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Independent on-line control of the two hands during bimanual reaching

Jörn Diedrichsen,[1,2] Rohit Nambisan,[1] Steve W. Kennerley[1,3] and Richard B. Ivry[1,4]
[1]Department of Psychology, University of California, Berkeley, USA
[2]Department of Biomedical Engineering, Johns Hopkins University, Baltimore, USA
[3]Department of Experimental Psychology, University of Oxford, Oxford, UK
[4]Helen Wills Neuroscience Institute, University of California, Berkeley, USA

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Abstract

Many studies on bimanual coordination have shown that people exhibit a preference for mirror-symmetric movements. We demonstrate that this constraint is absent when bimanual reaching movements are made to visual targets. We investigated the ability of humans to make on-line adjustments during such movements when one or both targets were displaced during the initial phase of the movements. Adjustments were as efficient during bimanual as unimanual movements, even when two adjustments had to be made simultaneously. When one target was displaced in the bimanual condition, the hand reaching to that target adjusted efficiently to the displacement. However, a small transient perturbation in the trajectory of the other hand was also observed. This perturbation was in the same direction as the displacement, rather than in mirror-symmetric direction. A control experiment demonstrated that these perturbations could be elicited by visual information alone, but that they were also influenced by whether an adjustment was required in the trajectory of the other hand. Our results demonstrate near independent control of the two arms during visually guided reaching. The subtle interference observed between the arms reflects interactions between target-related representations in visual coordinates rather than between movement-related representations in joint- or muscle-coordinates.

Introduction

Perhaps the most studied phenomenon in the bimanual coordination literature is the preference to produce mirror-symmetric trajectories (Kelso, 1995; Mechsner *et al*., 2001; Swinnen, 2002). For example, people have great difficulty producing simultaneously non-symmetric shapes such as a line and a circle (Franz, 1997). Furthermore, for a variety of repetitive movements, performance is more stable when the effectors move in a mirror-symmetric mode compared with when the movements follow the same direction in external space (asymmetric mode) (Kelso, 1984; Semjen *et al*., 1995).

While experimental studies are replete with examples of the preference for mirror-symmetric movements, this constraint is not obvious in everyday bimanual actions. For example, when simultaneously picking up a pen and a coffee cup, the two arms may follow very different trajectories and the hand shapes required to grasp the objects will differ. Nonetheless, our impression is that we can perform such tasks effortlessly.

One possible reason for the discrepancy between these everyday observations and the experimental literature is that most experimental tasks require movements that rely on internal guidance; for example the person might be instructed to produce target shapes from memory (e.g. draw circles or rotate the wrists). In contrast, most naturalistic actions are directed towards visible objects. We have shown that interference effects associated with the initiation of non-symmetric aiming movements are absent when the actions are directly cued by illuminating the target locations (Diedrichsen *et al*., 2001). This dissociation indicates that planning processes for visually guided aiming movements can occur in parallel for the two hands. However, most movements also require continuous monitoring and adjustments during execution. Similar to the planning processes that take place prior to movement initiation, these on-line control processes have been suggested to be a prominent source of bimanual interference (Spijkers & Heuer, 1995).

For unimanual movements, target displacement tasks have been used to study how people use visual information to adjust an on-going action. When a target stimulus is displaced during the initial phase of a reaching movement, an adjustment in the movement trajectory can be detected within 150 ms (Pelisson *et al*., 1986; Prablanc & Martin, 1992). Moreover, these adjustments can occur without awareness of the target displacement (Goodale *et al*., 1986) and sometimes occur involuntarily despite task instructions (Pisella *et al*., 2000). It is assumed that this corrective process also operates during reaching to stationary targets, providing a mechanism to minimize error that arises from noise associated with movement execution (Woodworth, 1899; Carlton, 1981; Desmurget & Grafton, 2000).

To date, it is unknown how people use visual information to control and adjust their actions during bimanual reaching movements. In the present report, we examine the responses to displaced targets under uni- and bimanual conditions. By comparing these conditions, we sought to determine if each hand is associated with an independent corrective process or whether adjustments during bimanual movements involve a common control process. The bimanual trials also provide a novel opportunity to assess the symmetry constraint during the correction of on-going movements.

Correspondence: Dr J. Diedrichsen, as above.[2]
E-mail: jdiedric@bme.jhu.edu

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Materials and methods

Subjects

Twelve participants (seven male, five female, ages 20–31 years) were recruited from the University of California, Berkeley community and consented to the experimental procedure. All participants were right-handed. The protocol was approved by the UC Berkeley Committee for the Protection of Human Subjects.

Apparatus and stimuli

A projection system was used to display virtual targets on a table surface. A LCD projector presented the stimuli onto a screen, which was mounted 48 cm above the table surface. Halfway between the screen and table was a mirror of the same size (100 × 70 cm). For participants looking down onto the mirror, the stimuli appeared to be located in front of them on the surface of the table.

Two unfilled white circles (2.4 cm diameter) were used to indicate the starting positions. Similar sized circles specified the target locations and were located 23 cm in front of the starting positions. Starting and target circles were presented 6 cm to the left and right of the midline. The targets could be displaced 3.5 cm to the left or right of the initial target position. A 3D movement recording system (Mini Bird, Ascension Technology, Burlington, VT, USA) was used to monitor the positions of the two hands. Small sensors (8 × 8 × 5 mm) were taped to the tip of each index finger providing an output signal of current position at a sampling rate of 140 Hz. In Experiment 1, two additional sensors were placed on the shoulders to monitor the orientation of the upper body, reducing the sampling rate to 70 Hz.

The mirror precluded vision of the hands. However, two small white dots (2 mm diameter) provided veridical information of the positions of the hands. The positions of these dots were updated at 60 Hz, with a delay of about 16 ms. The participants were unaware of this delay and had the impression that they were reaching directly across the table surface to the target circles with only the tips of their index fingers visible. Eye movements were recorded with an infrared eye tracker (sampling rate 60 Hz, 0.25 degree resolution, Model 504, Applied Science Laboratories, Bedford, MA, USA), with a remote camera pointed at the right eye of the participants through the mirror.

Experiment 1

In this experiment we tested on-line adjustments to target displacements during unimanual and bimanual reaching movements. One concern in a comparison of the uni- and bimanual conditions involves the role of eye movements: Eye and hand movements are closely coupled during unimanual reaches (Biguer *et al*., 1982; Neggers & Bekkering, 2000). During bimanual movements the eyes can fixate only on one of the targets at a time. To compare performance on bimanual and unimanual trials, we enforced fixation on a central non-target location for all conditions in the primary test blocks. At the end of the session, we also included four blocks of unimanual trials in which the participants were encouraged to saccade to the target. This allowed us to assess whether the on-line control of unimanual movements was affected by the constraint to maintain fixation.

Each trial began with the illumination of one (unimanual trials) or two (bimanual trials) starting circles (Fig. 1A). On unimanual trials, the participant placed one hand into the starting circle and rested the other hand near the edge of the table. On bimanual trials, the participant moved both hands into the starting circles. The participant was instructed to fixate on a cross positioned halfway between the locations where the two target circles would appear. The starting positions and fixation had to be maintained for 2–3 s; deviations from either restarted the inter-trial interval. Once these starting criteria were met, one (unimanual) or two (bimanual) targets appeared. The participants were instructed to move quickly, attempting to terminate their movement(s) within the target circle(s) while maintaining fixation on the centre cross. On 5% of the unimanual fixation and 1% of the bimanual trials, a saccade away from the fixation point was detected. These trials were excluded from further analysis.

Tangential velocity of the hand movements was calculated on-line. Target displacements were triggered when hand velocity exceeded 4 cm/s. Due to the refresh rate of the LCD projector, the maximal delay until target displacement was 16 ms. To avoid late corrective movements, the trial was terminated when the tangential velocity of both hands fell below 8 cm/s. The participants were then given feedback indicating whether the movement(s) terminated within the target circle(s).

The session began with four practice blocks of 16 trials each, in a fixed order of right unimanual, left unimanual and two bimanual blocks. Another round of practice blocks was included if the participants failed to achieve a mean movement time (MT) below 450 ms across the unimanual and bimanual trials. After reaching criterion, participants completed 10 test blocks, of 32 trials each. Fixation had to be maintained on the central cross during these blocks. Six blocks were bimanual and four were unimanual, with the order varied in a pseudo-random manner. Following these 10 blocks, four more unimanual blocks in the unimanual free-saccade condition were run. Here, the participants were instructed that fixation was no longer required and, in fact, that they should follow their natural tendency to saccade to the target location (and again, if the target was displaced). Each hand was tested on half of the unimanual blocks.

On unimanual blocks, the target remained stationary for half of the trials and was displaced, either to the left or right, on the other half of the trials. On bimanual blocks, each target was displaced on half of the trials: on eight trials both targets remained stationary, on 16 trials one of the targets moved, and on eight trials both targets moved. For the latter, the displacements were either in the same direction (asymmetric condition) or in opposite directions (symmetric condition). Equal numbers of displacements occurred for each hand and direction combination. These combinations of displacements gave rise to seven different movement conditions for each hand (Fig. 1B).

Because we were interested in performance difference in terms of endpoint error and adjustment speed following target displacements, we tried to keep the movements comparable in their kinematics. To ensure fast and relatively constant MTs across all conditions, participants were instructed to match their MTs to the performance on the last bimanual block during practice. After each block, feedback was provided indicating mean MT, the percentage of trials in which the movements terminated inside the targets, and the monetary bonus earned for that block. The bonus was designed to reward accuracy – provided participants were within ±50 ms of the target MT.

Experiment 2

In Experiment 2, we investigated the influence of distracting visual information on the on-line adjustments during unimanual and bimanual movements. In addition to a red circle marking the target position, a neighbouring distractor circle, outlined in green, was presented near each target. The targets were either 20 cm or 25 cm from the starting circles, with the distractor assigned to the other position. The positions were determined randomly for each side, resulting in four possible combinations of the target and distractor circles (i.e. both target locations close, both far, or one far and one close). The fixation cross was presented in the centre of the four circles at a distance of 22.5 cm from the starting circles, and fixation during each trial was monitored through eye movement recording. Target and distractor circles were

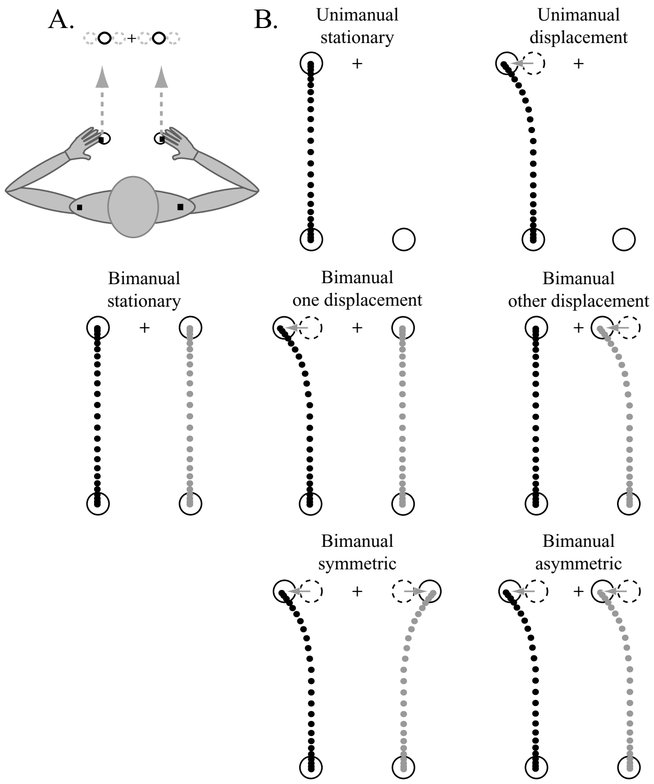

FIG. 1. Task and movement conditions in Experiment 1. (A) Participants placed their hands into the near circles to start each trial, and then fixated on the cross. At the appearance of the targets (black circles), they executed a unimanual or bimanual movement, reaching towards the target(s). As soon as the movement was initiated, one or both of the targets could be displaced to the left or the right (grey dotted circles). (B) Seven possible movement conditions for the left hand. In unimanual trials, the target could be either stationary (unimanual stationary) or displaced to either side (unimanual displacement). In bimanual trials, both targets could remain stationary (bimanual stationary), the left target could be displaced (bimanual one displacement) or the right target could be displaced (other displacement). When both targets were displaced, they could either jump in opposite directions (symmetric displacements) or in the same direction (asymmetric displacements). The movement conditions for the right hand are defined correspondingly. Thus, when the left hand executed a bimanual-one displacement movement, the right hand performed a bimanual-other displacement movement.

presented on both sides for uni- and bimanual trials. On bimanual blocks participants were instructed to reach to both target locations; on unimanual blocks they were instructed to reach for the target on the designated side and ignore the target on the other side. At movement onset, one of the four circles was displaced either to the left or to the right.

Data analysis

Kinematic and eye movement traces were resampled at 333 Hz and aligned to the moment of target displacement. For each movement we tested whether the target displacement occurred when the velocity exceeded 4 cm/s and stayed above this rate for at least 100 ms. Trials in which the displacement was triggered prematurely due to noise in the system or brief movements before true movement onset were excluded from further data analysis (approximately 1% of the trials in Experiments 1 and 2). Endpoint error was defined as the average distance between hand position at the end of the movement and the centre of the target circle.

To evaluate the manner in which on-going movements were adjusted, we focused on the analysis of lateral velocity, that is, movement orthogonal to the primary reach but parallel to the target (or distractor) displacements. We first calculated two average kinematic profiles: one for trials in which the target was displaced to the left and one for trials in which the target was displaced to the right. Onset of the adjustment was defined as the time point in which the lateral difference between the average profiles exceeded 2 cm/s for at least 45 ms. We also quantified the rapidity with which the adjustments were implemented by calculating the lateral spatial distance between the average position profiles to leftward and rightward displaced target 290 ms after the target displacement. Half this distance is reported in Tables 1 and 2, to indicate how much on average a movement adjusted relative to a movement to a stationary target. The 290 ms time point was chosen, because it corresponded to the peak velocity in the lateral direction in Experiment 1 and to the point in time at which perturbations were most pronounced for reaches to stationary targets when the other target (or distractor in Experiment 2) was displaced. Similar results were obtained when the analyses were repeated using various time points between 260 and 330 ms.

Results

Experiment 1

Unimanual fixation vs free-saccade condition

We first considered performance during unimanual trials with and without central fixation. As expected, a saccade towards the displaced target was detected on 90% of the trials in the free-saccade condition (Fig. 2B). The average time between the displacement of the target and the end of the saccade was 234 ms (SD = 20 ms). Participants were successful in maintaining fixation when required to do so (saccades detected on 5% of the fixation trials), but they were unable to move as fast as in the free-saccade condition (Table 1), $F_{1,11} = 6.25$, $P = 0.030$. Subjects also demonstrated a 12% increase in endpoint error when the target could not be fixated, $F_{1,11} = 16.44$, $P = 0.002$.

Consistent with previous results (Martin & Prablanc, 1991), movements to displaced targets took 15 ms longer than movements to stationary targets, $F_{1,11} = 41.0$, $P < 0.001$, and endpoint error increased, $F_{1,11} = 7.08$, $P = 0.02$. The cost in MT was partly due to the longer movement path required to reach the laterally shifted target, and was similar in the fixation and in the free-saccade condition.

We examined the kinematic traces to determine when the participants adjusted their movements. Figure 2C shows the velocity profiles perpendicular to the main movement direction, separated for trials requiring an adjustment for target displacements to the left or to the right. The onset time of the adjustment can be quantified as the time point at which the two kinematic profiles diverge. Consistent with previous studies (Prablanc & Martin, 1992), the adjustments were detectable in the kinematic traces at latencies under 200 ms (Table 1). Adjustments began on average 24 ms earlier in the free-saccade than in the fixation condition, $F_{1,11} = 18.94$, $P = 0.001$. To quantify how strong the initial adjustment was, we computed the spatial separation between average position traces for movements involving an adjustment and movements towards stationary targets. The results again indicated a larger adjustment (Table 1) when the participant was free to saccade to the target before and after displacement, $F_{1,11} = 57.77$, $P < 0.001$.

In summary, the requirement to maintain fixation on the central nontarget led to a significant increase in endpoint error and a delay in the onset of the adjustment to a displaced target. Although slightly delayed, the time course of the adjustments in the fixation condition was similar to that observed in a more naturalistic situation (free-saccade condition), and subjects could terminate their movements within the target in 65% of the trials even when central fixation was

TABLE 1. Kinematic measures for uni- and bimanual movements to stationary and displaced targets (Experiment 1)

	Stationary target				Displaced target				
	Unimanual movement		Bimanual movement		Unimanual movement		Bimanual movement		
	Free saccade	Fixation	Both stationary	Other displaced	Free saccade	Fixation	One target displacement	Symmetric displacement	Asymmetric displacement
Movement time (ms)									
Mean	393	421	410	412	409	436	422	428	422
(SD)	(56)	(73)	(63)	(64)	(54)	(67)	(60)	(64)	(62)
Endpoint error (cm)									
Mean	0.94	1.05	0.97	1.01	0.93	1.15	1.06	1.10	1.08
(SD)	(0.12)	(0.15)	(0.17)	(0.14)	(0.11)	(0.16)	(0.23)	(0.24)	(0.19)
Onset of adjustment (ms)									
Mean	–	–	–	–	153	178	173	177	175
(SD)	–	–	–	–	(6)	(18)	(11)	(12)	(14)
Spatial separation at 290 ms (cm)									
Mean	–	–	–	0.21	2.64	1.68	1.55	1.45	2.01
(SD)	–	–	–	(0.14)	(0.49)	(0.52)	(0.52)	(0.55)	(0.55)

Mean and (in parentheses) between-subject SD is reported. Movement times are measured from the moment of displacement until the hand moved slower than 8 cm/s. Endpoint error is calculated as the average distance from the movement endpoint to the centre of the target. The onset of adjustment refers to the interval from target displacement to the time at which there was a 2 cm/s difference in lateral velocity between trials involving inward and outward displacements. Spatial separation refers to the lateral distance of average position traces 290 ms after the displacement. [For simplicity, Table 1 presents the data collapsed over the left and the right hands. For completeness, hand was included as a factor in the ANOVAs. During unimanual trials, performance was slightly better with the dominant, right hand. Right-hand movements were 20 ms faster, $F_{1,11} = 8.69$, $P = 0.013$, endpoint error was reduced, $F_{1,11} = 6.86$, $P = 0.024$, and time of adjustment was earlier, $F_{1,11} = 8.042$, $P = 0.016$. However, unless specifically noted, the factor hand did not interact with the other variables.]

TABLE 2. Kinematic measures for unimanual and bimanual movements when either target or distractor circles are displaced (Experiment 2)

	Same-side target		Same-side distractor		Other-side target		Other-side distractor	
	Unimanual	Bimanual	Unimanual	Bimanual	Unimanual	Bimanual	Unimanual	Bimanual
Movement time (ms)								
Mean	420	417	400	398	396	400	397	398
(SD)	(56)	(52)	(53)	(57)	(55)	(57)	(53)	(57)
Endpoint error (cm)								
Mean	1.17	1.11	1.03	0.97	0.99	0.95	1.00	0.94
(SD)	(0.29)	(0.22)	(0.16)	(0.11)	(0.12)	(0.11)	(0.16)	(0.10)
Onset of adjustment (ms)								
Mean	198	198	197	194	–	209	211	–
(SD)	(21)	(21)	(25)	(30)	–	(20)	(24)	–
Spatial separation at 290 ms (cm)								
Mean	2.34	2.20	0.32	0.31	−0.02	0.14	0.11	0.06
(SD)	(0.58)	(0.55)	(0.14)	(0.17)	(0.09)	(0.12)	(0.16)	(0.11)

Mean and (in parentheses) between-subject SD is reported. For explanation of measures see Table 1.

maintained (compared with 75% when they were free to saccade to the target).

Independence of updating processes

We next compared trajectory adjustments between unimanual trials (with fixation) and bimanual trials. The latter consisted of three types of movements that required an on-line adjustment (Fig. 1B). In one condition, one target remained stationary and one target was displaced (bimanual-one condition). In the other two conditions, both targets were displaced – either in symmetric or asymmetric directions. Surprisingly, performance on bimanual trials was similar to, if not slightly better than, that observed on unimanual trials (Table 1). Movements were on average 11 ms faster in the bimanual conditions than in the unimanual condition, $t_{11} = 2.47$, $P = 0.03$. Similarly, the endpoint error was slightly lower in the bimanual conditions, although this effect only approached significance, $t_{11} = 1.97$, $P = 0.07$.

The time course of adjustments was similar in the unimanual, bimanual-one, bimanual-symmetric and asymmetric conditions (Fig. 2D). Most strikingly, the onset times of the movement adjustments following displacements did not differ across the four conditions, $F_{3,33} = 1.47$, $P = 0.239$. Although we found differences between the three bimanual conditions (see below), the size of the adjustment at 290 ms did not differ between the unimanual and bimanual conditions on average, $t_{11} < 1$.

In summary, the participants were able to adjust as proficiently to two target displacements during bimanual reaching as to one target displacement during unimanual reaching. This surprising ability is indicative of parallel updating processes for the two hands.

Interactions in allocentric coordinates

Although we failed to observe any general performance costs during bimanual reaching, we did observe subtle differences between the

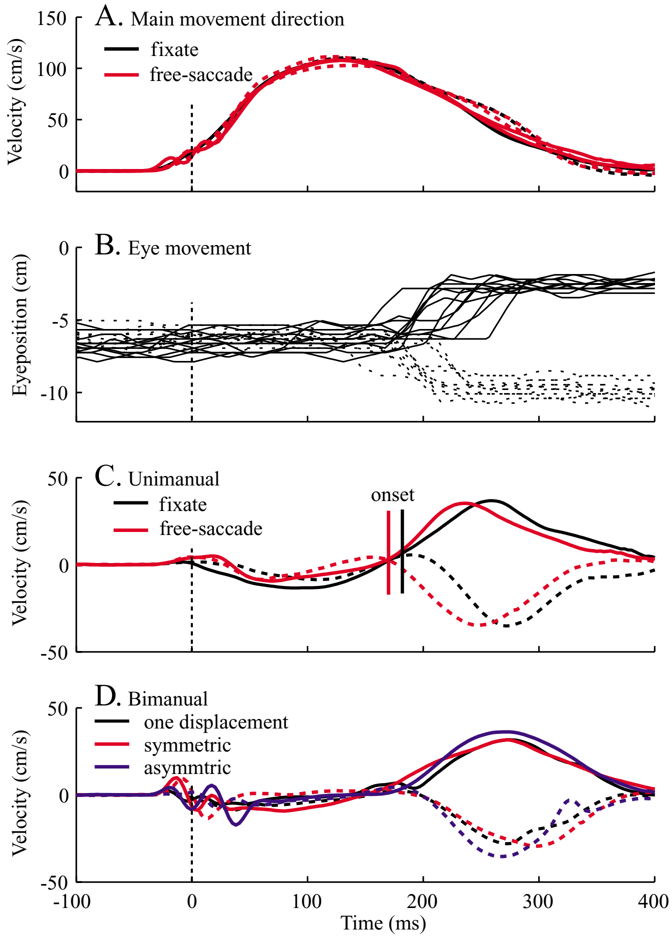

FIG. 2. Average hand-velocity traces for the left hand of one participant in Experiment 1. All traces were temporally aligned to the target displacement (0 ms). (A) Velocity in the main movement direction in unimanual fixate and free-saccade conditions. (B) Lateral eye position in the free-saccade condition. Initial fixation on the left target (−6 cm) was followed by an eye movement when the target was displaced to the right (solid) or left (dotted). Fixation was maintained on a central cross (0 cm, not shown) in the fixation condition. (C) Lateral velocity of the left hand when moving to a target displaced to the left (dotted) or right (solid). The onset of the adjustment in the free-saccade condition (red) was earlier than in the fixation condition (black). The initial negative lateral velocity corresponds to an outward curvature of the movement and can be observed across all conditions. (D) Lateral velocity in the three bimanual conditions. Adjustments followed a roughly equivalent time-course in all conditions.

bimanual conditions, indicative of interactions between the two hands (Table 1). While endpoint error did not differ, $F_{2,22} < 1$, movements were 6 ms slower in the symmetric condition than in the asymmetric condition and bimanual-one condition, $F_{2,22} = 4.60$, $P = 0.021$. Furthermore, the size of the adjustment (the lateral distance from non-adjustment trials 290 ms after target displacement, Table 1) was significantly larger in the asymmetric condition than in the symmetric or the bimanual-one displacement condition, $F_{2,22} = 39.14$, $P < 0.001$.

This finding is unexpected given that many theories of bimanual coupling emphasize on interactions that favour symmetrical movements with respect to the body midline. Swinnen *et al.* (1997, 1998) refers to this constraint as egocentric (a bias for movements to be mirror-symmetric), in contrast to an allocentric constraint (bias for the movements to follow the same direction in external space). They showed that, although both constraints can be observed in the same task, the egocentric constraint dictated interference in cyclical bimanual line drawing movements (Swinnen *et al.*, 2002). In contrast, in our visually guided reaching task, performance was consistently better when the targets were displaced in the same direction in external space.

Further evidence that the interactions in this task occur in allocentric coordinates comes from an effect observed in the bimanual-one condition. On these trials, one hand reached to a displaced target; the other hand reached to a stationary target. We refer to the latter movement as 'bimanual-other' to emphasize that it is the other hand's trajectory that required an adjustment following a target displacement (Fig. 1B). Optimal performance for the bimanual-other movement would involve a straight path trajectory to the stationary target. However, the results indicated that the trajectory for this hand consistently showed a slight perturbation (Fig. 3) and this perturbation was in the same direction as the target displacement for the other hand. For example, if the target for the right hand movement was displaced outward, the reaching movement of the left hand to a stationary target was briefly perturbed inward. This perturbation was corrected quickly with the direction of the lateral movement reversing within 100 ms, ensuring that the movement ended near the stationary target. To quantify the strength of the perturbation, we computed the lateral spatial separation in between the trajectories at 290 ms. As a baseline we used the lateral deviation from trials in which both targets remained stationary. The mean perturbation for the trajectory towards a stationary target was 0.21 cm, and the deviation was in the same direction as the target displacement (and movement adjustment) for the other

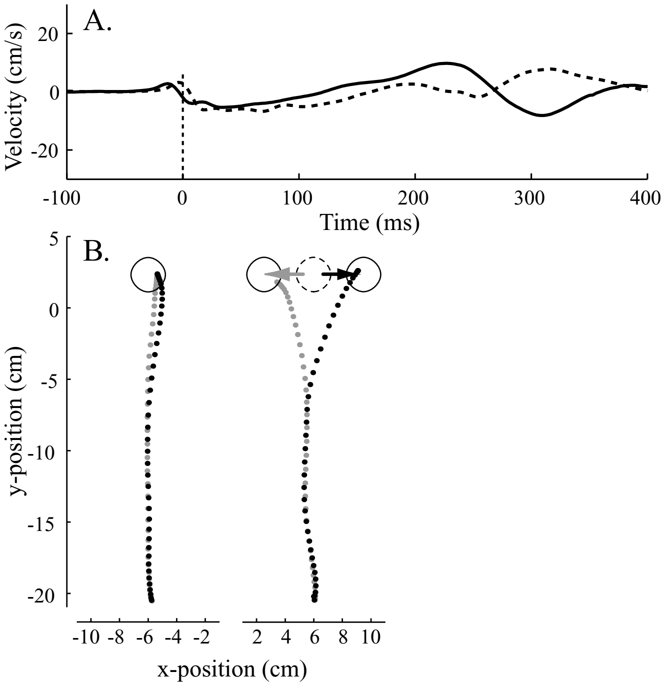

FIG. 3. A transient perturbation of the left-hand trajectory when the right hand adjusted for a target displacement. (A) Lateral velocity when the left hand moved to a stationary target while the right hand moved to a displaced target. A rightward adjustment of the right-hand movement produced an initial rightward perturbation of the left-hand trajectory (positive velocity, solid), followed by a correction that ensured that the movement terminated near the stationary target. Leftward displacement of the right-hand target produced an initial leftward perturbation of the left-hand trajectory (dotted). (B) Average position traces for the velocity data shown in (A). The right target was displaced either to the left (grey trace) or to the right (black trace). The left target remained stationary. While the right hand trajectory showed an adjusted for the target displacement, a transient perturbation was observed in the left-hand trajectory. This perturbation is in the same direction as the right target displacement (and movement adjustment), with direction defined in terms of allocentric coordinates.

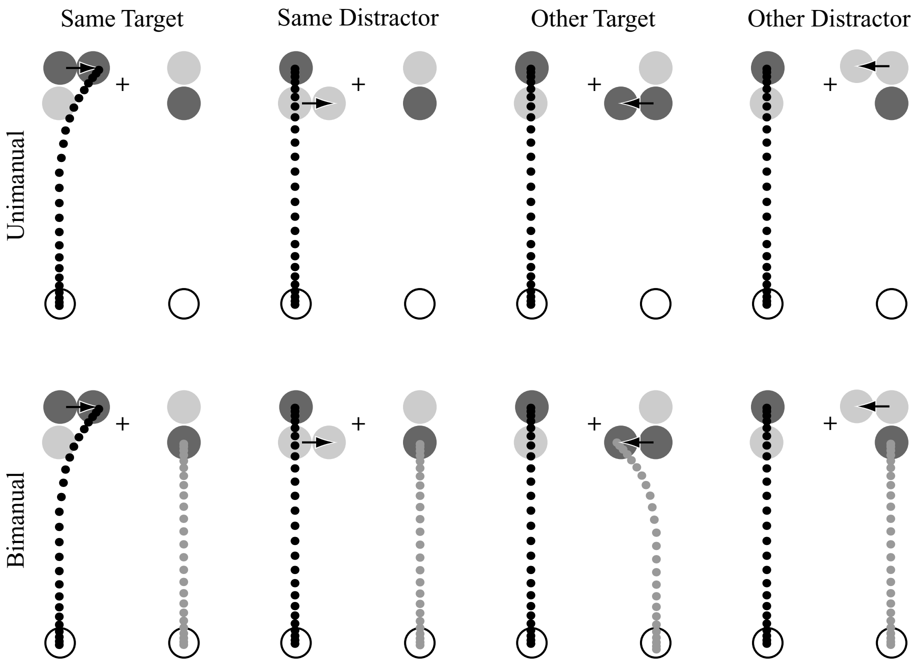

FIG. 4. Movement conditions for the left hand in Experiment 2. Red circles signified target locations (shown as dark grey disks), although no movement was required of the right hand on unimanual trials. Each target was accompanied by a green distractor (shown as light grey disks), presented either above or below the target. One of the four objects could be displaced, creating four conditions: the target of the movement (same target), the neighbouring distractor (same distractor), the target on the opposite side (other target) and the distractor on the opposite side (other distractor). Fixation was always on the central fixation cross. Conditions for the right hand were defined correspondingly.

hand, $t_{11} = 4.83$, $P = 0.001$. Although this perturbation was rather small and did not increase endpoint error, it was observed in 22 out of the 24 tested hands. Furthermore, we have replicated this effect in other studies with a different set of participants (Nambisan *et al.*, 2002).

We considered the hypothesis that the perturbation of the straight movement might be due to biomechanical factors. When a target is displaced, a rapid adjustment is made by the arm reaching towards that target. This adjustment might produce a slight rotation or lateral shift of the participant's trunk, resulting in a perturbation of the other hand in the same direction as the adjustment. To assess rotation and shift of the trunk, recording markers were placed on the shoulders of each participant (Fig. 1A). Contrary to the biomechanical hypothesis, on trials in which only one target was displaced, the trunk rotated in the opposite direction by 0.19 degrees, $t_{11} = 1.82$, $P = 0.09$, and shifted in the opposite direction by 0.11 cm, $t_{11} = 2.88$, $P = 0.013$. Thus, when the right hand responded to a displacement in the outward direction, the trunk rotated slightly counterclockwise and shifted to the left. This effect occurred simultaneously with the adjustment (between 190 and 290 ms) and was likely induced by interaction torques arising from the acceleration of the adjusting hand (Bastian *et al.*, 1996). If the other arm is modelled as a passive two-joint pendulum, these effects would be expected to create a perturbation of the hand in a mirror-symmetric direction. [We also assessed whether the difference between symmetric and asymmetric trials could be explained by shoulder rotation. While the torques generated by the two arm movements were balanced in the symmetric condition, we did observe a small, initial rotation against the direction of the adjustment in the asymmetric condition, followed later (after 320 ms) by a rotation in the direction of the adjustment (peaking at about 1 degree in the end of the trial). Based on this, we would have expected a cost on asymmetric trials in the early phase of the adjustment, because the arms would have had to compensate for the trunk rotation. The opposite was observed.] Thus, we conclude that the observed perturbations can not be accounted for by biomechanical influences and must rather be caused by a transient alteration of the motor command to the arm reaching toward the stationary target.

Experiment 1 summary

The participants were able to make simultaneous on-line adjustments when reaching for two separate targets. Endpoint error on trials in which both targets were displaced was similar to that found on trials in which only one target was displaced (either uni- or bimanual trials), and the timing of the adjustments was similar across all conditions. Despite an overall picture of parallel control, there were subtle interactions between the two movements on bimanual trials. These interactions led to coupling between the hands in terms of allocentric rather than egocentric, mirror-symmetric coordinates. Given that these interactions can not be explained by eye movements or biomechanical factors, we explore their source in the second experiment.

Experiment 2

Intermanual interactions in Experiment 1 were observed in allocentric coordinates, with the clearest demonstration occurring on bimanual trials in which only one target was displaced. In addition to the (appropriate) adjustment of the trajectory produced by the hand reaching towards the displaced target, there was a transient deviation in the same direction by the hand moving towards a stationary target. One hypothesis is that this perturbation results from interactions at a perceptual level. The displacement of the target generates a fast visual motion signal (Schmolesky *et al.*, 1998). This signal might be projected to both updating systems, causing an initial perturbation in the direction of the displaced target. The transient signal would be quickly offset by the persistence of the stationary target, allowing the updating process to re-adjust the trajectory so to terminate the movement at the appropriate location. We will refer to this idea as the 'perceptual-leakage' hypothesis to capture the idea that the salient visual displacement broadcasts to both updating systems. In the strongest form, the hypothesis predicts that transient motion signals cause a perturbation, regardless of the task relevance of the moving stimulus.

Alternatively the interaction could occur at later stages of processing. For example, the generation of a movement command 'Move Right' following a displacement of one target to the right might have a transient influence on both updating systems, similar to the way cross-talk was assumed to occur in the perceptual-leakage model. Here, the interactions occur between spatial representations guiding the movements (Heuer, 1993; Spijkers & Heuer, 1995; Heuer *et al*., 2001) rather than between purely perceptual representations. As noted in the Introduction, interference between signals involved in movement planning and execution have generally been assumed to cause a bias towards mirror-symmetric movements (see Heuer, 1993; Heuer *et al*., 2001; Cardoso de Oliveira, 2002). However, it is possible that visually guided movements are parameterized and planned in terms of visual rather than joint coordinates, which would give rise to an allocentric constraint.

Experiment 2 was designed to directly test the perceptual-leakage hypothesis. Two objects appeared on each side of fixation: a red target and a green distractor (Fig. 4). Either object could be displaced once the movement was initiated. If transient movement perturbations result from visual motion signals, it should be possible to induce such perturbations by the displacement of the distractor. This perturbation may be observed in the trajectory of the hand moving to the stationary target on the same side as the distractor (same-distractor condition). Moreover, a perturbation to a trajectory would be expected when a target or distractor on the other side was displaced (other-distractor and other-target conditions). Because fixation was always on the centre location, the unimanual and bimanual trials were perceptually very similar. Thus, perceptual leakage should even be evident on unimanual trials. Alternatively, if the perturbation reflects interactions at the level of response planning and execution, they should only be evident when the other hand adjusts to a target displacement, i.e. in the bimanual-other-target condition.

Unimanual vs bimanual

Restricting the analysis to data from trials in which fixation was maintained (97% of the trials), participants successfully matched MTs between the unimanual and bimanual conditions (Table 2), $F_{1,11} < 1$, and terminated the movements with equal endpoint error, $F_{1,11} = 2.24$, $P = 0.163$. The onset of the adjustment when moving to a displaced target (Fig. 5A) was slightly later than in Experiment 1. The presence of distractor circles and the fact that only one-quarter of the movements actually demanded an on-line adjustment (compared with half in Experiment 1) may be responsible for this difference. The onset of the adjustment was similar for unimanual and bimanual trials, $F_{1,11} < 1$, and the spatial separation at 290 ms was statistically equivalent, $F_{1,11} = 2.19$, $P = 0.166$. Thus, the results replicated the primary finding of Experiment 1, showing similar updating during uni- and bimanual reaches. [Again, the results are averaged across hands. The right hand moved 25 ms faster than the left in unimanual trials, but only 7 ms faster in bimanual trials, yielding a significant effect of hand, $F_{1,11} = 5.13$, $P = 0.045$, and hand × hand condition (unimanual vs bimanual) interaction, $F_{1,11} = 7.159$, $P = 0.022$. No significant differences between the hands, or interactions involving the hand factor were observed for spatial error or onset of adjustment.]

Perceptual-leakage vs movement-planning hypothesis

When reaching for a displaced target, MT increased by 20 ms, $F_{3,33} = 58.08$, $P < 0.001$, and endpoint error increased by 16% (Table 2), $F_{3,33} = 9.34$, $P < 0.001$. No significant differences between the remaining conditions was found, neither in the MTs, $F_{2,22} < 1$, nor in endpoint error, $F_{2,22} = 1.11$, $P = 0.346$.

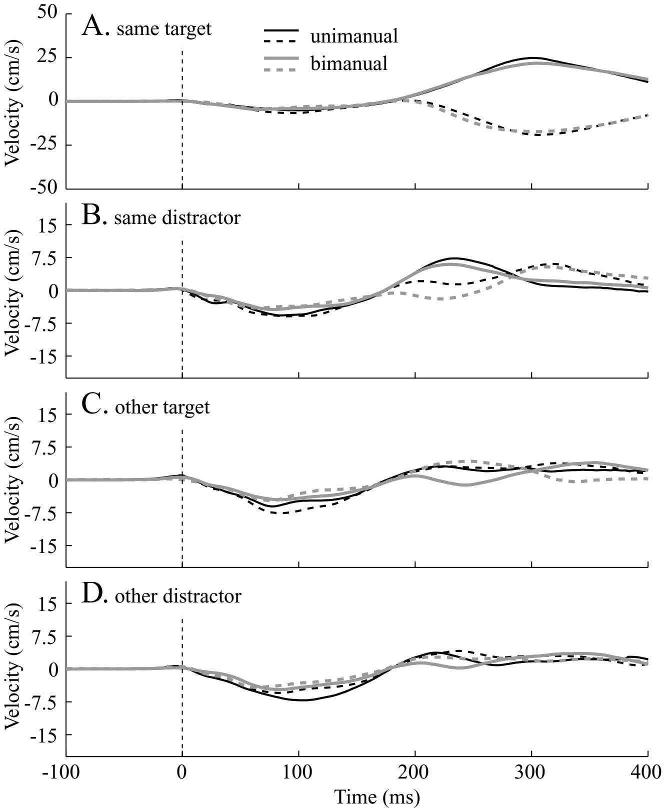

FIG. 5. Lateral velocity profiles for the left hand averaged over all participants in Experiment 2. (A) Rapid adjustments are visible when reaching to a displaced target, and these are comparable for unimanual (black) and bimanual (grey) trials. Solid traces indicate average lateral velocity when the target was displaced to the right and dotted traces when the target was displaced to the left. (B) When a neighbouring distractor was displaced, a perturbation in the direction of the displacement became evident about 200 ms after the displacement. This perturbation was corrected by the reversal of the lateral movement component (observe different scale than in A). (C) When the other target was displaced, a perturbation, again in the same direction as the displacement, was observed on bimanual trials. (D) A slight perturbation was observed when the other distractor was displaced.

In support of the perceptual-leakage hypothesis, we found transient perturbations of movements directed to a stationary target when the neighbouring distractor was displaced (Fig. 5B). The onset of this perturbation was as early as the onset of the adjustment when the target itself was displaced, $F_{1,11} = 2.51$, $P = 0.144$. Using the time window of 290 ms, the perturbation induced a spatial separation of 0.63 cm between the mean trajectories when the distractor was displaced to the right and when it was displaced to the left. Thus, the average size of the involuntary adjustment to either side was 0.32 cm – a highly significant perturbation both for unimanual, $t_{11} = 7.89$, $P < 0.001$, and for bimanual movements, $t_{11} = 6.24$, $P < 0.001$.

Interestingly, the timing and magnitude of the perturbation was similar in the unimanual and bimanual conditions; a direct comparison yielded no significant differences (both $t < 1$). Given our use of a blocked design, it was reasonable to expect participants to have attended to one side on the unimanual trials. This might have led them to be more adept in ignoring the irrelevant distractor. Instead, the results suggest that the perturbation reflects the operation of a preattentive updating process (Day & Lyon, 2000; Pisella *et al*., 2000).

The results of the other-target condition provide evidence for the movement-planning hypothesis. On bimanual trials, a perturbation was again observed (Fig. 5C). Similar to what was found in Experiment 1, the perturbation was 0.14 cm in the direction of the displaced target at 290 ms, $t_{11} = 4.16$, $P = 0.001$. However, the perturbation was not present in the unimanual condition, $t_{11} < 1$: the trajectory in reaching for a stationary target on unimanual trials was not perturbed when the 'target' on the other side was displaced. These results indicate that the perceptual-leakage hypothesis can not provide a complete account for the intermanual interactions. However, in favour of the perceptual-leakage hypothesis, we observed a small but significant perturbation when the distractor on the other side was displaced (Fig. 5D, Table 2), $t_{11} = 2.77$, $P = 0.018$, averaged over uni- and bimanual conditions.

Experiment 2 summary

The results indicate that interference may occur between both perceptual and action-related representations. When reaching for a stationary target, perturbations were observed when the neighbouring distractor was displaced and, although much smaller, when the distractor on the other side was displaced. This finding argues that interference can occur when the other hand is moving to a stationary target or even when the other hand is not moving at all. It would appear that these perturbations result from the visual movement of the distractors, consistent with the perceptual-leakage hypothesis. However, the perturbation in reaching toward a stationary object was strongest when the other arm was reaching toward a displaced target. This result suggests that interactions also occur between action-related representations. As in Experiment 1, all interactions were defined in an allocentric frame of reference.

Discussion

The present experiments demonstrate the efficiency of the human visuo-motor system in simultaneously controlling and adjusting two reaching movements. On measures of speed and endpoint accuracy, performance was comparable on conditions in which a single hand was used to reach to one target location or two hands were used to simultaneously reach to two target locations. The lack of a notable disruption to performance during bimanual reaching is especially striking in that the participants were able to readily modify movement trajectories, regardless of whether one or both targets were displaced. While much of the bimanual coordination literature has focused on interactions that constrain performance (e.g.Sherwood, 1994; Semjen *et al*., 1995; Spijkers & Heuer, 1995), these results are in accord with our starting observation that people do not find it difficult to reach for two different objects simultaneously.

The current experiments provide a first demonstration of parallel on-line control of two visually guided movements. While this skill did not seem to change critically with practice in this experiment, visually guided reaching movements are themselves highly practised and our findings emphasize the automaticity of the neural systems underlying this behaviour (Pisella *et al*., 2000; Glover, 2004). The efficiency with which the participants made the adjustments on bimanual trials argues for independent controllers rather than a dependency on shared resources such as a single updating process or a general attentional resource.

One limitation, however, is specific to bimanual reaching: whereas people typically look at the target location for a reaching movement (Biguer *et al*., 1982; Neggers & Bekkering, 2000), it is not possible to simultaneously fixate two objects. In fact, we did find that the speed and efficiency with which participants made on-line adjustments decreased when fixation at a non-target location was required compared with when they were free to move their eyes. However, overt eye movements are not a necessary condition for fast on-line adjustments; accuracy remained very high with only a slight delay in the onset of the adjustment, even when central fixation had to be maintained.

Despite the overall proficiency and independence of parallel adjustments, we found some subtle signs of interference between the actions of the two hands. In contrast to an extensive literature on the preference of the human motor system for mirror-symmetric movements (Kelso *et al*., 1979; Turvey *et al*., 1986; Swinnen, 2002; Swinnen *et al*., 2002), or movements that have real or anticipated mirror-symmetric perceptual consequences (Mechsner *et al*., 2001), the present study shows a preference for movement adjustments in the same direction in allocentric coordinates. When only one target was displaced, the trajectory of the hand reaching for the stationary target exhibited a transient perturbation in the same direction as the displacement. Furthermore, adjustments were faster and more accurate when the two targets were displaced in the same direction than in mirror-symmetric directions. These findings indicate that interference between the two hands during visually guided reaching movements leads to a allocentric rather than egocentric constraint (Swinnen *et al*., 1997). Consistent with these findings, Bogaerts *et al*. (2003) recently reported that isodirectional, but not mirror-symmetric, visual feedback stabilizes alternating hand movements.

What then is the nature of the neural codes that underlie bimanual interference in allocentric coordinates? Experiment 2 demonstrated that reaching movements to stationary targets can be perturbed by the displacement of a neighbouring distractor. These perturbations were again transient; a reversal of direction was observed within 100 ms of the perturbation onset, and the end points of the reaching movements were as accurate as on trials without perturbation. This finding is consistent with other studies demonstrating the influence of unrelated visual motion signals on ongoing reaching movements (Day & Lyon, 2000; Pisella *et al*., 2000; Whitney *et al*., 2003), and indicates that the spatial representations guiding these movements are easily influenced by visual input.

Nonetheless, our results indicate that a perceptual-leakage hypothesis does not provide a complete account of the intermanual interference effects. A pronounced perturbation of the trajectory to a stationary target occurred when the other hand was required to adjust to the displacement of its target. If that 'target' was displaced on unimanual trials, no perturbation was observed. Because central visual fixation was enforced in both conditions, the visual information was identical in the uni- and bimanual trials. [It is possible that the lack of a perturbation on the unimanual trials reflects a change in the focus of attention. On unimanual trials, the participants could covertly focus attention on the task-relevant side, thus attenuating the effect of stimulus information from the task-irrelevant side. While this hypothesis warrants further exploration, it would also suggest that we should have observed a difference between the unimanual and bimanual conditions on trials in which a neighbouring distractor was displaced.] Thus, interference might occur between visually driven neural codes that represent potential targets of reaching movements, as found in dorsal premotor cortex (Cisek & Kalaska, 2002) or area 5 of the parietal cortex (Andersen *et al*., 1985; Lacquaniti *et al*., 1995).

We propose a fundamental difference exists between interference effects observed during simple, visually guided, reaching movements and more complex internally guided movements. Movements planned and controlled without strong visual guidance are hypothesized to require greater involvement of the supplementary motor area (SMA) (Goldberg, 1985; Shima & Tanji, 1998; Debaere *et al*., 2003). Neural interactions between the two halves of the SMA are likely to be much more pronounced than between areas involved in visually guided reaching movements, consistent with the high density of transcallosal connections in the SMA (Rouiller *et al*., 1994). Furthermore, we hypothesize that interactions between the two halves of the SMA may be manifest in joint centred or egocentric coordinates, accounting for the strong egocentric constraint observed during complex coordinative behaviours like circle drawing (Carson, 1995; Semjen *et al*., 1995). In favour of this view, SMA activation is elevated during the production of asymmetric movements compared with symmetric movements (Jäncke *et al*., 1998, 2000; Debaere *et al*., 2001; Tracy *et al*., 2001). Furthermore, transcranial magnetic stimulation of the SMA disrupts the timing of asymmetric movements (Serrien *et al*., 2002; Steyvers *et al*., 2003) or induces phase transitions towards the more stable symmetric mode of coordination (Meyer-Lindenberg *et al*., 2002).

In contrast, the functional contribution of the SMA to simple visually guided reaching movements may be minimal (Shima & Tanji, 1998). Such movements have been associated with a distributed network of cortical areas including posterior parietal cortex (Desmurget *et al*., 1999; Pisella *et al*., 2000) and dorsal premotor cortex (Debaere *et al*., 2003). This may preclude strong interference associated with joint-centred coordinates. In the posterior parietal cortex, targets of reaching movements are represented in gaze-centred coordinates (Medendorp & Crawford, 2002). Because these representations are also used to guide eye movements (Medendorp *et al*., 2003), interactions between these visual representations would most likely cause interactions in allocentric rather than joint coordinates.

Our current results add to the recent literature demonstrating that visual (Swinnen *et al*., 1993; Mechsner *et al*., 2001) and haptic (Kelso *et al*., 2001) information can greatly attenuate the costs associated with asymmetric bimanual movements. Furthermore, the tendency towards spatially symmetric movements is greatly attenuated or abolished after callosotomy (Franz *et al*., 1996; Serrien *et al*., 2001; Kennerley *et al*., 2002; Diedrichsen *et al*., 2003). Taken together, these results indicate that the tendency to symmetry does not reflect constraints arising from hard-wired features of the motor pathways such as the interaction of crossed and uncrossed cortico-spinal projections (Cattaert *et al*., 1999). Rather, bimanual constraints may reflect inter-cortical interactions between neural codes that represent actions at an abstract level and are influenced by perceptual information.

The present results provide a demonstration that the tendency towards mirror-symmetric movements can be overridden, with people exhibiting a bias to move the limbs in the same spatial direction. We propose that bimanual movements planned in absence of an external spatial movement goal expose a strong mirror-symmetric bias because of their reliance on shared representations, and these representations tend to be based on egocentric reference frames. Visually guided movements, in contrast, exhibit a much higher degree of independence and the subtle interactions occur in a reference frame in allocentric coordinates.

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Abbreviations

MT, movement time; SMA, supplementary motor area.

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