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RESEARCH ARTICLE

Shared right-hemispheric representations of sensorimotor goals in dynamic task environments

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Abstract

Functional behaviour affords that we form goals to integrate sensory information about the world around us with suitable motor actions, such as when we plan to grab an object with a hand. However, much research has tested grasping in static scenarios where goals are pursued with repetitive movements, whereas dynamic contexts require goals to be pursued even when changes in the environment require a change in the actions to attain them. To study grasp goals in dynamic environments here, we employed a task where the goal remained the same but the execution of the movement changed; we primed participants to grasp objects either with their right or left hand, and occasionally they had to switch to grasping with both. Switch costs should be minimal if grasp goal representations were used continuously, for example, within the left dominant hemisphere. But remapped or re-computed goal representations should delay movements. We found that switching from right-hand grasping to bimanual grasping delayed reaction times but switching from left-hand grasping to bimanual grasping did not. Further, control experiments showed that the lateralized switch costs were not caused by asymmetric inhibition between hemispheres or switches between usual and unusual tasks. Our results show that the left hemisphere does not serve a general role of sensorimotor grasp goal representation. Instead, sensorimotor grasp goals appear to be represented at intermediate levels of abstraction, downstream from cognitive task representations, yet upstream from the control of the grasping effectors.

Keywords Bimanual · Coordination · Grasp · Goal representation · Sensorimotor · Switch costs · Motor · Representations

Introduction

To pursue goals despite the ever-changing world around us, we need to be able to change our action plans. For example, imagine your goal is to grab a cup placed on a table a few steps away and you plan to use your right hand to grasp it. But as you walk, perhaps your path swerves to the right to pass some chairs and you decide to grab the cup with your left hand because it is closer. Or you might realize that the cup is filled to the rim with coffee so you decide to grab the cup with fingers of both hands.

Grasps constitute a common type of actions and can serve as a model of goal-oriented behaviour because the underlying neural and computational mechanisms are already well understood (Galletti et al. 2003; Konen et al. 2013; Vingerhoets 2014). We know that the visuomotor control of grasp movements involves a dorsolateral network (Grafton et al. 1996; Ehrsson et al. 2000) within which the anterior portion of the intraparietal sulcus (aIPS in the human brain, AIP in the macaque brain; Culham et al. 2003; Frey et al. 2005) plays a key role in representing the sensorimotor aspect of action goals (Hamilton and Grafton 2006) as confirmed by several modes of research: (a) neurons in the aIPS are selectively tuned to the sight of object shapes (Murata et al. 2000) and provide the information required to find surface points at which to grasp an object (Blake 1993). (b) Functional imaging studies have found that observing another person's grasp movements activates the aIPS (e.g., Shmuelof and Zohary 2008); specifically, the aIPS is associated with encoding the goal of observed actions (Hamilton and Grafton 2006), is sensitive to the identity of the observed objects as well as grasp types (Shmuelof and Zohary 2005), and responds even when the observed action is performed on abstract geometric shapes (Ramsey and Hamilton 2010; Southgate et al. 2014). (c) Transcranial magnetic stimulation (TMS) of the aIPS disrupts grasps (Rice et al. 2006;

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Tunik et al. 2005, 2008). (d) Crucially, TMS disrupts grasps regardless of whether they are performed with thumb and index finger of one hand, or with the index fingers of the two hands (Le et al. 2014, 2017). What is more, bimanual grasp movements are disrupted as a whole rather than the movements of the two hands independently (Le et al. 2014, although see, 2017 for stimulation of a region posterior to aIPS).

However, much research has investigated grasping in scenarios where the action that is to be performed is known well in advance, that is, in relatively static task environments. For dynamic task environments, however, there is little understanding of how action goals are pursued despite sudden environmental changes that afford a different action to attain the same goal. That is, if one plans to grasp an object with the right hand but then suddenly finds that grasping with the left hand or both hands is more appropriate, the sudden change could either trigger a change in the representation of the grasp goal or the same sensorimotor goal representation could be used continuously.

Grasp goal representations could change given that the two cerebral hemispheres show a contralateral specialization for unimanual grasps with the right or left hand, respectively (Rice et al. 2006; Tunik et al. 2005, 2008). Thus, goal representations could either be remapped across hemispheres or re-calculated as grasp action plans change from the right to the left hand or to both hands.

However, re-calculating grasp goals might be computationally inefficient, and transferring information across the corpus callosum together with the need to overcome mutual inhibition between hemispheres (e.g., Nelson et al. 2009) could be too time consuming (Braun 1992; Ringo et al. 1994; Westerhausen et al. 2006). Thus, it might make sense to restrict most visual and visuomotor-plan computations to one hemisphere such that sensorimotor grasp goal representations could be used continuously. There is good evidence that both hemispheres carry information about grasp actions with the contra- as well as ipsilateral hand (e.g., Gallivan et al. 2013; Turella et al. 2016). In particular, the left hemisphere could serve a dominant role to encode goals given that in right-handed people there is a consistent left-hemisphere dominance for unilateral grasps: The left inferior parietal cortex near the aIPS is activated during right- as well as left-handed hand-object interactions (Naito and Ehrsson 2006), and TMS of the left aIPS impacts grip force control for both the right and left hands (Davare et al. 2007). Moreover, observations of grasp actions tend to activate the left more than the right aIPS (Shmuelof and Zohary 2005; Hamilton and Grafton 2006; Ramsey and Hamilton 2010; Southgate et al. 2014), and the left aIPS is more evenly responsive to grasping in both the left and right visual fields compared to the right aIPS (Shmuelof and Zohary 2006; Le and Niemeier 2014). Finally, planning to make hand movements is typically associated with left inferior parieto-frontal areas (see Johnson-Frey et al. 2005). In sum, it is possible that grasp control in the left hemisphere serves to maintain grasp goals when changes in the environment require changes in action plans.

If dynamic task environments caused grasp goal representations to be shared in the dominant left hemisphere, at the very least continued left-hemisphere control should be observed in scenarios where participants suddenly switch to grasping with both hands because bimanual grasps involve, at some level, motor areas in both hemispheres. As one caveat, research so far has found that bimanual grasps are governed more by areas in the non-dominant hemisphere (Le et al. 2017; also see; Le and Niemeier 2013a, b, 2014 for more evidence for a right-brain dominance for bimanual grasps), although these data were obtained in static task environments. As a second caveat, bimanual grasp control could be functionally entirely different from unimanual grasp control; TMS might have targeted bimanual grasp areas that are merely in close proximity to unimanual grasp areas (Le et al. 2014, 2017). Thus, unimanual and bimanual grasp goals might not share representations at all.

To test whether grasps are governed by shared goal representations, here we used a dynamic task environment. We employed a visuomotor priming paradigm (Bernardin and Mason 2011; Cant et al. 2005; Craighero et al. 1998; Neely et al. 2005) where participants always pursued the same goal of grasping an object while, most of the time, using the same single hand and only sometimes switching to bimanual grasps. We expected that switching to bimanual grasps should cost little time and timing should be similar if a shared goal representation within the left and/or right hemisphere was used, and times should be delayed and less similar if switching required a different goal representation.

Experiment 1

Methods

Participants

Sixteen healthy undergraduate students from the University of Toronto Scarborough participated in the experiment (11 females, mean age: 20.3 years). All participants had normal or corrected to normal vision, had no history of neurological disorders, and were right handed (Oldfield 1971). All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto and conformed to the ethical standards laid down in the Declaration of Helsinki.

Apparatus and procedure

Participants sat at a table in a dimly lit room. A button box, 15 cm in front of the body, served as start position for their two index fingers, and a pair of Plato goggles (Translucent Technology, Toronto) controlled their vision. At the start of each trial, the goggles turned transparent, revealing a black-painted wooden object ($5 \times 7 \times 2.5$ cm) 50 cm away from the participant on a pedestal (16.5 cm high). The object was either vertically or horizontally oriented following a random schedule and its largest side always faced the participant. 20 or 500 ms later, a beep signaled the participant to grasp the object along its horizontal axis as quickly as possible without sacrificing accuracy, and the pitch of this Go signal (counterbalanced across participants) indicated whether he or she should grasp with one hand, using thumb and index finger, or with two hands, using the two index and middle fingers (Fig. 1).

Participants were told that in each block (of 120 trials) unimanual grasps with the right, or the left hand, were more common than bimanual grasps. Thus, instructions and trial blocks served to prime motor plans for unimanual grasping and inflict switch costs for bimanual motor plans (Bernardin and Mason 2011) while keeping the goal of the action the same. In two “right-hand” blocks, participants grasped with their right hand 70% of the time but switched to bimanual grasping 30% of the time, in two “left-hand” blocks they grasped with the left hand 70% of the time and switched to bimanual grasps 30% of the time, and the four blocks were conducted in an ABBA or BAAB fashion.

Data analysis

Reaction times, previously demonstrated as a sensitive measure of sensorimotor processes of bimanual grasping (Le and Niemeier 2013a), were defined as the time between the GO signal and participants’ button release. Trials with reaction times three standard deviations above the mean were excluded together with trials with movement errors (grasping the object using the incorrect grasp; in total 16.1%). For the remaining trials, we determined median reaction times for each condition. Reaction times then entered a repeated-measures ANOVA with factors SOA (20 ms vs. 500 ms), Task (unimanual vs. bimanual), and Primed Hand (left hand vs. right hand).

Results and discussion

Reaction times ranged from 401 to 551 ms (Fig. 2a) and produced a significant Task × Primed Hand interaction ($F(1,15) = 5.09$, $p = 0.039$, $\eta^2 = 0.253$). This suggests that switching from unimanual to bimanual grasping caused delays only in right-hand blocks (averaged across both SOAs: 18 ms); left-hand blocks revealed almost no switch costs (averaged across both SOAs: 1 ms), although post hoc t-tests yielded no significant effects (right-hand blocks: $t(15) = 1.51$, $p = 0.151$; left-hand blocks: $t(15) = -0.12$, $p = 0.909$). As for the influence of SOAs on switch costs, Fig. 2a seems to suggest that switch costs become more prominent with longer SOAs; however, the Task × Primed Hand × SOA interaction did not reach significance ($F(1,15) = 1.84$, $p = 0.195$, note though that conducting

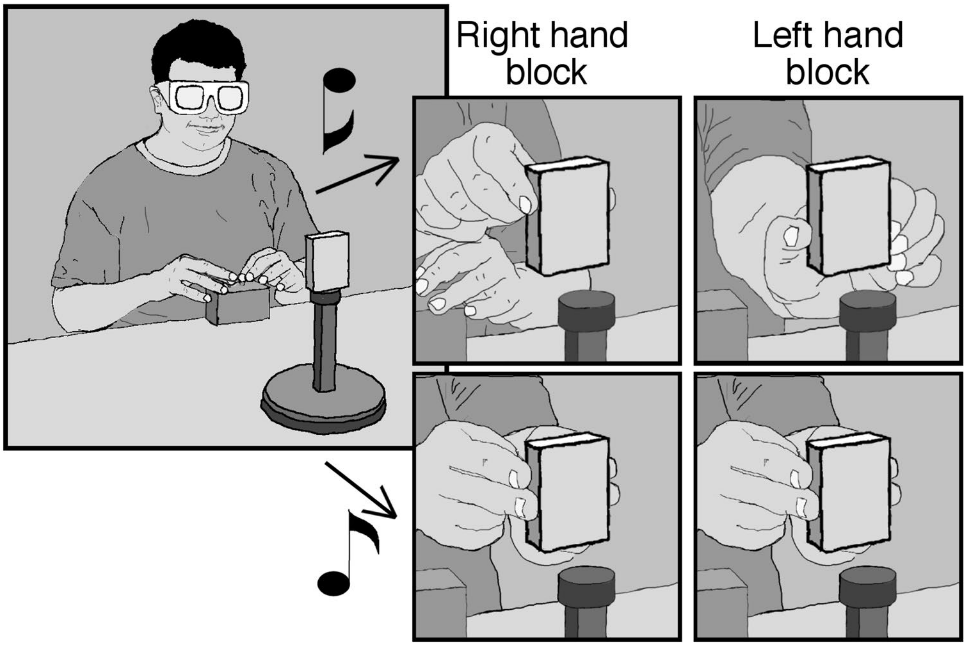


Fig. 1 Experimental set-up. Participants were primed to grasp and lift and object with one hand 70% of the time; 30% of the time they switched to bimanual grasping. Right-hand block: unimanual grasps were preformed with the right hand; left-hand block: unimanual grasps were performed with the left hand

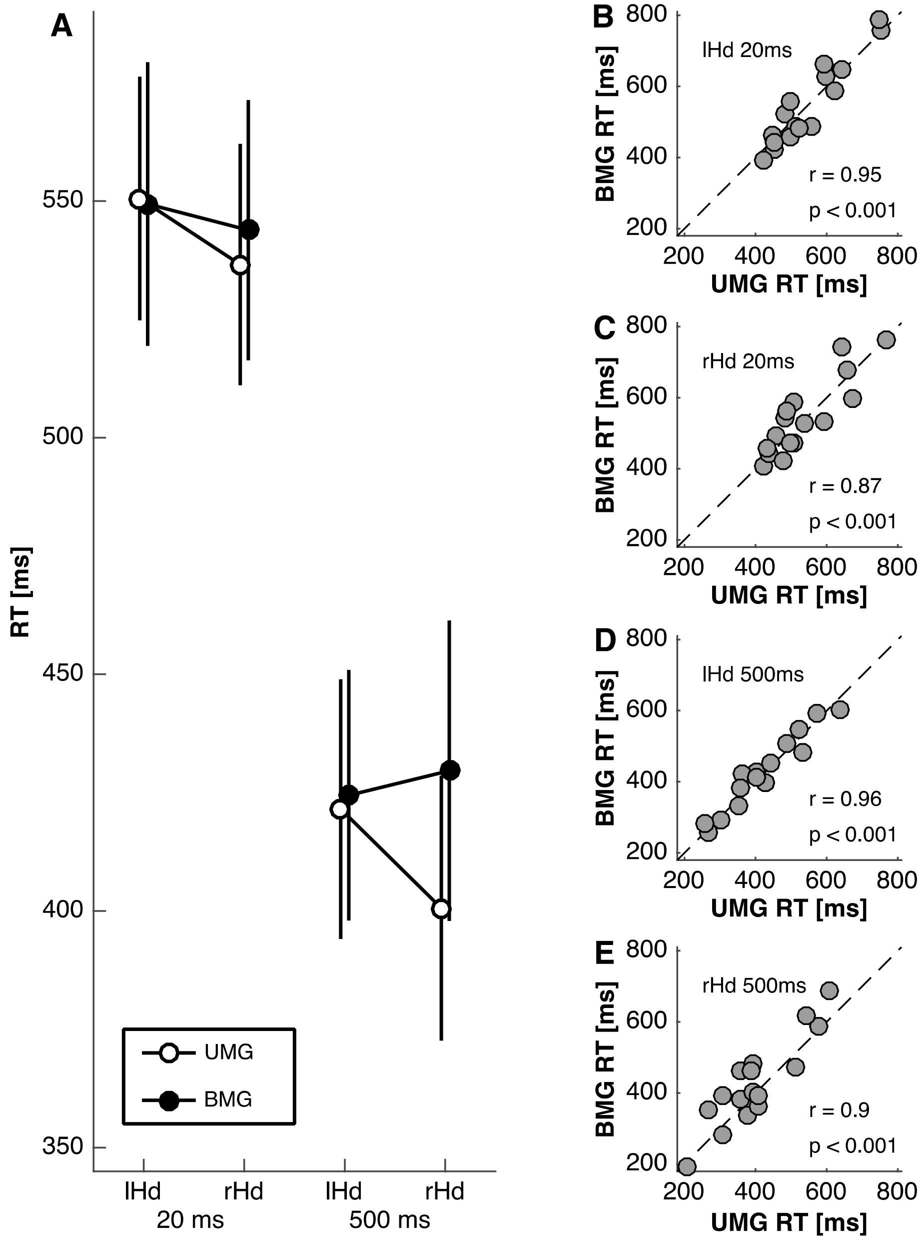


Fig. 2 Reaction times (RT) of the unimanual and bimanual grasping tasks. **a** Group-averaged reaction times plotted as a function of condition. Error bars represent standard errors. **b**–**e** Individual bimanual reaction times plotted as a function of unimanual reaction times. *UMG* unimanual grasp, *BMG* bimanual grasp, *lHd* left-hand blocks, *rHd* right-hand blocks. 20 and 500 ms represent stimulus onset asynchronies

exploratory two-way ANOVAs for each SOA level separately yields a significant Task × Primed Hand interaction for 500 ms: $F(1,15) = 7.57$, $p = 0.015$, but not for 20 ms: $F(1,15) = 0.64$, $p = 0.438$). Also, the main effect of SOA showed that the longer SOA significantly reduced reaction times ($F(1,15) = 215.27$, $p < 0.001$, $\eta^2 = 0.935$; all other effects and interactions: p's ≥ 0.148). Further, unimanual and bimanual reaction times were positively correlated (Fig. 2b–e). This argues against a trade-off of faster bimanual responses at the expense of slowed-down unimanual responses in left-hand blocks. What is more, correlations during left-hand blocks were higher than during right-hand blocks (we converted correlation coefficients to Fisher's *z* values and performed 10,000 bootstrapping steps of random sampling with replacement to calculate the 95% confidence intervals of correlation differences; all confidence intervals were larger than zero, indicating significance; $\mathrm{CI}(z)_{\mathrm{average}} = [0.291, 1.720]$, $\mathrm{CI}(z)_{\mathrm{20ms\ SOA}} = [0.017, 0.870]$, $\mathrm{CI}(z)_{\mathrm{500ms\ SOA}} = [0.141, 0.983]$), consistent with a greater overlap of neural structures for left and bimanual grasps.

In sum, Experiment 1 shows that priming of grasps with the right, but not the left hand incurs switch costs for bimanual grasping with reaction times for unimanual and bimanual grasping being more positively correlated in blocks that primed for left-hand actions. This suggests that, unlike grasping with the right hand, grasping with the left hand involves similar neural resources as bimanual grasping. Furthermore, these resources are likely associated with the right hemisphere (Le and Niemeier 2013a, b, 2014) and probably include grasp-related areas in right parietal cortex (Le et al. 2014, 2017). However, two alternative explanations need to be considered: (a) asymmetrical switch costs could come from asymmetries in inhibition at the level of motor cortices, that is, M1 in the left hemisphere might have inhibited M1 in the right hemisphere more strongly than the other way round (Duque et al. 2007) such that bimanual actions were delayed because it took longer to recruit the contralateral hand during right-hand blocks compared to left-hand blocks. (b) Right-hand blocks might show greater switch costs because they require switching from a common task (grasping with the right hand) to a less common task (grasping with both hands, although see Kilbreath and Heard 2005), whereas in left-hand blocks both tasks are uncommon.

Experiment 2

To test whether switch costs in right-hand blocks in Experiment 1 were caused by the left motor cortex inhibiting the right motor cortex on the level of motor execution (Duque et al. 2007), we repeated Experiment 1, except we replaced bimanual grasps with a pointing task of the non-primed hand. That is, participants were asked to switch to movements that are similar to how each hand moves during bimanual grasp movements. If the Experiment 1 results were merely due to asymmetrical interhemispheric inhibition and delayed recruitment of the non-primed left hand, we should see the same Task × Primed Hand interaction here. In addition, since grasping and pointing entail different goals and should share less neural resources with each other than the two types of grasping, we expect that a significant effect of Task in that overall pointing should be slower than grasping.

Methods

Participants

Twenty-one healthy individuals (15 females, mean age: 19.9 years) participated in Experiments 2. All participants had normal or corrected to normal vision, had no history of neurological disorders, and were right handed as confirmed by the Edinburgh Handedness Inventory (Oldfield 1971). All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto and conformed to the ethical standards laid down in the Declaration of Helsinki.

Apparatus and procedure

The apparatus and procedure were nearly the same as in Experiment 1 with left-hand and right-hand blocks containing 70% unimanual grasp trials. Unlike Experiment 1, however, 30% of the trials required participants to touch the object's centre using the index finger of their non-primed hand.

Data analysis

The data analysis was the same as in Experiment 1. We excluded 6.9% trials because participants made movement errors or because their reaction times deviated by at least three standard deviations from the mean.

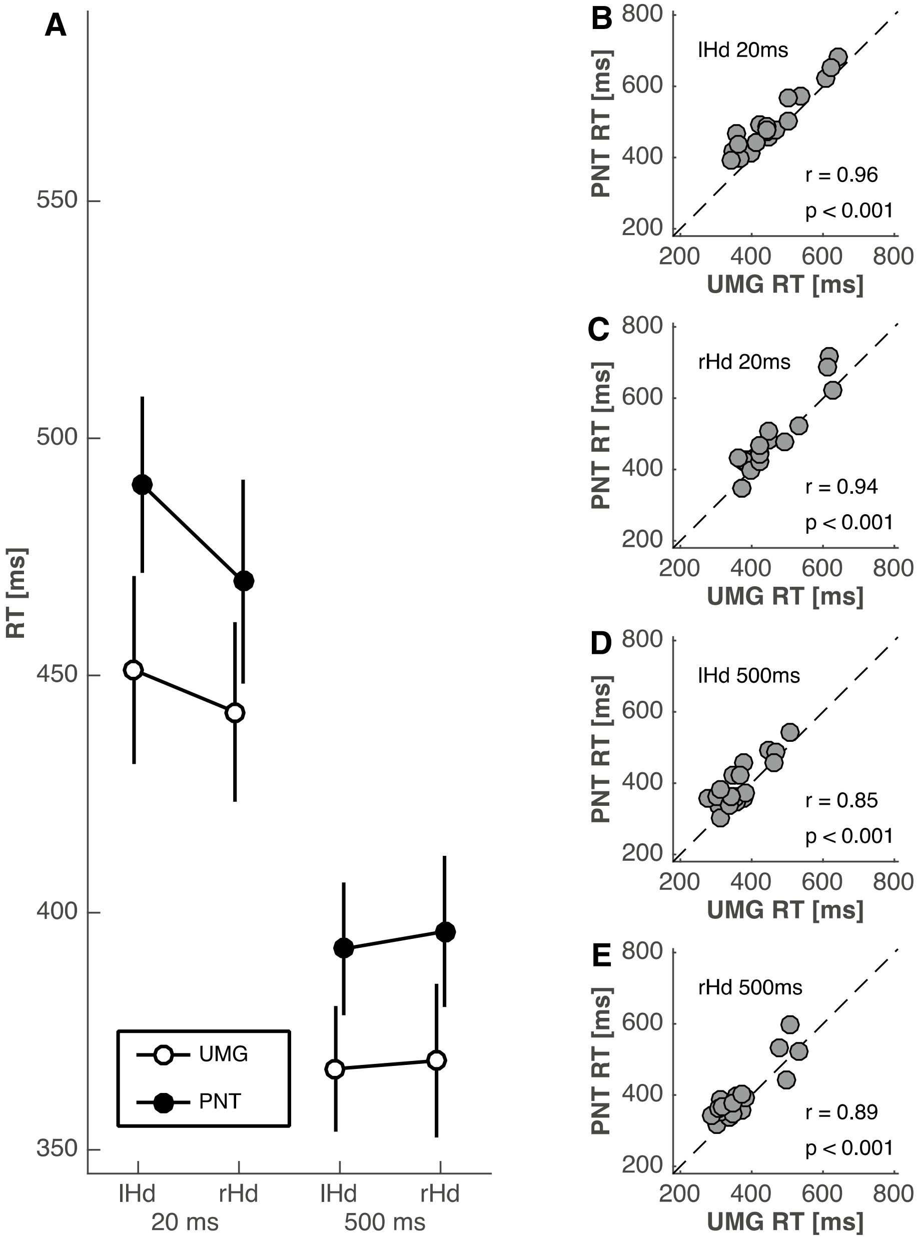
Results and discussion

Reaction times across all conditions ranged from 367 to 550 ms (Fig. 3a). There was a main effect of Task; as expected participants were faster when they grasped with the primed hand than when they had to switch to pointing with the other hand ($F(1,20) = 33.68$, $p < 0.001$, $\eta^2 = 0.627$). In addition, the longer SOA accelerated reaction times ($F(1,20) = 111.23$, $p < 0.001$, $\eta^2 = 0.848$), and SOA interacted with Primed Hand ($F(1,20) = 13.04$, $p = 0.002$), indicating that the left hand was slower than the right after 20 ms SOA but slightly faster after 500 ms SOA. Crucially, however, neither the Task × Primed Hand interaction ($F(1,20) = 0.48$, $p = 0.495$, $\eta^2 = 0.024$) nor the Task × Primed Hand × SOA interaction was significant ($F(1,20) = 2.12$, $p = 0.161$, $\eta^2 = 0.096$; all other F-tests: p's ≤ 0.137).

Correlations between reactions times were high as before (Fig. 3b–e) but there was no systematic difference between left-hand blocks and right-hand blocks (confidence intervals of Fisher's z transformed correlation differences after 10,000 bootstrapping steps: $\mathrm{CI(z)}_{\mathrm{average}} = [-0.760, 0.660]$, $\mathrm{CI(z)}_{\mathrm{20ms\ SOA}} = [-0.193, 0.606]$, $\mathrm{CI(z)}_{\mathrm{500ms\ SOA}} = [-0.699, 0.218]$).

To summarize, asking participants to switch from unimanual grasping to pointing with the respective other hand we did not replicate the asymmetrical switch costs from Experiment 1. In fact, the trends here are opposite to the trends in Experiment 1. This rules out the possibility that the asymmetry in the main experiment was caused by asymmetrical interhemispheric inhibition (Duque et al. 2007; Harris-Love et al. 2007). In the next experiment, we tested whether the asymmetrical switch costs in Experiment 1 were due to bimanual grasps being more 'novel' or 'unusual'.

Fig. 3 Reaction times (RT) of the unimanual grasping and pointing task. **a** Group-averaged reaction times plotted as a function of condition. Error bars represent standard errors. **b**–**e** Individual reaction times during the pointing task plotted as a function of reaction times during the grasping task. *UMG* unimanual grasp, *PNT* pointing with the respective opposite hand, *lHd* left-hand blocks, *rHd* right-hand blocks. 20 and 500 ms represent stimulus onset asynchronies



Experiment 3

In Experiment 1, participants might have taken longer to switch from right-hand grasping to bimanual grasping because it required switching from a more common or more practiced task to one that is novel and less practiced whereas switching from left-hand grasping to bimanual grasping might be about equally uncommon. To rule out this possibility, we repeated Experiment 1 but replaced bimanual grasps with unusual pointing of the non-primed hand. If the results from the main experiment were merely due to left-handed unimanual and bimanual grasps both being novel, then we should see the same Switch-Type effects as before.

Methods

Participants

Eighteen individuals (ten females, mean age: 21.3 years) participated in Experiment 3. All participants had normal or corrected to normal vision, had no history of neurological disorders, and were right handed as confirmed by the Edinburgh Handedness Inventory (Oldfield 1971). All procedures were approved by the Human Participants Review Sub-Committee of the University of Toronto and conformed to the ethical standards laid down in the Declaration of Helsinki.

Apparatus and procedure

The apparatus and procedure were the same as Experiment 1, with the exception that for Experiment 3, we asked participants to touch the object with the little finger of their non-primed hand with the palm facing upward.

Data analysis

The data analysis was equivalent to those of Experiment 1 and 2 with 18.5% trials being excluded.

Results and discussion

Reaction times across all conditions ranged from 384 to 548 ms (Fig. 4a). Participants were faster to grasp with one hand than to switch to the unusual pointing task with the opposite hand ($F(1,17) = 12.68$, $p = 0.002$, $\eta^2 = 0.427$), and they were faster with 500 ms SOA than 20 ms SOA ($F(1,17) = 177.98$, $p < 0.001$, $\eta^2 = 0.913$). However, there was no evidence for asymmetrical switch costs (Task × Primed Hand interaction: $F(1,17) = 0.43$, $p = 0.519$; Task × Primed Hand × SOA interaction: $F(1,17) = 0.387$, $p = 0.542$; all other F tests: p's ≥ 0.299). Although Fig. 4a suggests that at 500 ms SOA, there was a trend for a greater switch cost when participants were primed with

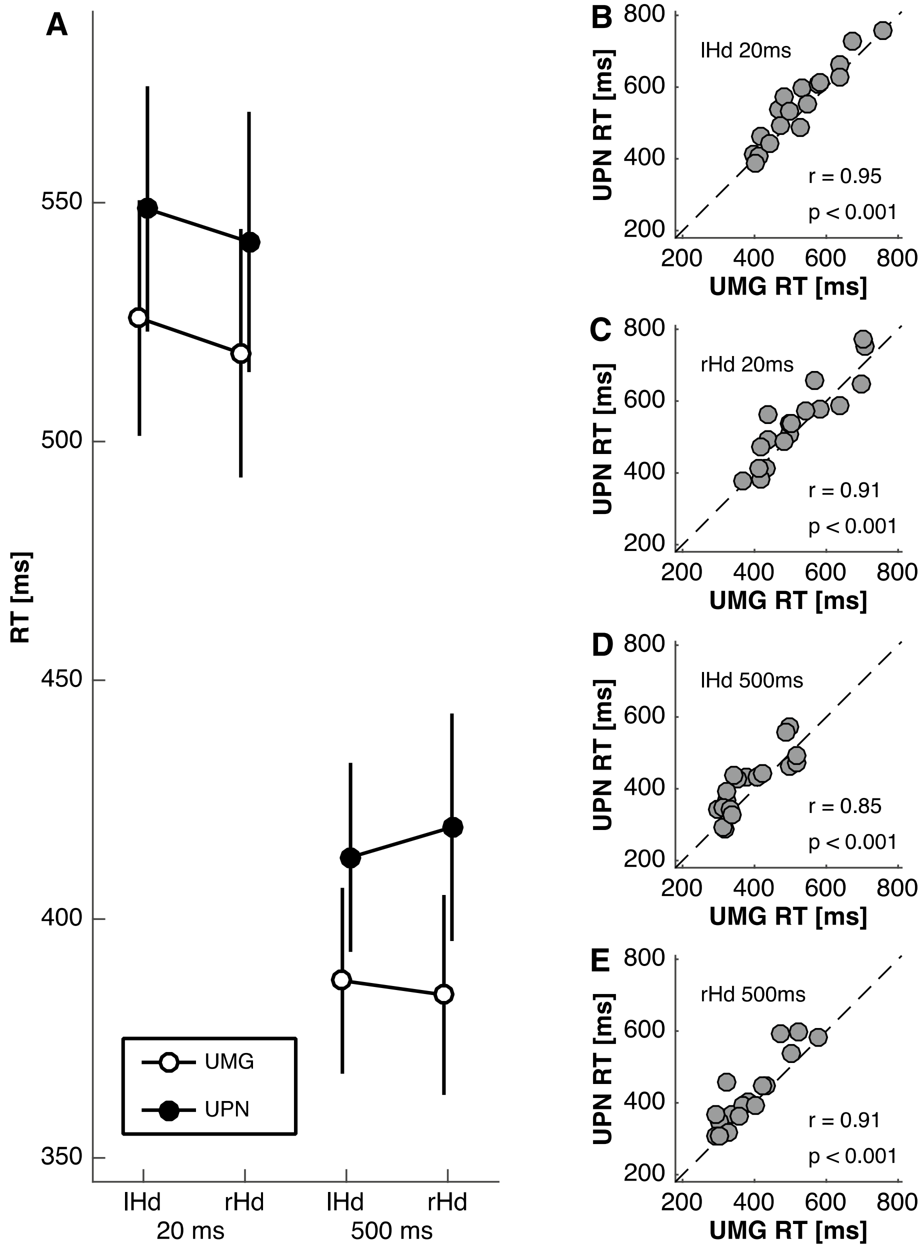


Fig. 4 Reaction times (RT) of the unimanual grasping and unusual pointing task. **a** Group-averaged reaction times plotted as a function of condition. Error bars represent standard errors. **b–e** Individual reaction times during the unusual pointing task plotted as a function of reaction times during the grasping task. *UMG* unimanual grasp, *UPN* unusual pointing with the respective opposite hand, *lHd* left-hand blocks, *rHd* right-hand blocks. 20 and 500 ms represent stimulus onset asynchronies

unimanual right-hand grasps, this trend was far from significant ($t(17) = 0.80$, $p = 0.44$).

Just like in Experiment 2, correlations between reactions times were high (Fig. 4b–e) but there was no systematic difference between left-hand blocks and right-hand blocks (confidence intervals of Fisher's *z* transformed correlation differences after 10,000 bootstrapping steps: $\mathrm{CI(z)}_{\mathrm{average}} = [-0.815, 0.576]$, $\mathrm{CI(z)}_{\mathrm{20ms\ SOA}} = [-0.143, 0.694]$, $\mathrm{CI(z)}_{\mathrm{500ms\ SOA}} = [-0.936, 0.193]$).

In sum, reaction times were slower for unusual pointing compared to unimanual grasping, which could be due to general switching- or priming-effects, or general longer reaction times for more unusual tasks. Either way, right-hand switches were not different from left-hand switches. These results are inconsistent with the asymmetrical switch costs from Experiment 1 and rules out the possibility that those results were merely due to 'novelty' effects.

Finally, for an omnibus analysis we compared correlations of primed and non-primed RTs across all experiments (Figs. 2b–e, 3b–e, and 4b–e). To this end, we calculated Fisher's *z* transformed correlations and averaged across SOAs (Fig. 5a). Next, we subtracted right-hand blocks from left-hand blocks and submitted the differences to linear contrasts. That is, we compared the difference in Experiment 1 with the averaged differences of Experiments 2 and 3, and we compared the difference in Experiment 2 with the difference in Experiment 3. Finally, we bootstrapped confidence intervals with 10,000 repetitions using a mixed design (i.e., within-subject comparisons for each experiment and between-subject comparisons across experiments). As shown in Fig. 5b, left-hand priming yielded significantly greater correlations in Experiment 1 compared to the other experiments, whereas there was no difference between Experiments 2 and 3.

General discussion

The aim of this study was to test grasp control in a dynamic task environment where the goal of the task remained the same but the execution of the movement changed. To this end, we used a visuomotor priming paradigm. Participants were primed to unimanually grasp an object using their right or left hand, and occasionally they would have to switch to a bimanual grasp. Switching from unimanual right-hand grasping to bimanual grasping resulted in significantly longer reaction times but switching from unimanual left-hand grasping to bimanual grasping did not. In addition, our control experiments found no equivalent lateralized switch costs when people switched to pointing or to an unusual pointing task. Further, reaction times during left hand and bimanual grasping were more similar than any other pair of actions.

Our results argue against the idea that the dominant left hemisphere assumes a general role of sensorimotor grasp goal representation in dynamic contexts. A special role of the left hemisphere could have been expected given that it is known to be dominantly involved in the observation of grasp actions (Shmuelof and Zohary 2005; Hamilton and Grafton 2006; Ramsey and Hamilton 2010; Southgate et al. 2014) and even plays a role in the control of left-hand grasps (e.g., Naito and Ehrsson 2006; Davare et al. 2007). Furthermore, for the sake of computational efficiency, it might make sense to restrict most visual and visuomotor-plan computations to one hemisphere to avoid re-computations of grasp goals or time-consuming transfer across hemispheres (Braun 1992; Ringo et al. 1994; Westerhausen et al. 2006). But if so, switching from right-hand to bimanual grasps should have delayed reaction times minimally. Instead, we observed significant delays that, at least for a stimulus onset asynchrony of 500 ms, were numerically nearly as big as the delays caused by switching effectors as well as sensorimotor goals in Experiments 2 and 3. What is more, the latter two

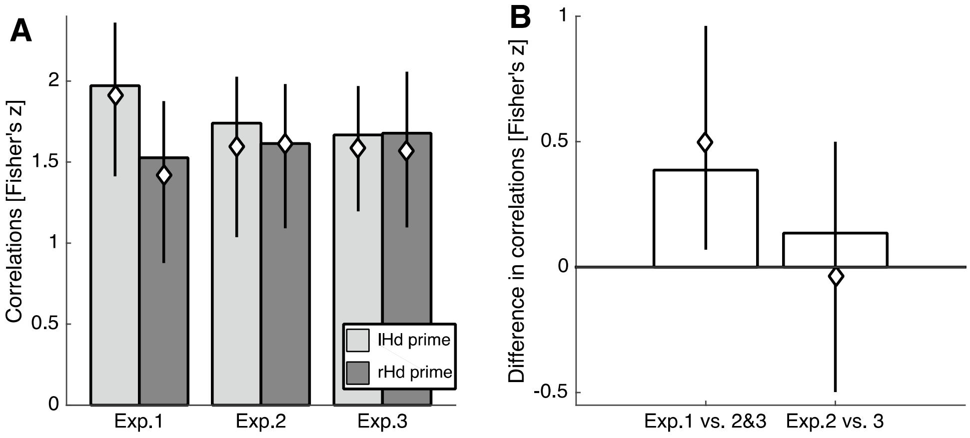


Fig. 5 Omnibus analysis. **a** Correlations between primed and non-primed RTs in left- and right-hand blocks across all three experiments. **b** Graphical depiction of bootstrapped confidence intervals of linear contrast results. Error bars that do not intersect with zero indicate significance. Bars: original Fisher's *z* transformed correlations; diamonds: bootstrapped medians of the *z* values; error bars: 95% confidence intervals after bootstrapping

experiments ruled out any simple explanations such as left-to-right interhemispheric inhibition between motor areas or delays caused by switching between usual and unusual tasks.

Of course, it could have been possible that switching from unimanual to bimanual grasping entailed entirely different sensorimotor processes. That is, bimanual grasping might constitute a form of grasping that is different from any form of unimanual grasping. Although previous TMS studies have suggested that bimanual grasp control is associated with parietal areas in the right hemisphere that are involved in the control of unimanual grasps (Le et al. 2014, 2017), the limitation of these studies is that TMS might stimulate several adjacent, but functionally unrelated, areas at once. But then switching from unimanual to bimanual grasping should have caused delays regardless of whether participants were primed to perform unimanual grasps with the left or right hand. In contrast, priming for left-hand grasps incurred nearly no switch costs at all and yielded high correlations in reaction times. Thus, our results add to the notion that bimanual visuomotor grasp control has important overlap with mechanisms underlying unimanual grasp control of the left hand consistent with earlier findings of a right-lateralization for bimanual grasping (Le and Niemeier 2013a, b; for further support for similarities between uni- and bimanual grasping see Ganel et al. 2017).

There are two potential limitations of our study. For one, it is possible that the asymmetrical switch costs in Experiment 1 arose from stronger left-to-right hemisphere inhibition on the level of goal representations, although to our knowledge such an asymmetry has not been reported. Evidence for asymmetrical inhibition does exist for the level of motor cortices (Duque et al. 2007). However, in Experiment 2, the contralateral hand made movements similar to those during bimanual grasp movements. Nevertheless, the experiment did not reproduce the asymmetrical switch costs of the first experiment.

Second, asymmetrical switch costs could be explained if bimanual coordination in general—rather than bimanual grasping specifically—shared fewer neural processes in the left hemisphere with right-hand grasping than resources in the right hemisphere with left-hand grasping. However, the contribution of the two hemispheres to bimanual control rather argues against such a notion. That is, hemisphere dominance depends on the form of bimanual coordination (for reviews Swinnen 2002, Swinnen and Wenderoth 2004). Specifically, coordination of parallel, asymmetric, or anti-phase movements involves structures in the right more than the left hemisphere (Sadato et al. 1997; Duque et al. 2009; Meister et al. 2010; Liuzzi et al. 2011). In contrast, a dominant role of the left hemisphere is found for the coordination of mirror or in-phase movements (Jäncke et al. 1998; Aramaki et al. 2006; Maki et al. 2008). At odds with this distinction, bimanual grasping (as a form of mirror movement) shows right-brain dominance (Le et al. 2014, 2017). It is not clear whether bimanual grasping differs from other forms of mirror coordination because the two hands share the same goal (see Duque et al. 2009; but see Liao et al. 2018 for the opposite conclusion). Further, we have previously examined bimanual grasping and bimanual pushing which both present the two hands with a common goal but we found only for the former task a left visual field preference (Le and Niemeier 2013a). In sum, asymmetrical switch costs as observed here are difficult to reconcile with current knowledge of hemisphere specialization of bimanual coordination. Moreover, the relationship between bimanual grasping and other forms of bimanual coordination remains unclear.

In conclusion, the results here rule out the possibility that the dominant left hemisphere serves a generalized role of maintaining sensorimotor grasp goal representations in dynamic task environments that afford sudden switches to bimanual action plans. Instead, we found that switching from left-hand to bimanual grasping came with little delay, consistent with shared neural structures in the right hemisphere, perhaps including the right aIPS, despite the fact that unimanual and bimanual grasps require substantially different forms of arm and finger motor control. Our results suggest that sensorimotor grasp goals are represented at intermediate levels of abstraction, downstream from cognitive representations of goals—yet upstream from control circuits for arm and finger movements.

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Author contributions A.L. and M.N. developed the study concept. All authors contributed to the study design. Data collection was performed by F.B.W., G.L., and R.A. Data analysis and interpretation were performed by A.L., under the supervision of M.N. A.L. drafted the paper, and all authors provided critical revisions. All authors approved the final version of the paper for submission.

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