Brief Report

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Kinematics of Reaching and Implications for Handedness in Rhesus Monkey Infants

ABSTRACT: *Kinematic studies of reaching in human infants using two-dimensional (2-D) and three-dimensional (3-D) recordings have complemented behavioral studies of infant handedness by providing additional evidence of early right asymmetries. Right hand reaches have been reported to be straighter and smoother than left hand reaches during the first year. Although reaching has been a popular measure of handedness in primates, there has been no systematic comparison of left and right hand reach kinematics. We investigated reaching in infant rhesus monkeys using the 2-D motion analysis software MaxTRAQ Lite+ (Innovision Systems). Linear mixed-effects models revealed that left hand reaches were smoother, but not straighter, than right hand reaches. An early left bias matches previous findings of a left hand preference for reaching in adult rhesus monkeys. Additional work using this kind of kinematic approach will extend our understanding of primate handedness beyond traditional studies measuring only frequency or bouts of hand use.* © *2011 Wiley Periodicals, Inc.* Dev Psychobiol

Keywords: *handedness; reaching; kinematics; primate; infant*

INTRODUCTION

Reaching paradigms have historically been a common method for assessing handedness in rhesus monkeys (*Macaca mulatta*: Deuel & Dunlop, 1980; Fagot, Drea, & Wallen, 1991; Lehman, 1978; Warren, 1953; Westergaard, Lussier, & Higley, 2001) as well as other primates. However, many investigators have argued that simple reaching, as traditionally measured by hand use frequency, is not a robust measure of hand preference (for reviews and discussion, see Fagot & Vauclair, 1991; Papademetriou, Sheu, & Michel, 2005; Rogers, 2009). Frequency of left or right hand use may not be sensitive to detecting asymmetries in reaching, particularly in adult subjects where reaching is considered to be a low-level task (Lilak & Phillips, 2007). By contrast, reaching is a highly demanding motor skill for infants. However, few studies have explored left–right differences in reaching among infant primates (e.g., Adams-Curtis, Fragaszy, & England, 2000; Hook & Rogers, 2000; Nelson et al., 2011; Westergaard, Bryne, & Suomi, 1998; Westergaard, Champoux, & Suomi, 1997).

Two-dimensional (2-D) and three-dimensional (3-D) motion analysis techniques offer an alternative and more powerful approach to examining early hand use asymmetries in reaching. These tools have been used to characterize the structure of reaching movements in human infants (for a review, see Berthier & Keen, 2006). Reach kinematics in human infants change rapidly in the first months of reaching and have not yet attained adult levels by 2 years of age. Two of the most notable changes in the quality of infant reaches during this time are improvements in reach straightness and reach smoothness. Infants transition from making multiple accelerations and decelerations in each reach to a single smooth acceleration and deceleration (Berthier

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& Keen, 2006; Konczak, Borutta, Topka, & Dichgans, 1995; Konczak & Dichgans, 1997; von Hofsten, 1991). Kinematic differences between arms do not emerge until after the onset of successful reaching around 16 weeks of age (Lynch, Lee, Bhat, & Galloway, 2008). In infants followed from 20 to 32 weeks of age using 2-D kinematic recordings, Morange-Majoux, Peze, and Bloch (2000) identified a right hand advantage for reaching such that the right hand was straighter and had a shorter movement time than the left hand. In a similar study using 3-D kinematics, Hopkins and Rönnqvist (2002) found that the right hand was smoother than the left hand for reaching in 6-month olds. Rönnqvist and Domellöf (2006) extended these findings to older infants, reporting that 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 the hands for straightness at 36 months. These findings of an early right bias are consistent with the 9:1 ratio of right hand preference observed in human adults (e.g., Annett, 2002). It should be noted however that the previous studies of human infants did not directly measure which hand the infant preferred to use given the choice of performing a task with either hand, with the exception of Rönnqvist and Domellöf (2006) who evaluated hand preference at the 36 month time point only. Those data were again consistent with the adult pattern, as the 36-month-old infants used their right hand 90% of the time or greater for precision throwing, drawing, and hammering.

Returning to rhesus macaques, the direction of hand use preference in these monkeys appears to be opposite from that of humans. Papademetriou et al. (2005) performed a meta-analysis of primate hand use studies examining reaching and identified a left hand preference at a ratio of 2:1 in a sample that largely consisted of adult subjects. The origins of this left bias remain elusive, as few studies have examined early asymmetries in rhesus infants. Nelson et al. (2011) reported a leftward pattern of neonatal asymmetries over the first month of life in a sample of 16 rhesus infants, including a left head orientation bias when monkeys were in a supine posture, a left hand preference for hand-to-face movements made also while supine, and a greater tactile reflex response to stimulation on the left arm and left leg. Frequency of left and right hand reaches to an object at midline were recorded when the same set of monkeys were 14–44 days old. Although there was a trend towards left hand preference, it did not reach statistical significance at the group level. Westergaard et al. (1997) measured hand preference for unimanual reaching in an older cohort of 19 monkeys aged 4–11 months and found a significant left hand preference. Hand preference for reaching in rhesus infants may emerge sometime after 1.5 months of age and be present by 4 months of age. Nevertheless, the general leftward pattern reported across studies in infant rhesus matches the leftward reaching preference observed in adult rhesus.

Although kinematic analyses have previously been used to examine reaching in macaques, these studies are limited by (1) adult subjects only; (2) small sample sizes ranging from 3 to 5 monkeys; (3) single arm measurements or no distinction made between the left and right arms (or the preferred and non-preferred arms); and (4) extensive pre-training to perform the reaching task(s) (Christel & Billard, 2002; Pizzimenti et al., 2007; Roy, Paulignan, Farnè, Jouffrais, & Boussaoud, 2000; Roy, Paulignan, Meunier, & Boussaoud, 2002, 2006). The current study was the first attempt to assess reach quality in both limbs while controlling for individual hand use preferences in a large cohort of infant rhesus monkeys ($N = 12$). The onset of reaching in rhesus monkeys is approximately 3–4 weeks of age and monkeys are capable of relatively independent finger movements (RIFM) at 4 months of age, although this ability does not become adult-like until 7 or 8 months of age (Lawrence & Hopkins, 1976). Reach quality was examined at approximately 4.5 months of age just after the onset of RIFM on a task involving reaching to and grasping a small food item. Frequency of hand use was also examined on a standard primate handedness task requiring bimanual coordination (TUBE task) at approximately 7.5 months when RIFM skills have become more advanced. We hypothesized that left hand reaches would be qualitatively different from right hand reaches, and predicted an early bias in favor of the left hand given the pattern of left hand preference for reaching observed in adult rhesus monkeys. More specifically, we predicted that left hand reaches would be smoother and straighter than right hand reaches, mirroring the pattern seen in early reach kinematics among developing human infants.

METHOD

Subjects

Data were analyzed from 12 nursery-reared rhesus monkey infants (*M. mulatta*) including 6 males and 6 females housed at the Laboratory for Comparative Ethology (LCE), Eunice Kennedy Shriver National Institute of Child Health and Human Development (NICHD) in Poolesville, Maryland. Monkeys were surrogate peer-reared according to standard LCE procedures as described by Ruppenthal (1979) and Shannon, Champoux, and Suomi (1998) as part of a larger protocol unrelated to the current study. Previous work has shown that monkeys reared with this paradigm show similar gross motor development to their mother-reared peers (Dettmer, Ruggiero, Novak, Meyer, & Suomi, 2008).

Reaching Task

Quality of left and right arm movements was assessed from a reaching task (Fig. 1A) given when monkeys were approximately 4.5 months of age ($M = 138 \pm 5$ days). 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 ipsilateral hand. The monkey's task was to reach to and pick up the food. 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 three blocks of five 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 (camcorder facing left or right profile of monkey) was alternated for each block of trials, with the starting configuration randomized across subjects.

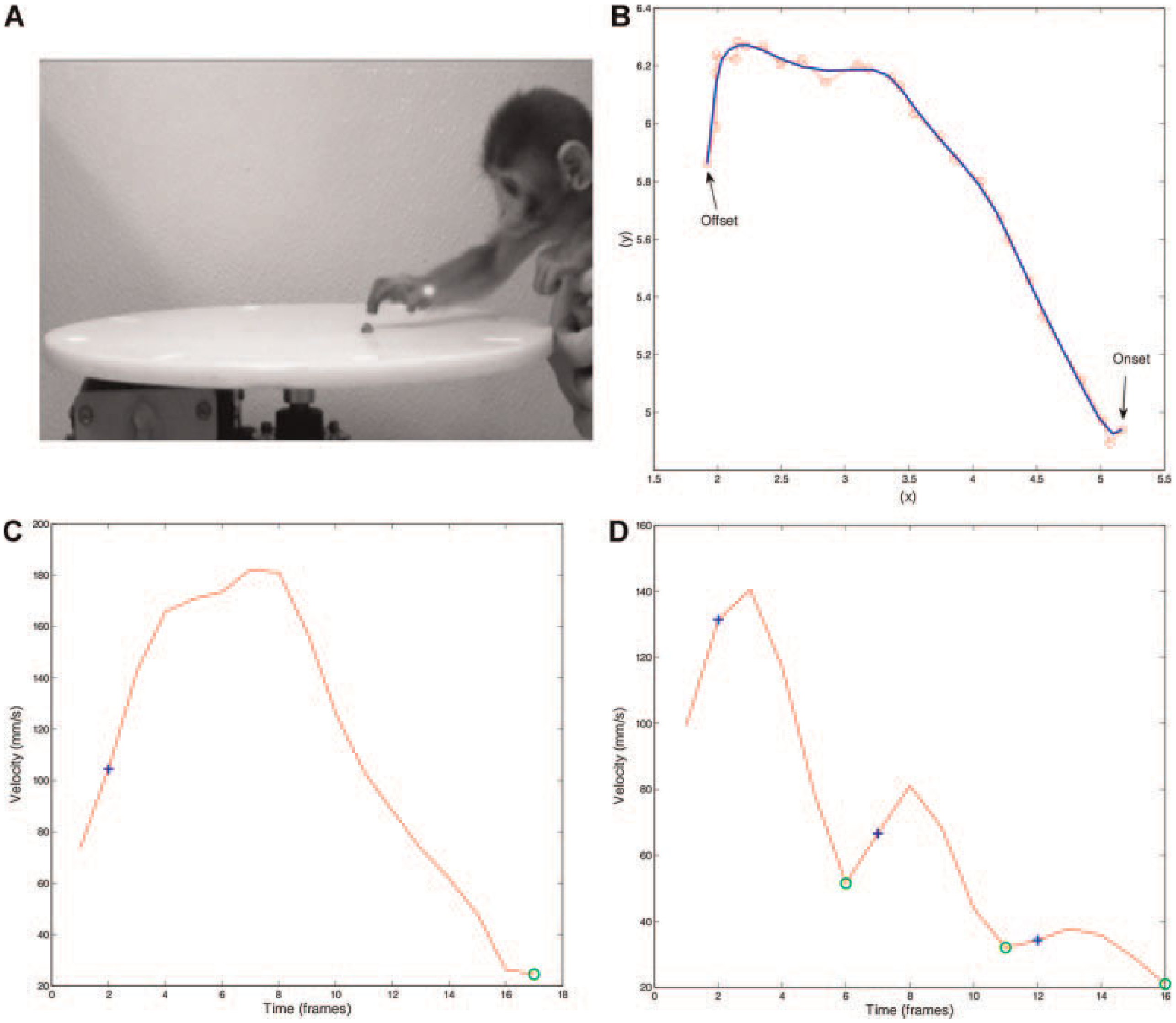

FIGURE 1 (A) Video still showing a monkey reaching for a grape slice with the right hand. Dot denotes point added to video with MaxTRAQ Lite+ to track the hand's movement in 2-D space. (B) Raw data (red) compared to filtered data (blue). (C) Example of a left-hand reach with one movement unit. A blue cross indicates the start of a movement unit and a green circle indicates the end of a movement unit. (D) Example of a right-hand reach with three movement units.

Handedness Groups

Monkeys were classified as left- or right-handed based on their performance on the coordinated bimanual TUBE task (Bennett, Suomi, & Hopkins, 2008; Hopkins, 1995) that was administered at 7.5 months of age ($M = 233 \pm 22$ days). Details of this work have been published elsewhere (Nelson et al., 2011). Briefly, monkeys must insert one or more fingers into a PVC tube to retrieve a food paste that has been smeared along the inside while using the opposing hand for stabilization. The criterion used to establish groups was 65% or greater use of one hand. There were six left-handed monkeys (range = 70–100% left hand use, $M = 81\%$, $SD = 14\%$) and six right-handed monkeys (range = 67–90% right hand use, $M = 82\%$, $SD = 10\%$). Gender was distributed equally across handedness groups. An additional four monkeys from this birth cohort were considered ambi-preferent on the TUBE task (percentage left hand use: male 1 = 50%, female 1 = 50%, male 2 = 53%, female 2 = 57%). Kinematic data from these monkeys were not analyzed, as there was no clear hand preference for statistical tests.

Kinematic Analysis

Reach quality was examined using 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/s) for reaches where the infant reached to and picked up the food (Fig. 1A). 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 toward 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.

Kinematic data were extracted and processed with Matlab (The MathWorks, Inc., Natick, MA) using custom programs. Data were low-pass filtered at a frequency of 6 Hz with a second order dual-pass Butterworth filter (see Fig. 1B). 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. Reach duration was the time in seconds between the onset and the offset of the reach. Straight-line distance corresponds to an estimated straight line between the starting position of the hand marker and the ending position of the hand marker. Path length refers to the length of the actual path the hand marker traveled. Reach straightness was computed by the ratio of hand path length to straight-line distance, with values closer to 1 indicating straighter reach movements. Movement units were computed with an algorithm derived from von Hofsten (1991) that has previously been used to characterize reaching in human infants. A movement unit was composed of a significant acceleration (defined as having a difference from the peak to the preceding valley of 20 mm/s and of having an average acceleration of 50 mm/s during the rise from the preceding valley to the peak) followed by a similarly sized deceleration. More simply, a movement unit consisted of a peak and the following valley in the hand-speed profile. Figure 1C,D depicts a reach with a single movement unit compared to a reach with multiple movement units.

A single observer digitized 100% of the reaches and was blind to hand preference condition. The same observer later reexamined approximately 20% of the data for intra-rater reliability. Intra-rater reliability was calculated by computing signed (Obs 1 − Obs 2) and unsigned [abs(Obs 1 − Obs 2)] differences between the two observations for each dependent variable. The median signed difference for reach average speed was 19 mm/s and more than 75% of the unsigned differences were less than 60 mm/s. For reach peak speed, the median signed difference was 6 mm/s and 75% of the unsigned differences were less than 70 mm/s. For reach duration, the median signed difference was 0% and 75% of the unsigned differences were less than .20 s. For reach smoothness (number of movement units), the median signed difference was 0. Approximately half of the unsigned differences were 0 and a third of the unsigned differences were 1. Finally, the median signed difference for reach straightness was 0% and 75% of the unsigned differences were less than .06.

Statistical Analysis

Dependent variables included reach average speed, reach peak speed, reach duration, reach smoothness, and reach straightness. Pearson's correlations between dependent variables averaged by monkey are given in Table I. Linear mixed effects models (Bates & Maechler, 2009) were used to examine the effects of handedness group (left-handed or right-handed), 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 described above using the statistical program R (R Development Core Team, 2009). This procedure estimates a mixed effects model for the data using both fixed and random effects where all the data from the subjects are included and a random effect is estimated for the subjects. In the model, deviations from an average effect that are due to individual subjects are

Table I. Correlations Between Dependent Variables

Parameters	Peak Speed	Duration	Smoothness	Straightness
Average speed	$.92^{*}$	$-.60^{**}$	$-.71^{**}$	.58
Peak speed	—	−.36	−.53	.57
Duration	—	—	$.85^{*}$	−.38
Smoothness	—	—	—	−.23
Straightness	—	—	—	—

$^{*}p < .001$.
$^{**}p < .05$.

Table II. Means and Standard Deviations for Reach Parameters as a Function of Group, Hand, and Preference

	Group		Hand		Preference	
Reach Parameters	Left	Right	Left	Right	Preferred	Non-Preferred
Average speed (mm/s)	248 ± 112	216 ± 80	247 ± 107	226 ± 95	235 ± 101	233 ± 100
Peak speed (mm/s)	474 ± 204	408 ± 167	478 ± 224	425 ± 167	443 ± 192	448 ± 191
Duration (s)	.58 ± .24	.53 ± .21	.56 ± .22	.56 ± .23	.56 ± .23	.55 ± .22
Smoothness[a]	1.98 ± 1.27	1.77 ± 1.05	1.68 ± 1.10*	2.01 ± 1.22*	1.86 ± 1.12	1.93 ± 1.28
Straightness[b]	1.17 ± .15	1.12 ± .13	1.13 ± .12	1.16 ± .16	1.15 ± .14	1.15 ± .15

Group = left handed versus right handed, Hand = left hand versus right hand, Preference = preferred hand versus non-preferred hand.

*$p = .009$.

[a] Measured by number of movement units. Values closer to 1 indicate smoother reaches.

[b] Measured by the ratio of hand path length to straight-line distance. Values closer to 1 indicate straighter reaches.

assumed to come from a normal distribution with zero mean and an estimated variance. Since each effect has two levels, all effects in the model are contained in single coefficients. Testing those coefficients corresponds to testing the effects of a standard ANOVA. Unlike ANOVA however, the mixed effects procedure is robust with unbalanced data where there are different numbers of trials from individual subjects (for comparisons to ANOVA, see Baayen, 2008a,b; Gueorguieva & Krystal, 2004; Krueger & Tian, 2004). Straight-line distance was used as a covariate to control for differences in arm sizes in models for average speed and peak speed. Duration was a covariate in models for smoothness. Values three times the interquartile range (IQR) were defined as outliers and excluded from analyses. Alpha was .05 for all tests. We note that *p* values were estimated from Markov chain Monte Carlo simulations (Baayen, 2008a,b) because of the challenges in calculating the degrees-of-freedom for error terms in mixed-effects models (Baayen, Davidson, & Bates, 2008). We report estimates of the regression coefficients from the model (*b*), standard errors of those coefficients (SE), and the *p* values for significant effects.

RESULTS

In total, 149 reaches were examined. An additional 31 trials were excluded from analysis either because the monkey did not participate or because the video segment was not suitable for 2-D analysis. The average number of digitized reaches from each monkey was 12 ($SD = 4$). Left-handed monkeys contributed 85 reaches and right-handed monkeys contributed 64 reaches to the analyses. There were 57 left hand reaches and 92 right hand reaches. Regardless of direction, 91 reaches were made by the preferred hand and 58 reaches were made by the non-preferred hand. Reaches were split equally by sex, with 74 reaches from male monkeys and 75 reaches from female monkeys. There were no sex differences for any of the reach parameters.

Means and standard deviations are given for each reach parameter as a function of handedness group (left-handed or right-handed), hand (left hand or right hand), or hand preference (preferred hand or non-preferred hand) in Table II. Overall, the left hand was found to be significantly smoother than the right hand as indicated by a smaller number of movement units, $b = -.38$, $\mathrm{SE} = .14$, $p = .009$ (Table II). Importantly, this finding was independent of individual monkeys' hand preferences.[1] Smoothness was moderately correlated with average speed such that smoother reaches were associated with faster speeds, $r = -.71$, $p = .010$ (Table I). However, there was no difference between hands for average speed. Although there was a trend for the left hand to be straighter overall as compared to the right hand, this difference was not statistically significant, $b = -.04$, $\mathrm{SE} = .02$, $p = .093$. There were no effects of hand on reach peak speed or reach duration. There were also no effects of handedness group or preferred hand on any of the reach parameters.

DISCUSSION

A kinematic approach has immense potential to add to the existing primate handedness literature that has to date only examined frequency or bouts of hand use at the behavioral level. The goal of this study was to demonstrate this technique by exploring the relationship between reach kinematics and hand preference

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[1] Smoothness and straightness were re-examined with reaches from three of the four other monkeys from this cohort included (those that did not have a hand preference). The remaining monkey, F1, had no kinematic data due to equipment failure. Greater smoothness in left hand reaches as compared to right hand reaches was confirmed with similar values to the original subset of lateralized infants ($N_{\mathrm{Reaches}} = 181$, $b = -.33$, $\mathrm{SE} = .11$, $p = .004$; LH = 1.49 ± 1.07, RH = 1.93 ± 1.18). There was no effect of hand on reach straightness, $b = -.03$, $\mathrm{SE} = .02$, $p = .196$.

as determined by the TUBE task in rhesus monkey infants. We were particularly interested in reach smoothness and reach straightness, as side differences have been found in these parameters in developing human infants. We expected to find biases in favor of the left hand given the pattern of left hand preference for reaching in adult rhesus monkeys. As predicted, the left hand was found to be significantly smoother than the right hand as quantified by fewer movement units for reaches to a stationary food item. However, there was no difference between the hands for reach straightness. These findings were independent of sex and monkeys' individual hand use preferences on the coordinated bimanual TUBE task. There were no differences between limbs for reach average speed, reach peak speed, or reach duration.

One possible explanation for why differences between the hands were not observed for reach straightness may be that monkeys' reaches at 4.5 months of age were already very straight. The means for the left and right hands were 1.13 ($SD = .12$) and 1.16 ($SD = .16$), respectively, suggesting that reach straightness was approaching floor levels (a straightness ratio of 1.00). Perhaps a side bias is present in early reaching but disappears over development much like in human infants where the right hand was reported to be straighter than the left hand at 5 months of age through the first year of life, yet there was no difference in straightness between the hands at 36 months of age (Hopkins & Rönnqvist, 2002; Morange-Majoux et al., 2000; Rönnqvist & Domellöf, 2006). These data cannot address this possibility in rhesus infants, as monkeys were sampled at only one time point. A goal of future work will be to evaluate straightness and other reach parameters at reach onset and subsequent later intervals using a longitudinal design.

There were also no effects of hand preference on reach kinematics in the current study. Hand preference was measured by the coordinated bimanual TUBE task, which has quickly become a standard measure in primate studies and is gaining popularity for use with human infants (e.g., Vauclair & Imbault, 2009). On the TUBE task, individual monkeys appear to have strong hand use preferences although there is no bias at the group level for either infant or adult rhesus monkeys (Bennett et al., 2008; Nelson et al., 2011; but see Westergaard et al., 1997). By contrast, the results from the current study suggest a group-wide difference between hands for reaching among infant rhesus monkeys in that left hand reaches were smoother than right hand reaches. Whether the left hand has any advantage over the right hand on reaching outcomes (e.g., success under challenge) in rhesus monkeys remains unknown. In a study of squirrel monkeys fishing for goldfish in either a bowl or a wading pool, there was no difference in the rate of successful capture between the preferred hand and the non-preferred hand, but significantly more attempts were made with the left hand than the right hand (King & Landau, 1993).

These findings favoring the left hand for reaching in monkeys are consistent with the Postural Origins Theory first proposed by MacNeilage, Studdert-Kennedy, and Lindblom (1987). According to this evolutionary framework, a division of labor between the left and right hands emerged in early prosimian primate species such that the left hand became specialized for reaching while the right hand was used for postural support in an arboreal environment. A shift to terrestriality in later primates enabled the right hand to be freed from postural control and become increasingly specialized for manipulation. Although speculative, monkeys may represent an intermediate group that retained a left hand preference for reaching, while beginning to develop a right hand preference for manipulation. Additional kinematic studies on primate reaching in conjunction with behavioral data may further inform this hypothesis.

The current study represents 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 primate species for reaching. Additional studies are needed to examine reach kinematics in other primate species, particularly other infant primates, as well as further work in rhesus monkeys. While preliminary, we hope that these results may serve as the basis for future studies and hypotheses regarding the relationship between reach quality and hand use in primates. Kinematic studies offer an exciting new perspective for this field as an additional tool in our toolkit for understanding handedness.

NOTES

The research described in this report was approved by the NICHD Animal Care and Use Committee, performed in accordance with the NIH Guide for the Care and Use of Laboratory Animals, and complied with the Animal Welfare Act. We are grateful to the LCE nursery staff for their assistance with data collection, particularly Angela Ruggiero, Michelle Miller, and Judy Songrady. We also thank Dr. Brian Umberger for his helpful advice on analyzing reach kinematics from 2-D video. This research was supported in part by funds from the Division of Intramural Research, NICHD. Dr. Nelson is now at the Center for Developmental Science at the University of North Carolina at Chapel Hill and Dr. Konidaris is at the MIT Computer Science and Artificial Intelligence Laboratory.

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