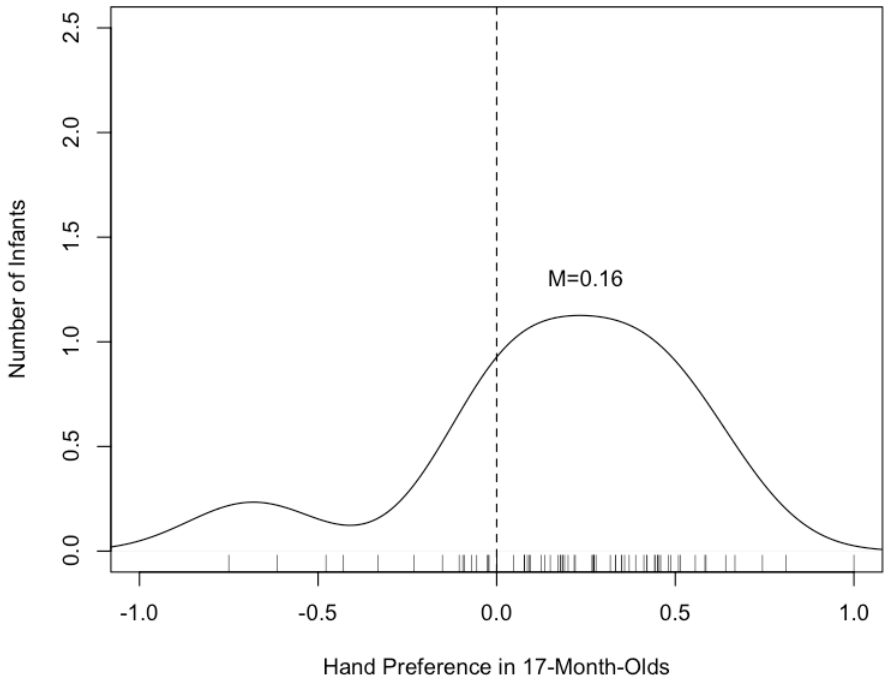

Figure 3.7. Hand preference distribution for 17-month-olds.

LI scores in 17-month-olds ranged from -0.75 to 0.67 (M=0.16, SD=0.37, **Figure 3.7**). The results of the one-sample t-test indicated a rightward trend in 17-month-olds that was marginally significant, $t(18)=1.878$, $P=0.077$. There was no difference between males and females for direction of hand preference from HI scores, $t(16.775)= 0.889$, $P>0.05$ (Males=0.08, Females=0.23). Degree of hand preference lateralization ranged from 0.00 to 0.75 (M=0.32, SD=0.24), and there was no difference between males and females on the absolute value of LI scores, which were used to determine the degree of hand preference lateralization, $t(16.743)= 1.203$, $P>0.05$ (Males=0.25, Females=0.38). Individually, 2 infants were classified as left-preferent, 8 infants were classified as right-preferent, and 9 infants were classified as ambi-preferent in the 17-month-old group.

Movement Quality

Infants were grouped into right or non-right (left and ambi combined) hand preference groups for linear mixed-effects modeling due to the lack of left-preferent infants in the 14-month-old group, and the small number of left-preferent infants overall (N=5). While this is a clear limitation, this division was necessary for statistical analyses. Hand use was recoded as preferred hand or non-preferred hand according to hand preference group. In the right-preferent group, the preferred hand was the right hand and the non-preferred hand was the left hand. In the non-right-preferent group, the preferred hand was designated as the left hand and the non-preferred hand was the right hand. The total number of infants as well as the gender of infants in each hand preference group is given in **Table 3.2**.

Table 3.2. Distribution of infant hand preference groups.

	NR	R		NR	R		NR	R
Males			*Females*			*Total*		
11 Months	15	6	11 Months	9	5	11 Months	24	11
14 Months	3	7	14 Months	5	3	14 Months	8	10
17 Months	6	3	17 Months	5	5	17 Months	11	8

NR = Non-right-preferent group, R = Right-preferent group.

For the fitting task, 303 trials were video coded. Of these, 174 had valid marker data for the reach to the ball component of the task (57%). There were 90 left-handed reaches and 84 right-handed reaches. 91 reaches were recoded as the preferred hand and 83 reaches were recoded as the non-preferred hand. By age group, there were 48 reaches from 11-month-olds (*N*=16), 63 reaches from 14-month-olds (*N*=13), and 63 reaches from 17-month-olds (*N*=8). The average number of reaches from each infant was 5 ± 3.

For the transport component of the fitting task (moving the ball from the platform to the top of the toy), 135 movements had valid marker data (45%). There were 71 left-handed transports and 64 right-handed transports. 70 transport movements were recoded as the preferred hand and 65 were recoded as the non-preferred hand. In this subset of the fitting task, 26 transport movements were from 11-month-olds (*N*=9), 50 movements were from 14-month-olds (*N*=12), and 59 movements were from 17-month-olds (*N*=8). The average number of transports from each infant was 5 ± 4.

Results from the reach and grasp portions of the fitting task are given in **Table 3.3.** Reach duration was shorter in the right hand than the left hand for the reach to the ball in the 11- and 14-month-olds, but the opposite was true for the 17-month-olds. An effect of hand preference was found for reaches to the ball such that the preferred hand was straighter than the non-preferred hand. For gripping the ball, an effect of gender by

hand preference was found. In females, the preferred hand was slower to grip the ball. In males however, the preferred hand was faster to grip the ball. There were no effects on reach average speed, reach peak speed, or reach smoothness; however, time to peak speed and percent to peak speed varied by gender, hand, and hand preference. Due to these complex interactions, reaches were not divided into segments for addition analyses.

Table 3.3. Results for the reach and grasp component of the fitting task in infants.

Parameter	*Effect*	*P-value*	*Means*
Reach Duration (ms)	Age x Hand	0.032	11: Right=638, Left=844 14: Right=731, Left=741 17: Right=745, Left=693
Reach Straightness (SLD/Path)	Pref	0.014	P=0.61, NP=0.52
Grip Ball (ms)	Gender x Pref	0.042	Females: P=1063, NP=981 Males: P=1033, NP=1371

Results from the transport portion of the fitting task are given in **Table 3.4.** A three-way interaction of gender by hand preference by age was found for transport average speed. In females, the non-preferred hand had a faster average speed than the preferred hand in every age group except 17-month-olds. In males, the preferred hand had a faster average speed in every age group. A number of effects on transport smoothness were found. First, transport movements became smoother with age. Second, an effect of gender by age was found. In 11 month-olds, males had smoother transports as compared to females; however, females had smoother transports in 14- and 17-month-olds. Third, age also interacted with gender and hand preference. In females, the non-preferred hand was smoother than the preferred hand in 14- and 17-month-olds but not 11-month-olds. In males, the preferred hand was smoother than the non-preferred hand in

all age groups. Fourth and finally, an interaction between hand and hand preference was also observed for transport smoothness. In the right-preferent group, the right hand was smoother than the left hand. In the non-right-preferent group, the right hand was also smoother than the left hand, but the difference between the hands was much smaller.

A number of effects on transport straightness were also found. In general transport movements became straighter with age. Age also interacted with gender on transport straightness. Males had straighter transport movements than females in the 11- and 14-month-old groups. Females were straighter than males however in the 17-month-old group. Finally, age and gender interacted with hand preference. In females at every age, the preferred hand was straighter than the non-preferred hand for transporting the ball. In males a different pattern was observed. In 11-month-olds, the non-preferred hand was straighter than the preferred hand. In 14-month-olds, the hands were virtually equivalent in transport straightness. In 17-month-olds, the preferred hand was straighter than the non-preferred hand, matching females of all ages. There were no effects on transport duration, transport average speed, or transport peak speed.

Moving on to the cup task, 532 trials were video coded. A greater number of infants participated in this task, possibly due to greater motivation because of the food involved. Of the trials that were identified for analysis, 375 reaches to the cup had valid marker data (70%). There were 198 left-handed reaches and 177 right-handed reaches. 196 reaches were recoded as the preferred hand and 179 were recoded as the non-preferred hand. For the cup task, 166 reaches were from 11-month-olds (N=27), 110 reaches were from 14-month-olds (N=18), and 99 reaches were from 17-month-olds (N=11). The average number of trials from each infant was 7 ± 3.

Table 3.4. Results for the transport component of the fitting task in infants.

Parameter	*Effect*	*P-value*	*Means*
Transport Avg. Speed (mm/s)	Age x Gender x Pref	0.043	11=Females: P=132, NP=175 11=Males: P=360, NP=169 14=Females: P=195, NP=290 14=Males: P=286, NP=203 17=Females: P=319, NP=299 17=Males: P=286, NP=246
Transport Smoothness (MUs)	Age	0.023	11m=4.38, 14m=3.16, 17m=2.98
Transport Smoothness (MUs)	Age x Gender	0.015	11m: Females=4.76, Males=3.67 14m: Females=3.10, Males=3.17 17m: Females=2.43, Males=3.83
Transport Smoothness (MUs)	Age x Gender x Pref	0.011	11=Females: P=4.69, NP=5.00 11=Males: P=3.25, NP=4.00 14=Females: P=4.00, NP=2.88 14=Males: P=2.90, NP=3.53 17=Females: P=2.78, NP=2.06 17=Males: P=2.73, NP=4.83
Transport Smoothness (MUs)	Hand x Pref	0.034	Right (P)=3.33, Left (NP)=3.71 Left (P)=3.08, Right (NP)=2.79
Transport Straightness (SLD/Path)	Age	0.020	11m=0.39, 14m=0.53, 17m=0.60
Transport Straightness (SLD/Path)	Age x Gender	0.009	11m: Females=0.36, Males=0.44 14m: Females=0.40, Males=0.56 17m: Females=0.67, Males=0.50
Transport Straightness (SLD/Path)	Age x Gender x Pref	0.010	11=Females: P=0.38, NP=0.29 11=Males: P=0.26 NP=0.59 14=Females: P=0.54, NP=0.37 14=Males: P=0.57, NP=0.55 17=Females: P=0.68, NP=0.67 17=Males: P=0.58, NP=0.44

Table 3.5. Results for the cup task in infants.

Parameter	*Effect*	*P-value*	*Means*
Reach Duration (ms)	Pref	0.031	P=876, NP=959
Reach Duration (ms)	Age x Hand x Pref	0.021	11: Right (P)=689, Left (NP)=980 11: Left (P)=934, Right (NP)=1016 14: Right (P)=975, Left (NP)=969 14: Left (P)=746, Right (NP)=835 17: Right (P)=1023, Left (NP)=992 17: Left (P)=799, Right (NP)=929
Reach Avg. Speed (mm/sec)	Gender x Hand x Pref	0.028	F: Right (P)=208, Left (NP)=244 M: Right (P)=171, Left (NP)=178 F: Left (P)=199, Right (NP)=198 M: Left (P)=212, Right (NP)=224
Reach Straightness (SLD/Path)	Gender	0.016	Females: 0.61, Males=0.52
Reach Straightness (SLD/Path)	Gender x Hand x Pref	0.032	F: Right (P)=0.65, Left (NP)=0.66 M: Right (P)=0.52, Left (NP)=0.47 F: Left (P)=0.60, Right (NP)=0.54 M: Left (P)=0.56, Right (NP)=0.53
Reach Straightness (SLD/Path)	Age x Hand x Pref	0.021	11: Right (P)=0.58, Left (NP)=0.61 11: Left (P)=0.51, Right (NP)=0.46 14: Right (P)=0.55, Left (NP)=0.56 14: Left (P)=0.71, Right (NP)=0.58 17: Right (P)=0.62, Left (NP)=0.50 17: Left (P)=0.64, Right (NP)=0.60
Grip Food (ms)	Age	0.0002	11m=3595, 14m=3082, 17m=2618
Grip Food (ms)	Gender	0.041	Females=3003, Males=3369
Grip Food (ms)	Gender x Pref	0.022	Females: P=2889, NP=3121 Males: P=3465, NP=3270
Grip Food (ms)	Age x Gender x Pref	0.042	11=Females: P=3477, NP=3691 11=Males: P=3375, NP=3861 14=Females: P=2513, NP=3253 14=Males: P=3456, NP=2923 17=Females: P=2075, NP=2433 17=Males: P=3663, NP=2538

Results from the cup task are given in **Table 3.5.** For reaches to the cup, an effect of hand preference was found on reach duration such that the preferred hand had a shorter duration than the non-preferred hand overall. Age and hand also interacted with hand preference on reach duration. For 11-month-olds, the preferred hand had a shorter duration than the non-preferred hand. The same pattern was found in the non-right-preferent groups only for the 14- and 17-month-olds. In the right-preferent groups for the two older ages, the non-preferred hand had a shorter duration than the preferred hand. A three-way interaction was also seen for reach average speed between gender, hand preference and hand. The non-preferred hand had a faster average speed than the preferred hand in both male and female right-preferent groups as well as non-right-preferent males. In non-right-preferent females, the hands were essentially equivalent for reach average speed.

An effect of gender was seen on reach straightness for reaches to the cup, with females having straighter reaches than males. Gender also interacted with hand and hand preference on reach straightness. The preferred hand was straighter than the non-preferred hand in right-preferent males, non-right-preferent females, and non-right-preferent males. For right-preferent females, reach straightness was about equal with each hand. Age also interacted with hand and hand preference on reach straightness. For 11- and 14-month-olds, the left hand was straighter regardless of hand preference group. For 17-month-olds however, the preferred hand was straighter than the non-preferred hand within each hand preference group.

Several effects were seen for time to grip the food that had been placed in the cup. In general, latency to remove the food from the cup decreased with age. There was also

an effect of gender on grip time, with females taking the food out of the cup faster than males. Gender interacted with hand preference as well, with the preferred hand being faster to grip the food than the non-preferred hand in females, but the non-preferred hand was faster than the preferred hand in males. Finally, age also interacted with gender and hand preference. The preferred hand was faster removing the food from the cup in both females and males in the 11-month-old group. For 14- and 17-month-olds, the preferred hand was faster in females, but the non-preferred hand was faster in males. Overall there were no effects on reach smoothness or reach peak speed for the cup task; however, time to peak speed and percent to peak speed varied by age, gender, hand, and hand preference. Like the fitting task, there were no main effects of either hand or hand preference on time to peak or percent to peak speed for reaches to the cup. Therefore, reaches were not divided into segments for further analyses.

Discussion

Overall there was a significant right hand preference at the group-level for 11-month-olds and 14-month-olds. Although the mean for the 17-month-olds was similar to the younger age groups, it did not reach statistical significance despite the large number of infants in the sample. Previous research has suggested that hand use undergoes change in infancy during periods of motor reorganization, such as during the transition to walking independently (e.g., Corbetta & Bojczyk, 2002). The majority of 11-month-old infants were not walking by the time of testing (83%). By contrast, nearly all of the 14-month-olds (89%) and the 17-month-olds (95%) were walking independently when they were assessed for hand use preference in the present study.

Because the target test ages were either before or after the walking transition, the lack of a group-level right hand preference seen in the 17-month-old group may have been the result of language, rather than motor, reorganization. Unfortunately, information regarding language development was not collected on the infants in the present study. In general however, infants experience a growth in vocabulary around 18 months, and hand preference for manipulation is correlated to hand preference for pointing during this period of language development, but not prior to it (Vauclair & Imbault, 2009). It may be that the high demand on the left hemisphere for speech and language development leads to a slight decrease in the use of the right hand for manipulation at 17 months compared to other points in infancy. The issue is confounded by the use of the hands for both language functions (e.g., pointing) as well as manipulative functions, and the debate over whether lateralized processes like language and handedness share the same underlying mechanism or operate independently.

Longitudinal studies are needed to further test the hypothesis that hand preference changes dynamically as major systems such as locomotion and language are reorganized over development (e.g., Corbetta & Thelen, 2002). A pilot study of this nature was conducted in a single infant (Infant X) from 9 months to 24 months of age using the hand preference protocol described for the present study. The results are plotted in **Figure 3.8**. Infant X had a strong left hand bias during the first assessment at 9 months of age. At 10 months of age, Infant X began taking steps and hand preference seemed to disappear. At 11 months of age, Infant X had a right hand bias, much like the 11-month-olds in the present study. Hand preference showed high variability between 12 and 13 months, corresponding to the period when Infant X began walking independently across a room.

At 14 months of age, Infant X had a strong right hand bias, again matching data from the present study. Finally, Infant X underwent a period of almost no bias from 16 to 18 months before returning to a right hand bias at 22 to 24 months of age. Although these data are anecdotal and may not be typical, they lend support to the findings from the present study and give credence to the hypothesis that hand preference changes dynamically in infancy.

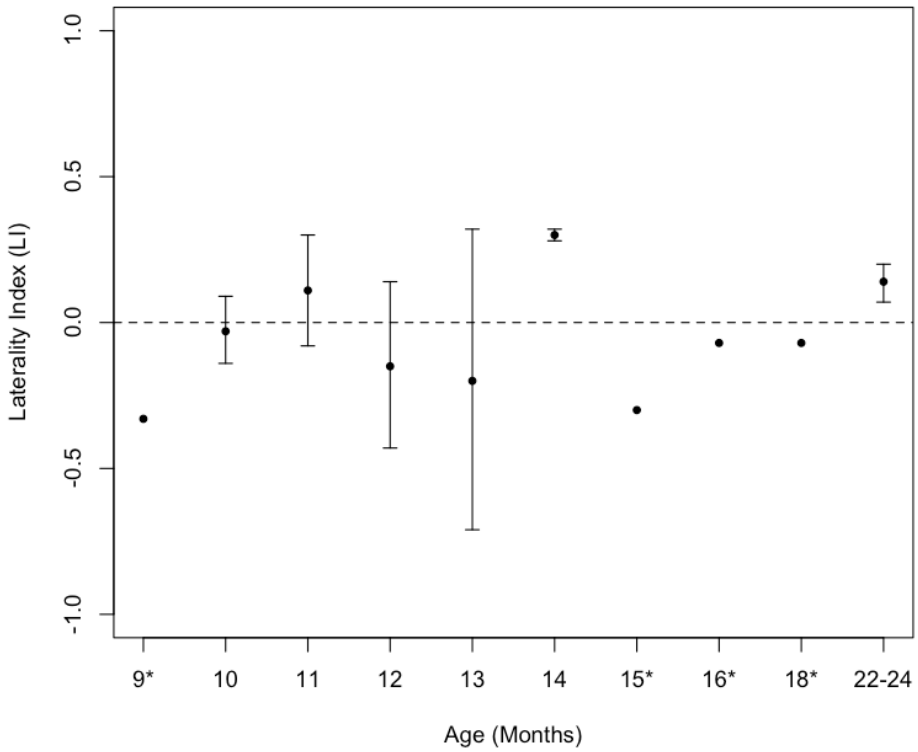

Figure 3.8. Hand use preference changes from 9 to 24 months in Infant X. Bars denote 95% confidence interval. Results may be atypical. *Denotes single assessment for age.

For the reaching tasks, there were a number of intuitive age effects. Babies' transport movements on the fitting task became both smoother and straighter with age, indicating that ability to fit improved. Babies also became quicker at removing the food from the cup. There were no other robust age-related changes for reaching to the ball,

grasping the ball, or reaching to the cup. Surprisingly, main effects of gender and interactions between gender and other factors were found for some of the variables, despite a lack of differences between males and females on the hand preference measure. These results may indicate that the relationship between movement quality and hand use varies with gender. Gender differences in motor skill have not been found for infants (Mondschein, Adolph, Tamis-LeMonda, 2000); however, males have been reported to outperform females on some motor tasks during childhood and later development (Thomas & French, 1985). It is possible that the gender effects observed here for movement quality are precursors for the motor differences between males and females noted later in life. Nevertheless, gender differences will be discussed with regards to interactions between hand use and hand preference only. Further interpretation is beyond the scope of this thesis.

In general, differences were observed between the preferred hand and the non-preferred hand, rather than the left and right hand. In the right-preferent group, the preferred hand was the right hand and the non-preferred hand was the left hand. In the non-right-preferent group, the preferred hand was considered to be the left hand and the non-preferred hand was consequently the right hand. For the predictions concerning hand preference, I had speculated that the preferred hand would have a shorter reach duration time and a straighter reach. I also predicted that the preferred hand would be faster to grasp the ball and to remove the food from the cup. For reaches to the cup, the preferred hand did have a shorter duration than the non-preferred hand. For reaches to the ball, reach duration varied by age and hand, with the right hand having a shorter duration in younger infants. There were no significant effects for transport duration. For reach

straightness, the preferred hand was straighter reaching to the ball and in most infants the preferred hand was also straighter reaching to the cup. For ball transport straightness, the preferred hand was straighter than the non-preferred hand for females in every age group. For males, the preferred hand was straighter when compared to the non-preferred hand in the older infants, but not in the 11-month-olds.

These data may suggest greater control in the use of the preferred hand compared to the non-preferred hand. In addition to these results on duration and straightness, findings on average speed also lend some support to the hypothesis that differences in movement quality reflect underlying hand preferences. For the reach to the cup, the preferred hand had a slower average reach speed compared to the non-preferred hand in the majority of infants. There were no effects on average speed for reaching to the ball. For transporting the ball, the preferred hand also had a slower average speed in females. For males however, the preferred hand had a faster average speed. Differences in average speed may reflect differences in control, with slower speeds indicating greater control and faster speeds indicating less control. Speed may be associated with smoothness, with faster movements also being smoother due to fewer corrections. The non-preferred hand was smoother than the preferred hand in most female infants for transporting the ball, whereas the preferred hand was smoother than the non-preferred hand in male infants. Although there were differences between males and females for average speed and smoothness, the direction of the findings appears consistent for transport movements.

For removing the food from the cup, the preferred hand was faster than the non-preferred hand in females at every age and also for males in the 11-month-old group. For males in the older age groups, the preferred hand was slower at getting the food out of the

cup than the non-preferred hand. The opposite effect was seen for time to grasp the ball. In females, the preferred hand was slower to grasp the ball and in males, the preferred hand was faster to grasp the ball. These differences may be related to the grasping demands of each task. A precision grip was needed for the cup task in contrast to the power grip or whole-hand grip required to pick up the ball. The actions that followed each grasp were also different. After the food was taken out of the cup, it was brought to the mouth and eaten on virtually all of the trials. This action of self-feeding would have been very familiar for the infant. In the present study, the average age infants began eating hard cereal was 8 ± 2 months (with the exception of 2 infants in the 11-month group that were not eating hard cereal at home at the time of the study). For the ball however, the object had to be moved to a specific location of the toy and thus may have required some additional planning on the part of the infant. Infants had less experience with fitting toys. Only 60% of parents reported that their 11-month-old had a similar fitting toy at home. Just over 80% of parents of infants in the older age groups reported having fitting toys at home. Parents also commented that although they had this type of toy, their child did not necessary perform fitting actions when playing with it spontaneously.

Prior work on movement quality in infants has only examined differences between left and right arm reaches and has not accounted for individual hand use preferences. In previous studies, a bias for the right hand was found such that the right hand was straighter, smoother, and had a shorter reach duration time than the left hand for infants at 6, 9, and 12 months of age (Morange-Majoux et al., 2000; Hopkins & Rönnqvist, 2002; Rönnqvist & Domellöf, 2006). The number of participants in each of

these studies was limited however, ranging from 8 to 17 infants. Given the hand use preference findings from the current study in addition to other published reports, it is likely that the majority of infants in these samples were right-preferent. It is possible that these effects could be attributed to hand preference, rather than differences between the hands. No main effects of hand were found for either the fitting task or the cup task in the current study.

One limitation of the current study was the potential of misclassifying infants' hand use preferences. Hand preferences were calculated from reaching to and manipulating a series of toys in a 7.5-minute play session in a laboratory setting. Infants were also constrained to sitting on a parent's lap and playing at a table. Under these conditions, infants' hand use patterns may have differed from their day-to-day hand use. Nevertheless, the preferred hand differed from the non-preferred hand on a number of movement characteristics, suggesting that the manner in which infants were divided into hand preference groups was largely accurate, even with the limitation of combining left- and ambi-preferent infants into a single category. Future work could attempt to increase the number of left-preferent infants in the sample. Additional analysis of the underlying distribution of infant hand use preferences would also be informative for understanding hand preference groups in infancy, and determining if left and ambi are truly separate.

A follow-up study could compare infants' hand use preferences measured in this study to hand use preferences in the same individuals as school-age children when handedness has stabilized to further examine the accuracy of infant handedness groups, and also to examine infant movement quality retrospectively. Differences in movement quality between the preferred and non-preferred hands for the fitting and cup tasks were

also examined in a control group of adults with stable hand use preferences in Experiment 4.

Finally, interpretations of these data are limited due to the cross-sectional design in that infants were observed only once. If hand use is truly fluid, future studies should incorporate a longitudinal design to further examine movement quality and handedness trajectory over development in the same infants.

Experiment 4: Movement Quality and Handedness in Human Adults

Handedness has been well studied in adults. The majority of adults are right-preferent, meaning they prefer to use the right hand on a variety of tasks (Annett, 2002). In addition to having clear hand preferences, adults also have a distinct hand performance advantage with the preferred hand on fine motor tasks. In a study by Triggs, Calvanio, Levine, Heaton and Heilman (2000), equal numbers of left- and right-preferent adults completed multiple measures of hand performance, including a peg moving task and a finger tapping task. Hand preferences were confirmed with standard hand use inventories. Triggs and colleagues showed that the right hand moved more pegs and tapped a key faster than the left hand in individuals classified as right-preferent. Accordingly, the left hand outperformed the right hand in individuals classified as left-preferent. Similar results of the preferred hand having greater proficiency than the non-preferred hand on tests of fine motor skill have been reported in other adult studies (e.g., Steenhuis & Bryden, 1999; Corey, Hurley & Foundas, 2001; Judge & Stirling, 2003).

Kinematic studies of reaching in adults commonly measure a single arm (i.e., the right) likely because the majority of people are right-preferent. Recent work has begun to

explore differences between the left and right arms for reaching tasks, but to date only right-preferent individuals have been examined (Sainburg & Kalakanis, 2000; Bagesteiro & Sainburg, 2002; Grosskopf & Kuhtz-Buschbeck, 2006; Wang & Sainburg, 2007). These studies have suggested a left hemisphere/right arm advantage for limb trajectory control and right hemisphere/left arm advantage for limb posture control (see Sainburg, 2002). However, it is difficult to draw conclusions from this work without equivalent studies in left-preferent participants who may show a different pattern of hemispheric specialization for motor control. To truly understand potential differences in arm reaching kinematics, the left and right arms must be compared in both left- and right-preferent adults on the same measures. It is unclear whether differences between arms for reaching kinematics can be attributed to a general specialization (i.e., left arm vs. right arm), or are the result of hand preference (i.e., preferred arm vs. non-preferred arm).

A comparison group of adults were tested on the infant hand performance measures of reaching to and fitting a ball into a toy and reaching to and removing a Cheerio® from a cup with both hands as described in Experiment 3. The purpose of adding an adult control group was to be able to compare the relationship between hand preference and hand performance in two very different populations: infants whose handedness may be fluid, and adults whose handedness is stable. These data also provided an important first look into potential hand-by-hand preference differences or hand specialization differences in reaching kinematics in both left- and right-preferent groups. Although adults have stable hand preferences that can be reliably measured, they also have accumulated experience with the preferred hand/arm in contrast to infants. If hand preference impacts both hand skill and arm kinematics, experience could create a

greater divergence between the preferred and non-preferred sides in adults compared to infants. Given the infant findings from Experiment 3 of hand preference effects on reach movement quality, I predicted that the preferred arm would differ from the non-preferred arm for reaching to the objects in each task, for transporting a ball to the top of a toy, and for placing a Cheerio® at a given location in adults. Furthermore, I predicted that the preferred hand would outperform the non-preferred hand on latency to grip a ball and latency to remove food from a cup.

Method

Participants

Twelve adults recruited from the University of Massachusetts Amherst campus participated in this study. The hand used to sign the study consent form determined the individual's eligibility to take part in the study as either left-preferent or right-preferent. Hand preference and gender were equally distributed across groups. There were 6 adults in the left-preferent group (males=3; females=3). The average age was 27.61 ± 4.72 years. There were 6 adults in the right-preferent group (males=3; females=3). The average age was 30.16 ± 3.36 years. Participants were blind to the objectives of the study, and were told that the purpose of the experiment was to examine reaching to differently sized objects (i.e., a ball and a Cheerio®) in infants and adults. Adults received monetary compensation for their participation.

Procedure

The University of Massachusetts Institutional Review Board (IRB) approved the following procedure. Adults participated in one session of approximately 30 minutes and completed two reaching tasks and a 10-item questionnaire. Before the study began, the primary investigator reviewed the informed consent with the participant (**Appendix G**), described the study procedure, and explained the motion capture equipment. Reaching tasks were recorded with a Sony Handycam® Hard Disc Drive DCR-SR45 digital camcorder that was positioned behind the experimenter to record the participant's behavior.

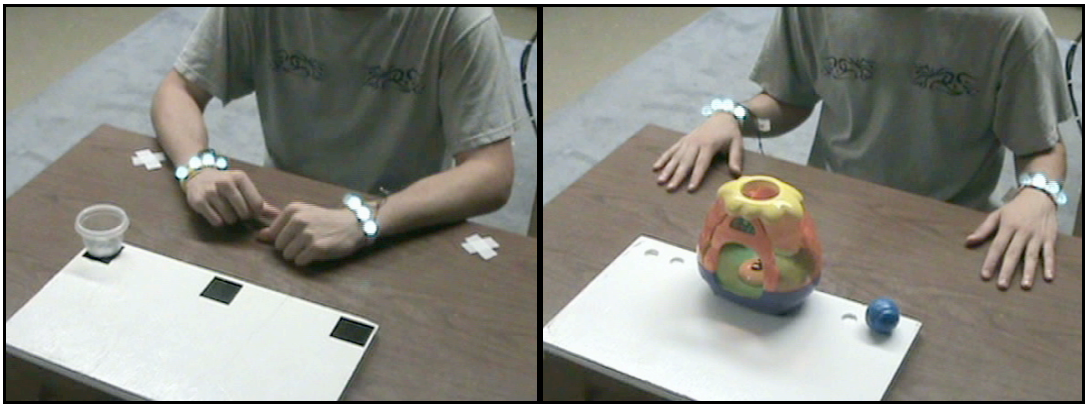

Figure 3.9. Left: Hand starting locations marked in tape on the testing table with an "X". Right: Adult participant with hands in the ready starting position prior to a fitting trial.

Participants wore four infrared markers embedded in Velcro® wristbands on each arm during the reaching tasks and their movements were tracked by a VZ4000 Visualeyez™ real-time motion capture system (PhoeniX Technologies Incorporated, see Experiment 3). Kinematic and behavioral data were synced with the NightShot Plus function on the camcorder. The participant sat across from the primary experimenter at the same testing table used for the infants. The participant was instructed to place his or

her hands flat on the table at two locations marked in tape with an “X” in a ready starting position prior to each trial (**Figure 3.9**).

For the fitting task, the experimenter demonstrated the fitting movement twice with each hand in the same manner done for the infant study prior to beginning fitting trials. Participants were instructed to reach to and pick up the ball, then place it in the top opening of the toy (**Figure 3.10**). Participants were given 12 trials total with the ball starting on alternating sides for each trial. Ball starting location (ipsilateral to preferred hand or ipsilateral to non-preferred hand) was counterbalanced across hand preference groups and participants. Following the demonstration by the experimenter, kinematic data capture was started and trials began. The participant was reminded to place his or her hands in the ready position before each trial. No instructions were given as to the speed at which the task should be completed.

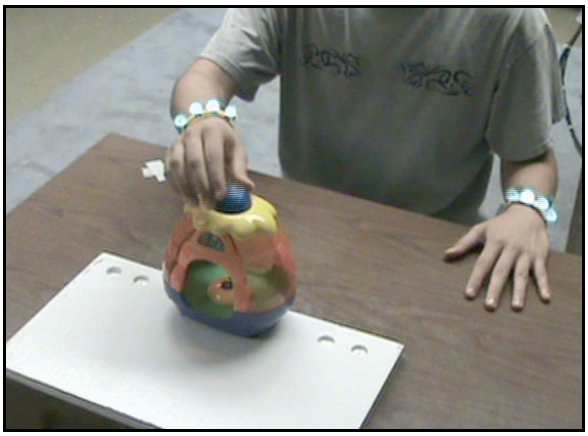

Figure 3.10. Adult fitting the ball with the right hand on the fitting task.

For the cup task, the experimenter placed a Cheerio® in one of the cups and the participant was instructed to reach to the cup, remove it, and place it back on the “X”

corresponding to that hand's starting position (**Figure 3.11**). Participants were given 12 trials total with the cup on alternating sides for each trial. Participants were again randomly assigned to cup starting location, with half of the participants starting with the cup on the same side as the preferred hand and the other half of the participants starting with the cup on the same side as the non-preferred hand. The participant was reminded to put his or her hands in the ready starting position before each trial, and no instructions were given regarding speed for retrieving the food. Kinematic data were captured continuously throughout each hand performance measure using the camera setup given in **Figure 3.4B**, and all sessions were videotaped for later analysis.

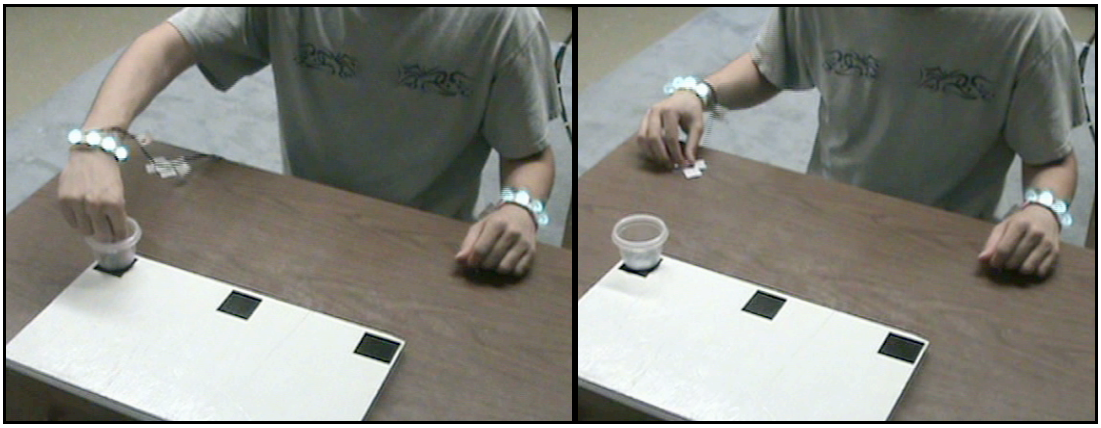

Figure 3.11. Left: Adult participant removing the Cheerio® with the right hand on the cup task. Right: Adult participant placing the Cheerio® on the "X" with the right hand.

Following completion of the reaching tasks, hand preference was examined in greater detail with a standard handedness questionnaire, the Edinburgh Handedness Inventory (Oldfield, 1971; **Appendix H**). This ten-question inventory addressed hand preference for writing, drawing, throwing, using scissors, using a toothbrush, using a knife without a fork, using a spoon, using a broom, striking a match, and opening the lid

of a box. The experimenter explained the questionnaire instructions in detail to each participant. Adults were told to read each item on the questionnaire and put checkmarks in the column(s) corresponding to the hand(s) they would normally use for that task. Two checkmarks in the same column indicated that the preference for using that hand was so strong they would never use the opposite hand for that item. One checkmark in each column indicated that they would use either hand for the item in question. The experimenter provided additional clarification for test items as needed, and checked each questionnaire for completeness after the participant had indicated their responses.

Data Analysis

Video data were reviewed frame-by-frame at 30 frames per second using MPEG Streamclip (Squared 5) for both reaching tasks. Behaviors were scored using the operational definitions given in Experiment 3 for the fitting and the cup tasks. An additional behavior called place Cheerio® was scored for adults on the cup task. Place time was defined as the first frame where the participant's hand was entirely removed from the cup to the first frame where the participant's finger(s) or hand touched the "X" on the testing table. Placing was not analyzed for infant participants because the majority of babies ate the food after removing it from the cup. The primary observer scored 100% of the data for each task. A second observer scored 25% of the fitting data and 25% of the cup data. Both observers had previously been trained on the coding system for infant data (Experiment 3). Inter-rater reliability for the adult data using a percent agreement score that allowed for a difference of 5 frames between observers was 97% for reach onset, 100% for ball contact, 100% for ball lift, and 100% for ball fit on the fitting task. Inter-

rater reliability was 100% for reach onset, 100% for enter cup, 100% for exit cup, and 100% for place Cheerio® on the cup task. Kinematic data were computed for the reach to the ball, the transport of the ball (fitting action), the reach to the cup, and the placing of the Cheerio® using custom Matlab programs described in Experiment 3 of this thesis.

Hand preference was characterized at both the group and individual levels. Analysis at the group level used a Laterality Index (LI) score. The LI was computed by subtracting the number of left responses from the number of right responses and then dividing by the total number of responses as indicated on the Edinburgh Handedness Inventory, $LI=(R-L)/(R+L)$. Hand preference values on this index range from -1.00 to 1.00 with negative values interpreted as a left bias and positive values interpreted as a right bias. One-sample t-tests against a hypothetical mean of 0 were performed on LI scores separated by hand preference group (left-preferent and right-preferent). Two sample t-tests were used to examine sex differences in LI scores. Analysis of hand use preferences at the individual level used the cutoffs established for the Edinburgh Handedness Inventory (Oldfield, 1971). Scores between -1.00 and -0.40 were considered left-preferent, scores between -0.39 and 0.39 were considered ambi-preferent, and scores between 0.40 and 1.00 were considered right-preferent.

Linear mixed effects models (Bates & Maechler, 2009) were used to examine the effects of hand (left or right), hand preference (hand use recoded as preferred hand or non-preferred hand), and gender (male or female) on each dependent variable for the reaching tasks using the statistical program R (R Development Core Team, 2009) as described in Experiment 3. For right-preferent adults, the preferred hand was the right

hand and the non-preferred hand was the left hand. For left-preferent adults, the preferred hand was the left hand and the non-preferred hand was the right hand.

Table 3.6. Values three times the interquartile range (IQR) for the fitting and cup tasks.

	Variable	*Values Excluded*	*Total Observations*
Fitting Task	Reach Duration	>1420 ms	131
	Reach Average Speed	None	132
	Reach Peak Speed	None	132
	Reach Straightness	<0.5972	131
	Reach Smoothness	>2 MUs	No variability for test
	Ball Grip Time	>1300 ms	131
	Transport Duration	>1280 ms	130
	Transport Average Speed	None	132
	Transport Peak Speed	None	132
	Transport Straightness	None	132
Cup Task	Reach Duration	None	129
	Reach Average Speed	>980 mm/s	127
	Reach Peak Speed	>2302 mm/s	127
	Reach Straightness	<0.2070	127
	Reach Smoothness	None	129
	Ball Grip Time	None	129
	Place Duration	None	129
	Place Average Speed	None	129
	Place Peak Speed	None	129
	Place Straightness	None	129

Outliers were identified from boxplots as values three times the interquartile range and were removed (**Table 3.6**). For reaching to the ball and to the cup, dependent variables included reach duration (ms), reach average speed (mm/s), reach peak speed (mm/s), reach smoothness (number of movement units), reach straightness (SLD/path), and grip time (ms). On the fitting task only, additional dependent variables included transport duration (ms), transport average speed (mm/s), transport peak speed (mm/s), and transport straightness (SLD/path) for the portion of the movement fitting the ball into the toy. On the cup task only, additional dependent variables included place duration (ms), place average speed (mm/s), place peak speed (mm/s), and place straightness

(SLD/path) for the portion of the movement placing the Cheerio® on the table on the "X". Finally, time to peak speed and percentage of the movement to peak speed were also analyzed for each task.

Results and Discussion

Laterality Index (LI) scores calculated from hand use preferences as indicated on the Edinburgh Handedness Inventory ranged from -0.40 to -0.90 for the left-preferent group. All of the adults in this group had significant left hand use preferences at the individual level. A one-sample t-test confirmed a population-level left bias, $t(5)=-8.174$, $P<0.001$, **Figure 3.12** (M=-0.70, SD=0.21). A two-sample t-test did not find an effect of gender on LI scores for the left-preferent group, $t(3.86)=-0.354$, $P>0.05$ ($M_{Males}=-0.67$, $M_{Females}=-0.73$). In the right-preferent group, one adult female was classified as being ambi-preferent with an LI score of 0.30. Her data were excluded from further analyses, as she did not meet the qualifications for a stable right hand preference. LI scores for the remaining 5 adults in the right-preferent group ranged from 0.70 to 1.00, and there was a population-level right bias for this subset, $t(4)=14.333$, $P<0.001$, **Figure 3.13** (M=0.86, SD=0.13). There was no difference between males and females for LI scores in the right-preferent group, $t(-2.43)=-0.500$, $P>0.05$ ($M_{Males}=0.90$, $M_{Females}=0.83$).

Valid marker data were processed from 100% of adult reaching trials, likely because of the controlled starting position of each hand. Results from the fitting task are presented in **Table 3.7**. For the reach to the ball, the right hand had a shorter duration and a straighter movement compared to the left hand. When reach straightness was further examined, the preferred hand was straighter than the non-preferred hand in the right-preferent group but the straightness ratios were virtually identical for the preferred and

non-preferred hands in the left-preferent group. An effect of gender was observed for reach straightness, with males executing straighter reaches to the ball compared to females. For gripping the ball, the right hand was faster in females but the left hand was slightly faster in males. Finally, the right hand reached a higher peak speed for the transport movement compared to the left hand regardless of hand preference group. There were no other effects for fitting transport. There were also no effects on reach average speed or reach peak speed for reaches to the ball; however, time to peak speed and percent to peak speed varied by gender, hand, and hand preference. Consequently, reaches were not divided further into segments for addition analyses. Of particular interest however was the main effect of hand on time to peak speed. Reach peak speed occurred earlier in the movement in the right hand as compared to the left hand for reaches to the ball.

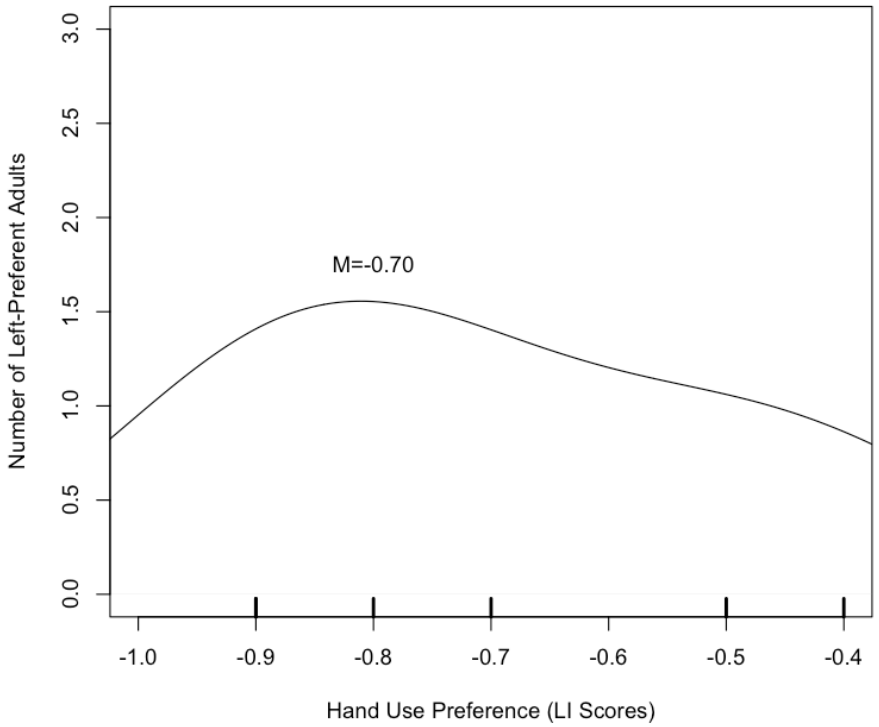

Figure 3.12. Hand use preference distribution for left-preferent adults.

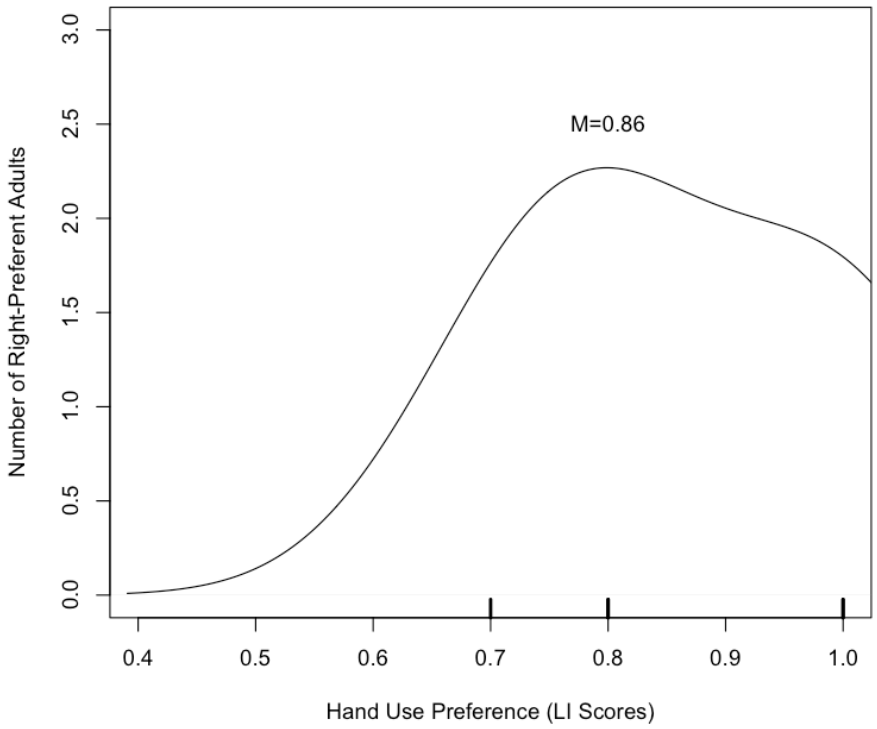

Figure 3.13. Hand use preference distribution for right-preferent adults.

Table 3.7. Results for the fitting task in adults.

Variable	*Effect*	*P-value*	*Means*
Reach Duration (ms)	Hand	0.016	Right=811, Left=854
Reach Straightness (SLD/Path)	Hand	0.012	Right=0.88, Left=0.86
Reach Straightness (SLD/Path)	Hand x Pref	<0.0001	Right (P)=0.84, Left (NP)=0.81 Left (P)=0.90, Right (NP)=0.90
Reach Straightness (SLD/Path)	Gender	0.015	Males=0.88, Females=0.85
Grip Ball (ms)	Gender x Hand	0.018	Females: Right=537, Left=579 Males: Right=618, Left=608
Transport Peak Speed (mm/s)	Hand	0.003	Right=641, Left=617

Results from the cup task are presented in **Table 3.8**. Similar to the reach to the ball, the right hand had a shorter duration and straighter movement for reaching to the cup. The right hand also had lower reach peak speeds compared to the left hand. There was also an effect of hand preference on reach peak speed, with the preferred hand having lower peak speeds. In addition, the preferred hand was straighter reaching to the cup than the non-preferred hand, although this effect may have been driven by the great disparity between hands in the right-preferent group. Like reaches to the ball, males also had straighter movements than females for reaches to the cup. For reach smoothness, a hand-by-hand preference effect was found such that the preferred hand was smoother in the right-preferent group, but the non-preferred hand was smoother in the left-preferent group. This pattern suggests that the right hand may have been smoother than the left hand, but the effect of hand alone on smoothness was not significant. There were no effects on reach average speed.

Reaches to the cup were not further divided into earlier and later segments for additional analyses because the time to peak speed and percent to peak speed for these reaches varied by gender, hand, and hand preference, creating complex interactions. Interestingly, reach peak speed occurred earlier in the movement in the right hand as compared to the left hand for reaches to the cup. The same pattern was observed for reaches to the ball. These findings match differences found between the right and left hands overall.

Table 3.8. Results for the cup task in adults.

Variable	*Effect*	*P-value*	*Means*
Reach Duration (ms)	Hand	0.004	Right=738, Left=780
Reach Duration (ms)	Gender x Hand x Pref	0.018	F: Right (P)=775, Left (NP)=879 M: Right (P)=752, Left (NP)=759 F: Left (P)=717, Right (NP)=678 M: Left (P)=797, Right (NP)=762
Reach Peak Speed (mm/sec)	Hand	0.019	Left=776, Right=762
Reach Peak Speed (mm/sec)	Pref	0.023	NP=780, P=761
Reach Smoothness (No. MUs)	Hand x Pref	0.030	Right (P)=1.61, Left (NP)=1.76 Left (P)=1.42, Right (NP)=1.28
Reach Straightness (SLD/Path)	Hand	<0.001	Right=0.89, Left=0.82
Reach Straightness (SLD/Path)	Pref	0.036	P=0.86, NP=0.85
Reach Straightness (SLD/Path)	Hand x Pref	0.005	Right (P)=0.87, Left (NP)=0.78 Left (P)=0.86, Right (NP)=0.91
Reach Straightness (SLD/Path)	Gender	0.010	Males=0.88, Females=0.82
Grip Cheerio (ms)	Gender x Hand Pref	0.005	F: Right (P)=730, Left (NP)=753 M: Right (P)=1116, Left (NP)=1073 F: Left (P)=906, Right (NP)=959 M: Left (P)=843, Right (NP)=800
Place Peak Speed (mm/sec)	Pref	0.029	NP=981, P=947
Place Straightness (SLD/Path)	Gender	0.037	Males=0.85, Females=0.82
Place Straightness (SLD/Path)	Gender x Hand x Pref	0.002	F: Right (P)=0.79, Left (NP)=0.78 M: Right (P)=0.90, Left (NP)=0.88 F: Left (P)=0.84, Right (NP)=0.85 M: Left (P)=0.83, Right (NP)=0.82

For gripping the cheerio, the preferred hand was faster than the non-preferred hand in both hand preference groups for females, but the non-preferred hand was faster than the preferred hand in both hand preference groups for males. An additional effect of gender was found on place straightness, such that males made straighter movements in putting the Cheerio® on the "X" compared to females. Males were also straighter at placing with their preferred hand than their non-preferred hand. In females, place straightness ratios were nearly equivalent in the preferred and non-preferred hands. Finally, the preferred hand had lower place peak speeds compared to the non-preferred hand, regardless of hand preference group. The preferred hand may have had greater hand control in reaching to the cup and placing the Cheerio® in a designated location. There were no effects on place duration, place average speed, or place smoothness.

In general, similar differences were observed between the right and left hands regardless of hand preference across tasks. For reaches to the ball and to the cup, the right hand had a shorter duration time and a straighter movement compared to the left hand. The right hand also had a lower peak speed and a smoother movement for reaches to the cup as opposed to the left hand. There were no effects on reach peak speed or reach smoothness for the fitting task. Moreover, the right hand reached its peak speed earlier in the movement than the left hand for both reaches to the ball and to the cup. Collectively, these data support previous findings for a right hand advantage in controlling reaching movements in adults (for review, see Goble & Brown, 2008); however, these interpretations are based on previous studies that compared the hands of right-preferent individuals only. In the current study, both left- and right-preferent participants were examined. A right hand bias still emerged with the inclusion of left-preferent adults,

suggesting that kinematic differences in arm movements in adults may in part be attributed to a right arm/left hemisphere specialization for particular motor movements.

Nevertheless, this is not to say that hand preference did not also impact adults' performance on the reaching tasks. The preferred hand was straighter than the non-preferred hand for reaches to the cup. The preferred hand also had a slower peak speed for reaches to the cup and for placing movements in moving the Cheerio® from the cup to the table. In addition, the preferred hand was straighter to place the Cheerio® in right-preferent adults; however, place straightness ratios were similar across hands in left-preferent adults. Right-preferent adults also had straighter reaches to the ball with the preferred hand compared to the non-preferred hand. Again, straightness ratios for ball reaches were similar in the preferred and non-preferred hands of left-preferent adults. Other studies that have examined the proficiency of the left and right hands in adult behavior have reported a greater difference between the preferred and non-preferred hands in right-preferent adults compared to left-preferent adults (e.g., Judge & Stirling, 2003). One explanation for this finding is that left-preferent individuals have been described as more likely to use their non-preferred hand as compared to right-preferent individuals (e.g., Mamolo, Roy, Rohr & Bryden, 2006). Thus left-preferent adults may have more experience using both hands on motor tasks, whereas right-preferent adults show a bias towards using the preferred hand.

Gender differences were also observed. Males had straighter reaches to the ball and to the cup, and also executed straighter placing movements for moving the Cheerio® compared to females, suggesting a possible male advantage in controlling movements. This finding corresponds to previous reports of gender differences in motor abilities, with

males outperforming females on particular tasks (Thomas & French, 1985). Different effects were found for grasping movements however. For grasping the Cheerio®, males were slower with their preferred hand while females were faster with their preferred hand. For grasping the ball, males were slower with their right hand whereas females were faster with their right hand. Although the statistical analyses controlled for differences in arm sizes by including straight-line distance as a covariate in the linear mixed-effects models, there may have been differences in hand sizes that led to the differential grasping patterns observed for the ball and the Cheerio®. It is clear from the current study that many variables affect reach quality in adults, including hand (left or right), hand preference (preferred or non-preferred hand), and gender. Additional discussion of these adult data in comparison to infant data from Experiment 3 can be found in the general discussion of this thesis (Chapter 4).

CHAPTER 4

GENERAL DISCUSSION

Human handedness differs from rhesus monkey handedness in the direction of asymmetry and the degree of asymmetry. Although both species show population-level hand preferences, approximately 90% of human adults are right-preferent whereas 68% of adult macaques are left-preferent (Annett 2002; Papademetriou et al., 2005). Despite these differences, the factors underlying a handedness trajectory may be similar across primates. Previous explanations of handedness including genetic models and environmental hypotheses do not appear to be sufficient (Provins, 1997). Rather, greater focus is needed on how these influences interact to establish handedness; in particular, species-typical development may weight these factors differently.

Experiment 1 examined the relationship between neonatal asymmetries and later hand use preference in infant rhesus monkeys. A group-level leftward supine head bias was found in monkey neonates that corresponded to greater activity in the left hand while supine; however, supine head orientation did not predict later hand preference as measured by reaching at 1 month of age or manipulation on a coordinated bimanual task measured at 6 to 9 months of age. In addition, the majority of monkeys also showed a greater response to tactile stimulation on the left side of the body in the first month of life. These data suggest that a left bias is present early in rhesus monkey development, and may be indicative of an early right hemispheric specialization in rhesus monkey development.

Nevertheless, the relationship between supine head orientation and hand preference is not the same in rhesus monkey infants as it is in human infants. A supine posture is common in human infants, but rarely occurs spontaneously in nursery-reared rhesus infants. This difference in early posture experience between species may explain the difference in the degree of hand asymmetry seen between humans and rhesus monkeys. Given additional supine experience as neonates, rhesus monkeys might develop stronger hand use preferences from an increase in asymmetrical hand experience in viewing and moving the hand ipsilateral to the head turn. This hypothesis could be directly tested with a nursery-rearing paradigm in rhesus monkeys, whereas it would be impossible to do with human infants. Future work could also compare neonatal biases with hand use preferences in adulthood, as hand preference may not be fully developed by late infancy in rhesus monkeys.

In Experiment 2, qualitative differences were found between the left and right hands for reaching in rhesus monkey infants. The left hand was smoother than the right hand overall. The left hand also reached higher peak speeds in the earlier portion of the reach and was faster on average than the right hand in the later portion of the reach. Smoother reaches coupled with higher peak speeds and faster average speeds suggests that left hand movements are ballistic, which is consistent with the postural origins theory of primate handedness (MacNeilage et al., 1987; MacNeilage, 2007). A ballistic left hand specialization for reaching in rhesus monkeys may have derived from earlier primates that relied on ballistic movements to capture moving insect prey. This is not to say that reaching in rhesus monkeys is entirely ballistic and incapable of correction and control,

but merely that the left hand may have retained some residual ballistic qualities from a feeding strategy of their primate ancestors.

A complimentary right hand bias for manipulation has also been proposed for monkeys. The coordinated bimanual TUBE task has been used to measure hand use for manipulation in removing food from a tube with one or more fingers. Contrary to the postural origins theory, rhesus monkeys do not show a right hand preference for this task (Experiment 1; Bennett, Suomi & Hopkins, 2008). It should be noted however that I did not examine the quality of fine motor skill in the right and left hands in these monkeys. In addition, data from Experiments 1 and 2 represent a restricted set of tasks for measuring hand use preferences, and hand use may vary by task or task demands in rhesus monkeys. Differences in hand ability may also vary based on the outcome measure used, such as error rate or the latency to complete a task (Rigamonti, Previde, Poli, Marchant & McGrew, 1998). Additional studies are needed that are targeted at understanding whether rhesus monkeys show a right hand advantage for manipulation, particularly tasks that require highly skilled motor movements.

Table 4.1. Hand use preference differences between monkeys and humans.

Group	Reaching	Manipulation
Rhesus monkeys	Left hand	Right hand*
Human infants	Right hand	Right hand
Human adults	Right hand	Right hand

*Suggested by postural origins theory (MacNeilage et al., 1987).

In contrast to nonhuman primates, there is no evidence for a division of labor between hands in humans for reaching and manipulation (**Table 4.1**). Rather, the right hand (left hemisphere) has been implicated in motor control in adults (Serrien, Ivry &

Swinnen, 2006; Goble & Brown, 2008). Results from Experiment 4 with adult humans are consistent with this pattern, with differences observed between the right and left hands regardless of hand preference group for two different reaching tasks. The right hand had a shorter duration time and a straighter movement when compared to the left hand for reaching to a ball and reaching to a cup. In addition, the right hand was smoother with a lower peak speed when reaching to the cup. Lower peak speeds, straighter movements, and shorter movement durations in particular may indicate greater motor control with the right hand for adults. Hand preference effects were also seen, but only for elements of the cup task that required fine motor skill. The preferred hand was straighter for reaches to the cup and also for placing the Cheerio® on the starting "X" as compared to the non-preferred hand. The preferred hand has previously been shown to be more proficient on fine motor tasks than the non-preferred hand in adults (Steenhuis & Bryden, 1999; Triggs et al., 2000; Hurley & Foundas, 2001; Annett, 2002; Judge & Stirling, 2003).

In contrast to adults, human infants showed an overall pattern of qualitative differences between the preferred and non-preferred hands for reaching, instead of the right and left hands in Experiment 3. Infants were examined once in a cross-sectional design at 11, 14, or 17 months. Infants were classified as right-preferent or non-right-preferent based on hand use during a play session prior to completing the reaching tasks. The non-right group included the small number of left-preferent infants observed, and subsequently the preferred hand was considered to be the left hand in the non-right-preferent group. The preferred hand was the right hand in the right-preferent group.

Human infant and adult data are compared in **Table 4.2**. For human infants, the preferred hand was straighter reaching to the ball and transporting the ball on the fitting task, and also straighter reaching to the cup. In addition, the preferred hand had a shorter duration time and a slower average reach speech on the cup task. Overall a significant population-level right hand use preference was found for 11- and 14-month-olds. The mean hand preference for 17-month-olds was similar to that of the younger age groups; however, a rightward bias was not significant at this age. These findings match previous studies that have reported a right hand use preference for reaching and manipulation in younger infants (Michel, Ovrut & Harkins, 1985; Michel, Tyler, Ferre & Sheu, 2006).

Table 4.2. Trends for infants and adults on the fitting and cup tasks.

Task		*Infants*	*Adults*
Fitting Task	Reach Duration	**Right hand**	**Right hand**
	Reach Straightness	**Preferred hand**	**Right hand**
	Reach Average Speed	No effects	No effects
	Reach Peak Speed	No effects	No effects
	Reach Smoothness	No effects	No effects
	Grip ball	**Preferred hand****	**Right hand***
	Transport Duration	No effects	No effects
	Transport Straightness	**Preferred hand**	No effects
	Transport Average Speed	**Non-pref. hand***	No effects
	Transport Peak Speed	No effects	**Right hand**
	Transport Smoothness	**Non-pref. hand***	No effects
Cup Task	Reach Duration	**Preferred hand**	**Right hand**
	Reach Straightness	**Preferred hand**	**Right/Pref. hand**
	Reach Average Speed	**Non-pref hand**	No effects
	Reach Peak Speed	No effects	**Left hand**
	Reach Smoothness	No effects	**Right hand**
	Grip food	**Preferred hand***	**Preferred hand***
	Place Duration	Not measured	No effects
	Place Straightness	Not measured	**Preferred hand**
	Place Average Speed	Not measured	No effects
	Place Peak Speed	Not measured	**Non-pref. hand**
	Place Smoothness	Not measured	No effects

*Females only. **Males only.

Overall, these human data suggest that differences in movement quality in infancy are due to hand preference, whereas differences in adulthood are largely due to hemispheric specialization. Several factors may account for this pattern of results including differential hand exposure in infancy and the developmental trajectory of hemispheric specialization. Infants initially have highly selective experience with their hands as compared to adults. Neonatal supine head orientation bias has been shown to correspond to hand preference for both the initial hand used for reaching as well as frequency of hand use for reaching at reach onset, indicating that hand use preferences are already present at 4 months of age in human infants (Michel, 1981). One prevailing hypothesis is that an early head turning bias induces other biases, including asymmetric visual regard of one hand and increased activity in that viewed hand (Coryell & Michel, 1978; Michel & Harkins, 1986). An early hand use preference could create further asymmetrical hand use experience in that the infant will use the preferred hand more than the non-preferred hand when learning additional motor skills.

More importantly, the skill of each hand will improve differentially with experience, causing the preferred hand to be more proficient on a task regardless of hand preference direction in infancy when motor skills are still developing. For the reaching measures described in this dissertation, the preferred hand may have been straighter than the non-preferred hand because the infant had greater control in the hand with the greater overall reaching experience. Despite a hand selection bias, the infant will also try the non-preferred hand on tasks some of the time, which could explain the fluctuations seen in hand use preference in longitudinal studies (Gesell & Ames, 1947; Corbetta & Thelen, 1999).

Hemispheric specialization may emerge gradually over development. Motor control appears to become increasingly lateralized to the left hemisphere. A specialization for motor control can explain why the right hand (left hemisphere) was found to have a straighter reach in a group of adults composed of both left- and right-preferent individuals. Hypothetical trajectories for hand efficiency from infancy to adulthood for a right-preferent individual are given in **Figure 4.1**. The right hand becomes increasingly more efficient with increased experience. The left hand also improves, but at a different rate since the left hand is used less often than the right hand. The right hand is always superior for reaching movements, at first because it is the preferred hand and ultimately because of a hemispheric specialization for reaching motor movements.

Similar hypothetical trajectories for hand efficiency in a left-preferent individual are given in **Figure 4.2**. In infancy, the left hand outperforms the right hand because the left hand has been used more often. As experience with the right hand accumulates and the hemispheres mature, the right hand eventually surpasses the left hand in controlling some motor movements like reaching. A left hand bias could still persist for practiced tasks such as writing and for other fine motor skills. These data are limited in that they cannot pinpoint when a hemispheric specialization for motor control, particularly reaching, may be established in human development. Additional studies evaluating the relationship between hand preference and the quality of left and right hand movements in human infants across development are needed. Computational simulations may be useful for modeling these hypothesized effects in differential hand experience that may account for hand preference effects on movement quality in infancy and hemispheric specialization effects on movement quality in adulthood.

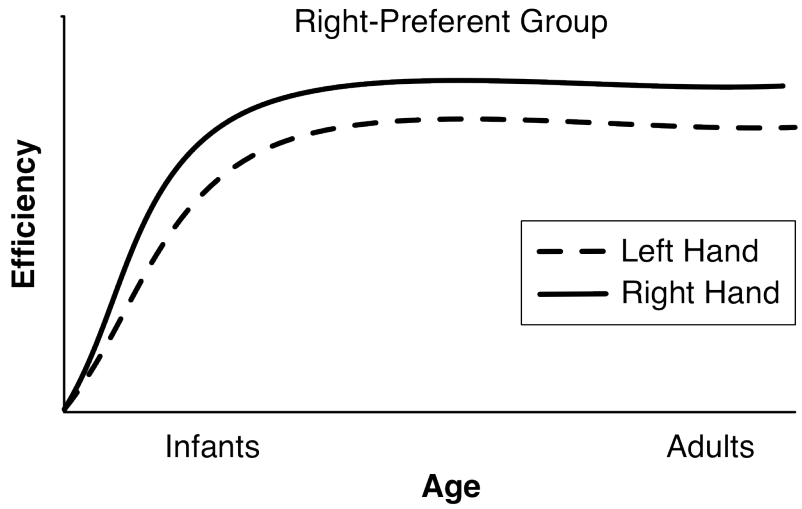

Figure 4.1. Hypothetical hand trajectories for hand efficiency in a right-preferent individual. The right hand outperforms the left hand in infants due to hand preference experience. The right hand outperforms the left hand in adults due to a left hemispheric specialization for motor control.

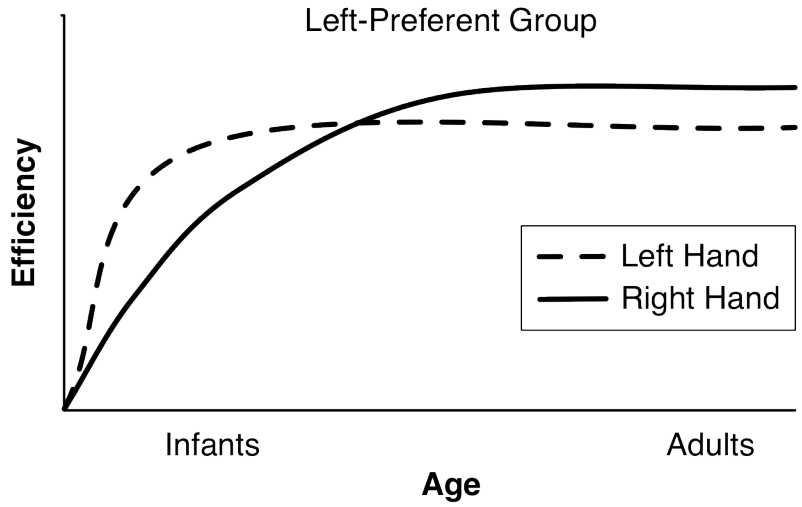

Figure 4.2. Hypothetical hand trajectories for hand efficiency in a left-preferent individual. The left hand outperforms the right hand in infants due to hand preference experience. The right hand outperforms the left hand in adults due to a left hemispheric specialization for motor control.

For rhesus monkey infants, no effect of hand preference on reach quality was observed at 4.5 months of age when monkeys were divided into either left and non-left groups or left, ambi, and right groups; however, hand preference may have been measured too early. Rhesus monkey infants differed from human infants in that individual monkeys had hand use preferences, but there was no bias at the group-level for either early infancy at the onset of reaching or later infancy for a manipulation task. Consequently, monkeys may have had similar experiences with each hand in infancy, resulting in the lack of a hand preference effect on movement quality. Another possibility is that hemispheric specialization is evident earlier in macaque development than human development, since macaques develop at a rate that is approximately four times faster than humans (Gunderson & Sackett, 1984). Future work should examine movement quality in monkey infants at the onset of successful reaching as well as in adult subjects to determine whether hand preference influences movement quality at other points across the lifespan, or if hand differences for reach quality in rhesus monkeys can be explained solely by hemispheric specialization.

Species-typical experience may play a critical role in a trajectory for handedness in primates. Neonatal supine experience creates a hand asymmetry that persists through development and impacts early movement quality in human infants. In rhesus monkeys, a similar mechanism could be in place but not fully activated given the group-level head turning bias, but weak hand use preference. For both humans and rhesus monkeys, hemispheric specialization appears to impact reach quality; however, such specializations occur in different hemispheres. In rhesus monkeys, a left hand/right hemisphere advantage for ballistic reaching was observed. The left hand was smoother, achieved a

greater early peak speed, and was faster on average in the later part of the reach. Rhesus monkeys may represent a transitional period in primates if motor skills are lateralized to separate hemispheres, with ballistic reaching specialized to the left hemisphere and manipulation specialized to the right hemisphere. In higher primates, all motor control may have shifted to the left hemisphere. This hypothesis merits further examination in other nonhuman primate species. In contrast, there was a right hand/left hemisphere advantage for motor control in adult humans. The right hand was straighter, had a shorter duration time, and had a lower peak speed than the left hand.

Hand preference has historically been attributed to experience in nonhuman primates, but not in the same manner suggested by this dissertation. Warren (1980) strongly advocated for experiential factors in determining hand use preference. To illustrate, one hand is chosen by chance, reinforced by the environment, and consequently used again in the future. Unlike explanations for human handedness, there are no genetic models for handedness in nonhuman primates. Recent evidence in chimpanzees showing that hand preference is heritable despite differences in rearing conditions has challenged the view that genetics are not involved in nonhuman primate hand preference (Hopkins, Bales & Bennett, 1994; Hopkins, 1999; Hopkins, Dahl & Pilcher, 2001; Hopkins, Wesley, Russell & Schapiro, 2006). Familial relationships for hand preference have also been examined in macaques. Westergaard, Lussier and Higley (2001) reported that hand preference direction was positively correlated in rhesus monkey mothers and their offspring, but no relationship was found between fathers and offspring. Although these data cannot exclude maternal environmental influence, a gene or set of genes linked to handedness may not be unique to humans.

Humans show a rightward pattern of asymmetry in a number of behaviors across development including early gestation fetal arm movements (Hepper, McCartney & Shannon, 1998; McCartney & Hepper, 1999; de Vries et al., 2001); fetal thumb-sucking (Hepper, Shahidullah and White, 1991); neonatal supine head orientation (Turkewitz, Gordon & Birch, 1965; Coryell & Michel, 1978; Michel & Goodwin, 1979; Michel, 1981); holding time duration (Caplan & Kinsbourne, 1976; Petrie & Peters, 1980; Hawn & Harris, 1983); infant reaching and manipulation (Michel, Ovrut & Harkins, 1985; Michel, Tyler, Ferre & Sheu, 2006); and adult hand use for a variety of tasks (Annett, 2002). The right shift theory proposed by Marian Annett implicated a single allele (RS) in the development of left cerebral dominance and right hand preference. Individuals with a copy of the RS allele are predisposed to right hand preference whereas individuals without the allele develop hand preference by chance. In addition, Annett (2006) demonstrated that chimpanzees are right shifted for hand use, although to a lesser extent than humans.

Increasing evidence of a leftward pattern of asymmetries in rhesus monkeys may suggest a left shift genetic factor or some other mechanism that predisposes monkeys to a left bias, resulting in a leftward neonatal supine head orientation, greater activity in the left hand while supine, greater response to tactile stimulation on the left side of the body, a leftward trend for unimanual reaching in infants, and a population-level left hand preference primarily for reaching in adult macaques. In addition, left hand reaching was found to be qualitatively different than right hand reaching in infant rhesus monkeys.

The ultimate explanation for handedness in either human or nonhuman primates will likely include a genetic mechanism such as a right or left shift factor as suggested by

Annett (2002). It will also account for environmental and experiential factors that may differentially shape a trajectory for hand preference, especially species-typical development. Finally, understanding handedness in primates will also include an evolutionary history as suggested by MacNeilage and collegues (1987). Further work examining the ontogeny of hand preference and hemispheric specialization in rhesus monkey infants, human infants, and other primate infants will contribute to a greater understanding of the interaction of various factors that give rise to primate laterality.

APPENDIX A

PRIMATE NEONATAL NEUROBEHAVIORAL ASSESSMENT

A. The infant's state is recorded before it is disturbed and removed from the cage.

B. Visual Orient

Swaddle the infant and hold with the left hand. With the right hand, hold the Tweety bird toy at the back of the infant's head and bring around the side slowly to the front. Repeat on the other side. Hold the toy above the head and slowly bring it down and repeat holding the toy below the head and slowly moving it up. For each direction the infant is scored as 0 = no orient, 1 = direct brief contact, 2 = direct prolonged contact.

C. Visual Follow

With the infant swaddled, hold the toy in front of the infant's face and move it horizontally. Repeat with a vertical movement. For each direction, the infant is scored as 0 = no follow, 1 = starts then stops, 2 = complete follow.

D. Reach and Grasp

This is scored while doing C and D from above. Do they reach and grasp at the toy? The categories are 0 = can't assess, 1 = swat, no finger flex, 2 = intent, grasp with flex.

E. Startle to Auditory

When the infant is swaddled and calm, hit the metal table behind it with a pair of metal scissors and look for a startle reflex. The categories are 0 = no startle, 1 = eye blink or head jerk, 2 = whole body jerk.

F. Orient to Auditory

When the infant is swaddled, hold it vertically with one side facing the tester. The tester makes smacking noises with his or her mouth. This is repeated with the infant facing in the other direction. The response is scored as 0 = no orient, 1 = partial orient, 2 = full orient with visual inspection.

G. Duration of Looking

This is calculated from the above testing. 0 = none, 1 = brief, 2 = prolonged. You can get an estimate by adding up previous visual scores. For example, if they add up to 20, duration of looking = 2. If they add up to 10, duration = 1, 5 = 0.5, and 0 = 0.

H. Distractible

Determined from the animal's performance up until now. The categories are 0 = none, 1 = slight, 2 = definite.

I. Attention

Determined from the animal's performance up until now. The categories are 0 = none, 1 = slight, 2 = definite.

J. Tactile Response

While the infant is held on the forearm without a blanket, gently rub the leg with a pen starting from the ankle and running to the hip. Repeat with the other leg. Then gently rub the pen from the wrist to the shoulder. Repeat with the other arm. The tactile response is scored 0 = no response, 1 = slight response, 2 = definite or exaggerated response.

K. Galants

While the infant is held on the forearm without a blanket, gently rub the back with a pen moving from the base of the skull to the tail on the side of the spine and repeat on the other side of the spine. The gallant is scored as 0 = no response, 1 = slight response, 2 = definite or exaggerated response.

L. Palmar Grasp

Start at the wrist and gently swipe your finger down the length of the hand. Repeat with the other hand. The response is scored as 0 = no grasp, 1 = weak grasp, digits closed loosely, 2 = strong grasp.

M. Plantar Grasp

Start at the heel and gently swipe your finger down the length of the foot. Repeat with the other foot. The response is scored as 0 = no grasp, 1 = weak grasp, digits closed loosely, 2 = strong grasp.

N. Inversion

With the infant swaddled in a blanket, hold the infant out and facing you. Bend over and swing the infant towards the floor. The response is scored as 0 = no response, 1 = slight response, 2 = definite aversion.

O. Head Posture Prone and Supine

Hold the infant with one hand around the belly so that the infant is facing downwards (prone). Hold the infant so that the infant is facing up (supine). The response for each is scored as 0 = flaccid, hanging down, 1 = head lift with limb semi flex, 2 = sustained head lift with semi flex.

P. Body Righting

Lay the infant on its back and record the time it takes to turn over and right itself. 0 = no righting in 15 seconds, 1 = rights in 5-15 seconds, 2 = rights in less than 5 seconds.

Q. Traction

Lay the infant on its back, holding onto the arms. Lift the infant up with the arms as if it were doing sit-ups. The response is scored as 0 = arms extend, head lag, 1 = arms moderately flexed, head lifted, 2 = resistance to extension with head turn.

R. Aversion on Back

This is scored based on how the infant reacted to P and Q. The response is scored as 0 = none-no vocalization, 1 = slight-short vocalizations, 2 = definite-vocalizations intense.

S. Labyrinthian Righting

Swaddle the infant, hold upright, then tilt to one side. Repeat with the other side. The response is scored as 0 = head in same plane as body, 1 = head partially rights, 2 = head rights 5 sec.

T. The following score the performance up until this point:

1. **Response speed:** 0 = slow (25% of time quick), 1 = moderate (75% of time quick), 2 = high (all responses quick)
2. **Response intensity:** 0 = low, "laid back", 1 = moderate, 2 = high, distresses intense in expression
3. **Soothability:** 0 = less than average- seldom intervention necessary, 1 = moderate- often intervention necessary, 2 = harder than average- continuous intervention necessary.
4. **Cuddliness:** 0 = none (extend) resists experimenter, 1 = slight- molds after experimenter cuddles, 2 = definite, molds and cuddles initially.
5. **Tremulousness:** 0 = none, 1 = slight (1-2 times), 2 = definite (3 or more times)

U. 5-minute isolation test

The infant is placed alone in an incubator cage. Nursery-reared infants are placed with a toy (Tweety bird) and the mother-reared infants are placed with a blanket in addition to the toy. The number of times the infant vocalizes is counted during the first minute of isolation. 5 minutes of behavioral data are then scored on a laptop. The behaviors recorded are the same as home-cage scoring.

V. The following categories score the animal's response to the isolation test:

1**. Calming self:** 0 = easy (calm 90% of time when alone), 1 = moderate (upset 50% of the time), 2 = harder than average (continuous distress).
2. **Motor activity:** (measure of environmental explore, locomotion, and motion) 0 = slight amount (25% moving), 1 = normal amount (50% moving), 2 = excessive continuous action.
3. **Coordination:** (for their age) 0 = poor, clumsy, 1 = adequate, 2 = excellent, agile
4. **Spontaneous Crawl:** 0 = absent, 1 = weak try, uncoordinated, 2 = coordinated
5. **Fine motor manipulation:** 0 = none, 1 = less than 10 sec, 2 = more than 10 sec.
6. **Passive** (passive score): 0 = none, 1 = slight (50% of time), 2 = definite (75% of time)

W. The following are scored in response to the temperament up to this point.

1. **Irritability**: 0 = extremely irritable, distress all items, 1 = slightly irritable, few items, 2 = no irritability- no distress.
2. **Self mouth:** 0 = none, 1 = slight, brief insertion, 2 = definite- 15 seconds or more in mouth.
3. **Temperament Rating Consolability:** 0 = cannot console infant, nothing works, 1 = consoles with difficulty (pick up, rock, and talk), 2 = easy to console (pick up only)
4. **Struggle During Test:** 0 = little struggle (25% of time), 1 = moderate amount (when appropriate), 2 = difficult to test (continuously).
5. **Predominant State:** 0 = alert, awake and aware, 1 = alert, but somewhat agitated, 2 = extremely agitated (body jerks and screams).
6. **Fearfulness:** 0 = none, bold, 1 = slight fear at first, 2 = definite- fearful often.

X. Maintenance Balance

Hold the infant perpendicular to the table with hind feet touching the table, then drop. Scored as 0 = fall, 1 = place arms out but fall, 2 = used arms for support and did not fall.

Y. Resistance- Passive MV

Push and pull the hands and feet. Look at muscle resistance. Scored as 0 = barely discernible resistance, 1 = moderate resistance (average), 2 = strong resistance.

Z. Active Power

Scored as 0 = unable to withstand slight resistance, 1 = active, able to withstand moderate resistance (average), 2 = powerful mv- difficult to restrain.

AA. Placing Response

Gently rub back of hand and foot against the side of a table or an edge. Scored as 0 = no response, 1 = slight evidence, 2 = definite response.

BB. Parachute

Hold the infant with one hand approximately 2 feet above the table. Move the infant very quickly towards the table. Scored as 0 = no extension, 1 = slight extension and opening hands, 2 = definite extension (opening hands).

CC. Rotation test

Swaddle the infant, hold at arm's length facing inward and spin in a circle. Repeat going in opposite direction (head free). Repeat both directions holding the head in place (head held). Does the head look in the direction of the spin (head free)? Scored as 0 = absent, 1 = weak - just discernible, 2 = good response. Do the eyes look in the direction of the spin (head held)? Scored as 0 = absent, 1 = weak - just discernible, 2 = good response.

DD. Restrain

Pin the infant on its back for 10 seconds. Record the response: 0 = resistance and vocalizes (25% of time or less), 1 = resistance and vocalizes (50% of time), 2 = resistance and vocalizes continuously.

EE. Persistence

Scored in response to the restraint. Rate as 0 = slight (few or none), 1 = definite (numerous attempts, but does quit), 2 = exaggerated (continuous attempts).

FF. Rooting

Draw a pen down the front of face. Repeat on either side of face. Score the response: 0 = absent, 1 = weak turn, 2 = full turn and lip grasp.

GG. The infant is weighed at the end of the Brazelton.

*Note: Half scores (0.5 and 1.5) can also be recorded for all categories.

APPENDIX B

INFANT STUDY RECRUITMENT LETTER

University of Massachusetts Amherst Child Study Center
Department of Psychology
Tobin Hall, 135 Hicks Way
Amherst MA 01003
Phone: 413.545.0535
Fax: 413.545.0996
Web: http://www.umass.edu/devpsych

Dear Parent,

Here at the University of Massachusetts Amherst, we have been conducting projects on children's development for more than twenty years. At this time we would like to tell you about an exciting study that is taking place at the Child Study Center. We are currently exploring how handedness develops in young infants. Specifically, we are interested in whether infants prefer to use one hand over the other during play and whether one hand is more skillful than the other on various motor tasks.

In this study, your child would wear markers on his or her wrists so that we can track the movement of each hand. There is no discomfort or risk associated with these markers. During the study your child would play with a series of different toys. The session is videotaped for later analysis. We are always happy to show you the videotape after the session and to discuss with you the findings of this study as well as other studies that we have conducted. All of the data that we collect will remain strictly confidential. Participation in this study is entirely voluntary, and if at any point during your visit you wish to terminate your participation, you may do so.

Your child would be eligible to participate in this study when he or she is 11-, 14-, or 17-months old. Appointments are scheduled two weeks before or after the testing age. The study consists of one visit of approximately 45 minutes and the parent remains with the child at all times. If you have another child who would be accompanying you, we are happy to arrange for an adult to entertain him/her during the session. If you would like to be a part of this study, please contact Dr. Neil Berthier via phone at 545-0535 or Eliza Nelson via email at lizanelson@gmail.com to schedule a visit. Thank you very much for considering this project.

Neil Berthier, Ph.D.
Professor of Psychology
(413)545-0535

Eliza Nelson, M.S.
Doctoral Candidate
lizanelson@gmail.com

APPENDIX C

INFANT CONSENT FORM

Consent Form

The Human Studies Research Committee has approved this study and the recruitment of subjects.

Purpose of Study
The study is designed to investigate hand preference and performance in human infants using a motion analysis system. In particular, we are examining whether there is a difference in left- and right-hand performance on various motor tasks and if so, whether this difference is correlated with the development of hand preference.

Procedure
Your infant will wear infrared markers on their left and right wrists. Your infant will sit on your lap while we present a series of attractive toys. Your infant will be encouraged to reach for and play with the toys. We are interested in assessing your infant's ability to manipulate objects with his/her hands. Please do not assist your child in any way during this experiment. The testing session will be videotaped so that we can later code your child's behavior. Testing will last about 30 minutes.

Possible Risks and Benefits
There is no risk to your child and no expected benefit.

Confidentiality of Records
The records generated by this study will be confidential. Videotapes and paper records will be stored in a locked room and will only be available to researchers involved in this study. Your child will not be individually identified in any publication or presentation that results from this experiment.

Request for More Information
Feel free to ask any question about our study. We will be happy to show you the videotape of your child at the end of the session. If you wish to speak with someone involved in this study regarding any problems or concerns you may have, contact the principal investigator, Professor Neil Berthier, via email at berthier@psych.umass.edu or by phone at (413) 545-0535. If you would like to discuss your rights as a participant in a research study or wish to speak with someone not directly involved in the study, you may contact the Human Subjects Review Board via email at HumanSubjects@ora.umass.edu or by phone at (413) 545-3428.

Voluntary Nature of Participation
Your participation in this study is purely voluntary. You may withdraw at any time for any reason.

I, _____, have explained to _____ the purpose of the research, the procedures required, and the possible risks and benefits to the best of my ability.

_____ _____
Researcher's Signature Date

I confirm that _____ has explained to me the purpose of the research, the study procedures that my child, _____, will undergo, and the possible risks and discomforts as well as benefits that my child may experience. I have read and I understand this consent form and will be given a copy. Therefore, I agree to give my consent to have my child participate as a subject in this research project.

_____ _____
Parent's Signature Date

APPENDIX D

INFANT VIDEO RELEASE FORM

VIDEO RELEASE

____ YES I, _____, hereby give my permission to the Child Study Center of the University of Massachusetts to show a brief segment of the videotape of my child, _____, for scientific or educational purposes. I understand that I may see the videotape before giving this permission. I understand that the Child Study Center may keep my child's tape as long as necessary for scientific or educational purposes.

____ NO I, _____, DO NOT give my permission to the Child Study Center of the University of Massachusetts to show a brief segment of the videotape of my child, _____, for scientific or educational purposes. I understand that the Child Study Center may keep my child's tape as long as necessary for scientific or educational purposes.

_____ NO I, _____, DO NOT give my permission to the Child Study Center of the University of Massachusetts to show a brief segment of the videotape of my child, _____, for scientific or educational purposes. ***Please destroy the tape of my child after it has been viewed.***

I understand that if I change my mind about my decision I should contact Neil Berthier at 545-0535 or berthier@psych.umass.edu.

I have read and I understand this consent form. I understand that I will receive a copy of this form.

_____ _____
Parent's Signature Date

_____
Researcher's Name

_____ _____
Researcher's Signature Date

APPENDIX E

INFANT DEVELOPMENTAL HISTORY FORM

SUBJECT # _____ TAPE # _____ AGE _____days EXPS _____
TEST DATE _____/_____/____ SEX M F **WKS GEST (**40 ± 2) _____

BIRTHDATE ____/_____/_____ MATERNAL AGE ____
BIRTH WT ____lbs _____oz (5 – 9 lbs) **BIRTH ORDER ____**

SIB NAMES & BIRTHDATES
1. _____ ____/____/____ 3. _____ ____/____/____
2. _____ ____/____/____ 4. _____ ____/____/____

DAYCARE Y N **AGE MOS ____** Currently ____Hrs/Day ____ Days/Wk
Other playgroup activities (hrs/day, days/wk)
_____
Wake _____ am **Sleep _____** pm **Other childcare _____** hrs/wk

SIT ONSET AGE MOS ____
(vertical sitting for 30 s with no hands; avg. 6, range 4 – 8)

BELLY ONSET AGE MOS ____
(any style, belly touch sometimes, 10 ft across room; avg. 7, range 5 – 8)

CRAWL ONSET AGE MOS ____
(hands/knees, hands/feet, 10 ft across room, no belly touching; avg. 8, range 6 – 10)

CRUISE ONSET AGE MOS ____
(sideways holding furniture for support; avg. 9, range 8 – 11)

WALK ONSET AGE MOS ____
(10 ft across room, no holding, no falling; avg. 12, range 10 – 14)

FALLS _____

SURFACE EXPERIENCE (1 or more times week)
WW/CPT AREA-RUG WOOD LINO TILE GRASS CONCRETE TUB
BED/MATT COUCH PILLOW GYM-MAT LEAVES SAND MUD WATER

HAVE TOY/SIMILAR TOY
BLOCKS HAMMER PHONE STK-RINGS POP-UPS FITTING TOY

DATE BEGAN EAT CEREAL/SIMILAR SIZE FOOD ITEM AGE MOS ____
DOES CHILD FEED SELF FROM A CUP OR SMALL DISH Y N

Breast-Fed starting ____ mos **Bottle-Fed** starting ____ mos **Mixed-Fed** starting ____ mos
Hand Pref of bottle feeders _____

ARE THERE ANY IMMEDIATE FAMILY MEMBERS WHO ARE LH? Y N
(If yes, who/relationship**)**_____

APPENDIX F

ADULT RECRUITMENT FLYER

UMASS AMHERST

Department of Psychology

PARTICIPANTS NEEDED FOR RESEARCH

We are looking for adult participants to take part in a study on reaching.

As a participant in this study, you would be asked to complete:
(1) Two reaching tasks and (2) a 10-question survey.

During the reaching tasks, you would wear infrared markers on each wrist.
These markers allow each hand to be tracked in 3-D space during reaching.
There is no risk or discomfort associated with wearing these markers.

The study takes approximately 30 minutes.
You will receive $5 for your participation.

For more information about this study, or to volunteer for this study,
please contact:

Eliza Nelson, Principal Investigator
enelson@cns.umass.edu

or Neil Berthier, Faculty Supervisor
berthier@psych.umass.edu

This study has been reviewed and approved by the Institutional Review Board
of the University of Massachusetts Amherst

Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu
Eliza Nelson enelson@cns.umass.edu

APPENDIX G

ADULT INFORMED CONSENT

Consent Form for Participation in a Research Study

University of Massachusetts Amherst

Principal Investigators: Eliza Nelson
Faculty Supervisor: Neil Berthier
Student Researchers: None
Study Title: The Quality of Hand Movements in Adults

1. WHAT IS THIS FORM?
This form is called a Consent Form. It will give you information about the study so you can make an informed decision about participation in this research study.

2. WHO IS ELIGIBLE TO PARTICIPATE?
Adults over 18 years of age with no known motor deficits are eligible to participate in this study.

3. WHAT IS THE PURPOSE OF THIS STUDY?
The purpose of this study is to investigate the quality of reaching movements to various objects using the left and right hands on different trials.

4. WHERE WILL THE STUDY TAKE PLACE AND HOW LONG WILL IT LAST?
The study will take place in Tobin 644 and will last approximately 30 minutes.

5. WHAT WILL I BE ASKED TO DO?
In the study you will be asked to sit at a table and complete two reaching tasks while wearing a bracelet containing infrared markers on each hand. On each trial, you will be instructed as to which hand to use. Your behavior will be videotaped, and your hand movements will be recorded from the markers and saved to a computer. At the end of the study, you will be asked to complete a short questionnaire.

6. WHAT ARE MY BENEFITS OF BEING IN THIS STUDY?
There are no direct benefits to you from this study.

7. **WHAT ARE MY RISKS OF BEING IN THIS STUDY**?
There is no more risk than would be encountered in everyday life/activity.

8. HOW WILL MY PERSONAL INFORMATION BE PROTECTED?
Participants will be assigned subject numbers upon entry to the study and these numbers will be used in all data records. Your contact information will be kept separately in a locked room and only researchers will have access to that information. Data records will either be physically secured by room lock or by password protection on computers and only the study researchers will have access to the records. The key linking your name to the data and videotapes will be destroyed three years after completion of the study. At the conclusion of this study, we intend to publish our findings and data will be presented in summary format. You will not be identified in any publications or presentations.

9. WILL I RECEIVE ANY PAYMENT FOR TAKING PART IN THE STUDY?
You will receive $5 for participating in this study.

10. PERMISSION TO RETAIN SEGMENTS OF VIDEO TAPES FOR TEACHING AND RESEARCH DEMONSTRATION.
When we present our research findings at a scientific meeting or to students in the classroom, the use of short (less than a minute) segments of video recordings is valuable. If you would like to give or deny us permission to use your recordings in this manner, please indicate below:

_____ I agree that segments of the recordings made of my participation in this research may be used for conference presentations.

_____ I **do not** want segments of the recordings made of my participation in this research to be used for conference presentations.

_____ I agree that segments of the recordings made of my participation in this research may be used for education and training of future researchers/practitioners.

_____ I **do not** want segments of the recordings made of my participation in this research to be used for education and training of future researchers/practitioners.

11. WHAT IF I HAVE QUESTIONS?
Take as long as you like before you make a decision. We will be happy to answer any question you have about this study. If you have further questions about this project or if you have a research-related problem, you may contact the principal investigator, Eliza Nelson (enelson@cns.umass.edu), the faculty supervisor Neil Berthier (berthier@psych.umass.edu or 413 545-0535) or the Chair of the Psychology Department, Melinda Novak (413 545-2387).
If you have any questions concerning your rights as a research subject, you may contact the University of Massachusetts Amherst Human Research Protection Office (HRPO) at (413) 545-3428 or humansubjects@ora.umass.edu.

12. CAN I STOP BEING IN THE STUDY?
You do not have to be in this study if you do not want to. If you agree to be in the study, but later change your mind, you may drop out at any time. There are no penalties or consequences of any kind if you decide that you do not want to participate. You will still receive $5 even if you decide not to continue in this study.

13. SUBJECT STATEMENT OF VOLUNTARY CONSENT
I have read this form and decided that I, _____, will participate in the project described above. The general purposes and particulars of the study as well as possible hazards and inconveniences have been explained to my satisfaction. I understand that I can withdraw at any time.

_____	_____	_____
Participant Signature	Print Name	Date

By signing below I indicate that the participant has read and, to the best of my knowledge, understands the details contained in this document and has been given a copy.

_____	_____	_____
Signature of Person Obtaining Consent	Print Name	Date

APPENDIX H

EDINBURGH HANDEDNESS INVENTORY

Edinburgh Handedness Inventory

Subject ID: _____

Date of Birth: _____

Sex: _____

Please indicate with a check (✓) your preference in using your left or right hand in the following tasks.

Where the preference is so strong you would never use the other hand, unless absolutely forced to, put two checks (✓✓).

If you are indifferent, put one check in each column (✓ | ✓).

Some of the activities require both hands. In these cases, the part of the task or object for which hand preference is wanted is indicated in parentheses. Please ask if you are unsure about any of the tasks/objects.

Task / Object	Left Hand	Right Hand
1. Writing		
2. Drawing		
3. Throwing		
4. Scissors		
5. Toothbrush		
6. Knife (without fork)		
7. Spoon		
8. Broom (upper hand)		
9. Striking a Match (match)		
10. Opening a Box (lid)		

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