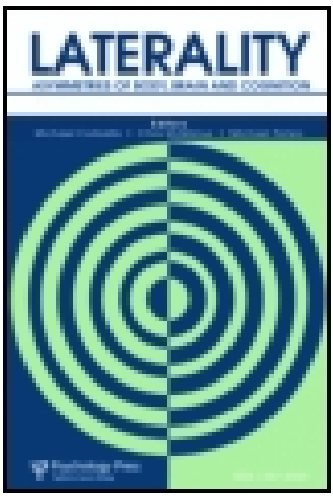
This article was downloaded by: [University of Lethbridge]
On: 23 January 2015, At: 09:10
Publisher: Routledge
Informa Ltd Registered in England and Wales Registered Number: 1072954
Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Laterality: Asymmetries of Body, Brain and Cognition
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/plat20

Evidence for right-hand feeding biases in a left-handed population

Jason W. Flindall[a], Kayla D. Stone[a] & Claudia L. R. Gonzalez[a]
[a] The Brain in Action Laboratory, Department of Kinesiology and Physical Education, University of Lethbridge, Lethbridge, AB, Canada
Published online: 26 Sep 2014.

CrossMark
Click for updates

To cite this article: Jason W. Flindall, Kayla D. Stone & Claudia L. R. Gonzalez (2014): Evidence for right-hand feeding biases in a left-handed population, Laterality: Asymmetries of Body, Brain and Cognition, DOI: 10.1080/1357650X.2014.961472

To link to this article: http://dx.doi.org/10.1080/1357650X.2014.961472

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at http://www.tandfonline.com/page/terms-and-conditions

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Laterality, 2014
http://dx.doi.org/10.1080/1357650X.2014.961472

Routledge
Taylor & Francis Group

Evidence for right-hand feeding biases in a left-handed population

Jason W. Flindall, Kayla D. Stone, and Claudia L. R. Gonzalez

The Brain in Action Laboratory, Department of Kinesiology and Physical Education, University of Lethbridge, Lethbridge, AB, Canada

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

We have recently shown that actions with similar kinematic requirements, but different end-state goals may be supported by distinct neural networks. Specifically, we demonstrated that when right-handed individuals reach-to-grasp food items with intent to eat, they produce smaller maximum grip apertures (MGAs) than when they grasp the same item with intent to place it in a location near the mouth. This effect was restricted to right-handed movements; left-handed movements showed no difference between tasks. The current study investigates whether (and to which side) the effect may be lateralized in left-handed individuals. Twenty-one self-identified left-handed participants grasped food items of three different sizes while grasp kinematics were captured via an Optotrak Certus motion capture array. A main effect of task was identified wherein the grasp-to-eat action generated significantly smaller MGAs than did the grasp-to-place action. Further analysis revealed that similar to the findings in right-handed individuals, this effect was significant only during right-handed movements. Upon further inspection however, we found individual differences in the magnitude and direction of the observed lateralization. These results underscore the evolutionary significance of the grasp-to-eat movement in producing population-level right-handedness in humans as well as highlighting the heterogeneity of the left-handed population.

Keywords: Grasp; Left-hand; Kinematics; Prehension; Asymmetries.

Many studies investigating kinematics of grasp-to-place or grasp-to-manipulate tasks have shown only minor differences between left- and right-handed movements. That is, despite a marked preference to use the right hand for grasping (Gonzalez, Ganel, & Goodale, 2006; Gonzalez & Goodale, 2009; Stone &

Address correspondence to: Jason Flindall, The Brain in Action Laboratory, Department of Kinesiology and Physical Education, University of Lethbridge, Lethbridge, Alberta T1K 3M4, Canada. E-mail: jason.flindall@uleth.ca

© 2014 Taylor & Francis

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Gonzalez, 2013), participants perform right- and left-handed movements with near identical kinematics (Flindall, Doan, & Gonzalez, 2014; Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana, Gordon, & Winstein, 2008). Recent research from our lab has shown that kinematic differences between left- and right-handed reach-to-grasp actions are not only identifiable, but are also robust and ubiquitous among right-handed individuals (Flindall & Gonzalez, 2013). These differences are intrinsically linked with task, however, which may explain why it has proven difficult to isolate them in previous kinematic analyses. Specifically, we established that when right-handed participants used their right (dominant) hands to grasp a small food item with the intention to eat it, they produced smaller maximum grip apertures (MGAs) during the pre-contact phase of the movement than if they used their non-dominant left hands. If participants grasped the same food items to instead place them into a receptacle near the mouth, then left- and right-handed movements shared similar kinematics. In other words, left-handed movements showed no differences between grasp-to-place or grasp-to-eat kinematics, and the kinematics of these tasks were identical to those seen in right-handed grasp-to-place actions. Right-handed grasp-to-eat actions, in contrast, displayed significantly smaller MGAs than grasps made in all other hand/task conditions.

The discovery of these task-dependent asymmetries favouring the right hand is supported by other studies highlighting differences in the grasp-to-place and grasp-to-eat movements, be they kinematic (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010, 2011), developmental (Sacrey, 2012; Sacrey, Arnold, Whishaw, & Gonzalez, 2013) or neural (Graziano, Aflalo, & Cooke, 2005; Graziano, Cooke, Taylor, & Moore, 2004). In terms of kinematics, Ferri et al. (2010) demonstrated that grasp-to-eat movements show greater automaticity than do grasp-to-place or grasp-to-feed movements. Regarding development, Sacrey et al. (2013) showed that a right-hand preference for grasp-to-eat movements develops in infants and toddlers several years earlier than the hand preference for grasp-to-place or grasp-to-manipulate movements. In electrophysiological studies involving macaques, Graziano and colleagues have shown that long-train stimulation of the primary motor cortex produced functional, multi-joint movements, including grasp-to-inspect and hand-to-mouth movements (Graziano et al., 2004, 2005). Taken together, these studies support a theory of primate motor cortex organized not around control of individual muscles, but rather around the production of goal-oriented actions.

Because the asymmetries in the grasp-to-eat movement we previously identified favoured the right hand, we postulated that this advantage may have strongly influenced the development of the right-handedness found at the population level in humans. However, that study did not address the behaviour of left-handed participants. Despite the fact that left-handers account for nearly 10% of the population (Annett, 1970; Briggs & Nebes, 1975), kinematic studies including left-handed participants are scarce. Multiple studies investigating behaviour among left-handers have shown that many are not simply mirror

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

images of right-handers (Bryden, Mayer, & Roy, 2011; Shen & Franz, 2005). Instead, "left-handed" describes a remarkably heterogenic group, in which up to 50% of members are behaviourally indistinguishable from their right-handed counterparts in terms of hand choice for grasping (Bryden et al., 2011; Gonzalez & Goodale, 2009; Gonzalez et al., 2006; Stins, Kadar, & Costall, 2001; Stone, Bryant, & Gonzalez, 2013) and/or of grasping kinematics (Boulinguez, Velay, & Nougier, 2001; Stins et al., 2001). Based on these studies, it is reasonable to anticipate that a significant proportion of the left-handed population would behave in a manner similar to the right-handers in our previous investigation (Flindall & Gonzalez, 2013). In other words, while some left-handers may show both a preference for and a kinematic advantage with left-handed grasp-to-eat movements, many self-identified left-handers should exhibit smaller MGAs when grasping-to-eat with their right (in this case, non-dominant) hands. In the present study, we investigated this possibility by looking at differences between grasp-to-eat versus grasp-to-place actions in the left and right hands of a left-handed population. A right-hand kinematic advantage would support a theory of left lateralized cortical structures producing grasp-to-eat actions, which in turn may have led to a species-wide preference for general right-hand use. In addition, it would rule out the simpler explanation that kinematic asymmetries arise from hand-use habits. Because we have previously argued that the earlier development of a right-hand preference for grasp-to-eat actions would translate into several additional years of experience in right-handed hand-to-mouth movements (Flindall & Gonzalez, 2013), we therefore (in the current study) assess kinematics among left-handed participants—a group in which an experience-based advantage would presumably favour the left (i.e., opposite) hand. If, instead, the advantage is predominantly lateralized to the right, or to both hands, then this would suggest that the advantage cannot be explained by experience alone.

Twenty-one self-reported left-handed participants grasped food items of three different sizes, using both their dominant and non-dominant hands in order to either (1) eat or (2) place the item into a bib located near the mouth. Based on the literature discussed above, we predicted two main outcomes from this research. First, we hypothesized that many left-handed participants would behave in a manner similar to the right-handed population, in that they would produce smaller MGAs when grasping with intent to eat, and that this behaviour would be lateralized to only one hand. Second, we predicted that the population would be heterogeneous with regard to which hand this behaviour is lateralized: that is, some participants would behave as mirror opposites to right-handers, producing smaller MGAs when grasping with their dominant hands (*left–left handers*). Other left-handers would behave as right-handers, producing smaller MGAs when eating with their non-dominant right hands (*right–left handers*). We predict this second group of right–left handers will constitute a significant portion of the left-handed population—perhaps as many as 50% (Derakhshan, 2006; Gonzalez & Goodale, 2009).

METHODS

Participants

Twenty-one left-handed university students (average age 21.8 years, 11 females) participated in the experiment. Handedness was self-reported by the participant and confirmed through a modified Edinburgh/Waterloo handedness questionnaire (Oldfield, 1971; Stone et al., 2013). All participants gave informed written consent prior to the onset of the study, in accordance with the principles expressed in the Declaration of Helsinki and with the approval of the University of Lethbridge Human Subjects Research Committee (protocol #2011-022). Participants were able to withdraw from the study at any time without consequence.

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Materials

The materials and procedures mirrored those of Flindall and Gonzalez (2013). Briefly, three infrared light emitting diodes (IREDs) were placed on the participant's hand; two on the distal phalanges of thumb and index finger, slightly proximal with respect to the nails, and one on the wrist at the medial aspect of the styloid process of the radius (proximal and medial with respect to the anatomical snuff box). An Optotrak Certus camera bar (Northern Digital, Waterloo, ON, Canada) recorded IRED position during each trial at 200 Hz for 5 s. Vision was restricted between trials using PLATO™ Liquid crystal glasses (Translucent Technologies, Toronto, ON, Canada) worn by the participant throughout the testing session. All experimental equipment was controlled using SuperLab 4.5 (Cedrus Corporation, San Pedro, CA, USA) and NDI First Principles (Northern Digital, Waterloo, ON, Canada).

Participants were seated before a self-standing height-adjustable triangular pedestal. The pedestal held individual cereal food items (presented one at a time) of three different sizes: SMALL (Cheerios®, mean diameter 11 mm), MEDIUM (Froot Loops®, mean diameter 15 mm), and LARGE (Oatmeal Squares®, mean length 21 mm). These targets were chosen based on their distinct sizes and familiarity. The distance to the pedestal was normalized to each participant's reach distance (100% of length from shoulder to index finger with elbow at full 180° extension). The height of the pedestal was adjusted for each participant not only such that the food was at a comfortable reach height (approximately level with the base of the sternum of the seated participant), but also such that the edge of the pedestal did not act as a direct obstacle during the reach-to-grasp movement (Whishaw et al., 2002).

Procedure

Participants sat behind the pedestal, with their hand placed comfortably on their lap (fingertips of thumb and index finger together) between trials. Targets were

Figure 1. Experimental design. Left: Participants begin all reach-to-grasp actions in a "start position" with their hand resting on their lap, thumb and index finger together (item shown: Froot Loops®). Centre: EAT task requires participant to eat the target after grasping. Right: PLACE task requires participant to grasp the target and place it in a bib hanging below his/her chin. Participants wore the bib throughout all blocks. PLATO™ liquid crystal glasses restricted participant vision between trials. Vision was unrestricted during grasps. All grasps were completed using only the index finger and thumb.

presented in a pseudo-random order, such that the participant was naive to the size of the food item until the beginning of the trial, when the goggles transitioned to their transparent state. After 1,000 ms of transparency during which the participant had full view of their hand and target, an audible go-signal ("beep") was presented, informing the participant that they should begin the reach-to-grasp movement "at a comfortable pace". After grasping the target between the thumb and index finger in a precision grip, participants would either (1) ingest the item completely (EAT condition) or (2) place the item in a bib hanging below their chin (PLACE condition; Figure 1). Investigators replaced food items between trials, while the liquid crystal goggles were in a closed (opaque) state. EAT and PLACE task conditions were presented in blocks of 25 trials (8 SMALL, 8 MEDIUM, 9 LARGE, randomized), with start order counterbalanced between participants. Participants were informed of task requirements at the beginning of each block. After both blocks were completed, IREDs were transferred to the participant's other hand, and the process was repeated. Hand start order was counterbalanced between participants.

Analyses

As the primary focus of the current study was to replicate the methods of Flindall and Gonzalez (2013) in a group of left-handers, kinematic analyses were limited to MGAs. MGA was measured as the peak resultant distance achieved between

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

the thumb and index finger prior to the time of grasp contact. Between hand comparisons required MGA calculations to be corrected for IRED placement, as grip aperture calculations were based on distance between the IREDs, rather than actual distance between-subject fingertips. Grip aperture corrections were accomplished via the method described in Flindall and Gonzalez (2013), wherein we averaged the resting grip apertures recorded per participant per hand, and subtracted that constant from all associated MGA values. This correction factor allows us to control for slight variations in IRED placement between the hands as well as variations in hand size within participants (Flindall & Gonzalez, 2013; Flindall et al., 2014).

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Data processing

Data were collected via NDI First Principles, kinematic calculations were performed on unfiltered data using Microsoft Excel 2010, and statistical analyses were completed using IBM SPSS Statistics 19.0. Each participant's MGA measurements were inspected for normalcy within each Hand/Task/Size condition. Three participants required MGA winsorization within condition, as their within-condition range of MGAs exceeded 20 mm (whereas the average within-condition MGA range for other participants was <9 mm). Outliers (MGA values more than 2 standard deviations outside the condition mean) were removed from analysis. An average of 3.2% of trials per participant (range 0–13%) were removed, with a further 3.0% of trials per participant (range 0–13%) lost due to either camera line-of-sight failure or participant error. In total, an average of 6.2% of trials were removed from each participant (range 0–15%). Remaining trials were averaged by condition, and further analyses were conducted on these averages. To assure that cleaning of the data did not bias the results, statistical analyses were conducted on both raw data (e.g., all trials included) and homogenized data. No differences were found between these two types of analyses. Significant results from homogenized data are reported below.

For our primary analysis, a three-way within-subject repeated measures analyses of variance [ANOVAs; Hand (LEFT/RIGHT) × Task (EAT/PLACE) × Size (SMALL/MEDIUM/LARGE)] was run on condition means. To enable comparisons of the current results with those of Flindall and Gonzalez (2013), a secondary analysis was conducted wherein the data were split by Hand used (LEFT/RIGHT), and separate two-way ANOVAs [Task (EAT/PLACE) × Size (SMALL/MEDIUM/LARGE)] were run on the resulting sets. This secondary analysis also allowed us to consider between competing hypotheses of whether a predicted effect of task appeared as a result of practice, or of a lateralization of brain structures responsible for producing grasp-to-eat actions. Alpha significance for all ANOVA results was set at $p < .05$, and estimate of effect size is reported using partial η^2.

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

RESULTS

Handedness questionnaire

All participants self-reported as left-handers. The average score was −22.1 (±2.8 *SE*; range −41 to +12) out of the possible range of −44 (*strongly left-handed*) to +44 (*strongly right-handed*). The results of the questionnaire suggest that four participants were of mixed handedness (scores from −12 to +12), despite self-identifying as left-handed. These participants were not excluded from analyses.

Primary analyses (within subjects)

Significant within-subject main effects and interactions are reported below. Between-subject means and standard errors of MGAs are reported in Table 1.

A main effect of size was observed, $F(2, 40) = 531.832$, $p < .001$, $\eta^2 = .964$, wherein participants scaled their MGA according to food size. Follow-up paired-sample *t*-tests indicated that all sizes were significantly different from one another, $t(20) < -14.5$, $p < .001$. A main effect of task was observed, $F(1, 20) = 7.115$, $p = .015$, $\eta^2 = .262$, wherein participants opened their hands less wide when grasping items in the EAT condition ($M = 28.481$ mm, $SE = 1.084$ mm) than they did in the PLACE condition ($M = 29.858$ mm, $SE = 1.155$ mm; Figure 2). No other main effects or interactions were observed.

Secondary analyses (within subjects, divided by hand)

In the original study (Flindall & Gonzalez, 2013), we found a significant Hand × Task interaction wherein the effect of task on MGA was lateralized to the dominant hand. In that study, we could not rule out the possibility that the MGA difference between the left and right hand was simply a result of increased practice with the dominant hand. If that were the case, then the left-handed participants tested in the current study should demonstrate the effect of task predominantly in their dominant (i.e., left) hands. To investigate this possibility, data from all

TABLE 1
MGA means and standard errors by hand, size and task

	Eat	*Place*
Left hand		
Small	22.7 ± 1.3	23.0 ± 0.9
Medium	27.2 ± 1.1	27.9 ± 1.1
Large	37.0 ± 1.3	37.6 ± 1.2
Right hand		
Small	23.9 ± 1.8	22.7 ± 1.3
Medium	29.0 ± 1.5	27.2 ± 1.1
Large	37.6 ± 1.5	37.0 ± 1.3

MGA values are reported in millimetres.

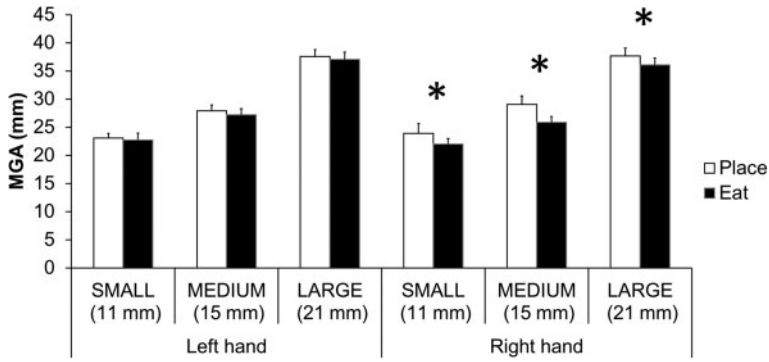


Figure 2. Average MGA during left- and right-handed movements towards small, medium, and large food items during place and eat tasks. Tasks were significantly different from each other during right-handed movements only ($p < .05$).

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

subjects were split by Hand condition (LEFT/RIGHT), and secondary two-way ANOVAs [Task (EAT/PLACE) × Size (SMALL/MEDIUM/LARGE)] were run on the resulting data sets. If the task effect were due to practice, then left-handed participants should show the effect predominantly in their left hands. If instead the task effect were due to a lateralized brain network responsible for producing grasp-to-eat movements, then (depending on the direction of lateralization) the task effect should be observed either in the right, or both, hands. Significant within-subject main effects and interactions are reported.

Significant main effects of size were found for both left, $F(2, 40) = 284.178$, $p < .001$, $\eta^2 = .934$, and right-handed, $F(2, 40) = 312.944$, $p < .001$, $\eta^2 = .940$, MGAs. Follow-up t-tests revealed that MGAs for all food sizes were significantly different from one another in both left-handed, $t(20) < -11.5$, $p < .001$, and right-handed, $t(20) < -11.5$, $p < .001$, grasps. When participants used their right hands, a main effect of task was again observed, $F(1, 20) = 5.332$, $p = .032$, $\eta^2 = .210$, with the EAT condition ($M = 27.98$, $SE = 1.06$) producing smaller MGAs than the PLACE condition ($M = 30.20$, $SE = 1.54$). This effect was not significant during the participant's dominant left-handed movements, $F(1, 20) = 0.728$, $p = .404$, $\eta^2 = .035$. It should be noted that although this analysis suggests a left hemisphere (right hand) lateralization for grasp-to-eat actions, the initial omnibus ANOVA failed to demonstrate a Hand × Task interaction, thus the data should be interpreted with caution. It is possible that the heterogeneity within the participant population was great enough to mask an interaction. The heterogeneity of the participant pool is investigated in our tertiary analysis.

Tertiary analysis (individual analyses)

In the previous study involving right-handed participants, the observed Hand × Task interaction was found in all participants. However, as shown by numerous

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

studies, left-handers represent a less homogenous group with respect to lateralization as compared to right-handers. For this reason we investigated each participant included in the primary and secondary analyses on an individual basis. After averaging participant data across each condition, we did a case-by-case search for the expected pattern: that is, a smaller average MGA for EAT versus PLACE, consistent across all three food sizes, lateralized to one hand. As expected, this pattern was not found in all left-handers; instead, eight participants did not demonstrate the effect consistently [either the task effect was not consistent across all food sizes (n = 5), or was in the direction opposite to that expected (i.e., PLACE < EAT; n = 3)). Of the remaining 13 participants, 7 demonstrated the effect only in their right hands ("right–left handers"), consistent with the results of our secondary analyses. Four more participants demonstrated the expected effect, but restricted to their *left* hands ("left–left handers"). The remaining two participants demonstrated the expected effect in both hands ("ambidextrous"), though the effect was stronger during right-handed movements in both cases.

Handedness correlation results

To determine whether our results (and the effective grouping of left–left handers, right–left handers, and ambidextrous) was linked with degree of left-hand preference as measured by the modified Edinburg/Waterloo handedness questionnaire, we determined the average difference between Eat and Place MGAs for the right and left hands of each participant. This analysis non-categorically measured the size of the effect for each participant. For example, if a participant displayed the task effect in their left hand only, this difference would be a positive value for their left hand (larger MGA in Place condition – smaller MGA in Eat condition), and a near-zero value for their right hand (representative of an insignificant difference between Eat and Place MGAs). Larger values are associated with larger differences between tasks. A Pearson correlation analysis was conducted to determine the degree of association between left- and right-handed task difference values and the scores on the modified Edinburg/Waterloo handedness questionnaire. No significant correlation was found, for either hand ($r^2 < .025$, $p > .54$), indicating that degree of handedness as measured by the modified Edinburg questionnaire is unrelated to degree of lateralization measured from the size of our within-hand difference between tasks.

Monte Carlo analysis

Monte Carlo analysis is a mathematical tool wherein random samples are generated to simulate the behaviour of a complex system (Hammersley & Handscomb, 1964). These samples may then be observed in order to infer the processes governing that system (Kalos & Whitlock, 2008). Monte Carlo analysis may also be used to test whether an observed sample distribution

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

TABLE 2
Number of occurrences of *n* randomly generated participants belonging to one of our assigned groups in 10,000 sample randomizations

Group	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10–21*	*Expected proportion (%)*	*Actual proportion (%)*
Left–left handers	2817	3577	2319	960	256	65	6	0	0	0	0	5.93	19.04
Right–left handers	2725	3766	2280	877	267	72	11	2	0	0	0	5.94	33.33
Ambidextrous	9196	782	22	0	0	0	0	0	0	0	0	0.39	9.52
Any	618	1878	2647	2348	1461	700	252	75	15	6	0	12.27	61.91

Expected proportions are calculated by summing all group membership occurrences over 10,000 randomizations and dividing by generated population size (210,000).

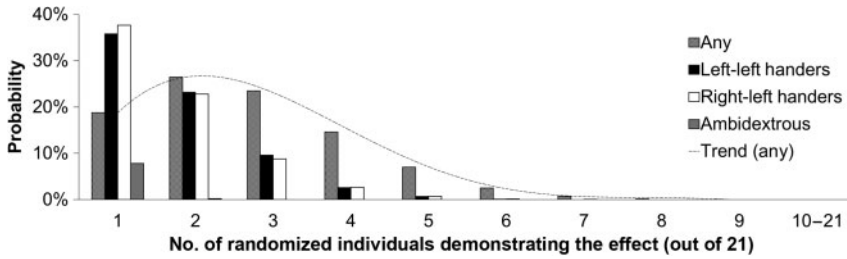


Figure 3. Probability of observing group membership of x (1–21) in a randomly generated sample (n = 21), for three groups (left–left handers, right–left handers and ambidextrous). Membership in our participant sample was 7, 4 and 2, respectively, for a total membership of 13 of 21 (61.91%). The dotted line represents the total expected membership in any of these three groups (y = 1E-05x^6 − 0.0003x^5 + 0.0024x^4 + 0.0038x^3 − 0.1151x^2 + 0.371x − 0.0743, R^2 = 0.9996).

differs from one predicted by a random null model (Roth, Kang, Batty, & Barthélemy, 2011; Trakhtenbrot & Kadmon, 2006). To test whether our effective groupings of left–left handers, right–left handers and ambidextrous could be attributed to random chance or experimenter bias, we generated sample MGA data for each participant, and analyzed the results according to the methods described in our tertiary analysis. Random MGAs were generated using Microsoft Excel 2010, using the means and standard deviations of a participant's experimental MGAs, collapsed across hand and task. We did not collapse across size, as we observed a robust effect of size, persistent in all participants. The resulting random MGAs were again averaged across each condition, and analyzed according to the same methods as described in our tertiary (subject-by-subject) analysis. The data were randomized 10,000 times, and the numbers of left–left handers, right–left handers and ambidextrous "participants" were tallied during each randomization. The results of these tallies are reported in Table 2, along with the expected and actual proportion for each lateralization. Figure 3 shows the probability of observing group membership of n out of 21 for each of the 3 groups, along with the probability of observing group membership of n for any of the 3 groups.

A one-group chi-square test was conducted to evaluate whether the group distribution as observed in our participant sample (n = 21; 19.0% left–left handers, 33.3% right–left handers, 9.5% ambidextrous, 38.1% none) differed significantly from the randomly generated population (n = 210 000; 5.93% left–left handers, 5.94% right–left handers, 0.39% ambidextrous, 87.73% none). The participant sample group membership proportion was found to be significantly different from the randomized population, $\chi^2(3, N = 21) = 83.433$, $p < 5.63e^{-18}$.

DISCUSSION

We have recently shown that right-handed participants produce smaller MGAs when reaching to grasp food items with their dominant right hands, but only

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

when they intend to eat those food items (Flindall & Gonzalez, 2013). If instead participants grasped the items to place them in a receptacle near the mouth, both dominant and non-dominant hands produced equally large MGAs. In the current study, this effect was investigated in a group of left-hand dominant participants. Twenty-one adults used their dominant and non-dominant hands to grasp small, medium and large food items to either eat them or place them in a receptacle near the mouth. A main effect of task was found wherein grasp-to-eat actions produced significantly smaller MGAs than did grasp-to-place actions. This is the first study (of which we are aware) to show that the end goal of a reach-to-grasp action will affect the kinematics of that action in a population of left-handed individuals. This task-specific distinction also supports the theory of a goal-oriented organization of the human motor cortex, again for the first time in a left-handed population. To facilitate comparisons between our current results and those of our previous study (Flindall & Gonzalez, 2013), we performed two additional (i.e., secondary and tertiary) analyses on our data. In our secondary analysis, when we inspected dominant (left-) and non-dominant (right-) handed movements separately, the effect of task was found to be significant only during right-handed movements. This result supports the theory of a lateralized advantage for grasp-to-eat movements as discussed in our previous study (Flindall & Gonzalez, 2013), one that is unlikely to be a result of experience alone. While it should be noted that no Hand × Task interaction was observed in the initial omnibus ANOVA, this effect is also in agreement with the results of multiple behavioural and kinematic analyses of left-handers which show that many adult left-handed persons behave in a manner similar to that of the general right-handed population with regard to grasping (Begliomini, Nelini, Caria, Grodd, & Castiello, 2008; Bryden et al., 2011; Gonzalez & Goodale, 2009; Gonzalez et al., 2006; Stins et al., 2001; Stone et al., 2013). In our tertiary analysis, when we inspected participants on an individual basis, we found that the direction of lateralization of the main effect of task was not consistent throughout the group. The lateralized effect of task (i.e., smaller MGAs to eat, rather than place) was found in the right hand in seven participants, the left hand in four participants, both hands in two participants and not consistently present (in either hand) in the remaining eight participants. This is in direct contrast to our previous study, where we found that the task effect was lateralized to the right hand in every one of our 12 adult participants (Flindall & Gonzalez, 2013). The non-homogenous nature of the tested population may also be responsible for the lack of Hand × Task interaction in the initial omnibus ANOVA. Furthermore, the hand and degree to which the grasp-to-eat advantage manifested did not correlate with degree of left-hand preference as measured by a handedness questionnaire. Taken together, these results support the postulation that left-handed individuals are not always mirror images of right-handers, nor are they always identical to right-handers in terms of kinematic behaviour; rather, they represent a heterogeneous population in terms of degree and direction of functional lateralization (Bryden

et al., 2011; Curt, Maccario, & Dellatolas, 1992; Gonzalez & Goodale, 2009; Gonzalez et al., 2006; Steenhuis & Bryden, 1999; Steenhuis, Bryden, Schwartz, & Lawson, 1990; Stins et al., 2001; Stone et al., 2013; Triggs, Calvanio, Levine, Heaton, & Heilman, 2000). These results are discussed in detail below.

Previous studies have shown that actor intent may have significant influence on the kinematic execution of a movement. Studies have reported differences in the reach-to-grasp phases of throwing and placing actions (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987), lift and show actions (Ferri et al., 2011) and feed and place actions (Ferri et al., 2010; Flindall & Gonzalez, 2013). As has been previously demonstrated, participants in the current investigation produced smaller MGAs when the target object was to be placed in the mouth, rather than simply in a location near the mouth. Unlike previous investigations however, the current study investigated task-related behavioural differences in left-handed individuals. We show that the right-hand grasp-to-eat accuracy advantage previously identified in right-handers may be lateralized to either hand in left-handed persons. This accuracy advantage may be evolutionarily significant, as numerous reach-to-grasp studies have shown that MGA is sensitive to target uncertainty, and that increases in uncertainty are linked with larger MGAs (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Flindall, 2012; Gentilucci, Toni, Chieffi, & Pavesi, 1994; Harvey et al., 2001; Jakobson & Goodale, 1991; Schettino, Adamovich, & Poizner, 2003; Wing, Turton, & Fraser, 1986). It has been proposed that larger MGA production may be a strategy to increase confidence in uncertain grasps by increasing the margin for error (Jakobson & Goodale, 1991). The fact that this kinematic advantage is inconsistently lateralized in left-handers suggests that, despite the probable link between grasp-to-eat lateralization and the evolution of handedness (Goodale, 1990; MacNeilage, Studdert-Kennedy, & Lindblom, 1987; Rogers, 2002; Whishaw, 2003), the neural basis for the grasp-to-eat advantage may be distinct from that for overall hand preference. Future research into the grasp-to-eat movement will be directed by this possibility.

Research has shown that a significant proportion of the population (9–14%) identify as left-handed (Annett, 1967). As left-handed individuals represent a group whose members are less consistently lateralized in terms of language processing (Gonzalez & Goodale, 2009; Jörgens, Kleiser, Indefrey, & Seitz, 2007; Matsuo et al., 2002; Sommer, Ramsey, Mandl, & Kahn, 2002; Szaflarski et al., 2002), facial recognition areas (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Willems, Peelen, & Hagoort, 2010), motor and premotor cortex activation patterns during simple movements (Cabinio et al., 2010; Matsuo et al., 2002; Verstynen, Diedrichsen, Albert, Aparicio, & Ivry, 2005) and hand preference for grasping (Bryden et al., 2011; Gonzalez & Goodale, 2009; Gonzalez et al., 2006; Stins et al., 2001; Stone et al., 2013), they are often excluded from study cohorts to reduce variance and increase statistical sensitivity [for review, see Willems, Van der Haegen, Fisher, and Francks (2014)]. This presents a problem, as any conclusions drawn from studies which exclude left-handed participants can

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

only be generalized to 86–91% of the population. In addition, such studies cannot reliably discuss evolutionary processes leading to right-hand dominance if they explicitly exclude the main source of variability in populations. Thus, a comprehensive analysis of prehension in the human population remains to be defined. In a previous study on right-handers, we found evidence that supports a theory of distinct neural networks regulating grasping tasks which are similar in their mechanics but differ in terms of end-goal (Flindall & Gonzalez, 2013). When right-handed people used their dominant hands, grasp-to-place movements directed towards food items presented with larger MGAs than did grasp-to-eat movements directed towards the same items. The goal of the present study was to investigate the existence of this effect in left-handed individuals. We confirmed the presence of this effect in a left-handed population but, in contrast with our previous study, the effect was not consistently lateralized to the dominant hand. That is to say, the left-handed participants in the current study do not represent as homogenous a group as did the right-handers investigated previously. Grasp-to-eat actions still often presented with smaller MGAs than did grasp-to-place actions directed towards the same targets, however whether this presented in the left or right hand varied between participants. This finding is significant as it expands the theory of a functionally organized human motor cortex to include all people, where it could previously only be applied to right-handers. In addition, by including left-handed participants we not only gathered data from a more representative sample, but we also provide evidence that the behaviours by which we should define handedness are not consistently lateralized. This study adds to the growing body of literature that describes left-handed persons in terms of mixed lateralization of multiple behaviours. With regard to kinematic advantages in grasp-to-eat behaviour, we show here that left-handed people who, as a group are inconsistent in terms of direction and degree of lateralization, may contain a majority who are lateralized in the same manner as are right-handed people. This supports the hypothesis that population level right-handedness may have evolved as a result of this lateralized right-hand advantage of the grasp-to-eat action (Flindall & Gonzalez, 2013; see also Goodale, 1990; MacNeilage et al., 1987; Rogers, 2002; Whishaw, 2003) and argues for the inclusion of left-handers in future kinematic and behavioural analyses. However, it also calls into question whether the current parameters by which we define handedness may be trusted to accurately predict an individual's behavioural lateralization.

In comparison to right-handed individuals, left-handed individuals are less consistently lateralized in terms of both behaviour and cortical organization (Willems et al., 2014). For example, some left-handers may prefer to use their right hands for certain fine motor skills, while others may display a rightward bias for power movements, such as those required in competitive sports (Peters, 1990). The current study found inconsistent lateralization of an advantage for grasping an object to eat, adding to this pattern of heterogeneity among left-handers. Handedness is most often determined based on hand use for a single

task (e.g., writing) or a small number of skilled and unskilled tasks assessed via questionnaire; these methods of classification overlook the significance of variability for behaviour within an individual. Handedness questionnaires, for example, focus mainly on a small number of skilled tasks, while ignoring bimanual tasks or tasks part of a functional chain (e.g., making a cup of tea; Scharoun & Bryden, 2014). Furthermore, questionnaires often do not address the confines imposed by context (Mamolo, Roy, Bryden, & Rohr, 2005; Mamolo, Roy, Rohr, & Bryden, 2006; Scharoun & Bryden, 2014). For example, one might prefer to open a door with her dominant hand while travelling through a familiar pathway in one direction, while consistently preferring her non-dominant hand while travelling in the other. In the current study, we found that lateralization of the grasp-to-eat advantage did not correlate with participant responses on a modified Edinburgh/Waterloo handedness questionnaire. While initially surprising, this finding is in accordance with several previous studies which have shown no correlation between hand preference/performance as measured by a behavioural task and that measured via questionnaire (Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Gonzalez et al., 2006; Peters, 1990; Porac & Coren, 1981; Steenhuis & Bryden, 1999). Because right-handers are more likely to be consistently lateralized in terms of multiple behaviours (Steenhuis & Bryden, 1999), handedness questionnaires may still demonstrate reliability in confirming the label of "right-handed". However, in light of the unpredictable lateralization of specific behaviours in self-identified left-handers, we propose that handedness questionnaires for left-handers should be interpreted with a certain degree of scepticism. If left-handed participants are unpredictably lateralized, then behavioural and kinematic investigations should not exclude them simply as a matter of course. Future behavioural studies should include left-handed participants not only to search for additional similarities between left- and right-handed people, but also to broaden the body of literature that describes this significant proportion of our global population.

To summarize, the current study investigated the lateralization of kinematic advantages in the grasp-to-eat task in left-handed people. While the kinematic advantage in question was present in 62% of left-handers, unlike right-handers the direction and degree of lateralization was inconsistent and unpredictable among those tested, demonstrating both the heterogeneity of the left-handed population, and the fact that the observed lateralized advantage is unlikely to be resultant from preference-related experience. These findings also reinforce the theory that population-level right-handedness has its origins at least partially in the grasp-to-eat movement. Finally, these results highlight the often unpredictable lateralization of specialized behaviours in left-handed people.

Manuscript received 22 May 2014
Revised manuscript received 27 August 2014
Revised manuscript accepted 30 August 2014
First published online 25 September 2014

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

REFERENCES

Annett, M. (1967). The binomial distribution of right, mixed and left handedness. *Quarterly Journal of Experimental Psychology*, *19*, 327–333. doi:10.1080/14640746708400109

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology*, *61*, 303–321. doi:10.1111/j.2044-8295.1970.tb01248.x

Badzakova-Trajkov, G., Häberling, I. S., Roberts, R. P., & Corballis, M. C. (2010). Cerebral asymmetries: Complementary and independent processes. *PLoS ONE*, *5*(3), e9682. doi:10.1371/journal.pone.0009682

Begliomini, C., Nelini, C., Caria, A., Grodd, W., & Castiello, U. (2008). Cortical activations in humans grasp-related areas depend on hand used and handedness. *PLoS ONE*, *3*(10), e3388. doi:10.1371/journal.pone.0003388

Berthier, N. E., Clifton, R. K., Gullapalli, V., McCall, D. D., & Robin, D. (1996). Visual information and object size in the control of reaching. *Journal of Motor Behaviour*, *28*, 187–197. doi:10.1080/00222895.1996.9941744

Boulinguez, P., Velay, J.-L., & Nougier, V. (2001). Manual asymmetries in reaching movement control. II: Study of left-handers. *Cortex*, *37*(1), 123–138. doi:10.1016/S0010-9452(08)70562-8

Briggs, G. G., & Nebes, R. D. (1975). Patterns of hand preference in a student population. *Cortex*, *11*, 230–238. doi:10.1016/S0010-9452(75)80005-0

Bryden, P. J., Mayer, M., & Roy, E. A. (2011). Influences of task complexity, object location, and object type on hand selection in reaching in left and right-handed children and adults. *Developmental Psychobiology*, *53*(1), 47–58. doi:10.1002/dev.20486

Cabinio, M., Blasi, V., Borroni, P., Montagna, M., Iadanza, A., Falini, A., & Cerri, G. (2010). The shape of motor resonance: Right-or left-handed? *NeuroImage*, *51*, 313–323. doi:10.1016/j.neuroimage.2010.01.103

Curt, F., Maccario, J., & Dellatolas, G. (1992). Distributions of hand preference and hand skill asymmetry in preschool children: Theoretical implications. *Neuropsychologia*, *30*(1), 27–34. doi:10.1016/0028-3932(92)90011-A

Derakhshan, I. (2006). Laterality of the command center in relation to handedness and simple reaction time: A clinical perspective. *Journal of Neurophysiology*, *96*, 3556–3556. doi:10.1152/jn.00852.2006

Ferri, F., Campione, G. C., Dalla Volta, R., Gianelli, C., & Gentilucci, M. (2010). To me or to you? When the self is advantaged. *Experimental Brain Research*, *203*, 637–646. doi:10.1007/s00221-010-2271-x

Ferri, F., Campione, G. C., Dalla Volta, R., Gianelli, C., & Gentilucci, M. (2011). Social requests and social affordances: How they affect the kinematics of motor sequences during interactions between conspecifics. *PLoS ONE*, *6*(1), e15855. doi:10.1371/journal.pone.0015855

Flindall, J. W. (2012). *Manual asymmetries in the kinematics of reach-to-grasp actions*. Lethbridge: Master of Science, University of Lethbridge.

Flindall, J. W., Doan, J. B., & Gonzalez, C. (2014). Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality: Asymmetries of Body, Brain and Cognition*, *19*, 489–507. doi:10.1080/1357650X.2013.862540

Flindall, J. W., & Gonzalez, C. (2013). On the evolution of handedness: Evidence for feeding biases. *PLoS ONE*, *8*(11), e78967. doi:10.1371/journal.pone.0078967.t002

Gentilucci, M., Toni, I., Chieffi, S., & Pavesi, G. (1994). The role of proprioception in the control of prehension movements: A kinematic study in a peripherally deafferented patient and in normal subjects. *Experimental Brain Research*, *99*, 483–500. doi:10.1007/BF00228985

Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, *95*, 3496–3501. doi:10.1152/jn.01187.2005

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Gonzalez, C. L., & Goodale, M. A. (2009). Hand preference for precision grasping predicts language lateralization. *Neuropsychologia*, *47*, 3182–3189. doi:10.1016/j.neuropsychologia.2009.07.019

Gonzalez, C. L., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, *182*, 275–279. doi:10.1007/s00221-007-1090-1

Goodale, M. A. (1990). *Vision and action: The control of grasping*. Norwood, NJ: ABLEX.

Graziano, M. S., Aflalo, T. N., & Cooke, D. F. (2005). Arm movements evoked by electrical stimulation in the motor cortex of monkeys. *Journal of Neurophysiology*, *94*, 4209–4223. doi:10.1152/jn.01303.2004

Graziano, M. S. A., Cooke, D. F., Taylor, C. S. R., & Moore, T. (2004). Distribution of hand location in monkeys during spontaneous behavior. *Experimental Brain Research*, *155*(1), 30–36. doi:10.1007/s00221-003-1701-4

Grosskopf, A., & Kuhtz-Buschbeck, J. P. (2006). Grasping with the left and right hand: A kinematic study. *Experimental Brain Research*, *168*, 230–240. doi:10.1007/s00221-005-0083-1

Hammersley, J. M., & Handscomb, D. C. (1964). *Monte Carlo methods* (Vol. 1). London: Methuen.

Harvey, M., Jackson, S. R., Newport, R., Krämer, T., Morris, D. L., & Dow, L. (2001). Is grasping impaired in hemispatial neglect? *Behavioural Neurology*, *13*(1), 17–28.

Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, *86*, 199–208. doi:10.1007/BF00231054

Jörgens, S., Kleiser, R., Indefrey, P., & Seitz, R. J. (2007). Handedness and functional MRI-activation patterns in sentence processing. *Neuroreport*, *18*, 1339–1343. doi:10.1097/WNR.0b013e32825a67db

Kalos, M. H., & Whitlock, P. A. (2008). *Monte Carlo methods*. New York, NY: John Wiley & Sons.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences*, *10*, 247–263. doi:10.1017/S0140525X00047695

Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2005). The performance of left-handed participants on a preferential reaching test. *Brain and Cognition*, *57*, 143–145. doi:10.1016/j.bandc.2004.08.033

Mamolo, C. M., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality*, *11*, 465–492.

Marteniuk, R. G., MacKenzie, C. L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. *Canadian Journal of Psychology/Revue canadienne de psychologie*, *41*, 365–378. doi:10.1037/h0084157

Matsuo, K., Kato, C., Ozawa, F., Takehara, Y., Isoda, H., Isogai, S., … Nakai, T. (2002). Manipulo-spatial processing of ideographic characters in left-handers: Observation in fMRI. *Magnetic Resonance in Medical Sciences*, *1*(1), 21–26. doi:10.2463/mrms.1.21

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*(1), 97–113. doi:10.1016/0028-3932(71)90067-4

Peters, M. (1990). Subclassification of non-pathological left-handers poses problems for theories of handedness. *Neuropsychologia*, *28*, 279–289. doi:10.1016/0028-3932(90)90021-F

Porac, C., & Coren, S. (1981). *Lateral preferences and human behavior*. New York, NY: Springer-Verlag.

Rogers, L. J. (2002). Lateralization in vertebrates: Its early evolution, general pattern, and development. *Advances in the Study of Behavior*, *31*, 107–161. doi:10.1016/S0065-3454(02)80007-9

Roth, C., Kang, S. M., Batty, M., & Barthélemy, M. (2011). Structure of urban movements: Polycentric activity and entangled hierarchical flows. *PLoS ONE*, *6*(1), e15923. doi:10.1371/journal.pone.0015923.g009

Sacrey, L. A. R. (2012). *Development and degeneration of the sensory control of reach-to-eat behaviour* (Doctoral thesis). Department of Neuroscience, University of Lethbridge, Lethbridge.

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Sacrey, L. A. R., Arnold, B., Whishaw, I. Q., & Gonzalez, C. (2013). Precocious hand use preference in reach-to-eat behavior versus manual construction in 1- to 5-year-old children. *Developmental Psychobiology*, *55*, 902–911.

Scharoun, S. M., & Bryden, P. J. (2014). Hand preference, performance abilities, and hand selection in children. *Frontiers in Psychology*, *5*, 82. doi:10.3389/fpsyg.2014.00082

Schettino, L. F., Adamovich, S. V., & Poizner, H. (2003). Effects of object shape and visual feedback on hand configuration during grasping. *Experimental Brain Research*, *151*, 158–166. doi:10.1007/s00221-003-1435-3

Shen, Y.-C., & Franz, E. A. (2005). Hemispheric competition in left-handers on bimanual reaction time tasks. *Journal of Motor Behavior*, *37*(1), 3–9. doi:10.3200/JMBR.37.1.3-9

Sommer, I., Ramsey, N., Mandl, R., & Kahn, R. (2002). Language lateralization in monozygotic twin pairs concordant and discordant for handedness. *Brain*, *125*, 2710–2718. doi:10.1093/brain/awf284

Steenhuis, R., & Bryden, M. (1999). The relation between hand preference and hand performance: What you get depends on what you measure. *Laterality: Asymmetries of Body, Brain and Cognition*, *4*(1), 3–26. doi:10.1080/713754324

Steenhuis, R. E., Bryden, M. P., Schwartz, M., & Lawson, S. (1990). Reliability of hand preference items and factors. *Journal of Clinical and Experimental Neuropsychology*, *12*, 921–930. doi:10.1080/01688639008401031

Stins, J. F., Kadar, E. E., & Costall, A. (2001). A kinematic analysis of hand selection in a reaching task. *Laterality: Asymmetries of Body, Brain and Cognition*, *6*, 347–367. doi:10.1080/713754421

Stone, K. D., Bryant, D. C., & Gonzalez, C. L. R. (2013). Hand use for grasping in a bimanual task: Evidence for different roles? *Experimental Brain Research*, *224*, 455–467. doi:10.1007/s00221-012-3325-z

Stone, K., & Gonzalez, C. (2013, April). *Grasping without vision: Hand preference in sighted and congenitally blind individuals*. Paper presented at the Cognitive Neuroscience Society Annual Meeting, San Francisco, CA.

Szaflarski, J. P., Binder, J. R., Possing, E. T., McKiernan, K. A., Ward, B. D., & Hammeke, T. A. (2002). Language lateralization in left-handed and ambidextrous people: fMRI data. *Neurology*, *59*, 238–244. doi:10.1212/WNL.59.2.238

Trakhtenbrot, A., & Kadmon, R. (2006). Effectiveness of environmental cluster analysis in representing regional species diversity. *Conservation Biology*, *20*, 1087–1098. doi:10.1111/j.1523-1739.2006.00500.x

Tretriluxana, J., Gordon, J., & Winstein, C. J. (2008). Manual asymmetries in grasp pre-shaping and transport–grasp coordination. *Experimental Brain Research*, *188*, 305–315. doi:10.1007/s00221-008-1364-2

Triggs, W. J., Calvanio, R., Levine, M., Heaton, R. K., & Heilman, K. M. (2000). Predicting hand preference with performance on motor tasks. *Cortex*, *36*, 679–689. doi:10.1016/S0010-9452(08)70545-8

Verstynen, T., Diedrichsen, J., Albert, N., Aparicio, P., & Ivry, R. B. (2005). Ipsilateral motor cortex activity during unimanual hand movements relates to task complexity. *Journal of Neurophysiology*, *93*, 1209–1222. doi:10.1152/jn.00720.2004

Whishaw, I. Q. (2003). Did a change in sensory control of skilled movements stimulate the evolution of the primate frontal cortex? *Behavioural Brain Research*, *146*(12), 31–41. doi:10.1016/j.bbr.2003.09.027

Whishaw, I. Q., Suchowersky, O., Davis, L., Sarna, J., Metz, G. A., & Pellis, S. M. (2002). Impairment of pronation, supination, and body co-ordination in reach-to-grasp tasks in human Parkinson's disease (PD) reveals homology to deficits in animal models. *Behavioural Brain Research*, *133*, 165–176. doi:10.1016/S0166-4328(01)00479-X

Downloaded by [University of Lethbridge] at 09:10 23 January 2015

Willems, R. M., Peelen, M. V., & Hagoort, P. (2010). Cerebral lateralization of face-selective and body-selective visual areas depends on handedness. *Cerebral Cortex*, *20*, 1719–1725. doi:10.1093/cercor/bhp234

Willems, R. M., Van der Haegen, L., Fisher, S. E., & Francks, C. (2014). On the other hand: including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews Neuroscience*, *15*, 193–201.

Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, *18*, 245–260. doi:10.1080/00222895.1986.10735380

Downloaded by [University of Lethbridge] at 09:10 23 January 2015