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In the present study, we manipulated the perceived demand of an ecologically valid task to investigate the possible presence of manual asymmetries in a reach-to-grasp action. Participants reached, grasped and sipped from a water glass under low (nearly empty) and high (nearly full) demand conditions. Participants reached to grasp in closed-loop, open-loop and delay visual conditions. Manual asymmetries were found in movement time, peak velocity and maximum grip aperture variability. Consistent with reach-to-point literature: (1) right-handed actions were completed in less time than left-handed actions in visually and memory-guided conditions; (2) right-handed movements were more accurate (i.e., produced more consistent maximum grip apertures) than left-handed movements in visually guided conditions. The results support a theory of left-hemisphere specialization for visual control of action.

Keywords: Prehension; Demand; Kinematics; Asymmetries; Left hand.

Manual asymmetries in visually guided reaching actions are well established in the literature. Many studies have demonstrated that right-handed people perform pointing and aiming movements in less time, with higher peak velocities, and with greater end-point accuracy when using their dominant hand (Elliott & Chua, 1996; Elliott et al., 1993; Fisk & Goodale, 1985; Roy & Elliott, 1989). It has

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been suggested that these asymmetries stem from a left hemisphere visual processing advantage; specifically, that the right hand/left hemisphere system is better able to process visual feedback of the ongoing movement, and is able to integrate this information more efficiently into online corrections (Flowers, 1975; Roy, Kalbfleisch, & Elliott, 1994). In support of this suggestion, it has been shown, for example, that when a target shift occurs during a reaching movement, regardless of the direction of the shift the target is reacquired more quickly by the right hand than the left hand (Elliott, Lyons, Chua, Goodman, & Carson, 1995).

In contrast, manual asymmetries in the grasping movement have been more difficult to demonstrate. This is intriguing, as common reach movements (e.g., reach-to-point or reach-to-aim) and grasp movements share similar limb transport phases (i.e., proximal–distal movement of the hand), and differ only in how the hand pre-shapes according to object features during grasps. In one study, investigators asked participants to reach for, grasp and remove a small peg from a hole into which it was fit (Grosskopf & Kuhtz-Buschbeck, 2006). This study revealed no significant kinematic differences between right- and left-handed movements. In another study (Tretriluxana, Gordon, & Winstein, 2008), participants were asked to reach-to-grasp targets of different sizes. The authors report that the only difference between the hands was in "preparatory aperture" (an inflection in the early grip aperture–time curve) exhibited by the left hand, with no other kinematic asymmetries in the grasp. The authors of these studies concluded that despite their manipulations, and excluding some very minor differences in the early grasp behaviour, the left and right hands were essentially equal in terms of grasp performance.

Several studies have shown that manual asymmetries in the kinematics of pointing/aiming movements are contingent upon task difficulty (Roy & Elliott, 1989; Roy et al., 1994; van Doorn, 2008). For example, van Doorn (2008) asked participants to touch a fixed target using a stylus while speed and precision requirements of the task were varied. In the high-precision condition, participants were required to hit the exact centre of the target. It was found that the time to complete the movement ("movement time") was significantly longer for the left hand in all conditions, but especially in those in which precision was emphasized. Perhaps by increasing the difficulty of a task, such hand differences could be found in the kinematics of the grasp. In other words, it is possible that hand differences in the grasp movement may not become significant until the visuomotor system is challenged by a demanding task.

The purpose of the current study was to investigate if manual asymmetries in *grasping* movements are contingent on task demands. Previous research has shown that right-handed grasp movements are affected by demand manipulations (Marteniuk, Mackenzie, Dugas, Liske, & Eickmeier, 1987; Savelsbergh, Steenbergen, & Van der Kamp, 1996). In a seminal experiment, Marteniuk et al. (1987) asked participants to reach for and grasp either a tennis ball or a light bulb. The tennis ball and the light bulb shared similar physical dimensions, and only differed in the fact that one would be perceived as more fragile than the other. Marteniuk et al. found that grasps directed towards the light bulb were associated with prolonged deceleration phase trajectories and overall longer movement times (Marteniuk et al., 1987). In the present study, we manipulated task demands without changing the external dimensions of the target (participants reached for and grasped the same object), but rather by changing the difficulty of the task. In a manipulation similar to that described in Steenbergen, Marteniuk, and Kalbfleisch (1995), participants in the current study were required to grasp a glass of water that was either nearly empty (*low* demand condition) or nearly full (*high* demand condition). Based on reaching literature, we hypothesized that any manual asymmetries observed would be most apparent in the high demand condition. Furthermore, we expected kinematic differences in the grasp between these two demand conditions; specifically, we predicted that the grasps performed in the low demand condition would be faster and more accurate (e.g., with less variable maximum grip apertures) than grasps performed in the high demand condition. In studies such as ours where a single target is used for all trials, scaling differences in grip aperture cannot be assessed, and averaging of maximum grip apertures across trials masks potential "errors" in grip formation elicited by less-practiced or more difficult tasks. Variability of maximum grip aperture (MGA) therefore becomes the most suitable measure of accuracy in such grasps (Mon-Williams & Bingham, 2011).

Because hand differences in reaching movements have been attributed (at least in part) to asymmetries in hemispheric processing of visual stimuli and feedback (Flowers, 1975; Roy et al., 1994), we tested participants under three different visual conditions. In the *closed-loop* visual condition, constant visual feedback of both the hand and the target was available throughout the task; in the *open-loop* condition, vision was removed 100 ms after the go signal, limiting the influence of visual feedback on the latter, non-ballistic phase of the movement; in the *delay* condition, vision was occluded 2000 ms prior to the go signal, leaving the movement to be performed entirely from memory (Hu, Eagleson, & Goodale, 1999). If visual feedback is responsible for the reported right hand advantages during aiming and pointing movements, then we hypothesized similar advantages in the grasping movement under conditions where full or recent visual feedback was available. We expected fewer or no differences between grasps in the *delay* condition.

METHODS AND PROCEDURES

Participants

Fifteen self-reported right-handed individuals (8 females; mean age 21.7 years) took part in the experiment. 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. Each participant was tested individually.

Materials

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 snuffbox) (Figure 1). An Optotrak Certus[1] camera bar [*Northern Digital, Waterloo, ON, Canada*], positioned overhead, recorded IRED position during each trial at 200 Hz for 8 s. Visual conditions were controlled via Plato Liquid-crystal glasses [*Translucent Technologies, Toronto, ON, Canada*], worn by the participant throughout the test. Visual conditions were planned and controlled using Superlab 2.0 (*Cedrus Corporation, San Pedro, CA, USA)*. Reach-to-grasp target was a cylindrical, untapered water glass, 80 mm tall and 67 mm in diameter at the mouth and base.

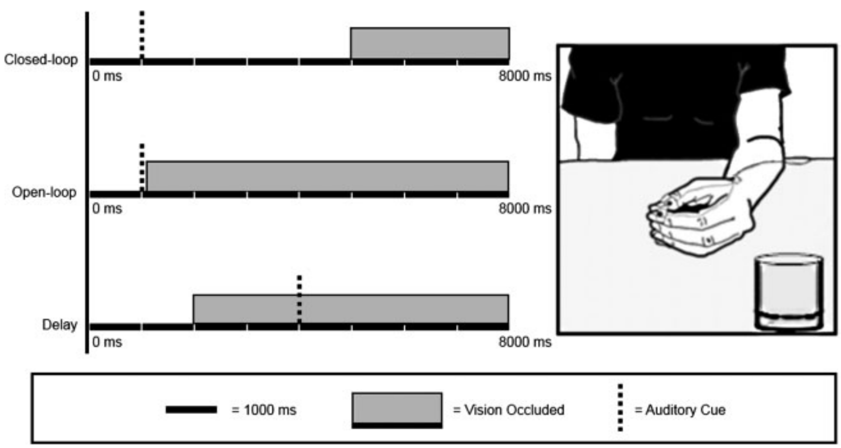

Figure 1. Experimental design. Timeline of visual conditions. Auditory cue was followed by movement onset in the direction of the target. (Insert: resting position, showing typical IRED marker sites and typical placement of the target glass.)

[1] The resolution of this system is 0.01 mm, with an advertised accuracy of 0.1 mm.

Procedure

Participants were seated facing a table (*W* = 107 cm, *D* = 77 cm, *H* = 67 cm) on which the target glass was placed at a viewing distance of approximately 60 cm. A 1 × 1 cm adhesive piece of white tape was placed at the edge of the table signalling the resting location (~30 cm from the target). The target placement randomly varied (within 5–10 cm) around the participant's midline between trials; this precaution was taken to prevent pre-planning of the movement (Goodale, Kroliczak, & Westwood, 2005). Before each trial, participants placed the wrist and the lateral edge of the hand on the resting location, with thumb and forefinger touching in such a way that all three markers were visible to the overhead camera (Figure 1).

Each trial began with the Plato goggles in a closed (opaque) state. Recording began at the beginning of each trial when the goggles opened (i.e., became transparent), allowing the participants to locate the target and plan their grasp. Participants were instructed to wait for an audible go signal before reaching for, grasping and taking a sip of water from the glass "as quickly and accurately as possible". Participants were further instructed to ensure that they did not spill the contents of the glass. Timing of the go signal varied with visual condition (Figure 1). In the closed- and open-loop conditions, the go signal was presented 1000 ms after the goggles "opened" to their transparent state. The goggles remained open a further 4000 ms during the closed-loop condition, giving the participant full vision throughout the duration of the reach and grasp. In the open-loop condition, the goggles closed 100 ms following the go signal, such that the movement was executed with recent but not ongoing visual input. In the delay condition, the goggles remained open for 2000 ms at the beginning of the trial, closed, and a 2000 ms delay period was observed before presentation of the go signal. This delay conservatively reflects the maximum amount of time in which the dorsal visual stream is able to store visual feedback to be used in generating movement (Elliott & Calvert, 1990; Hu et al., 1999); therefore, in this condition, both the planning and execution phases of the movement were completed entirely from memory. Each participant reached for the same glass in all trials. The water content of the target glass was varied with demand condition. For the low demand condition, the water level was within 10 mm from the base of the glass. In the high demand condition, the glass was filled to within 10 mm of its rim. We varied Vision and Demand in a 3 × 2 factorial design, repeating each condition 8 times, resulting in 48 trials per hand (96 trials total). Conditions were presented in a pseudo-random order, in right and left hand blocks. Right/left hand starting order was randomly assigned and counter-balanced. Trials were judged successful and included in statistical analysis if and only if the participant: (1) began from a proper resting state (fingertips together at the resting location), (2) correctly waited for the go signal to begin and (3) did not knock over or otherwise spill the glass or its contents.

Analyses

We determined kinematic parameters using finite differences in the two-step method.[2] All kinematic calculations were performed using Microsoft Excel 2007/2010, and statistical analyses were completed using PASW Statistics 18.0.0. Condition means were analysed via repeated measures analyses of variance (ANOVAs) on a variable by variable basis.

Reach kinematics. Reach kinematics were measured from the wrist marker. *Reaction time* (RT) was defined as the time following the go signal at which a participant achieved a resultant equal to 5% of their peak velocity. *Peak velocity* (PV) was defined as the maximum speed the participants achieved during their reach towards the target. We calculated velocity as a resultant in absolute terms using a finite differences model (Schneck & Bronzino, 2003). The time of grasp contact was defined as the point at which (1) the subject's outward speed dropped below 0.02 ms, and (2) their corrected grip aperture plateaued at the approximate diameter of the target glass. Trials in which these two conditions were not synchronized to within 10 frames (±.05 s) were removed from the analysis. *Movement time* (MT) was calculated as the difference between RT and the time of grasp contact, and represents the span during which the participant reached outward towards the target glass.

Grasp kinematics. Grasp kinematics were measured from the thumb and index finger markers. *Maximum grip aperture* (MGA) was measured as the peak resultant distance achieved between the thumb and index finger IREDs prior to the time of grasp contact. In trials where the participant adjusted their initial grasp after brief contact with the object, only the first MGA was recorded, even if the second MGA was found to be larger; this ensured that only visually influenced MGAs (as opposed to those with additional somatosensory feedback afforded by the initial contact with the target) were included in the analysis. MGA values were corrected for IRED placement using the average of the 10 smallest grip apertures recorded during rest per participant per hand; this correction factor allows us to control for slight variations in IRED placement between the hands as well as differences in hand size within participants.[3] *Variability of MGA* (vMGA) was included as a dependent variable reflecting

[2] Using the two-step method, average speed at time n is calculated by determining displacement between times $n - 1$ and $n + 1$, and dividing that displacement by the elapsed time between those two points. The method can be expressed by the $v = [P(n + 1) - P(n - 1)]/\Delta t$, where v is velocity, P is position, n is a single point in the output data, and Δt is the time elapsed between points $n - 1$ and $n + 1$.

[3] Analyses were also conducted on uncorrected MGA data, which confirmed that all reported main effects and interactions were still present.

consistency in grasp production (Aglioti, DeSouza, & Goodale, 1995; Fukui & Inui, 2006; Mon-Williams & Bingham, 2011; Wing, Turton, & Fraser, 1986). vMGA was calculated for each hand as the standard deviation of the MGAs achieved during the eight trials of each Vision X Demand condition.

RESULTS

An average of 8.8% of trials per subject (± 5.9%) were missing critical data or were considered failures, and as such were excluded from the analysis. Failed trials were those in which participants either did not properly wait for the go signal to begin the grasp or spilled during transport to the mouth. No participants knocked over a glass during any trials. A paired-sample *t*-test, used to compare the failure rate between participants' left- and right-handed movements, demonstrated that the failure rate did not differ between hands ($p > .5$). The data from remaining trials were averaged across condition, and repeated measures ANOVAs were used on a variable by variable basis. Significant (or approaching significant[4]) main effects and interactions are reported below.

The results of a three-way repeated measures ANOVAs [RMA; Vision (Closed-Loop/Open-Loop/Delay) × Hand (Left/Right) × Demand (High/Low)] revealed that the vision manipulation had a profound effect on all kinematic measures ($F(2, 28) > 45$, $p < .001$, $\eta^2 > 0.750$). To rule out the possibility that this large main effect of visual manipulation masked the effect(s) of the other factors (Hand and Demand), we conducted three separate two-way ANOVAs (Hand × Demand), one for each visual condition (see Grosskopf & Kuhtz-Buschbeck, 2006 for a similar analysis). Results are reported as either reach or grasp kinematics, within each visual condition (closed-loop, open-loop and delay). Means and standard errors of all measurements are reported in Table 1. ANOVA results (*F*-values and effect size) are reported in Table 2.

Closed loop

Reach kinematics. A main effect of Hand on MT nearly reached significance ($F(1,14) = 3.849$, $p = .070$, $\eta^2 = 0.216$). Participants completed reach-to-grasp movements slightly sooner with the right hand ($M = 946$, $SE = 40$ ms) than with the left hand ($M = 978$, $SE = 39$ ms). A main effect of Demand was observed on MT ($F(1,14) = 42.908$, $p < .001$, $\eta^2 = 0.754$). Reaches took longer to complete in the high demand condition ($M = 988$, $SE = 40$ ms) than they did in the low demand condition ($M = 937$, $SE = 38$ ms).

[4] Effects that are only approaching significance ($.05 < p < .1$) are labelled as such. While we do not claim that these results are definitive, we nevertheless feel that their inclusion is warranted. In all cases where we discuss borderline effects, effect strengths are moderate ($0.3 < \eta^2 < 0.5$).

TABLE 1
Means and standard errors [Mean (*SE*)] are reported for all reach and grasp kinematic measures

			RT (ms)	*PV (ms)*	*MT (ms)*	*MGA (mm)*	*vMGA (mm)*
Closed-loop	Left	Low	447 (29)	0.780 (0.04)	960 (39)	82.3 (2.1)	3.77 (0.4)
		High	419 (21)	0.772 (0.04)	996 (39)	82.2 (2.1)	3.21 (0.4)
	Right	Low	454 (26)	0.792 (0.04)	913 (39)	83.9 (2.5)	2.40 (0.2)
		High	430 (30)	0.787 (0.04)	979 (42)	83.4 (2.3)	2.76 (0.2)
Open-loop	Left	Low	460 (26)	0.749 (0.05)	1146 (44)	90.4 (2.6)	4.11 (0.4)
		High	452 (41)	0.721 (0.05)	1238 (56)	90.5 (2.7)	4.39 (0.5)
	Right	Low	431 (21)	0.737 (0.03)	1092 (56)	90.1 (2.7)	3.83 (0.5)
		High	454 (24)	0.753 (0.04)	1200 (58)	89.8 (2.8)	3.32 (0.4)
Delay	Left	Low	374 (19)	0.660 (0.04)	1334 (48)	95.2 (2.9)	4.05 (0.6)
		High	376 (17)	0.632 (0.03)	1427 (45)	93.5 (2.6)	3.42 (0.4)
	Right	Low	375 (12)	0.665 (0.03)	1289 (49)	94.1 (3.1)	3.56 (0.5)
		High	379 (14)	0.651 (0.03)	1388 (53)	93.8 (3.3)	2.89 (0.3)

Grasp kinematics. A main effect of Hand was observed on vMGA, $F(1,14) = 18.588$, $p < .001$, $\eta^2 = 0.570$). Specifically, when participants grasped a glass with their right hand, their MGAs were significantly less variable ($M = 2.58$, $SE = 0.21$ mm) than they were when using their left hand ($M = 3.49$, $SE = 0.32$ mm). We also found a significant Hand × Demand interaction in vMGA ($F(1,14) = 4.531$, $p = .05$, $\eta^2 = 0.244$). Pairwise comparisons revealed that the right hand responded to the demand manipulation, but the left hand did not ($p > .1$). Specifically, vMGAs were lower in the low demand condition than in the high demand condition ($t(14) = 2.4$, $p < .05$) for right-handed movements only (Figure 2).

TABLE 2
ANOVA results [*F* values (η^2)] are reported for all reach and grasp kinematic measures

		RT	*PV*	*MT*	*MGA*	*VMGA*
Closed-loop	Hand	0.15 (0.01)	0.43 (0.03)	3.85 (0.22)†	1.32 (0.09)	18.59 (0.57)*
	Demand	3.00 (0.18)	0.46 (0.03)	42.91 (0.75)*	0.79 (0.05)	0.16 (0.01)
	Hand × Demand	0.03 (0.00)	0.02 (0.00)	3.94 (0.22)	0.83 (0.06)	4.53 (0.24)*
Open-loop	Hand	0.34 (0.02)	0.26 (0.02)	2.96 (0.17)	0.17 (0.01)	3.96 (0.22)†
	Demand	0.24 (0.02)	0.33 (0.02)	47.64 (0.77)*	0.16 (0.01)	0.18 (0.01)
	Hand × Demand	0.89 (0.06)	6.11 (0.30)*	0.25 (0.02)	0.63 (0.04)	1.23 (0.08)
Delay	Hand	0.03 (0.00)	0.48 (0.03)	4.59 (0.25)*	0.10 (0.01)	2.00 (0.13)
	Demand	0.12 (0.01)	3.61 (0.21)†	21.77 (0.61)*	5.81 (0.29)*	5.54 (0.28)*
	Hand × Demand	0.00 (0.00)	0.36 (0.02)	0.08 (0.01)	1.76 (0.11)	0.01 (0.00)

Significant results ($p < .05$) are marked with an asterisk (*). Borderline effects ($.05 < p < .1$) are marked with a cross (†).

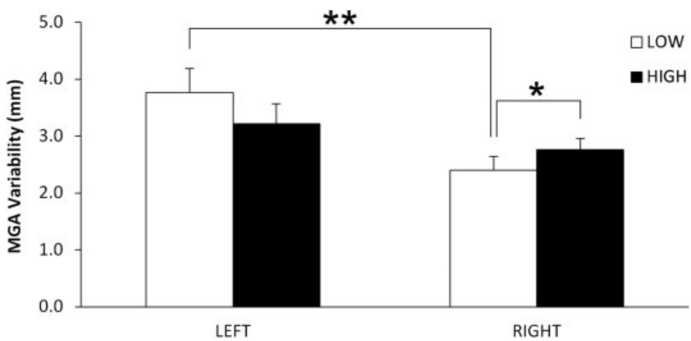

Figure 2. Hand × Demand interaction on vMGA in the closed-loop visual condition. Right-hand reach-to-grasp movements are significantly less variable than are left-hand reach-to-grasp movements in the low demand condition ($p < .001$). In the high demand condition, there is no significant variability difference between hands. A significant difference was also found between demand conditions in the right-handed movements only, where MGAs were more variable in the high demand condition ($p < .05$).

Additionally, there was a significant difference between hands in the low demand condition, where right hand MGAs were significantly less variable than left hand MGAs ($t(14) = 4.397$, $p < .001$) (Figure 2).

Open loop

Reach kinematics. A significant effect of Demand was found on MT ($F(1,14) = 47.638$, $p < .001$, $\eta^2 = 0.773$). Reaching for a glass took longer in the high demand condition ($M = 1219$, $SE = 55$ ms) than in the low demand condition ($M = 1119$, $SE = 48$ ms). A significant interaction of Hand × Demand was observed on PV ($F(1,14) = 6.109$, $p = .027$, $\eta^2 = 0.304$). Pairwise comparisons showed that right-handed PVs were similar in both demand conditions; however, left-handed PVs were significantly lower ($t(14) = 2.3$; $p < .05$) in the high ($M = 0.721$, $SE = 0.05$ ms) than in the low ($M = .749$, $SE = 0.05$ ms) demand condition (Figure 3).

Grasp kinematics. A borderline effect of Hand was found in the vMGA ($F(1,14) = 3.956$, $p = .067$, $\eta^2 = 0.220$) where MGA was more variable for the left hand ($M = 4.25$, $SE = 0.37$ mm) than for the right hand ($M = 3.58$, $SE = 0.42$ mm).

Delay

Reach kinematics. For MT, there was a main effect of Hand ($F(1,14) = 4.589$, $p = .050$, $\eta^2 = 0.247$) and a main effect of Demand ($F(1,14) = 21.768$, $p < .001$, $\eta^2 = 0.609$) but no significant interaction ($p > .1$). Reach-to-grasp movements made with the left hand took longer ($M = 1381$, $SE = 45$ ms) than their right-handed equivalents ($M = 1339$, $SE = 49$ ms). Also, when reaching for a glass in the high demand condition, reaches took longer to complete ($M = 1407$, $SE = 47$ ms) than

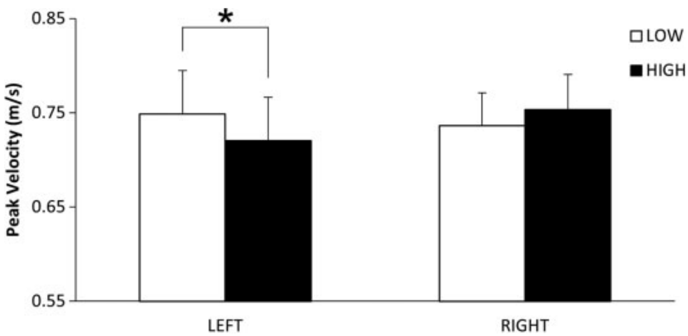

Figure 3. Hand × Demand interaction on PV in the open-loop visual condition. Left-hand reach-to-grasp movements reach significantly higher peak velocities in the low demand condition than they do in the high demand condition. The reverse is true for right-handed reach-to-grasp movements, which reach higher PVs in the high demand condition than they do in the low demand condition, though this difference is not significant ($p > .05$).

they did in the low demand condition (M = 1312, SE = 47 ms). A borderline effect of Demand was found for PV ($F(1, 14) = 3.614$, $p = .078$, $\eta^2 = 0.205$). Reach-to-grasp movements in the low demand condition (M = 0.662, SE = 0.03 ms) reached higher PVs than movements in the high demand condition (M = 0.642, SE = 0.03 ms).

Grasp kinematics. Main effects of demand were found in MGA ($F(1,14) = 5.805$, $p = .030$, $\eta^2 = 0.293$), and vMGA ($F(1,14) = 5.541$, $p = .034$, $\eta^2 = 0.284$). Grasps directed towards glasses in the high demand condition had smaller MGAs (M = 93.6, SE = 2.8 mm) than did grasps in the low demand condition (M = 94.7, SE = 2.9 mm). Variability of MGA was lower in the high (M = 3.15, SE = 0.31 mm) than in the low (M = 3.81, SE = 0.47 mm) demand condition. No other main effects or interactions were observed.

DISCUSSION

The purpose of the study was to investigate the possibility of manual asymmetries in the reach-to-grasp movement. Based on reaching studies in which participants aimed at or pointed to a target, we hypothesized that increasing task demands would elicit kinematic differences between the hands. In the current study, participants reached for, grasped and took a sip of water from a drinking glass. The glass was either nearly empty or nearly full, so as to vary the demands required to pick it up and to transport it to the mouth without spilling any water (Steenbergen et al., 1995). We tested participants under three visual conditions, reasoning that manual asymmetries would be linked with visual-feedback availability. Our hypotheses regarding the effects of these manipulations were as follows: first, the kinematics of the reach-to-grasp action would be affected by the demand manipulation; second, kinematic asymmetries between the hands would be larger in the high demand condition and third, manual asymmetries would be contingent upon visual feedback availability. Consistent with our first hypothesis, we found that the demand manipulation had a significant effect on nearly all kinematic measures. Regarding our second hypothesis, we were able to identify manual asymmetries in both reach and grasp kinematics—however, contrary to our prediction, these asymmetries were present in both demand conditions. Concerning our third hypothesis, with the exception of movement time, significant manual asymmetries were limited to reach-to-grasp actions benefitting from full or recent visual feedback. These findings are discussed in detail below.

Research has shown that regardless of handedness, people complete reaching movements (i.e., aiming and pointing) faster and with greater end-point accuracy when using the right hand (Boulinguez, Nougier, & Velay, 2001; Boulinguez, Velay, & Nougier, 2001; Elliott & Chua, 1996; Elliott et al., 1993; Fisk & Goodale, 1985; Roy & Elliott, 1989; van Doorn, 2008; Woodworth, 1899). These results lend support to the suggestion that the left hemisphere may be more specialized for visuomotor control, a speculation that dates to early twentieth-century work from Woodworth and Liepmann (Liepmann, 1925; Woodworth, 1899). Previous reach-to-grasp studies, however, had reported negligible asymmetries between the left and right hands (Grosskopf & Kuhtz-Buschbeck, 2006; Tretriluxana et al., 2008). However, these studies used objects such as solid wooden pegs (Grosskopf & Kuhtz-Buschbeck, 2006) and tape-wrapped cylinders (Tretriluxana et al., 2008) as targets, neither of which carry any negative consequences in the event of mishandling. In contrast, the drinking glass used in our experiment carried a risk of spilling, particularly in the high demand condition when the glass was full. Our results showed that this demand manipulation affected both reach and grasp kinematics. Consistent with the results reported by Steenbergen et al. (1995), we found that in all visual conditions, movement times directed to full glasses were significantly longer than those towards nearly empty glasses. This finding is also consistent with that of Savelsbergh et al. (1996), who found that grasps directed towards transparent cylinders perceived as fragile had longer movement times than grasps directed towards solid targets matched for size and weight. Although during the closed- and open-loop conditions our demand manipulation affected other kinematic measures (depending on the hand used), demand had the largest effect in the delay condition. In the delay condition, movement times were greater, peak velocities were lower, and grasps had smaller and less variable maximum grip apertures when the glass was full. We speculate that actions executed in a delay condition are more strongly affected by changes in perceived demand because movements in this condition are guided by memory. Memory-guided actions are known to be vulnerable to illusory influence because they are based entirely on perception (e.g., Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu & Goodale, 2000). Because the physical characteristics of the glass remained the same between conditions, we assume that it was the level of water that changed the perceived demands of the task. While the direction of our effect on reaching kinematics was expected (i.e., increased demand resulting in lower PVs and longer MTs (Elliott & Chua, 1996; Steenbergen et al., 1995), the effect on grasp kinematics was somewhat unexpected. In keeping with the reach-to-point literature, we predicted that difficult grasps (those directed towards high-demand targets) would be less accurate; specifically, they would have larger and more variable MGAs. When vision was available, we observed the predicted effect on vMGA within right-handed grasps. In contrast, left-handed grasps were equally variable in both high and low demand conditions. In memory-guided grasps, we observed an effect of demand opposite of that expected, with the high demand condition producing smaller and less variable MGAs regardless of hand used. The results from the current study provide additional evidence that the demands of a task do indeed influence kinematics of reaching (Fitts, 1954; Heath & Binsted, 2007; Kudoh, Hattori, Numata, & Maruyama, 1997; Roy & Elliott, 1989) and grasping (Castiello, Bennett, & Stelmach, 1993; Mon-Williams & Bingham, 2011; Savelsbergh et al., 1996; Steenbergen et al., 1995; Wing et al., 1986). We discuss these findings in detail below.

Hand differences were detected as main effects and/or interactions in movement time, peak velocity and variability of maximum grip aperture. With respect to movement time, our results showed that in the delay condition, right-handed reach-to-grasp movements were completed in less time than are left-handed movements; this effect was also observed as a trend of borderline significance in the closed-loop condition. These results are consistent with the reach-to-point literature, in which several studies have shown that the movement time advantage right-handed people have for their dominant hands in visually guided reaches is also present in reaches guided by memory (Roy & Elliott, 1986, 1989; Roy et al., 1994). The results of these studies led Roy and colleagues to conclude that hemispheric asymmetries in visual-feedback processing capability were *not* the source of movement time asymmetries in the reach-to-point movement; rather, since lateral kinematic differences are also present in memory-guided reaches, the left-hemisphere/right-hand system must be more efficient at processing feedback in general, be it visual or proprioceptive in origin. Our results expand this conclusion to cover the reach-to-grasp movement. In the current study, left-handed grasps achieved lower PVs in the high demand (full glass) condition. This was not the case for right-handed movements, which achieved similar (comparatively high) PVs in both demand conditions. While this same Hand × Demand interaction was observed by Steenbergen et al. (1995), in our study this effect was present only in the open-loop condition. Because of this, we speculate that in the absence of continuous visual feedback, the right-hemisphere/left-hand system was more vulnerable to changes in the *perceived* demands of the task. In other words, it is possible that movements executed by the left hand are more easily influenced by perceptual information, so that when grasping a full glass the left-hand system is more "cautious," which is reflected by lower peak velocities in the reach. This speculation is supported by studies showing that left-handed, but not right-handed, reach-to-grasp movements are susceptible to visual illusions and visual context (Adam, Müskens, Hoonhorst, Pratt, & Fischer, 2010; Gonzalez, Ganel, & Goodale, 2006; but see de Grave, Brenner, & Smeets, 2009; van der Kamp, de Wit, & Masters, 2012), and that the asymmetries produced by the illusions manifest most strongly in the initial, ballistic phase of the reach-to-grasp movement (Glover & Dixon, 2002). However, while in the current study the effect on PV was of statistical significance and moderate strength ($\eta^2 > 0.3$), it was not accompanied by a significant difference in either movement time ($p > .6$) or deceleration phase duration ($p > .1$; unreported). Although a mere speculation, it is possible that these higher PVs are due to decreases in the slope of the velocity curve, in both the positive (acceleration) and negative (deceleration) directions. Concerning grasp kinematics during visually guided grasps, our results showed more consistent maximum grip apertures when participants used their right, as opposed to their left, hands. Previous studies have shown that visually guided reach-to-point actions performed with the right hand have greater end-point accuracy than do actions performed with the left hand (for review, see Grouios, 2006). However, end-point accuracy in reach-to-grasp movements is difficult to assess, as a manipulatable object may have an infinite number of points from which it can be successfully grasped (Klatzky, Pellegrino, McCloskey, & Doherty, 1989). Instead, accuracy of the grasp may be evaluated from the MGA measurement. vMGA is a measurement of the inter-trial differences between MGAs; as such, it is sometimes considered a measurement of uncertainty or perceptual and/or motor inconsistency in the formation of the grasp (Mon-Williams & Bingham, 2011). Accurate and efficient reach-to-grasp movements demonstrate consistent MGAs that closely scale to the size of the target. In studies such as ours, in which a single target is used, grip aperture *scaling* cannot be assessed and the vMGA becomes the most valid measure of accuracy available.

Previous researchers have shown that variability is increased by either reducing visual feedback (Wing et al., 1986) or increasing task difficulty (Mon-Williams & Bingham, 2011). In the current investigation, we observed inconsistent effects of demand on vMGA across our visual feedback conditions. vMGA was significantly different between the hands in the closed-loop condition, near significantly different in the open-loop condition and similar between hands in the delay condition. In all cases, right-handed grasps were less variable than left-handed grasps (though this difference was not always significant). We also observed a Hand × Demand effect in the closed-loop condition where grasps directed towards full glasses had higher vMGAs than did those directed towards empty glasses, but exclusively in grasps performed with the right hand. Despite the fact that demand only affected the right-handed grasps, it should be noted that right-handed grasps were consistently less variable than left-handed grasps in both high and low demand conditions. This finding is in accordance with the dynamic dominance hypothesis of handedness (Sainburg, 2002), which posits that intersegmental dynamics are more easily controlled in the dominant limb. This theory predicts that right-handed people will be able to more easily control joint dynamics for their right hands; we observed this in the form of less variable right-handed maximum grip apertures. However, this observation was only found in the closed-loop condition. The *trend* was present in the open-loop condition, but the difference failed to reach statistical significance. In the delay condition, we observed a consistent effect of demand across both hands, but in the reversed direction; both left- and right-handed grasps were less variable in the high demand condition. The effect observed in the closed-loop condition is in agreement with the reach-to-point literature, which has shown that more difficult aiming movements (i.e., of increased amplitude, to smaller targets, and/or of higher speed) show less accuracy than aiming movements of comparatively low demand (Fitts, 1954; Heath & Binsted, 2007; Roy & Elliott, 1989) and are in general more accurate when performed with the right hand (Elliott et al., 1993; Mieschke, Elliott, Helsen, Carson, & Coull, 2001; Roy & Elliott, 1989). Our results in the closed-loop condition are also consistent with reach-to-grasp studies investigating the end-state comfort effect (Rosenbaum et al., 1990), which show that the right hand is more responsive to grasp requirements than the left hand (Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Janssen, Meulenbroek, & Steenbergen, 2011). In contrast to visually guided reach-to-grasp movements, we observed an opposite effect of demand in the delay condition, in that more difficult grasps produced more consistent MGAs. We argue that this result was due to a greater influence of perception on the grasping movement when it is guided by memory. Specifically, the full glass may have been *perceived* as a more constant threat, resulting in a reduced margin of error for the grasp. This speculation is supported by the concurrent main effect of demand on MGA observed in these delayed grasps, wherein full glasses elicited significantly smaller MGAs than did empty glasses. Because the right-hand advantage in consistency observed in the closed-loop condition was not maintained in memory-guided movements, the findings of the present study support the view of a left hemisphere specialization for visuomotor integration in the right-hand dominant population (Crajé, van der Kamp, & Steenbergen, 2009; Elliott et al., 1995; Flowers, 1975; Goodale, 1988; Liepmann, 1925; Roy et al., 1994; Woodworth, 1899). Whether this specialization is consistent in the left-handed population remains to be seen. Based on results of previous studies showing that left-handers are not a homogenous group in terms of hemispheric lateralization or even hand preference for grasping tasks (Gonzalez et al., 2006; Stone, Bryant, & Gonzalez, 2013), as well as studies showing that left-handers often behave as right-handers in terms of pointing

(Boulinguez, Velay, et al., 2001) and grasping (Derakhshan, 2006; Hughes, Reißig, & Seegelke, 2011) behaviour, we speculate that a left-hemisphere/right-hand advantage for visuomotor integration would be present in perhaps as many as half of all left-handers. This speculation will be addressed in future studies.

Aside from the demands associated with our task, it is possible that the nature of the task itself may have highlighted differences between the hands. It has been argued elsewhere that natural tasks might be better at detecting manual asymmetries during grasping (Seegelke, Hughes, & Schack, 2011). Our results support this speculation, as we identified previously unobserved manual asymmetries by using an ecologically valid task. Ecologically valid tasks are not commonly used in the laboratory to (presumably) avoid complications regarding control and reproducibility; we contend that such tasks are of particular *strength* in the laboratory as they allow researchers to avoid the potential confound of experimental learning (Bennett, Marchetti, Iovine, & Castiello, 1995; Latash & Jaric, 2002). Drinking from a glass has been used in past research to highlight significant effects of task difficulty on the kinematics of the reach-to-grasp motion in healthy (Latash & Jaric, 2002) and neuro-pathological populations (Doan, Whishaw, Pellis, Suchowersky, & Brown, 2006). By using such a familiar, everyday task, we might have prompted more natural behaviour, allowing identification of asymmetries otherwise masked by artificial procedures and/or protocols. In sum, by utilizing an ecologically valid task of varying demand, this study uncovered manual asymmetries in the reach-to-grasp action.

Finally, a puzzle remaining to be solved is the relationship between hand preference and kinematic differences between the hands during reach-to-grasp actions. Many studies have shown a marked right hand preference for grasping, in both right- and left-handed populations (Gonzalez et al., 2006). Unimanual and bimanual tasks have shown that the right hand is preferred when picking up various types of objects, including 3D geometric shapes (Gabbard, Tapia, & Helbig, 2003), cards (Bishop, Ross, Daniels, & Bright, 1996; Calvert, 1998; Carlier, Doyen, & Lamard, 2006), toys (Bryden & Roy, 2006; Sacrey, Karl, & Whishaw, 2012), tools (Mamolo, Roy, Bryden, & Rohr, 2004, 2005; Mamolo, Roy, Rohr, & Bryden, 2006), and blocks (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008; Stone et al., 2013). If grasping movements are more often executed with the right hand, should this not translate into better, more accurate movements? One thing that becomes clear from this investigation (and those of others) is that kinematic differences between the hands during reach-to-grasp movements are subtle. If there are no prominent, obvious kinematic asymmetries in the visually guided reach-to-grasp movement (as there are for pointing and aiming movements), then our preference for such grasps must arise from some other source. Perhaps the preference is a remnant of asymmetries present in the reach; or there may be a metabolic cost to reaching/grasping integration (or left-hand use in general) of which we are unaware. Alternatively, prehension may be coupled with the development of other motor processes, such as praxis and speech, that are predominantly contained within the left hemisphere. These possibilities should guide future research into hemispheric asymmetries in visuomotor integration.

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REFERENCES

Adam, J. J., Müskens, R., Hoonhorst, S., Pratt, J., & Fischer, M. H. (2010). Left hand, but not right hand, reaching is sensitive to visual context. *Experimental Brain Research*, *203*, 227–232. doi:10.1007/s00221-010-2214-6

Aglioti, S., DeSouza, J., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679–685. doi:10.1016/S0960-9822(95)00133-3

Bennett, K., Marchetti, M., Iovine, R., & Castiello, U. (1995). The drinking action of Parkinson's disease subjects. *Brain*, *118*, 959–970. doi:10.1093/brain/118.4.959

Bishop, D., Ross, V., Daniels, M., & Bright, P. (1996). The measurement of hand preference: A validation study comparing three groups of right-handers. *British Journal of Psychology*, *87*, 269–285. doi:10.1111/j.2044-8295.1996.tb02590.x

Boulinguez, P., Nougier, V., & Velay, J.-L. (2001). Manual asymmetries in reaching movement control. I: Study of right-handers. *Cortex*, *37*(1), 101–122. doi:10.1016/S0010-9452(08)70561-6

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

Bryden, P., & Roy, E. (2006). Preferential reaching across regions of hemispace in adults and children. *Developmental Psychobiology*, *48*, 121–132. doi:10.1002/dev.20120

Calvert, G. (1998). Quantifying hand preference using a behavioural continuum. *Laterality: Asymmetries of Body, Brain and Cognition*, *3*, 255–268.

Carlier, M., Doyen, A.-L., & Lamard, C. (2006). Midline crossing: Developmental trend from 3 to 10 years of age in a preferential card-reaching task. *Brain and Cognition*, *61*, 255–261. doi:10.1016/j.bandc.2006.01.007

Castiello, U., Bennett, K., & Stelmach, G. (1993). The bilateral reach to grasp movement. *Behavioural Brain Research*, *56*(1), 43–57. doi:10.1016/0166-4328(93)90021-H

Crajé, C., van der Kamp, J., & Steenbergen, B. (2009). Visual information for action planning in left and right congenital hemiparesis. *Brain Research*, *1261*, 54–64. doi:10.1016/j.brainres.2008.12.074

de Grave, D. D., Brenner, E., & Smeets, J. B. (2009). The Brentano illusion influences goal-directed movements of the left and right hand to the same extent. *Experimental Brain Research*, *193*, 421–427. doi:10.1007/s00221-008-1638-8

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

Doan, J., Whishaw, I. Q., Pellis, S. M., Suchowersky, O., & Brown, L. (2006). Motor deficits in Parkinsonian reaching: Dopa-sensitivity influenced by real-word task constraint. *Journal of Motor Behavior*, *38*(1), 45–59. doi:10.3200/JMBR.38.1.45-59

Elliott, D., & Calvert, R. (1990). The influence of uncertainty and premovement visual information on manual aiming. *Canadian Journal of Psychology/Revue canadienne de psychologie*, *44*, 501–511. doi:10.1037/h0084263

Elliott, D., & Chua, R. (1996). Manual asymmetries in goal-directed movement. In D. Elliott & E. Roy (Eds.), *Manual asymmetries in motor performance* (pp. 143–158). Boca Raton, FL: CRC Press.

Elliott, D., Lyons, J., Chua, R., Goodman, D., & Carson, R. G. (1995). The influence of target perturbation on manual aiming asymmetries in right handed individuals. *Cortex*, *31*, 685–697. doi:10.1016/S0010-9452(13)80020-2

Elliott, D., Roy, E. A., Goodman, D., Carson, R. G., Chua, R., & Maraj, B. K. (1993). Asymmetries in the preparation and control of manual aiming movements. *Canadian Journal of Experimental Psychology*, *47*, 570–589. doi:10.1037/h0078856

Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral space. *Experimental Brain Research*, *60*(1), 159–178. doi:10.1007/BF00237028

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*, 381–391. doi:10.1037/h0055392

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology*, *66*(1), 39–52. doi:10.1111/j.2044-8295.1975.tb01438.x

Fukui, T., & Inui, T. (2006). The effect of viewing the moving limb and target object during the early phase of movement on the online control of grasping. *Human Movement Science*, *25*, 349–371. doi:10.1016/j.humov.2006.02.002

Gabbard, C., Tapia, M., & Helbig, C. R. (2003). Task complexity and limb selection in reaching. *International Journal of Neuroscience*, *113*, 143–152. doi:10.1080/00207450390161994

Gentilucci, M., Chieff, S., Daprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologia*, *34*, 369–376.

Glover, S., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: Support for a planning/control model of action. *Attention, Perception, & Psychophysics*, *64*, 266–278. doi:10.3758/BF03195791

Gonzalez, C., 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

Gonzalez, C., Ganel, T., Whitwell, R., Morrissey, B., & Goodale, M. A. (2008). Practice makes perfect, but only with the right hand: Sensitivity to perceptual illusions with awkward grasps decreases with practice in the right but not the left hand. *Neuropsychologia*, *46*, 624–631. doi:10.1016/j.neuropsychologia.2007.09.006

Goodale, M. A. (1988). Hemispheric differences in motor control. *Behavioural Brain Research*, *30*, 203–214. doi:10.1016/0166-4328(88)90149-0

Goodale, M. A., Kroliczak, G., & Westwood, D. A. (2005). Dual routes to action: Contributions of the dorsal and ventral streams to adaptive behavior. *Progress in Brain Research*, *149*, 269–283. doi:10.1016/S0079-6123(05)49019-6

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

Grouios, G. (2006). Right hand advantage in visually guided reaching and aiming movements: Brief review and comments. *Ergonomica*, *49*, 1013–1017. doi:10.1080/00140130600665349

Heath, M., & Binsted, G. (2007). Visuomotor memory for target location in near and far reaching spaces. *Journal of Motor Behaviour*, *39*, 169–177. doi:10.3200/JMBR.39.3.169-178

Hu, Y., Eagleson, R., & Goodale, M. A. (1999). The effects of delay on the kinematics of grasping. *Experimental Brain Research*, *126*(1), 109–116. doi:10.1007/s002210050720

Hu, Y., & Goodale, M. A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience*, *12*, 856–868.

Hughes, C. M., Reißig, P., & Seegelke, C. (2011). Motor planning and execution in left- and right-handed individuals during a bimanual grasping and placing task. *Acta Psychologica*, *138*(1), 111–118. doi:10.1016/j.actpsy.2011.05.013

Janssen, L., Beuting, M., Meulenbroek, R., & Steenbergen, B. (2009). Combined effects of planning and execution constraints on bimanual task performance. *Experimental Brain Research*, *192*(1), 61–73. doi:10.1007/s00221-008-1554-y

Janssen, L., Meulenbroek, R. G. J., & Steenbergen, B. (2011). Behavioral evidence for left-hemisphere specialization of motor planning. *Experimental Brain Research*, *209*(1), 65–72. doi:10.1007/s00221-010-2519-5

Klatzky, R. L., Pellegrino, J. W., McCloskey, B. P., & Doherty, S. (1989). Can you squeeze a tomato? The role of motor representations in semantic sensibility judgments. *Journal of Memory and Language*, *28*(1), 56–77. doi:10.1016/0749-596X(89)90028-4

Kudoh, N., Hattori, M., Numata, N., & Maruyama, K. (1997). An analysis of spatiotemporal variability during prehension movements: Effects of object size and distance. *Experimental Brain Research*, *117*, 457–464. doi:10.1007/s002210050241

Latash, M. L., & Jaric, S. (2002). Organization of drinking: Postural characteristics of arm-head coordination. *Journal of Motor Behavior*, *34*(2), 139–150. doi:10.1080/00222890209601936

Liepmann, H. (1925). Apraktische störungen [Apraxic disorders]. In H. Curschmann & F. Kramer (Eds.), *Lehrbuch der nervenkrankheiten* [Textbook of nervous diseases] (pp. 408–416). Berlin: Springer.

Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and Cognition*, *55*, 349–351. doi:10.1016/j.bandc.2004.02.041

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., Dugas, C., Liske, D., & Eickmeier, B. (1987). Three dimensional movement trajectory in a Fitts' task: Implications for control. *Quarterly Journal of Experimental Psychology*, *39A*, 629–647.

Mieschke, P. E., Elliott, D., Helsen, W. F., Carson, R. G., & Coull, J. A. (2001). Manual asymmetries in the preparation and control of goal-directed movements. *Brain and Cognition*, *45*(1), 129–140. doi:10.1006/brcg.2000.1262

Mon-Williams, M., & Bingham, G. P. (2011). Discovering affordances that determine the spatial structure of reach-to-grasp movements. *Experimental Brain Research*, *211*(1), 145–160. doi:10.1007/s00221-011-2659-2

Rosenbaum, D. A., Marchak, F., Barnes, H. J., Vaughan, J., Slotta, J. D., & Jorgensen, M. J. (1990). Constraints for action selection: Overhand versus underhand grips. In M. Jeannerod (Ed.), *Attention and performance 13: Motor representation and control* (pp. 321–342). Hillsdale, NJ: Lawrence Erlbaum Associates.

Roy, E. A., & Elliott, D. (1986). Manual asymmetries in visually directed aiming. *Canadian Journal of Psychology*, *40*, 109–121. doi:10.1037/h0080087

Roy, E. A., & Elliott, D. (1989). Manual asymmetries in aimed movements. *Quarterly Journal of Experimental Psychology*, *41A*, 501–516.

Roy, E. A., Kalbfleisch, L., & Elliott, D. (1994). Kinematic analyses of manual asymmetries in visual aiming movements. *Brain and Cognition*, *24*, 289–295. doi:10.1006/brcg.1994.1017

Sacrey, L. A. R., Karl, J. M., & Whishaw, I. Q. (2012). Development of rotational movements, hand shaping, and accuracy in advance and withdrawal for the reach-to-eat movement in human infants aged 6–12 months. *Infant Behavior and Development*, *35*, 543–560. doi:10.1016/j.infbeh.2012.05.006

Sainburg, R. L. (2002). Evidence for a dynamic-dominance hypothesis of handedness. *Experimental Brain Research*, *142*, 241–258. doi:10.1007/s00221-001-0913-8

Savelsbergh, G., Steenbergen, B., & Van der Kamp, J. (1996). The role of fragility information in the guidance of the precision grip. *Human Movement Science*, *15*(1), 115–127. doi:10.1016/0167-9457(95)00039-9

Schneck, D. J., & Bronzino, J. D. (2003). *Biomechanics: Principles and applications*. Boca Raton, FL: CRC Press.

Seegelke, C., Hughes, C., & Schack, T. (2011). An investigation into manual asymmetries in grasp behaviour and kinematics during an object manipulation task. *Experimental Brain Research*, *215*(1), 65–75. doi:10.1007/s00221-011-2872-z

Steenbergen, B., Marteniuk, R. G., & Kalbfleisch, L. E. (1995). Achieving coordination in prehension: Joint freezing and postural contributions. *Journal of Motor Behavior*, *27*, 333–348. doi:10.1080/00222895.1995.9941722

Stone, K. D., Bryant, D. C., & Gonzalez, C. (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

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

van der Kamp, J., de Wit, M. M., & Masters, R. S. (2012). Left, right, left, right, eyes to the front! Müller-Lyer bias in grasping is not a function of hand used, hand preferred or visual hemifield, but foveation does matter. *Experimental Brain Research*, *218*(1), 91–98. doi:10.1007/s00221-012-3007-x

van Doorn, R. R. A. (2008). Manual asymmetries in the temporal and spatial control of aimed movements. *Human Movement Science*, *27*, 551–576. doi:10.1016/j.humov.2007.11.006

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

Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychological Review*, *3*(Monograph suppl.), 1–119.