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RESEARCH ARTICLE

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Handedness and Reach-to-Place Kinematics in Adults: Left-Handers Are Not Reversed Right-Handers

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ABSTRACT. The primary goal of this study was to examine the relations between limb control and handedness in adults. Participants were categorized as left or right handed for analyses using the Edinburgh Handedness Inventory. Three-dimensional recordings were made of each arm on two reach-to-place tasks: adults reached to a ball and placed it into the opening of a toy (fitting task), or reached to a Cheerio inside a cup, which they placed on a designated mark after each trial (cup task). We hypothesized that limb control and handedness were related, and we predicted that we would observe side differences favoring the dominant limb based on the dynamic dominance hypothesis of motor lateralization. Specifically, we predicted that the dominant limb would be straighter and smoother on both tasks compared with the nondominant limb (i.e., right arm in right-handers and left arm in left-handers). Our results only partially supported these predictions for right-handers, but not for left-handers. When differences between hands were observed, the right hand was favored regardless of handedness group. Our findings suggest that left-handers are not reversed right-handers when compared on interlimb kinematics for reach-to-place tasks, and reaffirm that task selection is critical when evaluating manual asymmetries.

Keywords: Handedness, kinematics, reaching

At least 85% of the adult human population is right handed (Annett, 2002). Although adult handedness is considered stable, variations can arise according to how it is measured. Efforts have been made to distinguish hand preference (i.e., a bias in the use of one hand over the other) from hand performance (i.e., a bias in the proficiency of one hand over the other). The relationship between preference and performance is not clear cut, and disentangling the links between these two types of hand biases remains a target for advancing our understanding of the lateralization of motor skill (Bryden, 2016). In general, asymmetries observed in hand use have been interpreted as behavioral markers for hemispheric specialization due to the crossed innervation of the vertebrate motor system.

As Mutha, Haaland, and Sainburg (2013) have pointed out, the natural assumption many investigators make regarding laterality in the motor system is that the dominant hand/limb is universally superior to its nondominant counterpart (i.e., “preferred” always equals “proficient”). By contrast, the dynamic dominance hypothesis of motor lateralization, which has emerged from the literature on interlimb asymmetries in adult reach kinematics, has argued that each hemisphere is specialized for particular control processes, and that the hemispheres work together in a complementary fashion (Mutha et al., 2012; Sainburg, 2002, 2005, 2014). According to the dynamic dominance hypothesis, each limb is specialized for different aspects of motor control—the dominant limb for predictive control under stable conditions, and the nondominant arm for impedance control under unstable conditions. Because much of the dynamic dominance hypothesis was derived from observations of right-handers (identified by hand preference questionnaires), this model has also been characterized as left hemisphere (right/dominant arm) and right hemisphere (left/nondominant arm) motor specializations (Bagesteiro & Sainburg, 2002, 2003; Coelho, Przybyla, Yadav, & Sainburg, 2013; Duff & Sainburg, 2007; Mutha et al., 2013; Sainburg & Kalakanis, 2000; Sainburg & Schaefer, 2004; Shabbott & Sainburg, 2008; Tomlinson & Sainburg, 2012; Wang & Sainburg, 2007; Yadav & Sainburg, 2014). Notably, the dynamic dominance hypothesis was developed from a series of studies that have examined reaching without an explicit grasping component.

Few studies have examined differences in the kinematics of the two limbs of left-handers under similar testing conditions to right-handers described above. Wang and Sainburg (2006) reported a mirrored pattern for left-handers (left/dominant arm) compared with right-handers on a visuomotor rotation task involving interlimb transfer, suggesting an effect of dominance rather than an absolute difference between the arms. Initial movement direction improved in the dominant limb whereas spatial accuracy improved in the nondominant limb, consistent with the dynamic dominance hypothesis. Przybyla, Good, and Sainburg (2012) similarly reported that the dominant arm was better coordinated than the nondominant arm in left-handers, matching previous findings in right-handers. However, interlimb asymmetries were reduced in left-handers compared with right-handers, which may reflect a cultural effect of living in a right-handed world, or the fact that left-handers are more heterogeneous in their hand use patterns compared with right-handers. One goal of the present study was to expand the work on left-handers, and compare the interlimb kinematics of right-handed adults versus left-handed adults on two reaching and grasping tasks that we have used previously in infants (Nelson, Konidaris, & Berthier, 2014).

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Of interest to the present study are additional kinematic predictions beyond interlimb dynamics that can be derived from the dynamic dominance hypothesis for the dominant arm—straighter and smoother hand-paths to optimize predictive control. Reach straightness refers to how closely the path of the hand adheres to the straight-line distance between the hand and its intended target; values closer to 1 denote straighter reaches (Churchill, Hopkins, Rönnqvist, & Vogt, 2000). Reach smoothness is determined with an algorithm that counts the peaks in the hand-speed profile; one acceleration and deceleration in hand speed is one movement unit, and values closer to 1 denote smoother reaches (von Hofsten, 1979, 1991). These parameters of reach straightness and reach smoothness are the same aspects of motor control that have interested investigators studying infants, both in understanding the development of motor control (Berthier & Keen, 2006; Corbetta & Thelen, 1996, 1999; Fetters & Todd, 1987; Konczak, Borutta, Topka, & Dichgans, 1995; Konczak & Dichgans, 1997; Mathew & Cook, 1990; Rönnqvist & Domellöf, 2006; von Hofsten, 1979) as well as the development of laterality (Hopkins & Rönnqvist, 2002; Lynch, Lee, Bhat, & Galloway, 2008; Morange-Majoux, Peze, & Bloch, 2000; Rönnqvist & Domellöf, 2006; Souza, de Azevedo Neto, Tudella, & Teixeira, 2012). We previously reported that while asymmetries in hand use are observed in some infants, hand preference was not systematically related to interlimb asymmetries during reaching and grasping with the intent to perform a secondary action (fitting task: reach for and place a ball into the opening of a toy; cup task: reach for and remove a Cheerio from inside a cup) in infants 11–14 months old (Nelson et al., 2014).

An outstanding question is whether hand preference influences reaching and grasping kinematics in a systematic manner on the fitting task and cup task in adults, whose hand use patterns are established. Although there has been a longstanding interest in comparing hand preference to hand performance in understanding the phenomenon of handedness in adults (e.g., Borod, Caron, & Koff, 1984; Coelho et al., 2013; Corey, Hurley, & Foundas, 2001; Healey, Liederman, & Geschwind, 1986; Judge & Stirling, 2003; Nicholls, Thomas, Loetscher, & Grimshaw, 2013; Przybyla, Coelho, Akpinar, Kirazci, & Sainburg, 2013; Rigal, 1992; Steenhuis & Bryden, 1999; Todor & Doane, 1977; Triggs, Calvanio, Levine, Heaton, & Heilman, 2000), there has been little continuity between infant and adult studies, in large part due to the differences in manual abilities between these two demographics, as well as the variety of measures that have been used. By utilizing experimental tasks that can be performed by both groups (i.e., fitting task and cup task) and the same dependent variables derived from quantitative three-dimensional motion capture (e.g., reach straightness and reach smoothness), we hope to better characterize the relations among hand use, laterality, and motor control across development. Moreover, by using a task that can be performed by infants, we hope to establish norms to which developing kinematics may be compared.

Although not originally designed to test the dynamic dominance hypothesis, the fitting task and the cup task we first created for infants utilize stable conditions with everyday tasks of picking up familiar objects (i.e., ball or Cheerio) under visual feedback; features that are seemingly ideal for dominant arm performance in adults. Critically, the fitting and cup tasks are reach-to-grasp actions with secondary goals, as opposed to reach to touch/aim/point. Therefore, these tasks provide a novel test of the dynamic dominance hypothesis. We predicted that the dominant arm would be straighter and smoother than would the nondominant arm in both left-handed and right-handed adults on the fitting task and cup task in accordance with the dynamic dominance hypothesis. Although we had no a priori prediction for average reach speed in the dynamic dominance hypothesis framework, we also examined average reach speed effects given the interaction we found in previous research with infants using this paradigm (Nelson et al., 2014).

Methods

Participants

Twenty-two adults participated in this study. Adults had normal or corrected to normal vision and no known motor impairments. Hand preference was assessed after the experimental reaching tasks were completed using the Edinburgh Handedness Inventory (EHI; Oldfield, 1971; see Procedure section). Data from one left-handed woman were not usable due to error with the motion capture equipment. Data from another woman were excluded because the participant did not meet criteria for right-handedness. Although the participant signed the consent with her right hand, she indicated other activities on the questionnaire that she completed with the left hand and thus could not be considered right-handed by the study criteria (see Handedness Groups section). The final sample used in the statistical analyses was 20. There were 10 adults in the left-handed group (men = 5; women = 5). The average age was 27.61 ± 4.72 years old. There were 10 adults in the right-handed group (men = 5; women = 5). The average age was 30.16 ± 3.36 years old. Participants were blind to the objectives of the study. The University of Massachusetts Amherst Institutional Review Board approved the protocol. Participants received $5 compensation for their time.

Procedure

Adults participated in one session of approximately 30 min and completed two reaching tasks and a 10-item handedness questionnaire. Before the study began, the primary investigator reviewed the informed consent with the participant, described the study procedure, and explained the motion capture equipment. Reaching tasks were recorded with a Sony Handycam digital camcorder (Sony Corporation of America, New York, NY) that was positioned behind the experimenter. Participants wore Velcro wristbands containing 5-mm infrared-emitting markers for kinematic recordings during the two reaching tasks, and completed equal numbers of left- and right-hand trials on each task. Adults were instructed to place their hands flat on the table at two locations marked in tape with an "X" in a ready starting position prior to each trial (Figure 1A and 1B).

Reaching Tasks

Adults reached for a ball (fitting task, Figure 1C) or a Cheerio (cup task, Figure 1D) during two experimental reaching tasks. These tasks were originally designed for use in infants and have been described in detail elsewhere (Nelson et al., 2014). Briefly, the fitting task required the participant to reach to a ball and place it into the top of a toy. Small wells on either side of the toy held the ball in place prior to each trial. The cup task required the participant to reach to a cup and take out a Cheerio. Adults then placed the Cheerio on the starting "X"; this was the only procedural difference from prior testing with infants, who consumed the Cheerio after each trial. Because we asked adults to put the Cheerio on the table after each trial, we considered both the fitting and the cup tasks to be grasp-to-place tasks. The experimenter demonstrated each task twice with each hand. Following the demonstration, the participant completed 12 trials per task in accordance with the infant protocol. Ball and cup starting location were counterbalanced across handedness groups and participants within each task. The participant was reminded to place his or her hands in the ready position before each trial, and was told to use the hand ipsilateral to the object to be grasped. No instructions were given as to the speed at which the tasks should be completed.

Handedness Groups

Following completion of the reaching tasks, hand use was examined with the Edinburgh Handedness Inventory (for a recent review and discussion on the use of the EHI, see Edlin et al., 2015). This 10-item questionnaire addressed hand use 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. Adults were instructed to read each item on the questionnaire and put checkmarks in the column(s) that corresponded 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 test item. A laterality quotient (LQ) was calculated for each participant using the formula, $[(R-L)/(R+L)]*100$, where R represents the number of right hand checkmarks and L represents the number of left hand

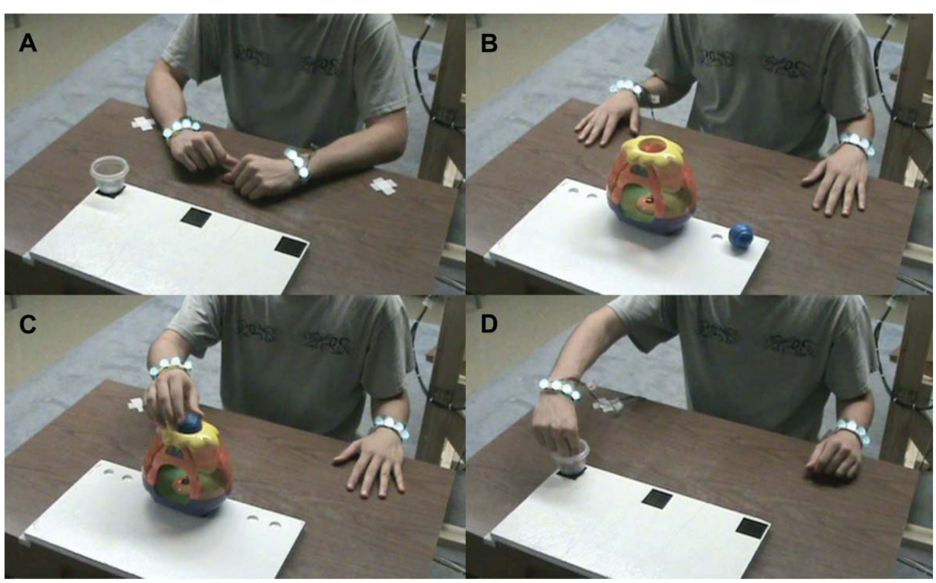

FIGURE 1. (A) Hand starting locations marked in tape on the testing table with an "X." (B) Adult with hands in the ready starting position prior to a trial on the fitting task. (C) Adult completing a trial on the fitting task. (D) Adult completing a trial on the cup task.

checkmarks. Scores between −100 and −40 were considered left handed, and scores between 40 and 100 were considered right handed.

Video Analysis

Videotape of the reaching tasks was reviewed frame by frame using MPEG Streamclip (Squared 5 srl, Rome, Italy) to determine the onset and offset of reaches. For the fitting task, the onset of the reach was defined as the first frame of directed movement toward the ball and the offset of the reach was defined as the first frame where the hand contacted the ball. Grip time was defined as the first frame where the participant contacted the ball to the first frame where the participant lifted the ball off the platform. The primary observer scored 100% of the data and a second observer scored approximately 25% of the data. Interrater reliability using a percent agreement score that allowed for a difference of five frames between observers was 97% for reach onset, 100% for reach offset, and 100% for ball lift for the fitting task.

For the cup task, the onset of the reach was defined as the first frame of directed movement toward the cup and the offset of the reach was defined as the first frame where the participant's hand entered the cup. Grip time was defined as the first frame where the participant's hand entered the cup to the first frame where the participant's hand was entirely removed from the cup. The primary observer scored 100% of the data and a second observer scored approximately 25% of the data. Interrater reliability using percent agreement as in the previous task was 100% for reach onset, 100% for reach offset, and 100% for cup exit for the cup task.

Kinematic Analysis

Kinematic data were captured continuously throughout each reaching task at 100 Hz using a Visualeyez three-dimensional real-time motion capture system (VZ4000, Phoenix Technologies Incorporated, Burnaby, Canada). Kinematic data were synchronized with behavioral data from the digital camcorder during data processing, and extracted and processed with MATLAB software version R2016b (The MathWorks, Natick, MA) using custom programs. Data were processed from a single marker with valid data from the wristband array. Data were low-pass filtered at 4 Hz with a fourth-order dual-pass Butterworth filter. A loss of up to 30 kinematic frames or one third of a second was interpolated with a cubic spline. The onset of the reach was further refined by an algorithm that searched for the minimal velocity in a 30 kinematic frame window prior to the behaviorally coded start of the reach. A three-point differentiation technique was used to calculate speed (mm/s^2). The average speed was the mean speed of the hand during the reach.

Reach duration, straight-line distance, path length, and reach smoothness were calculated. Reach duration was the time in milliseconds between the onset and offset of the reach, and was used as a covariate in statistical models. Straight-line distance was a calculation of the estimated straight line between the starting position of the hand marker and the ending position of the hand marker. Path length corresponded to the length of the actual path of the hand marker. Straightness was computed by the ratio of path length to straight-line distance and values near 1 indicated straighter reaches (Churchill et al., 2000). Smoothness was characterized using movement units with an algorithm derived from von Hofsten (1991). A movement unit was composed of a significant acceleration (defined as having a difference from the peak to the preceding valley of 200 mm/s^2 and of having an average acceleration of 500 mm/s^2 during the rise from the preceding valley to the peak) followed by a similarly sized deceleration. Visually, a movement unit consisted of a bell curve in the hand-speed profile.

Statistical Analysis

Dependent variables for the reaching tasks included average speed (mm/s), smoothness (number of movement units), straightness (ratio of path length to straight-line distance), and grip time (ms). Left-handers were analyzed separately from right-handers. Linear mixed-effects models (Bates, Maechler, & Bolker, 2012) were used to examine the effect of hand (left or right) within each handedness group for each dependent variable using the statistical program R (R Development Core Team, 2011). Duration and straight-line distance were used as covariates to control for differences in arm length where appropriate for our dependent variables. Outliers were defined as values three times the interquartile range and were excluded from analyses. The p values were estimated from Markov chain Monte Carlo simulations (Baayen, 2011; Baayen, Davidson, & Bates, 2008). Estimates of the model regression coefficients (b), 95% CI of those coefficients, and estimated p values are reported.

Results

Handedness

LQ scores calculated from the EHI ranged from −90 to −40 for left-handed participants. A two-sample t test did not find an effect of gender on LQ scores among left-handers, $t(7.157) = -1.037$, $p > .05$, $M_{MEN} = -60 \pm 21.21$, $M_{WOMEN} = -72 \pm 14.83$. For right-handed participants, LQ scores ranged from 70 to 100. A two-sample t test revealed that there was similarly no gender difference for right-handers, $t(6.969) = 0$, $p > .05$, $M_{MEN} = 86 \pm 8.94$,

TABLE 1. Means and Standard Errors for Reach Parameters as a Function of Handedness Group and Hand on the Fitting Task

	Right-handers		Left-handers	
Reach parameter	Left hand	Right hand	Left hand	Right hand
Average speed (mm/s)	399 ± 7.2	381 ± 7.3	401 ± 15.1	413 ± 12.1
Smoothness (movement units)	1.00 ± 0	1.00 ± 0	1.42 ± 0.117	1.25 ± 0.067
Straightness	1.20 ± 0.016[a]	1.15 ± 0.010[a]	1.11 ± 0.007	1.12 ± 0.009
Grip time (ms)	608 ± 12.1	586 ± 14.2	552 ± 17.0	520 ± 16.2

Note. Smoothness could not be analyzed in right-handed adults because participants performed at floor levels. For smoothness data, values closer to 1 indicate smoother reaches. Straightness was measured by the ratio of hand path length to straight-line distance; values closer to 1 indicate straighter reaches.
[a]Significant difference between hands.

$M_{\text{WOMEN}} = 86 \pm 13.42$. Because we did not find an effect of gender on LQ scores, analyses of the reaching and grasping tasks were collapsed across gender within handedness groups for each task.

Fitting Task

In right-handers, 120 trials were video coded for the fitting task. Of these, 119 trials had valid marker data (99%), including 59 left-hand reaches and 60 right-hand reaches. In left-handers, 120 trials were video coded for the fitting task. Of these, 117 trials had valid marker data (98%), including 58 left-hand reaches and 59 right-hand reaches. Means and standard errors are given for each reach parameter as a function of handedness group (right-handers or left-handers) and hand (left or right) in Table 1 and the corresponding model estimates are given in Table 2. Trial-by-trial data averaged across participants for each kinematic variable are given in Figure 2. Reach smoothness could not be examined in right-handers, because participants performed at floor levels for this variable on the fitting task. There was a main effect of hand on reach straightness for right-handers on the fitting task. As predicted, the right hand was straighter than the left hand in right-handers for reaches to the ball. There were no other main effects of hand on reach average speed, reach smoothness, or grip time in right-handers. Contrary to our predictions, there were no main effects of hand on reach average speed, reach smoothness, reach straightness, or grip time for left-handers on the fitting task. In other words, the left (preferred) hand in left-handers did not outperform the right (nonpreferred) hand on any of the target movement parameters on the fitting task.

TABLE 2. Estimates of the Model Regression Coefficients, 95% CI of Those Coefficients, and Estimated *p* Values for the Fitting Task by Handedness Group

	b	95% CI	*p*
Right-handers			
Average speed	7.55	[−12.07, 27.17]	.43
Smoothness	—	—	—
Straightness	0.03	[0.01, 0.05]	.02
Grip time	21.46	[−5.45, 48.37]	.13
Left-handers			
Average speed	–9.66	[−27.35, 8.03]	.37
Smoothness	0.23	[0.008, 0.45]	.06
Straightness	–0.004	[−0.02, 0.01]	.50
Grip time	21.04	[−2.42, 44.50]	.11

Note. Smoothness could not be analyzed in right-handed adults because participants performed at floor levels.

Cup Task

In right-handers, 120 trials were video coded for the cup task. Of these, 118 trials had valid marker data (98%), representing 59 left-hand reaches and 59 right-hand reaches. In left-handers, 120 trials were video coded for the cup task. Of these, 118 trials had valid marker data (98%), representing 58 left-hand reaches and 60 right-hand reaches. Means and standard errors are given for each reach parameter as a function of handedness group and hand in Table 3 and model estimates are given in Table 4. Trial-by-trial data averaged across participants for each kinematic variable are given in Figure 3. In right-handers, there were main effects of hand on average reach speed, reach smoothness, and reach straightness, but not on grip time. Overall, the right hand was slower on average compared with the left hand in right-handers on the cup task. In addition, the right hand was smoother and straighter than the left hand for reaches to the Cheerio in right-handers. Similar to right-handers and contrary to our predictions, the right hand was smoother and straighter than the left hand in left-handers on the cup task. However, there was no effect of hand on average reach speed or grip time for reaches to the Cheerio in left-handers. These results suggest that the left hand had no advantage in left-handers on the target movement parameters of average reach speed, reach smoothness, reach straightness, or grip time for the cup task.

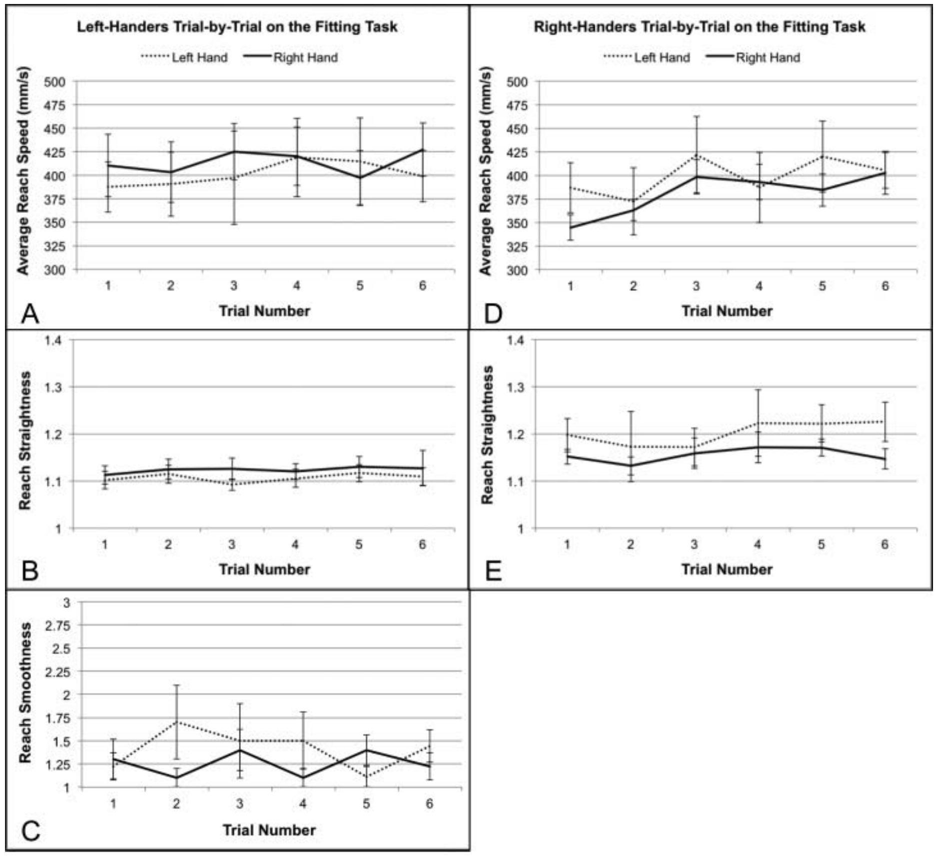

FIGURE 2. Trial-by-trial data averaged across participants for the fitting task. (A–C) Left-handers, (D, E) right-handers.

Discussion

The primary goal of this study was to examine the relations between limb control and handedness in adults. Three-dimensional recordings were made of each arm on two reaching and grasping tasks: adults reached to a ball and placed it into the opening of a toy (fitting task), or reached for a cup with a Cheerio inside, which they placed on the table in a predesignated location after each trial (cup task). Participants were categorized as left- or right-handed for analyses using the EHI questionnaire that was completed at the end of the visit following the experimental tasks. We hypothesized that limb control and handedness were related, and predicted that we would observe side differences favoring the dominant limb based on the dynamic dominance hypothesis of motor lateralization (Mutha et al., 2012; Sainburg, 2002, 2005, 2014). Specifically, we predicted that the dominant limb would be straighter and smoother on both reaching and grasping tasks compared with the nondominant limb (i.e., right arm in right-handers and left arm in left-handers). Our results only partially supported these predictions for right-handers, but not for left-handers.

When differences between hands were observed, the right hand was favored regardless of handedness group. This effect was seen most strongly on the cup task. The performance of right-handers on the cup task was consistent with our predictions. The right arm was straighter and smoother compared with the left arm in accordance with the dynamic dominance hypothesis for optimized predictive control (Bagesteiro & Sainburg, 2002; Mutha et al., 2013; Sainburg, 2002; Sainburg & Kalakanis, 2000; Sainburg & Schaefer, 2004; Schaefer, Haaland, & Sainburg, 2007, 2009; Shabbott & Sainburg, 2008; Tomlinson & Sainburg, 2012; Yadav & Sainburg, 2014). The right arm was also slower on average than the left arm in right-handers, lending further support for a precision control mechanism in the dominant limb. However, the right arm was also straighter and smoother in left-handers on the cup task, which is contrary to our predictions. There was no difference between arms for average speed in left-handers. Thus, there was no advantage for the preferred left hand/limb in left-handers for retrieving a Cheerio and placing it on the table. These results differ from prior work comparing left-handers to right-handers on reaching tasks where the effects were mirrored (Przybyla et al., 2012; Wang & Sainburg, 2006).

TABLE 3. Means and Standard Errors for Reach Parameters as a Function of Handedness Group and Hand on the Cup Task

	Right-handers		Left-handers	
Reach parameter	Left hand	Right hand	Reach parameter	Left hand
Average speed (mm/s)	495 ± 13.9[a]	466 ± 9.0[a]	541 ± 22.0	539 ± 14.4
Smoothness (movement units)	1.97 ± 0.132[a]	1.47 ± 0.078[a]	1.75 ± 0.144[a]	1.38 ± 0.083[a]
Straightness	1.23 ± 0.021[a]	1.13 ± 0.009[a]	1.14 ± 0.012[a]	1.11 ± 0.009[a]
Grip time (ms)	910 ± 30.2	892 ± 31.8	834 ± 30.3	857 ± 28.4

Note. For smoothness data, values closer to 1 indicate smoother reaches. Straightness was measured by the ratio of hand path length to straight-line distance; values closer to 1 indicate straighter reaches.
[a]Significant difference between hands.

There are two procedural differences that may explain the differences between studies. First, adult studies typically utilize large blocks of trials, giving the participant more experience with each stimulus type, which could allow for learning effects. Using our infant protocol, we ran a much smaller number of trials and eliminated any learning or practice effects (cf., Berthier, Clifton, Gullapalli, McCall, & Robin, 1996). As illustrated in Figures 2 and 3, there were minimal changes in the kinematic variables over the test session. Second, we examined complex actions where the participant not only had to grasp an object, rather than simply touch or point to it, but then also perform a secondary action of placing the object in a new location. Therefore, the demands of the tasks used to test dynamic dominance varied greatly between studies. Future researchers should examine left-right differences as a function of task type to better understand how task constraints shape interlimb asymmetries. Overall, our results from the cup task support a more general right-hand/left-hemisphere specialization for fine motor skill, independent of handedness (Goble & Brown, 2008; Gonzalez, Ganel, & Goodale, 2006; Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Goodale, 1988; Serrien, Ivry, & Swinnen, 2006).

TABLE 4. Estimates of the Model Regression Coefficients, 95% CI of Those Coefficients, and Estimated *p* Values for the Cup Task by Handedness Group

	b	95% CI	*p*
Right-handers			
Average speed	32.44	[7.62, 57.26]	.01
Smoothness	0.49	[0.22, 0.76]	.001
Straightness	0.09	[0.06, 0.12]	<.001
Grip time	17.09	[−41.69, 75.87]	.59
Left-handers			
Average speed	31.33	[−7.68, 70.34]	.11
Smoothness	0.46	[0.16, 0.76]	.003
Straightness	0.04	[0.02, 0.06]	.01
Grip time	−27.28	[−96.70, 42.14]	.46

We also found a slight advantage for the right hand in right-handers on the fitting task. The right hand was straighter than the left hand in right-handers, in part supporting our prediction. We were unable to examine smoothness in right-handers, however, as there was no variability in movement units between the hands. In left-handers, our predictions were not supported, as no differences were found between the hands on any of the target variables. Taken together, our results suggest that the fitting task was not ideal for identifying hand performance differences as relevant to our hypothesis. Grosskopf and Kuhtz-Buschbeck (2006) administered a similar task in right-handers only in which participants were asked to reach to a peg, pick it up, and insert it in another location. While they reported that the dominant (right) hand was faster to insert, there were no kinematic differences between the hands (note: straightness and smoothness were not examined in that study). Seegelke, Hughes, and Schack (2011) similarly reported no kinematic differences between the left and right hands in right-handers grasping cylinders and moving them to targets. Importantly, they noted that their task did not require as much precision as other studies, and they argued that the degree to which any asymmetry may be expressed is dependent on task context and complexity.

Studies ranging from infants to adults have consistently found that action intent influences reach kinematics (e.g., Armbrüster & Spijkers, 2006; Claxton, Keen, & McCarty, 2003; Wilmut, Byrne, & Barnett, 2013). Both the cup task and the fitting task can be classified as grasp to place as performed by the adults in this study, so why did the reach kinematics differ so greatly? Rather than intent, the difference in patterning between the two tasks might have been due to the precision required. Participants used a whole hand power grip on the fitting task. The starting wells that held the ball were quite shallow, so it was not particularly challenging to lift the ball. In addition, placing the ball into the top of the toy did not require a great deal of accuracy for adults; the ball easily fit into the opening. By comparison, participants utilized a thumb and index finger precision grip for removing the Cheerio from inside the small cup and placing it on the

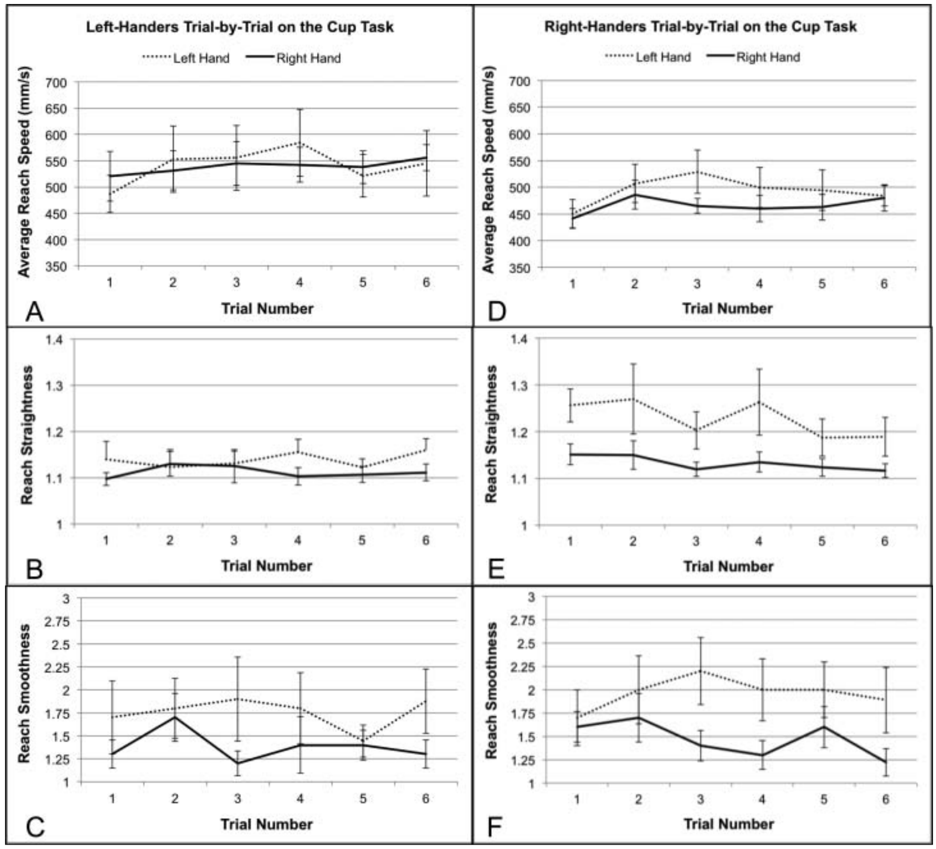

FIGURE 3. Trial-by-trial data averaged across participants for the cup task. (A–C) Left-handers, (D, E) right-handers.

"X" on the table. The difference in grasping skill required may explain the kinematic differences observed between tasks. We suggest that task complexity may be defined in a number of ways including but not limited to (a) the number of steps in the action, (b) the intent of the action, and (c) the grip type needed to perform the action. In typical development, such task constraints are independent of person-level dexterity or ability.

One limitation of the present study was that we did not measure coordination between reaching and grasping, or evaluate grasp kinematics on our experimental tasks. Tretriluxana, Gordon, and Winstein (2008) reported a left hand advantage for aperture preshaping and a right hand advantage for coordinating hand transport and grasping in right-handers completing reach-to-grasp movements. In a series of studies by Flindall and colleagues, grasp kinematics were compared for reaching to and eating a Cheerio versus placing it in a large opening of a bib (Flindall & Gonzalez, 2013, 2014, 2015; Flindall, Stone, & Gonzalez, 2015). Maximum grip aperture was smaller for right hand grasp-to-eat movements compared with grasp-to-place in young children and adults regardless of handedness group. Most recently, Flindall and Gonzalez (2016) replicated their right hand maximum grip aperture effect with inedible targets that were comparable in size to Cheerios, and have suggested that the advantage is tied to more general hand-to-mouth movements. However, there was no condition requiring the Cheerio to be placed in a precise location, as in the present study. It is not clear whether the kinematic advantage for grasping is related to target size, the end goal of the movement, or a combination. Future work could compare reach and grasp kinematics for small targets such as Cheerios with various endpoints (e.g., place imprecise, place precise) that can clarify the right-hand reaching and grasping advantages identified across multiple studies.

Another limitation of the present study is that we did not include tasks that would highlight nondominant/left arm advantages, such as those without visual feedback or with unexpected changes (Sainburg, 2014). Previous work with right-handers has found that the left arm had better accuracy and precision in spatial positioning compared with the right arm (Bagesteiro & Sainburg, 2003; Duff & Sainburg, 2007). A reduced but similar effect was observed in left-handers for the right arm (Przybyla et al., 2012). However, Boulinguez, Velay, and Nougier (2001) reported a left arm advantage in initiating movement and adjusting amplitude online that was independent of handedness. Because left-handers are rarely included in kinematic studies and handedness studies often focus on the dominant arm (i.e., right), more data are needed to evaluate this component of the dynamic dominance hypothesis. We are also not aware of any developmental studies that have utilized no-vision or perturbation conditions and compared arm kinematics as well as hand preference. These studies are critically needed to evaluate the origins of arm/hemisphere advantages in development.

Returning to our original experiment in infants that motivated the present study, there is a sharp contrast in the type and extent of asymmetries exhibited by adults on the fitting and cup task that were not observed around the first year of life (Nelson et al., 2014). Two caveats are important to mention. First, recent work by Michel, Babik, Sheu, and Campbell (2014) suggests that there are multiple trajectories in the development of infant handedness, which was not captured by our prior work. For example, some infants may be characterized by an early consistent rightward trajectory and their reach kinematics could be different than infants who initially display no preference, but trend toward the right or left. Second, the dependent variables of interest (i.e., reach smoothness, reach straightness, and average reach speed) continue to be refined over the first years of life and have not reached adult values by 2 years of age (Berthier, 2011). We can only speculate when adult-like patterns of asymmetries may appear on our tasks, particularly the cup task where we observed more robust effects. With adult benchmarks in place, a longitudinal design is needed to fully characterize the relations between asymmetries observed in manual behavior, and those in reach-to-grasp kinematics across early development.

Summary and Conclusions

Laterality is not unique to humans, and has been well documented in vertebrate and invertebrate animals (for reviews, see Frasnelli, 2013; Frasnelli, Vallortigara, & Rogers, 2012; Rogers, Vallortigara, & Andrew, 2013; Vallortigara & Rogers, 2005). Investigators working in laterality in any model share the same basic tenet: behavioral biases are thought to reflect asymmetric brain function. One hypothesis has summarized the work on behavioral laterality across various animal species and proposed a division of labor wherein the left hemisphere has been associated with routine or learned behavior, and the right hemisphere has been associated with unexpected or arousing behavior (MacNeilage, Rogers, & Vallortigara, 2009; Rogers & Vallortigara, 2015; Rogers et al., 2013; Vallortigara & Rogers, 2005). Avoiding duplication of function and increasing computational efficiency offers a clear evolutionary advantage regardless of brain size, and it is plausible that motor control would similarly benefit from such organization. Sainburg (2014) overlaid the dynamic dominance hypothesis onto this division of labor framework, supported largely by the work in right-handers where the right hand (left hemisphere) excels at stable conditions and the left hand (right hemisphere) excels at unstable conditions. The work by Sainburg and colleagues has suggested that the system is reversed in left-handers. However, we have shown that left-handers look like right-handers on a task requiring fine motor skill, which suggests that the hemispheres may be matched, not mirrored. To complicate matters, we did not find a robust pattern of hand/hemisphere bias on our other task, and we argue that any theory of laterality must be mediated by task difficulty level, as well as address ontogeny. We are not the first to argue that measurement is a critical variable in laterality research, and future work is needed using a variety of tasks across handedness groups to refine these theories and understand if, when, and how laterality serves as an organizing principle for motor control in human development.

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