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Head Orientation and Handedness Trajectory in Rhesus Monkey Infants (*Macaca mulatta*)

ABSTRACT: *In human and chimpanzee infants, neonatal rightward supine head orientation bias predicts later right hand use preference. In an evolutionarily older primate species such as the rhesus monkey, a left hand preference has been reported, but there are no data on head orientation biases. Supine head orientation bias was measured experimentally in 16 rhesus monkey neonates and compared with prone head orientation bias as well as with various measures of hand use preference. A group-level leftward supine head bias was found 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 or manipulation on a coordinated bimanual task. These data suggest that a trajectory for handedness in rhesus monkeys may be different from that of humans and chimpanzees.* © 2010 Wiley Periodicals, Inc. Dev Psychobiol 53: 246–255, 2011.

Keywords: handedness; laterality; head orientation; neonatal; primate

INTRODUCTION

Humans are widely considered to be right-handed, with at least 85% 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 in both rightward and leftward developing infants.

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 than their left hand. Similarly, infants with a left supine head bias viewed their left hand more than their right hand. 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 than their left hand, and infants with a left head bias moved their left hand more than their right hand. 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 2–5 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 use 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. In addition, we were interested in whether neonatal head orientation preferences corresponded to later hand use preferences in rhesus monkeys observed longitudinally from birth to late infancy.

We determined whether infant rhesus monkeys showed prone or supine head orientation biases as neonates, and then measured hand use for three different activities: hand-to-face contacts while supine, unimanual reaching to objects, and manipulation on a coordinated bimanual task. We also report data from neonatal developmental tests that measured responses on both sides of the body. We expected to find a supine, but not prone, head orientation bias given previous work in human, chimpanzee, and capuchin infants. Furthermore, we 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, we 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, we also predicted that head orientation bias would correspond to later hand use for reaching as well as hand use for manipulation.

METHODS

Subjects

Subjects were 16 healthy, full-term infant rhesus macaques (*Macaca mulatta*) housed at the Laboratory for Comparative Ethology (LCE), Eunice Kennedy Shriver National Institute 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. It is important to note that infant monkeys had visual, auditory, and olfactory access to other infant monkeys at all stages of nursery-rearing, daily interactions with human caregivers, daily play interactions with other infants, and were provided with a multi-directional surrogate. Rhesus monkeys reared with this high-quality surrogate show similar gross motor development to their mother-reared peers (Dettmer, Ruggiero, Novak, Meyer, & Suomi, 2008). Extensive research has shown that surrogate peer-rearing results in normal development and appropriate reproductive and maternal behavior. Furthermore, previous research comparing about 500 surrogate peer-reared monkeys with over 1,000 mother peer-reared monkeys failed to find any group differences in survival rates, growth, disease, bite wounds, pregnancy outcome, or neonatal deaths (Sackett, Ruppenthal, & Davis, 2002).

Briefly, infants were separated from their mother 24–72 hr 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 given 2-hr 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. 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.

Procedure

Primate Neonatal Neurobehavioral Assessment (PNNA).
All monkeys were administered the PNNA (Schneider, Champoux, & Moore, 2006) on days 7, 14, 21, and 30 by experimenters trained to 90% inter-rater agreement. The PNNA is a 20-min 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 we 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. For orient to auditory, an experimenter swaddled the monkey vertically with one side facing the tester 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. 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 s. 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 s. 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 s intervals, resulting in a total of 10 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° toward the infant's left shoulder. For a right head position, the chin had to be turned greater than 45° toward the infant's right shoulder. When the chin was turned less than 45° toward either shoulder, the position of the head was scored as midline. In total, 240 data points were collected per infant (40 per test day × 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-hr intervals from 0800 to 2000 for the first month of life for a total of seven 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. 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 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 × 30 days).

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. 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. Digit-sucking was considered to be a distinct behavior from hand-to-face contacts. Although instances of digit-sucking were noted as left or right hand, these data were subsequently not analyzed due to insufficient observations, including four monkeys that never engaged in the behavior during supine head orientation testing.

Reaching to objects. Hand use preference for reaching to objects was examined repeatedly when monkeys were between 14 and 44 days of age. This age range 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, an experimenter held the monkey vertically, supporting its lower half. A second experimenter presented a toy on a testing table at the monkey's midline. 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 in which the infant successfully reached to and obtained the toy were scored for frequency of left, right, or bimanual hand use.

Coordinated bimanual TUBE task. Monkeys were given the coordinated bimanual TUBE task (Hopkins, 1995; Bennett, Suomi, & Hopkins, 2008) when they were 6–9 months of age. 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. 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 nonconsecutive 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.

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

DS values were computed for each of the target behaviors measured over the first month of life in the PNNA assessments (Table 1). Palmar grasp DS values ranged from −3.00 to 1.00 ($M = -0.41$, $SD = 1.11$). Individually, seven monkeys showed a greater palmar grasp response in the left hand, five monkeys showed a greater response in the right hand, and four monkeys were

Table 1.   Difference Score Values by Subject and Sex for Palmar Grasp, Plantar Grasp, Tactile Arm Response, Tactile Leg Response, and Orient to Auditory Components of the Primate Neonatal Neurobehavioral Assessment (PNNA) Administered During the First Month of Life

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

Values 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.

equally responsive in both hands. This distribution of palmar grasp scores did not differ from an unbiased distribution, $\chi^2 = 4.50$, $df = 2$, $p > 0.05$. 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, $\chi^2 = 2.38$, $df = 2$, $p > 0.05$, with six infants showing a greater reflex response in the left foot, five infants showing a greater reflex response in the right foot, and five 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, $\chi^2 = 8.50$, $df = 2$, $p < 0.05$, and tactile leg reflex, $\chi^2 = 9.38$, $df = 2$, $p < 0.01$. Individually, nine monkeys showed a greater response to left arm tactile stimulation, three monkeys showed a greater response to right arm tactile stimulation, and four monkeys had an equal response to tactile stimulation in both arms. Similarly, nine monkeys showed a greater response to left leg tactile stimulation, four monkeys showed a greater response to right leg tactile stimulation, and three monkeys had an equal response to tactile stimulation in both legs. Arm and leg DS scores were not related however, $r = 0.194$, $p > 0.05$.

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, $\chi^2 = 0.38$, $df = 2$, $p > 0.05$, with three monkeys rated as having a greater orient response to auditory stimuli presented on the left side, four monkeys rated as having a greater orient response to auditory stimuli presented on the right side, and nine 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 ($p > 0.05$). Two-tailed Pearson correlations did not reveal any significant relationships between DS values ($p > 0.05$).

Head Orientation

LI scores were computed for each head orientation posture measured over the first month of life. Data for each head orientation measure are plotted in Figure 1. Supine head orientation LI scores across all trials ranged from −0.66 to 0.37 ($M = -0.19$, $SD = 0.23$, Tab. 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
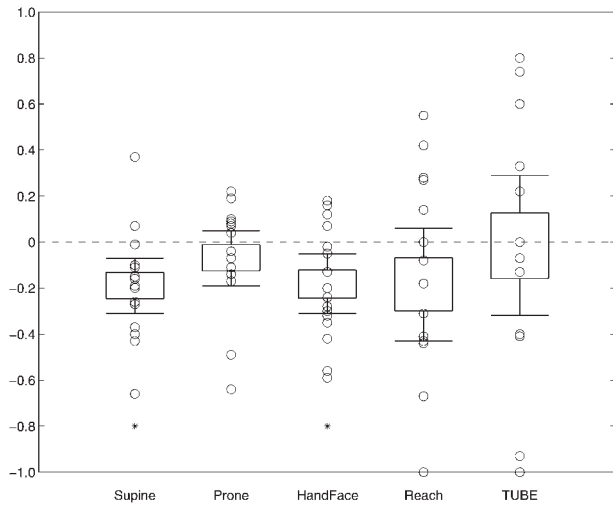
FIGURE 1 Distribution of Laterality Index (LI) scores for each head orientation and hand use measure. Boxes represent the group mean and standard error on each task. Whiskers signify 95% confidence intervals. Asterisks denote significant group-level biases as determined by one-sample *t*-tests with an alpha level of 0.05.

15 s 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

Table 2. Head Turning Preferences by Subject and Sex for Supine and Prone Postures

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

Preferences 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.

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 ($M = -0.07$, $SD = 0.23$, Tab. 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

LI scores were computed for each hand use measure. Data for each hand use task are plotted in Figure 1. 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 ($M = -0.18$, $SD = 0.24$, Tab. 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 and 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 3. No bias was found at the group-level,

Table 3. Hand Use Preferences by Subject and Sex for Hand-to-Face Contacts, Reaching, and the Coordinated Bimanual TUBE Task

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

Preferences 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.

$t(15) = −1.580$, $p > 0.05$, $M = −0.18$, $SD = 0.47$. 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 6–9 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 ($M = −0.02$, $SD = 0.57$, Tab. 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 co-ordinated bimanual task. Hand use on the TUBE task was not correlated to 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, $r = −0.223$, $p > 0.05$.

Does Head Orientation Predict Hand Preference?

A linear regression analysis found that direction of supine head orientation bias predicted direction of hand use preference for hand-to-face contacts, $F(1,14) = 11.450$, $p < 0.01$, $r^2 = 0.45$ (Fig. 2). 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 6–9 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, $F(1,14) = 0.069$, $p > 0.05$, $r^2 < 0.01$).

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.
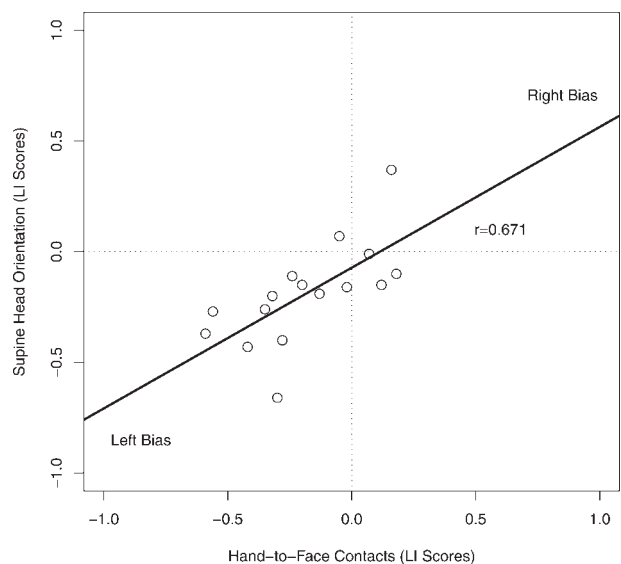

FIGURE 2 Supine head orientation preference corresponds to hand use preference for hand-to-face contacts. The greater the leftward head bias, the greater the left hand bias. LI scores were calculated by the formula $LI = R − L/R + L$, where LI = Laterality Index, R = right response, L = left response. Positive scores indicate a right bias and negative scores indicate a left bias.

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 6–9 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. Asymmetric supine hand experience (i.e., hand-to-face contacts) was therefore limited to the experimental testing of supine head orientation and thus may have been insufficient for establishing hand use preference. Moreover, macaque infants develop at a rate that is approximately four times as fast as human infants (Gunderson & Sackett, 1984), further limiting the role of potential supine experience during the prereaching period in influencing later hand use 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). An attempt was made to examine hand use preference for digit-sucking while supine during head orientation testing, but most monkeys either engaged in this behavior infrequently or not at all. Digit-sucking may play an important role in influencing handedness when monkeys are in other postures or contexts throughout development. The current study however cannot address that possibility.

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 4–11 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 3–6 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, 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.

We reported evidence of a population-level leftward neonatal asymmetry in rhesus monkeys infants 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 group-level preferences or relationships to earlier behavioral asymmetries. We suggest that the limited supine experience of rhesus monkey infants prior to the onset of reaching compared to that of human infants differentially affected the relationship between early head positioning and later hand preference, although we acknowledge that other factors may be involved in a trajectory for handedness, and that similar patterns in behavior may not share the same underlying mechanisms across species. Head orientation may not be the best predictor of hand preference, particularly for rhesus monkey infants. In addition, hand preference may not have been fully developed at 6–9 months of age in this cohort of monkeys, given the finding that a number of previous studies in adult macaques have reported a group-level left hand bias (for review, see Papademetriou et al., 2005). Nevertheless, these data are novel in that they demonstrate population-level asymmetries in behavior over the first month of life in rhesus monkeys and suggest that species-typical experience may differentially shape trajectories for handedness in primates.

Our interpretations of these data are limited in that we cannot speculate about how these findings 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. We are unaware of any 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.

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