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RESEARCH ARTICLE

The left cerebral hemisphere may be dominant for the control of bimanual symmetric reach-to-grasp movements

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Abstract

Previous research has established that the left cerebral hemisphere is dominant for the control of continuous bimanual movements. The lateralisation of motor control for discrete bimanual movements, in contrast, is underexplored. The purpose of the current study was to investigate which (if either) hemisphere is dominant for discrete bimanual movements. Twenty-one participants made bimanual reach-to-grasp movements towards pieces of candy. Participants grasped the candy to either place it in their mouths (grasp-to-eat) or in a receptacle near their mouths (grasp-to-place). Research has shown smaller maximum grip apertures (MGAs) for unimanual grasp-to-eat movements than unimanual grasp-to-place movements when controlled by the left hemisphere. In Experiment 1, participants made bimanual symmetric movements where both hands made grasp-to-eat or grasp-to-place movements. We hypothesised that a left hemisphere dominance for bimanual movements would cause smaller MGAs in both hands during bimanual grasp-to-eat movements compared to those in bimanual grasp-to-place movements. The results revealed that MGAs were indeed smaller for bimanual grasp-to-eat movements than grasp-to-place movements. This supports that the left hemisphere may be dominant for the control of bimanual symmetric movements, which agrees with studies on continuous bimanual movements. In Experiment 2, participants made bimanual asymmetric movements where one hand made a grasp-to-eat movement while the other hand made a grasp-to-place movement. The results failed to support the potential predictions of left hemisphere dominance, right hemisphere dominance, or contralateral control.

Keywords Discrete bimanual movements · Lateralisation · Grasp-to-eat · Grasp-to-place

Introduction

It is well known that the contralateral hemisphere is dominant for the control of unimanual movements (Kandel et al. 2000). A right-handed reach-to-grasp movement is controlled by the left hemisphere, while left-handed movements are predominantly controlled by the right hemisphere. The neural control of bimanual movements (i.e. movements that require the hands to move concurrently, though not necessarily cohesively) is more complex. The left hemisphere is dominant for the control of continuous bimanual movements (reviewed by Serrien et al. 2006); however, the lateralisation of motor control for discrete bimanual movements is underexplored. The purpose of the current study was to investigate patterns of hemispheric dominance for discrete bimanual movements. The lateralisation of bimanual reach-to-grasp movements was probed by comparing the kinematics of grasp-to-eat and grasp-to-place movements. Unimanual grasp-to-eat and grasp-to-place movements have kinematic

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asymmetries in maximum grip aperture (MGA) that have been used to infer the laterality of the movement's locus of control (e.g. Flindall and Gonzalez 2013). We examined how this difference in MGA (i.e. smaller MGAs with the right hand for grasp-to-eat movements compared to grasp-to-place movements) manifests during discrete bimanual movements to investigate patterns of hemispheric dominance.

The most commonly studied continuous bimanual movements are in-phase and anti-phase coordination patterns. Both coordination patterns are stable at low movement frequencies, but only in-phase coordination is stable at higher frequencies. Anti-phase coordination destabilises and tends to transition into in-phase coordination as frequency increases (Kelso 1997). This transition from anti-phase to in-phase is typically led by the right limb; that is, at higher frequencies, the movement pattern of the right limb remains stable while that of the left limb gradually shifts to match the pattern of the right limb (e.g. Byblow et al. 1994). In general, this means that movements of the right limb are far more likely to affect movements of the left limb than vice versa. This pattern of transfer implies that the left hemisphere has considerably more influence over bimanual movements than does the right hemisphere.

The stronger influence of the right limb on the left limb is seen in other ways during continuous bimanual coordination. The strength of spatiotemporal coupling between limbs has been assessed by mechanically perturbing one limb during in- and anti-phase coordination and examining how the coordination pattern is re-established. When the right limb is perturbed, movements of both limbs contribute to the recovery of the coordination pattern. In contrast, when the left limb is perturbed, it is predominantly the left limb that re-establishes the coordination pattern (de Poel et al. 2007). This again suggests that movement of the right limb has primacy over movement of the left limb. This primacy may be observed in more complex movement patterns as well. Multi-frequency coordination patterns, for example, are more stable when the right limb performs the higher frequency movements (e.g. 1L:2R) than when the left limb does (e.g. 2L:1R; Byblow et al. 1998). These results also support the theory of left hemisphere dominance for the control of continuous bimanual movements. This pattern is also seen with other types of continuous bimanual movements; for example, finger tapping (e.g. Peters 1981), circle drawing (e.g. Franz et al. 2002), and force production (e.g. Kennedy et al. 2016) all show examples of right hand/left hemisphere priority of control.

Spatiotemporal coupling has also been shown for *discrete* bimanual movements, including bimanual pointing movement and bimanual reach-to-grasp movements. Temporal coupling is stronger than spatial coupling in both bimanual pointing movements (Kelso et al. 1979, 1983) and bimanual reach-to-grasp movements (Bingham et al. 2008; Blinch et al. 2018; Dohle et al. 2000; Jackson et al. 1999; Mason and Bruyn 2009). For bimanual reach-to-grasp movements, the spatial coupling of the grip apertures to targets with difference sizes is comparatively weak (c.f. Blinch et al. 2018); that is, when one hand reaches for a large target, and the other hand reaches for a small target, each hand will shape itself appropriately for its own target with little intermanual interference. Jackson et al. (1999) reported that the MGAs of bimanual reach-to-grasp movements were independently scaled. Both Dohle et al. (2000) and Mason and Bruyn (2009) found weak spatial coupling not only at MGA, but between grip apertures throughout the entire movement.

In terms of the hemispheric dominance of discrete bimanual movements (specifically, pointing or reach-to-grasp movements), this has been investigated by only a few studies (Le and Niemeier 2013; Sherwood 1994; Walter and Swinnen 1990). One such study involved participants making rapid bimanual reversal movements (Sherwood 1994). When the target distance for one movement is short and the other long, the short-distance movement often overshoots its target, which is called spatial coupling. Spatial coupling is larger when the left arm has a short-distance target and the right arm has a long-distance target than when target distance is reversed; in other words, the left arm is more likely to overshoot the shorter distance than is the right arm. This, again, suggests that left hemisphere/right limb movements have a stronger influence on right hemisphere/left limb movements than the converse when producing discrete bimanual movements. A counter example of lateralised control for discrete bimanual movements comes from a study where participants were asked to make a unidirectional movement with one arm and a double-reversal movement with the other (Walter and Swinnen 1990). Performance of the double-reversal movement caused spatial coupling and altered the kinematics of the unidirectional movement. Interestingly, interference in the unidirectional movement was larger when the left arm made the double-reversal movement than when the right arm did; that is, the right hemisphere/left arm system had a stronger influence on the left hemisphere/right arm's movement than vice versa. In contrast with the conclusions of Sherwood (1994), this finding implies that the right hemisphere is dominant for the control of discrete bimanual movements.

As the lateralisation of motor control for discrete bimanual movements is underexplored, we developed a new task to test it. Our experiment relied on the well-established, task-dependent kinematic asymmetries in MGAs for unimanual reach-to-grasp movements. Multiple studies show that both the planning and execution of reach-to-grasp movements are influenced by the end-goal of the movement. That is, the kinematics of a reach-to-grasp action, measured prior to object contact, are at least partially determined by the intention or purpose of the action. Interestingly, these kinematic differences are often independent of those imposed by mechanical constraints of the environment in which the action is performed. Such differences have been described between communicative and non-communicative grasp-to-lift actions (Wilmut et al. 2013), grasp-to-lift and grasp-to-throw movements (Ansuini et al. 2008; Armbrüster and Spijkers 2006; Marteniuk et al. 1987; Wilmut et al. 2013), grasp-to-lift and grasp-to-place movements (Ansuini et al. 2006, 2008; Wilmut et al. 2013), and, relevant for the current study, between grasp-to-eat and grasp-to-place movements (Ferri et al. 2010; Flindall and Gonzalez 2013, 2014, 2016, 2017; Flindall et al. 2015; Naish et al. 2013).

Imagine a piece of cereal within arm's reach; after an outward reach-to-grasp movement to acquire the cereal, you will either put it in your mouth (grasp-to-eat) or put it in a similarly sized receptacle near your mouth (grasp-to-place). The final goal of your action (whether 'to eat' or 'to place') will affect the kinematics of your initial reach-to-grasp movement in a consistent way. Specifically, the initial prehension of a grasp-to-eat movement produces a smaller MGA than does a grasp-to-place movement (Flindall and Gonzalez 2013). Critically, this difference in MGA occurs only during right-handed movements (left-handed movements show no such task-dependent kinematic difference) and cannot be explained in terms of the mechanical requirements of the final goal. In the case of differences between grasp-to-lift and -throw, or grasp-to-lift and -place actions, task-dependent kinematics have generally been interpreted as adjustments that serve the precision or speed requirements of the secondary (post-grasp) movement (Fleming et al. 2002). For example, an aggressive, ballistic secondary action (e.g. a grasp-to-throw movement) will have a shorter movement time, more abrupt deceleration phase, and higher peak velocity (cf. Armbrüster and Spijkers 2006) than a comparatively more gentle and precise secondary action, such as a grasp-to-lift (Ansuini et al. 2008; Armbrüster and Spijkers 2006; Wilmut et al. 2013), or a grasp-to-place or -fit movement (Marteniuk et al. 1987). However, with respect to grasp-to-eat and grasp-to-place movements, functional explanations fail to explain the observed kinematic differences. As stated above, Flindall and Gonzalez have repeatedly shown that right-handed grasp-to-eat movements produce significantly smaller MGAs than right-handed grasp-to-place movements, or left-handed movements of either type (Flindall and Gonzalez 2013, 2014, 2015; Flindall et al. 2015); this signature persists even though the targets in eat and place tasks are identical (Flindall and Gonzalez 2016), and when the direction, distance, and precision requirements of the post-grasp movement are controlled for (Flindall and Gonzalez 2017). Since this grasp-to-eat signature is consistently found only in right-handed movements, it is an ideal measure with which to investigate potential inter-limb kinematic interference during bimanual grasping.

Experiment 1

In the first experiment, we investigated which (if either) hemisphere was dominant for discrete bimanual symmetric movements. We examined bimanual symmetric reach-to-grasp movements where both arms make either simultaneous grasp-to-eat movements or simultaneous grasp-to-place movements. There are three possible outcomes, corresponding to left hemisphere dominance, right hemisphere dominance, or discrete contralateral control (i.e. neither hemisphere is dominant). If the left hemisphere is dominant for bimanual reach-to-grasp movements, then its influence should extend to the movements of both hands. Given the left hemisphere lateralization of the grasp-to-eat action, left hemisphere control should cause smaller MGAs for both hands during bimanual grasp-to-eat movements compared to bimanual grasp-to-place movements. Alternatively, if the right hemisphere is dominant for bimanual reach-to-grasp movements, then bimanual grasp kinematics should follow the pattern observed during left-handed unimanual actions; that is, MGAs in both hands should be similar between grasp-to-eat and grasp-to-place movements. Finally, it is possible that neither hemisphere exerts overt control over the other, and, as in unimanual movements, each hemisphere controls the contralateral hand during bimanual reach-to-grasp movements. In this case, each hand's MGA should mimic the patterns observed during unimanual movements. The right hand should produce smaller MGAs during grasp-to-eat movements than during bimanual grasp-to-place movements, while the left hand should show identical MGAs during both types of movement. Based on previous research suggesting left hemisphere control for continuous bimanual movements, we predicted that the left hemisphere would also be dominant for discrete bimanual movements; that is, MGAs would be smaller for both hands during bimanual grasp-to-eat movements than during bimanual grasp-to-place movements, mimicking the pattern observed in right-handed unimanual movements for these goals.

Methods

Participants

Twenty-one volunteer participants (mean age of 21.5 ± 4.6 years, 15 female and 6 male) were recruited from the university community. All participants were right-handed by self-report [mean score of 0.92 ± 0.11 (SD) on a modified version of the Edinburgh (Oldfield 1971) and Waterloo (Brown et al. 2006) handedness questionnaires (see Stone et al. 2013 for the questionnaire)] and reported that they had normal or corrected-to-normal vision. The Human Subject Research Committee at the University of Lethbridge approved the study.

Apparatus

Participants were seated at a table. On the table were two 1X1 Lego bricks (7.8 × 7.8 × 11.4 mm), 6 cm in from the edge of the table and 15 cm apart. These served as the home positions for all movements, which were pincer grasped at the beginning of each trial. Participants were seated so that their midsagittal plane was centred between the home positions. The target objects for the reach-to-grasp movements were placed at a comfortable reach distance ("a reach distance requiring one to fully extend his/her elbow to complete the reach, while keeping their back firmly against the chair") in front of the left and right home positions. This reach distance ranged from 22.0 to 28.5 cm for the different participants. The target objects were Rockets[1] (11.7 mm radius; Ce De Candy Company) or SweeTarts (18.1 mm radius; The Willy Wonka Candy Company) candies; objects of different sizes were included to confirm that participants were scaling their grip apertures appropriately to individual targets, which are hereinafter referred to as the small and large target objects, respectively.

We tracked each participant's movement via three infrared light-emitting diodes, attached to the distal phalanx of the thumb, the distal phalange of the index finger, and the dorsal tubercle of the radius on both upper limbs. An Optotrak Certus motion capture system (Northern Digital) sampled diode positions at 400 Hz. (Two participants had their data accidentally recorded at 100 Hz; their data were subsequently resampled to 400 Hz.) Participants wore PLATO visual occlusion spectacles (Translucent Technologies) that limited their access to visual information between trials, such that they would not be able to pre-plan their movements while the experimenter prepared the upcoming trial.

Procedures

All trials began with the spectacles closed to occlude visual information. If not already grasping the home positions from the end of the previous trial, participants used somatosensation and memory to find and grasp the left and right home positions with ipsilateral pincer grasps. They grasped the left and right home positions with their left and right hands. Trials began with the spectacles opening (transitioning to a transparent state), and participants previewed the target objects (two objects for each trial, positioned 10 cm apart, at arm's length) for 1 s. The left hand always reached for the left object and the right hand always reached for the right object. The target objects were always the same size as each other, either both small or both large. A tone played after the 1-s foreperiod, signalling participants to "reach and grasp the objects at a comfortable pace, with an emphasis on accuracy over speed". While both blocks required bimanual movements, the specific instructions for after the participants grasped the objects varied by block. In the bimanual eat block (left hand eat, right hand eat; Eat–Eat), participants were instructed to place both objects in their mouth. Similarly, in the bimanual place block (Place–Place), participants were instructed to bring both objects to a bib hanging just below their chin. Following each trial, participants either (a) placed their hands on the surface of the table and waited for the 5-s recoding interval of the Optotrak to end (signalled by the closing of the spectacles), or (b) returned both hands to the home positions, according to their personal preference. In the Eat–Eat block, after bringing both items to their mouth, participants were given the choice to either consume the candy or spit them into a nearby trash receptacle before preparing for the next trial. Note that either action, eating or spitting, causes smaller MGAs for unimanual movements with the right hand compared to the left hand (Flindall and Gonzales 2014).

Design

Participants completed the modified Edinburgh–Waterloo handedness questionnaire. This was followed by two blocks of reach-to-grasp movements: Eat–Eat and Place–Place. The order of the blocks was counterbalanced across participants. The blocks were two-choice reaction time tasks. The action performed in each block was the same for every trial, but the target objects were varied, always either both small or both large. Each block consisted of 30 trials, 15 where both objects were small and 15 where both objects were large. Targets of different sizes were presented according to a pseudo-random order to discourage participants from anticipating target size and pre-planning their movement.

Data analysis

The following procedures were performed separately for data from the left and right hands. The position data were filtered with a low-pass Butterworth filter (dual-pass, 2nd-order) with a cutoff frequency of 20 Hz. Tangential velocity of the wrist was calculated with a 3-point central difference method. We calculated grip aperture as the distance between the finger and thumb diodes normalised to the size of the home position during the foreperiod to account for variability in diode placement between hands

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[1] Marketed as Smarties in the United States.

and to correct for distance between the digit pads and the diodes. To determine movement initiation, we isolated the first time after the go signal that tangential velocity of the wrist exceeded 5% of its peak for each trial. Grasp onset of the target object was calculated by taking the maximum of an objective function based on multiple sources of information (Schot et al. 2010). Our objective function was calculated by combining the following criteria: after movement initiation, grip aperture approaching the target size, finger markers close to the target amplitude, and low tangential velocity of the wrist. Movement initiation and grasp onset were visually inspected for each trial and corrected when necessary.

The main dependent variable was MGA of each hand, measured from movement onset of the earlier hand to grasp onset of the later hand. All kinematic variables reported were measured between these two temporal points—this method maintains the spatiotemporal data kinematic variables measured from both hands with respect to each other, facilitating between-hand/within-task comparisons (Blinch et al. 2018). We also examined the spatiotemporal evolution of grip aperture. To facilitate comparisons between trials and participants, we time normalised grip aperture trajectories by interpolating each trial into 100 frames. This converted the trajectories from time in milliseconds to percent time, allowing us to average trajectories across trials, conditions, and (for producing figures) participants. This form of trajectory analysis is commonly used for reach-to-grasp movements (e.g. Jeannerod 1981). These trajectories were examined solely during the outward reach-to-grasp phase of the movement, as the Optotrak markers were often occluded during the return, grasp-to-eat/place phase, as the hands would rotate toward the participant and away from the Optotrak to successfully bring the items to their destination.

Each trial was labelled as “good” or “bad”. Types of bad trials included anticipation (reaction time < 100 ms), fumbling or dropping the target object(s) with one or both hands, or occlusion of Optotrak markers during the reach-to-grasp phase of the movement. In total, 3.3% of all trials were bad and excluded from data analysis. MGA was analysed with a 2 Goal (eat, place) by 2 Hand (left, right) repeated measures ANOVA; preliminary analyses included target size (big, small) as a third factor, but because (a) size (as a factor) did not interact with our other factors, and (b) effects of target size on reach-to-grasp kinematics are both extremely robust and reported extensively elsewhere, we collapsed across size for all analyses reported here. This ANOVA was followed up with two a priori between-task comparisons: the left hand in the Eat–Eat condition was compared to the left hand in the Place–Place condition, and the right hand in the Eat–Eat condition was compared to the right hand in the Place–Place condition. These comparisons were one-tailed paired samples *t* tests, as we predicted that MGAs in the Eat–Eat condition would be smaller than those produced in the Place–Place condition.

We compared grip aperture trajectories throughout movement execution, from 1 to 100% time, with repeated measures functional ANOVAs (Ramsay and Silverman 2005). We used test statistics $\mathcal{D}_n$ and $\mathcal{E}_n$, and the permutation approach to approximate their null distributions (Smaga 2019b). The tests based on $\mathcal{D}_n$ and $\mathcal{E}_n$ are repeated measures counterparts of an omnibus F test of an ANOVA. Test statistic $\mathcal{D}_n$ is an adaptation of the globalising pointwise F test by Zhang and Liang (2014) to repeated measures analysis, and test statistic $\mathcal{E}_n$ is an adaptation of the $F_{\max}$-test by Zhang et al. (2019). These test statistics are extensions of test statistic C_n (Martínez-Camblor and Corral 2011; Smaga 2019a). Importantly, simulation studies have shown that these implementations of $\mathcal{D}_n$ and $\mathcal{E}_n$ outperform other implementations and C_n in terms of size control and power (Smaga 2019b). We used pointwise tests (Ramsay and Silverman 2005) for all pairwise comparisons between eat and place movements. These tests were nondirectional as we did not have predictions for how grip aperture would unfold during the entire trajectory. The Benjamini and Hochberg (1995) procedure was used to control the false discovery rate. Eating and placing tasks, with each hand, were compared with separate functional ANOVAs.

While MGA and grip aperture trajectory were our primary variables of interest, we also analysed other common kinematic variables to ensure that any differences in maximum grip aperture, grip aperture trajectories, or both could not be explained as a by-product of another (functional) aspect of the movement. Specifically, we examined movement time, synchrony/asynchrony at movement initiation and grasp onset, and grasp orientation at grasp onset. Movement time was analysed with the same ANOVA as MGA. Synchrony was calculated by subtracting the time of an event for the right hand from the time of the same event for the left hand—negative values indicated that the left hand led, whereas positive values indicated that the right hand led. Synchrony at movement initiation and grasp onset were analysed with a paired samples *t* test comparing the Eat–Eat and Place–Place conditions. For grasp orientation at grasp onset, the grasp of the left hand was typically rotated counterclockwise from vertical and the right hand was rotated clockwise from vertical. To facilitate comparisons between hands, grasp orientation of the left hand was converted to degrees counterclockwise from vertical and the right hand was converted to degrees clockwise from vertical. If, for example, the grasp orientations of the left and right hands in the Eat–Eat condition are 105° and 75°, with vertical being 90°, then the converted grasp orientation of the left hand is 15° ($105° - 90° = 15°$ counterclockwise from vertical) and the right hand is also 15° ($90° - 75° = 15°$ clockwise from vertical). Analysis of grasp orientation required circular

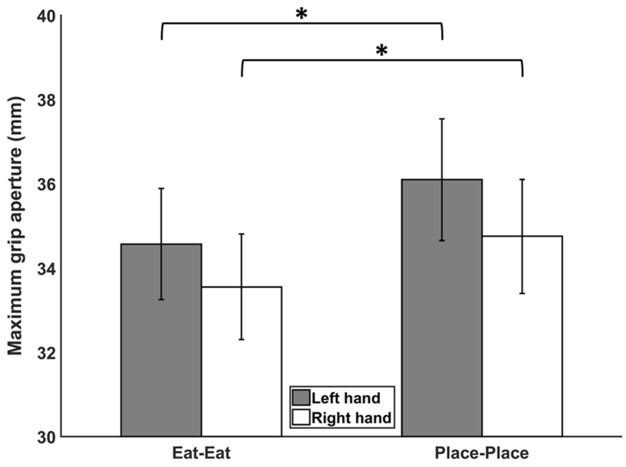

Fig. 1 Grand mean maximum grip aperture for both hands in the two bimanual symmetric conditions (Experiment 1). Error bars are 95% within-participant confidence intervals (Cousineau 2005; Morey 2008). $^{*}p \leq 0.05$

statistics; specifically, grasp orientations were compared between hands and between conditions with parametric Hotelling paired samples tests.

Reported values, unless otherwise noted, are means and 95% within-participant confidence intervals (Cousineau 2005; Morey 2008). An example of these values is 100, [90, 110], where 100 is the mean and the 95% within-participant confidence interval is 90–110. Effect sizes are reported using either partial eta-squared (η^2_{p}; for ANOVAs) or Cohen's d (for *t* tests; calculated with the pooled standard deviation).

Results

Participants were instructed to "reach and grasp the objects at a comfortable pace, with an emphasis on accuracy over speed". This caused a grand mean initiation time of 386 ms, [353, 418] and a grand mean movement time of 859 ms, [792, 925] (between-participant confidence intervals). We use the term initiation time instead of reaction time because participants were not given the typical reaction time task instructions of reacting as quickly and accurately as possible.

Maximum grip aperture

Grand mean MGA for both hands in the two conditions are shown in Fig. 1. There was a significant main effect of goal, $F(1, 20) = 4.4$, $p = 0.048$, $\eta^2_{\mathrm{p}} = 0.18$. The main effect of hand and the goal by hand interaction were not significant, $F(1, 20) = 1.9$, $p = 0.188$, $\eta^2_{\mathrm{p}} = 0.09$, $F(1, 20) = 0.4$, $p = 0.550$, $\eta^2_{\mathrm{p}} = 0.02$. Consistent with the main effect of Goal, the a priori, one-tailed *t* tests showed that MGAs in the Eat–Eat condition were smaller than those in the Place–Place condition, for both the left hand and the right hand, $t(20) = 2.0$, $p = 0.028$, $d = 0.23$, $t(20) = 1.9$, $p = 0.039$, $d = 0.21$. MGA represents grip aperture at just one point during movement execution; as such, it may fail to capture differences in grip aperture development over time. Next, we examined the evolution of grip aperture throughout movement execution.

Grip aperture trajectories

Sample mean functions of grip aperture trajectories are shown in Fig. 2; each graph compares eating and placing trajectories between conditions for either the left hand (Fig. 2, left) or the right hand (Fig. 2, right). The trajectories showed the typical pattern of grip aperture rapidly increasing after movement initiation, reaching MGA around 70% of movement execution, and then rapidly decreasing to the size of the object at grasp onset (Jeannerod 1981). Recall that MGA was smaller when eating than when placing when using the left hand. This was not the case for grip aperture trajectories of the left hand, where eating and placing were not significantly different, $\mathcal{D}_n = 0.057$, $\mathcal{E}_n = 0.058$, $ps \geq 0.111$. In contrast, the functional ANOVAs on the grip aperture trajectories of the right hand were slightly above and below our threshold for statistical significance, $\mathcal{D}_n = 0.069$, $\mathcal{E}_n = 0.045$. Like the left hand, the right hand produced smaller MGAs when eating compared to placing. Unlike the left hand, however, this trend was visible in the grip aperture trajectory of the right hand around the time of MGA, from 59 to 77% (Fig. 2, right), though the difference was not statistically significant at the 0.05 level ($0.068 \leq ps \leq 0.100$).

Movement characteristics

Grand mean movement time was 859 ms, [792, 925] (between-participant confidence interval). Movement time was not significantly affected by goal, hand, or the interaction between goal and hand, $F(1, 20) < 0.1$, $p = 0.833$, $\eta^2_{\mathrm{p}} < 0.01$, $F(1, 20) < 0.1$, $p = 0.920$, $\eta^2_{\mathrm{p}} < 0.01$, $F(1, 20) = 0.7$, $p = 0.419$, $\eta^2_{\mathrm{p}} = 0.03$. The movements of the left and right hands were initiated and reached grasp onset relatively synchronously. Asynchrony analysis revealed that asynchrony of the hands at movement initiation was not significantly different between Eat–Eat (− 3.4 ms, [− 6.5, − 0.3]) and Place–Place conditions (− 0.9 ms, [− 3.9, 2.2]), $t(20) = -1.2$, $p = 0.236$, $d = 0.20$. The asynchrony of the hands at grasp onset was also not significantly different between Eat–Eat (− 1.9 ms, [− 10.4, 6.7]) and Place–Place conditions (− 3.8 ms, [− 12.3, 4.8]), $t(20) = 0.3$, $p = 0.744$, $d = 0.06$. Grasp orientation at grasp onset for the left hand (17.1°, [13.3, 20.9]) and the right hand (14.4°, [10.4, 18.5]) in the Eat–Eat condition were not significantly different from one another, $F(2, 19) = 1.0$, $p = 0.372$. Grasp orientations of the left (14.5°, [10.6, 18.4]) and right hands (12.4°, [8.2,

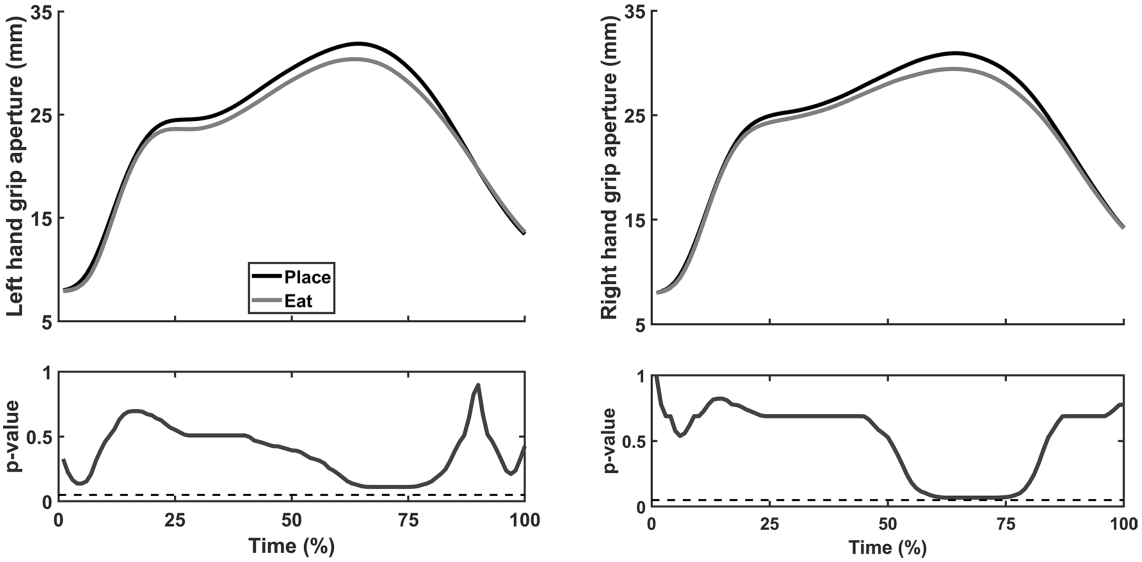

Fig. 2 The top graphs show the sample mean functions of grip aperture trajectories from movement initiation to grasp onset for bimanual symmetric movements (Experiment 1): Eat–Eat vs. Place–Place (left hand) and Eat–Eat vs. Place–Place (right hand). The bottom graphs show the associated p values from the pointwise tests, comparing grip aperture between tasks at each percentile. The dashed line is the threshold for statistical significance, $\alpha = 0.05$

16.5]) were also not significantly different in the Place–Place condition, $F(2, 19) = 0.6$, $p = 0.563$. The grasp orientation of the left hand was significantly different between tasks, $F(2, 19) = 4.639$, $p = 0.023$. The grasp orientation of the right hand was not significantly different between tasks, $F(2, 19) = 3.2$, $p = 0.065$.

Discussion

We hypothesised that the left hemisphere would be dominant for bimanual symmetric movements, manifesting as smaller MGAs (in both hands) for bimanual grasp-to-eat movements (Eat–Eat) than for bimanual grasp-to-place movements (Place–Place). The results of MGA and grip aperture trajectory analysis of the right hand's movement both supported our hypothesis. Furthermore, it is unlikely that the observed differences were caused by other characteristics of the movements, as movement time, asynchrony, and orientation the hands when grasping were symmetric between hands and consistent between conditions. Based on previous studies that imply a left hemisphere origin for the grasp-to-eat action, these results suggest that the left cerebral hemisphere may be dominant for the control of bimanual symmetric reach-to-grasp movements. This conclusion is in line with many studies that have shown the left hemisphere is also dominant for *continuous* bimanual movements (e.g. Byblow et al. 1994, 1998; de Poel et al. 2007; Franz et al. 2002; Kennedy et al. 2016; Peters 1981). This is somewhat surprising as the motor control of continuous and discrete bimanual movements is unique (e.g. Heuer and Klein 2005; Semjen 2002). The many differences between continuous and discrete bimanual movements had led to separate theoretical paradigms for each class of bimanual movements (Swinnen and Wenderoth 2004); that is, dynamical systems for continuous bimanual movements and information processing for discrete bimanual movements. There are, of course, commonalities between continuous and discrete bimanual movements (e.g. Amazeen 2002; Monno et al. 2002). We suggest that another one of these commonalities is that both movement types, continuous and discrete, are predominantly controlled by the left hemisphere. A natural extension from Experiment 1 is to investigate whether bimanual reach-to-grasp movements with asymmetric goals are similarly controlled; this was the purpose of Experiment 2.

Experiment 2

In the second experiment, we investigated which (if either) hemisphere was dominant for discrete bimanual asymmetric movements. We examined bimanual asymmetric reach-to-grasp movements where one hand made a grasp-to-eat movement while the other hand made a grasp-to-place movement. As in Experiment 1, the same three possibilities for hemispheric control apply: left hemisphere dominance, right hemisphere dominance, or contralateral control. Recall from the "Introduction" that only two studies have investigated the hemispheric dominance of discrete bimanual asymmetric movements (Sherwood 1994; Walter and Swinnen 1990), and that these studies have contradictory conclusions: Sherwood (1994) argued that the left hemisphere is dominant for discrete bimanual asymmetric movements whereas Walter and Swinnen (1990) argued that the right hemisphere is dominant. We, therefore, did not have a strong prediction for which of the three possibilities of hemispheric control was most likely.

If the left hemisphere exhibits dominance for the control of bimanual asymmetric movements, then bimanual grasp kinematics should follow the pattern observed during right-handed unimanual actions; MGAs should be smaller for eating movements than placing movements across both types of bimanual asymmetric reaches (Eat–Place and Place–Eat). In other words, the smaller grasp-to-eat plan should be used for eating movements with the right hand (Eat–Place) and transferred to the right hemisphere for eating movements with the left hand (Place–Eat). Alternatively, if the right hemisphere is dominant for bimanual reach-to-grasp movements, then bimanual grasp kinematics should follow the pattern observed during left-handed unimanual actions; that is, MGAs, for both left and right hands, should be similar for grasp-to-eat and grasp-to-place tasks. Finally, bimanual asymmetric reach-to-grasp movements might be controlled independently by each hand's contralateral hemisphere; that is, the left hemisphere controls the right hand and the right hemisphere controls the left hand. In this scenario, each hand's MGA should mimic those observed during unimanual movements; the right hand should have smaller MGAs for grasp-to-eat movements than grasp-to-place movements, while the left hand should have comparable MGAs for grasp-to-eat and grasp-to-place movements.

Methods

The same 21 volunteer participants from Experiment 1 were tested in Experiment 2. They were tested in two additional blocks for Experiment 2 immediately following Experiment 1. The method in both experiments was similar, and so we will note only the differences in Experiment 2. Participants completed two blocks of bimanual asymmetric reach-to-grasp movements: Eat–Place and Place–Eat. The order of the blocks was counterbalanced across participants. The blocks were two-choice reaction time tasks. The action performed in each block was the same for every trial, but the target objects were varied, always either both small or both large.

In total, 2.4% of all trials were bad and excluded from data analysis for one or more of the reasons reported in Experiment 1 (see "Data analysis"). As in Experiment 1, MGA was collapsed across size and analysed with a 2 Goal (eat, place) by 2 Hand (left, right) repeated measures ANOVA. This ANOVA was followed up with two a priori between-task comparisons: the left hand in the Eat–Place condition was compared to the left hand in the Place–Eat condition, and the right hand in the Place–Eat condition was compared to the right hand in the Eat–Place condition. These comparisons were two-tailed paired sample *t* tests, as we did not favour one of the three predictions over the others. The same two comparisons were made for grip aperture trajectories: the left hand in the Eat–Place condition was compared to the left hand in the Place–Eat condition, and the right hand in the Place–Eat condition was compared to the right hand in the Eat–Place condition.

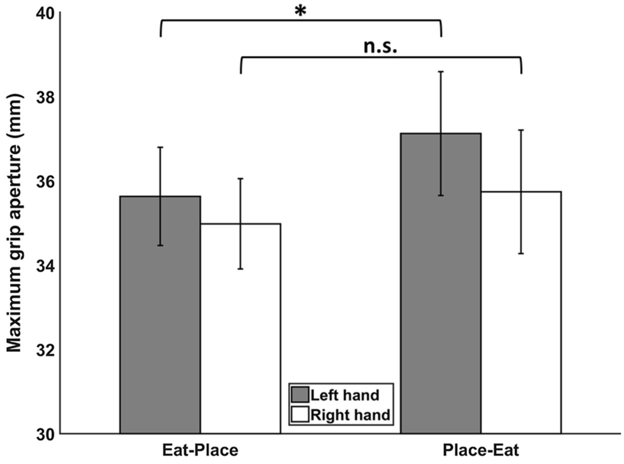

Fig. 3 Grand mean maximum grip aperture for both hands in the two bimanual asymmetric conditions (Experiment 2). Error bars are 95% within-participant confidence intervals (Cousineau 2005; Morey 2008). $*p \leq 0.05$

Results

The grand mean initiation time was 382 ms, [345, 418] and the grand mean movement time was 842 ms, [768, 917] (between-participant confidence intervals).

Maximum grip aperture

Grand mean MGA for both hands in the two conditions is shown in Fig. 3. The main effects of goal and hand were not significant, $F(1, 20) = 1.9$, $p = 0.180$, $\eta_p^2 = 0.09$, $F(1, 20) = 1.1$, $p = 0.318$, $\eta_p^2 = 0.05$. There was, however, a significant goal by hand interaction, $F(1, 20) = 10.2$, $p = 0.005$, $\eta_p^2 = 0.34$. The asymmetric conditions were analysed with two two-tailed *t* tests. These comparisons revealed that the left hand had a smaller MGA when eating (35.6 mm, [34.5, 36.8]) compared to placing (37.1 mm, [35.7, 38.6]; Eat–Place vs. Place–Eat), $t(20) = 3.1$, $p = 0.006$, $d = 0.22$. The MGA of the right hand was slightly larger when eating (35.7 mm, [34.3, 37.2]) compared to placing (35.0 mm,

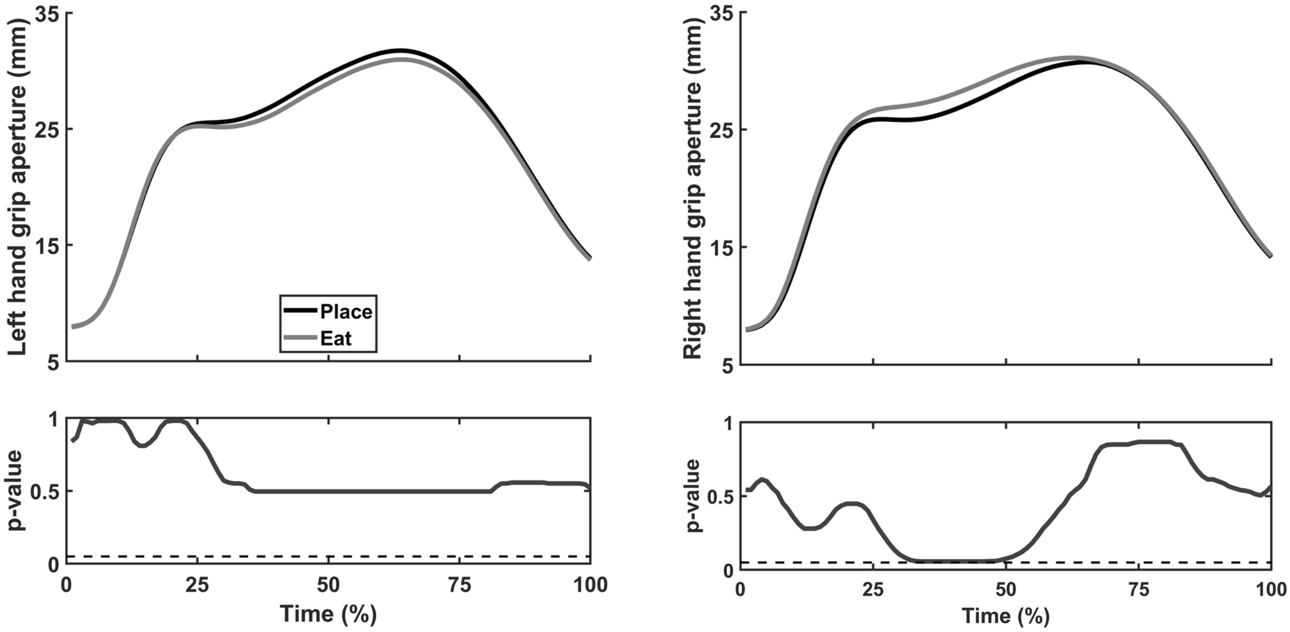

Fig. 4 The top graphs show the sample mean functions of grip aperture trajectories from movement initiation to grasp onset for bimanual asymmetric movements (Experiment 2): Eat–Place vs. Place–Eat (left hand), and Place–Eat vs. Eat–Place (right hand). The bottom graphs show the associated p values from the pointwise tests. The dashed line is the threshold for statistical significance, $\alpha = 0.05$

[33.9, 36.1]; Place–Eat vs. Eat–Place), but they were not significantly different, $t(20) = 1.9$, $p = 0.068$, $d = 0.11$.

Grip aperture trajectories

Sample mean functions of grip apertures are shown in Fig. 4; each graph compares eating and placing for either the left hand (Fig. 4, left) or the right hand (Fig. 4, right). Recall that for MGA in the asymmetric conditions, the left hand produced smaller MGAs when eating than when placing. This effect did not appear in the left-hand grip aperture trajectories, where eating and placing were not significantly different, $\mathcal{D}_n = 0.276$, $\mathcal{E}_n = 0.498$, $ps \geq 0.496$. In contrast, the MGA analysis suggested that the right hand had comparable MGAs when eating and placing. Statistical analysis on right-hand grip aperture trajectories, however, were statistically significant, $\mathcal{D}_n = 0.049$, $\mathcal{E}_n = 0.046$. Pointwise tests suggested a nonsignificant trend for grip apertures while placing to be smaller than eating before MGA, from 31 to 51%, $0.057 \leq ps \leq 0.100$. The likely reason the omnibus tests ($\mathcal{D}_n$ and $\mathcal{E}_n$) were significant and the pointwise tests were not significant is that the omnibus test are more powerful than the pointwise tests. This is also the case for an omnibus F test and pointwise tests from an ANOVA.

Movement characteristics

Grand mean movement time was 842 ms, [768, 917] (between-participant confidence interval). Movement time was not significantly affected by goal, hand, or the interaction between goal and hand, $F(1, 20) = 2.8$, $p = 0.112$, $\eta_p^2 = 0.12$, $F(1, 20) = 0.1$, $p = 0.800$, $\eta_p^2 < 0.01$, $F(1, 20) = 1.3$, $p = 0.266$, $\eta_p^2 = 0.06$. Asynchrony analysis revealed that Eat–Place movements were initiated with significantly greater asynchrony (−5.0 ms, [−7.8, −2.3]) than Place–Eat movements (−0.8 ms, [−3.6, 2.0]), $t(20) = -2.3$, $p = 0.035$, $d = 0.33$. Asynchrony at grasp onset was also significantly different between Eat–Place (−7.9 ms, [−16.8, 1.1]) and Place–Eat (6.0 ms, [−3.0, 15.0]) conditions, $t(20) = -2.3$, $p = 0.033$, $d = 0.41$. Grasp orientation at grasp onset for the left hand (15.2°, [10.4, 20.1]) and the right hand (12.4°, [7.7, 17.1]) in the Eat–Place condition was not significantly different from one another, $F(2, 19) = 1.5$, $p = 0.244$. Grasp orientations of the left (16.1°, [12.0, 20.3]) and right hands (14.0°, [9.6, 18.5]) were also not significantly difference in the Place–Eat condition, $F(2, 19) = 0.5$, $p = 0.628$. The grasp orientation of the left hand was not significantly different between tasks, $F(2, 19) = 2.0$, $p = 0.168$. The grasp orientation of the right hand was significantly different between tasks, $F(2, 19) = 4.0$, $p = 0.036$.

Discussion

These results are difficult to interpret because they do not align with any of our three hypotheses (i.e. left hemisphere dominance, right hemisphere dominance, or contralateral control). The MGA results for the left hand do suggest that the left hemisphere may be dominant for the control of bimanual asymmetric reach-to-grasp movements. The results for the right arm, however, do not support the left hemisphere hypothesis. In fact, the results for the right arm do not support any of the three hypotheses. We, therefore, believe that bimanual asymmetric reach-to-grasp movements require further experimentation to determine their hemispheric dominance. One possibility to explore is that the lateralisation of discrete bimanual asymmetric movements may depend on the task; the hemisphere in control may depend on the functional goals of the movements, rather than their simple mechanical requirements. In other words, one may need to consider the combined goal of the bimanual movement rather than the separate goals of the two unimanual movements. This would fit with the theory that bimanual movements, especially asymmetric ones, are not simply the sum of two unimanual movements (Blinch et al. 2015; Kelso et al. 1979; Swinnen and Wenderoth 2004). Perhaps this approach could explain why grip aperture of both hands in the Eat–Place condition was smaller than in the Place–Eat condition. We attempted to formulate such a post hoc explanation, but we were unconvinced by our many formulations. Proper interpretation of these unpredicted results likely requires more empirical evidence than currently available.

General discussion

The purpose of the current study was to investigate which, if either, cerebral hemisphere is dominant for the control of bimanual reach-to-grasp movements. We investigated the hemispheric control of both bimanual symmetric (Experiment 1) and bimanual asymmetric movements (Experiment 2).

Bimanual symmetric reach-to-grasp movements

Based on research on continuous bimanual movements, we hypothesised that the left hemisphere would exhibit more control over bimanual symmetric reach-to-grasp movements than the right hemisphere. Since the left hemisphere has a processing advantage for grasp-to-eat movements (which manifests as smaller MGAs for grasp-to-eat than grasp-to-place movements when using the right hand; see Flindall and Gonzalez 2013; Flindall et al. 2015), we hypothesised that a left hemisphere dominance for bimanual reach-to-grasp movements would manifest as smaller MGAs for grasp-to-eat movements than for grasp-to-place movements in both hands. This prediction was supported by the results: MGAs were indeed smaller during bimanual grasp-to-eat movements than they were during bimanual grasp-to-place movements. Grip apertures tended to be smaller for grasp-to-eat than grasp-to-place movements in the immediate moments before and after MGA, from about 60 to 80% of movement execution. These results, again, suggest that the left hemisphere may be dominant for the control of bimanual reach-to-grasp movements.

Our finding that the left hemisphere may be dominant for discrete bimanual movements agrees with many studies that have shown the left hemisphere is also dominant for continuous bimanual movements (e.g. Byblow et al. 1994, 1998, de Poel et al. 2007, Franz et al. 2002, Kennedy et al. 2016 and Peters 1981). There are only a few studies that have investigated lateralisation during discrete bimanual movements. The result of Sherwood (1994) also suggested that the left hemisphere is dominant for discrete bimanual movements, but the results of Walter and Swinnen (1990) supported the opposite, that the right hemisphere is dominant. However, both of those studies investigated dominance for discrete bimanual asymmetric movements, which may have different dominance than the bimanual symmetric movements tested in Experiment 1. There is at least one behavioural study that examined the lateralisation of discrete bimanual symmetric movements (Le and Niemeier 2013), and they argued that the right hemisphere is dominant.

Le and Niemeier (2013) asked participants to make a bimanual reach-to-grasp movement to grasp-to-lift or reach-to-push a small wooden block. The reach-to-grasp movements involved using both hands to pick up one block; the middle and index fingers of the left hand were placed on the left side of the block, and the middle and index fingers of the right hand were placed on the right side of the block. To lift the block, the hands needed to work together, like a pair of tongs. Hemispheric contribution was manipulated by asking participants to fixate to one side of the to-be-grasped block; when the participant fixated to the left, for example, then the block was in the right visual field and the visual information would reach the left hemisphere first. Le and Niemeier reasoned that if the left hemisphere is dominant for these movements, then movements should be easier to make when the block is in the right visual field (and vice versa if the right hemisphere is dominant). They found the movements were easier (e.g. shorter reaction time, smaller MGA) when the block was in the left visual field. In comparison, no movement asymmetries were found in the reach-to-push condition, which was computationally less demanding; together, these results suggested a right hemisphere advantage for programming bimanual reach-to-grasp movements.

The control of the movements tested by Le and Niemeier (2013) and the bimanual reach-to-grasp movements in Experiment 1 have several key differences. First, we investigated bimanual movement production via concurrent unimanual movements while they investigated a bimanual task that would be impossible to perform without coordinated effort from the left and right hands. It is quite possible that hemispheric lateralisation depends on the type of discrete bimanual movement. This could also explain the contrasting results for different types of bimanual asymmetric movements [e.g. those tested in Experiment 2 or those tested by Sherwood (1994) and by Walter and Swinnen (1990)]. Second, our studies used different approaches to measure the hemispheric specialisations of the sensorimotor system. We manipulated the goal of the task and the hand that produce the movement while they manipulated the visual field of the target object. The divided visual field paradigm used by Le and Niemeier is well established, but it requires precise methodology to work properly. The study by Le and Niemeier had two large departures from the well-established divided visual field paradigm. First, the stimulus was visible for 2500 ms in the study by Le and Niemeier. The recommended stimulus duration is less than 100 or 150 ms to prevent anticipatory saccades or saccades and exposure of the stimulus to a central visual field (e.g. Bourne 2006, Hunter and Brysbaert 2008; Pelletier et al. 2007). Second, in Le and Niemeier's study, participants fixated 15° from central placement of the to-be-grasped block, which would have seriously degraded the usefulness of visual information to the sensorimotor system (Bourne 2006). The recommended fixation is between 2.5 and 3.0° to ensure adequate visual acuity of the stimulus (Bourne 2006).

We have two criticisms of the study by Le and Niemeier (2013). First, one of the dependent variables that showed an advantage when the block was in the left visual field was MGA. MGA was smaller when the block was in the left visual field than in the right visual field. This, however, occurred only when the block was oriented horizontally (grip surface of 50 by 24 mm); MGA was comparable in both visual fields when the block was oriented vertically (grip surface of 87 by 50 mm). These results suggest that the right hemisphere was dominant when the grip surface was slightly smaller and neither hemisphere was dominant when the grip surface was slightly larger. That the grip surface affected MGA and hemispheric dominance suggest a more complex interpretation than that offered by the authors. Second, and perhaps more importantly, Le and Niemeier also tested movements where participants used their index and middle fingers of both hands to push the block off the pedestal. In this condition, the maximum reach apertures (so called because no grasp was performed in this condition) of these pushing movements also responded to block orientation, though the direction of the effect was the opposite; when the block was oriented horizontally, maximum reach aperture was smaller when the block was in the right visual field than when the block was in the left visual field. By their own logic, this suggests that the left hemisphere is dominant for bimanual reach-to-push movements. Le and Niemeier argued that this result did not suggest that the left hemisphere is dominant because, "it is unclear whether measures of [maximum reach aperture] can be considered as criteria for functional reaches". We are unconvinced by this argument; to us, maximum reach aperture seems as relevant to their grasping movements as to their pushing movements. In both grasp and push conditions, finger placement on the target (which naturally determines MGA/maximum reach aperture in their bimanual grasp/push movements) needs to be precisely controlled to efficiently lift or push the block. Without efficient inter-limb coordination, both movements will fail.

Visuomotor grasping circuit

Many of our concerns with the study by Le and Niemeier (2013) were addressed in a follow-up study that relied on transcranial magnetic stimulation (TMS) for direct evidence of right hemisphere dominance when bimanually grasping a single object (Le et al. 2014). To provide context for that study, we will briefly review the neural mechanisms of unimanual reach-to-grasp movements. The visuomotor grasping circuit is well understood from macaque neurophysiological research (reviewed by Castiello and Begliomini 2008). The grasping circuit consists of three areas: anterior intraparietal area (AIP), ventral premotor cortex (vPMC; area F5), and dorsal premotor cortex (dPMC; area F2). It has been proposed that the AIP determines the possible types of grasps based on the representation of the target object. The vPMC then selects one of these grasps and prepares a motor command. A copy of the motor command, the efference copy, is sent to the vPMC. The vPMC uses the efference copy and sensory feedback for online control of the grip aperture (Castiello and Begliomini 2008). This visuomotor grasping circuit has also been researched in humans with neuroimaging and TMS. The anterior intraparietal sulcus (aIPS; the human homologue of the macaque area AIP) has received the most attention, the vPMC and the dPMC, in comparison, are underexplored and lacking consensus (e.g. Begliomini et al. 2007, Cavina-Pratesi et al. 2010 and Davare et al. 2006).

The role of the aIPS in humans was investigated with a series of TMS studies by Grafton and colleagues (Rice et al. 2006, 2007; Tunik et al. 2005). Tunik et al. had participants make unimanual reach-to-grasp movements with their right hands to a rectangular object. That object was rotated at movement initiation 180 or 90°. The 180° rotation did not necessitate a change in the size of the grip aperture during movement execution, and so it was called the no perturbation condition. The 90° rotation required the grip aperture to increase during movement execution; it was called the perturbation condition. Single-pulse TMS was applied to the aIPS in the left hemisphere (contralateral to the hand used for grasping) in attempt to disrupt the grasp. Impairments to grip aperture in the perturbation occurred when stimulation was within 65 ms of object perturbation. These results suggested that the aIPS in the left hemisphere is involved in the online control of grasping movements with the right hand. Rice et al. (2006) conducted a similar experiment but with paired-pulse TMS, with the first pulse at movement initiation and the second 100 ms after movement initiation (during early movement execution). The perturbation condition showed, once again, that TMS to the left hemisphere impaired grip aperture of the right hand. The novel results were in the no perturbation condition, where TMS also affected grip aperture. Rice and colleagues concluded that the aIPS in the left hemisphere is involved in the online monitoring of grasping movements with the right hand, regardless of whether there is a perturbation. These two previous studies (Tunik et al. 2005; Rice et al. 2006) did not test movements with the left hand or stimulation of the aIPS in the right hemisphere. This, however, was the purpose of their third study (Rice et al. 2007). In this experiment, the target object was not perturbed; instead, differently sized rectangles, which necessitated smaller or larger grip apertures, were presented for each trial. TMS was applied to both left aIPS and right aIPS, in separate blocks, and its effect was measured on grasps made with either the ipsilateral or contralateral hand. Results showed that stimulation of the left aIPS impaired only grasping with the right hand and grasping with the left hand was impaired by only stimulation of the right aIPS. These results support that the online control of unimanual grasping movements is mediated by the contralateral aIPS (c.f. Davare et al. 2007).

To summarise, there is wide support that the aIPS is involved in the online control of unimanual grasping, and that each hand is controlled by the aIPS in the contralateral hemisphere. We now return to Le et al. (2014), who questioned which hemisphere mediated the online control of bimanual grasping movements. They stimulated the aIPS in either the left or right hemisphere at movement initiation. Participants made bimanual reach-to-grasp movements where both hands grasped a single object. The object was occasionally perturbed at movement initiation by rotating it, as was done by Tunik et al. (2005) and Rice et al. (2006). Le and colleagues found that stimulation to only the right aIPS impaired the bimanual grasp. Le et al. concluded that the right hemisphere is dominant for bimanually grasping one object, which was consistent with their previous behavioural results (Le and Niemeier 2013). However, this is inconsistent with our conclusion from the present study, that the left hemisphere may be dominant for bimanual symmetric reach-to-grasp movements. We suggest that these different conclusions might be caused by differences between the types of bimanual reach-to-grasp movements. Recall that the bimanual grasps by Le and Niemeier (2013) and Le et al. (2014) involved one object that both hands worked together to grasp, whereas our grasps involved two objects that were grasped independently, one by each hand. These are both bimanual grasps, but they are unique movements that likely require different coordination within the visuomotor grasping circuit. Some evidence for this comes from a neuroimaging study that investigated brain activation in untrained medical students learning to use endoscopic surgical instruments (Karabanov et al. 2019). Their bimanual reach-to-grasp movements involved each hand making separate reach-to-grasp movements, and so they were like the bimanual grasps in the current study and unlike the bimanual grasps in the studies by Le and Niemeier (2013) and Le et al. (2014). Karabanov et al. looked at changes in activity from baseline (scan 1) to the third (scan 3) endoscope session. They found a significant increase in activity in the left aIPS (as well as the left vPMC). They concluded, as we did, that the visuomotor grasping pathway for bimanual movements is led by the left hemisphere.

Hemispheric dominance of left-handed people

An area for future research is to investigate hemispheric dominance of left-handed people making bimanual symmetric reach-to-grasp movements. For continuous bimanual movements, most (e.g. de Poel et al. 2008, Stucchi and Viviani 1993 and Treffner and Turvey 1996), but not all (e.g. de Poel et al. 2007, Franz et al. 2002 and Swinnen et al. 1996), studies on left-handed people support a theory of right hemisphere dominance. Recall that the left hemisphere is dominant for right-handed people. It is challenging to make a conclusion about the hemispheric dominance of left handers because there is a dearth of studies in the kinematic literature comparing behaviour between right- and left-handed people. Left handers are often excluded from behavioural and neuroimaging studies for several reasons (Willems et al. 2014), most commonly to maintain homogeneity among participants. While right handers in general have a strong and consistent preference for using their dominant hands (Peters 1981; Prichard et al. 2013), left handers are far more heterogeneous in terms of hand preference for everyday tasks, as determined by both self-report (Borod et al. 1984; Chapman and Chapman 1987; Flindall and Gonzalez 2019; Peters 1981; Steenhuis and Bryden 1999) and more direct measures of performance (Bryden et al. 2000; Peters 1981). This heterogeneity has led some researchers to label left handers according to their reported consistency of preference between tasks, rather than the strength of that preference within tasks. Consistent left handers prefer to use their left hands for virtually all common activities, while inconsistent left handers use their non-dominant (right) hands for one or more inventoried actions (Prichard et al. 2013). Adding to this confusion is the fact that, among many self-identified left handers, kinematic performance (and often hand preference itself) in prehension is indistinguishable from that of right handers, despite significantly different responses on handedness inventories (Boulinguez et al. 2001; Bryden et al. 2011; Gonzalez et al. 2014; Gonzalez and Goodale 2009; Stins et al. 2001). A final point of confusion is that, where studies involving left handers do exist, researchers typically do not discriminate between consistent and inconsistent left handers. This may contribute to the perception of an overall weaker and more variable lateralization among the left-handed population in general. In sum, while right handers are generally left hemisphere dominant for continuous bimanual movements, and some evidence suggests that consistent left handers (at least) are right hemisphere dominant for continuous bimanual movements, inconsistent left handers may not have a group-wide dominant hemisphere for continuous bimanual coordination.

Conclusions

The purpose of the current study was to investigate which, if either, cerebral hemisphere is dominant for the control of bimanual reach-to-grasp movements. In agreement with research on continuous bimanual movements, the results of Experiment 1 suggested that the left hemisphere may be dominant for bimanual symmetric movements. There are, admittedly, only a few studies on the hemispheric contributions of discrete bimanual movements. Notably, Le and Niemeier (2013) and Le et al. (2014) have shown evidence for right hemisphere dominance. We suggest that the critical difference between those studies and the current study is the type of discrete bimanual movement tested. The movements in the current study involved two objects that were grasped separately by each hand, and the movements by Le and Niemeier and Le et al. involved one object that was grasped by both hands working together. These two types of discrete bimanual movements likely require different coordination within the visuomotor grasping circuit, which may be under opposite hemispheric control. We also examined hemispheric contributions to bimanual asymmetric movements (Experiment 2). The results did not fit with any of our three predictions of left hemisphere dominance, right hemisphere dominance, or contralateral control. We tentatively suggest that the control of bimanual asymmetric movements may depend on the complex interactions between the goals of each hand. This idea fits with the theory that bimanual movements, especially asymmetric ones, are not simply the sum of two unimanual movements (Blinch et al. 2015; Kelso et al. 1979; Swinnen and Wenderoth 2004).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Informed consent was obtained from all individual participants included in the study.

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