Generalization of Visuomotor Learning Between Bilateral and Unilateral Conditions

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Wang J, Sainburg RL. Generalization of visuomotor learning between bilateral and unilateral conditions. J Neurophysiol 102: 2790–2799, 2009. First published September 16, 2009; doi:10.1152/jn.00444.2009. A long history of behavioral and physiological research has suggested that bilateral coordination invokes unique neural processes that are not involved in unilateral movements. This hypothesis predicts that motor learning should show limited transfer between unilateral and bilateral conditions, which is consistent with a recent finding that indicated partial, but not complete, transfer of learning between the two conditions. However, during learning of new motor skills, transformations must also be made between visual and proprioceptive coordinate systems, a process that may occur upstream to the processes that differentiate bilateral from unilateral movements. We now investigate whether visuomotor adaptations are shared between unilateral and bilateral movement conditions. Our results indicate substantial transfer from bilateral to subsequent unilateral conditions for both arms. Interestingly, whereas the nondominant arm never showed complete adaptation to visual rotation under bilateral conditions, this interference, or lack of improvement, in bilateral performance did not disturb the visuomotor adaptation process or transfer, as reflected by superb unilateral performances immediately following the bilateral conditions. These findings unambiguously indicate that visuomotor adaptation can extensively generalize between bilateral and unilateral conditions, thus suggesting a substantial overlap in the neural processes underlying visuomotor transformations between the two movement conditions. Our findings provide support for a two-stage model of motor planning, in which the visuomotor transformation process precedes the processes that convert the visuomotor plan into effectorspecific commands that incorporate bilateral synergies and that result in the forces that determine motion.

INTRODUCTION

The idea that bilateral movements recruit unique neural processes has been supported not only by previous behavioral research (Kelso 1979; Swinnen 2002; Wiesendanger and Serrien 2004), but also by lesion (Brinkman 1981, 1984) and imaging studies (Donchin et al. 2002; Sadato et al. 1997; Toyokura et al. 1999). However, the nature of these processes remains largely unknown. For example, such processes might simply synchronize the individual movements of each limb, recruiting the same neural circuitry as that of unilateral movements. This hypothesis leads to a prediction that motor learning should transfer between unilateral and bilateral movements. Alternatively, the motor control system might recruit the neural processes that are unique to bilateral movements, which would predict substantially limited transfer between unilateral and bilateral conditions. This latter hypothesis is partly supported by a recent finding reported by Nozaki and colleagues (2006), which indicated partial, but not complete, transfer of learning between these movement conditions when subjects adapted to novel dynamic conditions. Based on their findings, the authors suggested that bilateral movements might recruit circuits that do not simply act to synchronize the controllers for each limb. Instead, they argued that bilateral movement conditions might recruit synergies that are unique to control of the two arms together. However, the extent of transfer shown in the study by Nozaki et al. appears to be >50%, which leaves a question of whether it can be considered a strong piece of evidence to support the idea of unique neural circuits involved in bilateral movements. This calls for further investigation of the nature of such bilateral control processes.

It is plausible that the pattern of generalization between bilateral and unilateral conditions may differ, depending on the nature of sensorimotor transformations involved in a given motor task. In fact, we have hypothesized that transformations between visual and proprioceptive coordinates, or visuomotor transformations, occur upstream in the planning process to the mechanisms that underlie adaptation to novel dynamic conditions. Previous research has suggested that these two processes may be subserved by unique neural mechanisms. Whereas some investigators suggested that visuomotor and dynamic adaptations are subserved by distinct neural mechanisms (Krakauer et al. 1999), others argued that they are not independently represented in the nervous system (Tong et al. 2002). However, previous findings from our laboratory (Sainburg and Wang 2002; Wang and Sainburg 2004) showed that the direction of information transfer across the arms depends on the nature of the underlying sensorimotor transform. Specifically, adaptation to novel visuomotor rotations shows different patterns of transfer than adaptation to novel dynamic conditions. Other research has shown that when visual and proprioceptive information about the initial limb configuration is dissociated prior to movement, subjects rely more heavily on visual information to plan the direction and distance of hand motion and on proprioceptive information to transform this plan into the commands associated with the forces required to carry out the motion (Bagesteiro et al. 2006; Lateiner and Sainburg 2003; Sober and Sabes 2003, 2005). These findings collectively indicate that the nature of sensorimotor transformations involved in a given task plays an important role in determining the pattern of generalization across movement conditions and that the extent of generalization between unilateral and bilateral movements may depend on the nature of the sensorimotor transformation in question as well.

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These above-cited findings also lead to the idea that recruitment of bilateral synergies might occur downstream to control processes associated with visuomotor transformations. It is generally thought that visuomotor transformations occur upstream to dynamic transformations, during which the neural commands associated with the forces required to carry out a motion are specified (Ghez et al. 1991; Kawato et al. 1988; Sainburg 2002). Because of this, it is plausible that the selection of effectors used for either a unilateral or a bilateral task may occur during the dynamic transformation process, whereas the visuomotor transformation process involved in these tasks may be independent of these effectors. If this were the case, generalization of visuomotor adaptation between two different effectors (e.g., unilateral vs. bilateral movements) might be substantially greater than that of dynamic adaptation. Therefore we now investigate the pattern of generalization between bilateral and unilateral reaching movements following adaptation to a novel visuomotor condition. Findings from three experiments in the present study reveal substantial transfer from bilateral to unilateral conditions.

METHODS

Subjects

Subjects were 24 neurologically intact right-handed adults (14 female, 10 male), ranging in age from 18 to 28 yr. Handedness of the subjects was determined using the Edinburgh Handedness Inventory. They were recruited from the university community and were paid for their participation. Informed consent was obtained prior to participation.

Apparatus

Subjects sat facing a table with both arms supported over a horizontal surface, positioned just below shoulder height, by a frictionless air-jet system (Fig. 1A). A start circle, target, and cursor representing the index finger position were projected onto a horizontal 52-in. liquid crystal display TV positioned above the arm (Fig. 1B). A mirror, positioned parallel and below this TV, reflected the visual display, to give the illusion that the display was in the same horizontal plane as the hand. Calibration of the display ensured that this projection was veridical. Position and orientation of each limb segment were sampled at 103 Hz using the Flock of Birds (Ascension Technology, Burlington, VT) magnetic 6 degrees of freedom movement-recording system. Positions of the following three bony landmarks on each arm were digitized: 1) index finger tip; 2) the lateral epicondyle of the humerus; and 3) the acromion, directly posterior to the acromioclavicular joint. As sensor data were received from the Flock of Birds, positions of these landmarks were computed by our custom software. For detailed information, see Sainburg and Wang (2002).

Experimental design

We conducted three experiments in this study. In the first experiment, we examined the effect of visuomotor adaptation with one arm on bilateral adaptation to the same task, as well as the effect of the bilateral adaptation on subsequent performance with the arm opposite to that used in the initial adaptation session. This is analogous to a therapeutic situation, for example, in which a hemiparetic patient would learn a motor task with the nonparetic arm first, then with both arms, and finally with the paretic arm, to see whether the paretic arm might benefit from the preceding training sessions with one or both arms.

In the second experiment, we attempted to replicate the effect of bilateral training on subsequent unilateral performance observed in experiment 1, with the potential effect of initial unilateral training on...
the subsequent opposite arm performance removed; thus the experimental paradigm was similar to that of experiment 1, except that it started with a bilateral adaptation session, followed by a unilateral session. Finally, we examined the retrograde effect of bilateral adaptation on subsequent performance with the same arm that was used in the initial unilateral training. The experimental paradigm was again similar to that of experiment 1 (i.e., preunilateral adaptation, bilateral adaptation, postunilateral adaptation), except that the same arm was used during both the pre- and postunilateral sessions.

Each experiment consisted of three (experiment 2) or four sessions (experiments 1 and 3): baseline (no visual rotation), preunilateral adaptation, bilateral adaptation, and postunilateral adaptation sessions. The baseline session was provided so that subjects could become familiar with our reaching task in general, using both arms simultaneously. During the adaptation sessions, the position of the cursor was rotated 30° counterclockwise (CCW) relative to the start circle. For each trial, one of eight targets (Fig. 1C: 2 cm in diameter), presented in a pseudorandom sequence, was displayed prior to movement. During the bilateral adaptation session, however, the direction of visual rotation was always the same (i.e., extrinsically consistent) for both arms, whereas the target direction was opposite (i.e., intrinsically consistent) between them. Each session consisted of 192 trials, organized into 24 cycles, with each cycle containing eight consecutive trials (i.e., a set of movements made toward all eight target directions). Subjects were instructed to move directly from the starting circle to the target (13 cm in distance) using a single, rapid motion in response to an auditory “go” signal. The start circle for each arm was placed laterally (i.e., 20 cm from midline), as illustrated in Fig. 1C. During the movement, visual feedback was provided as a screen cursor. At the end of each trial, knowledge of results (KR) was provided in the form of a hand path between the starting circle and the target and by points awarded for spatial accuracy (two-dimensional [2D] distance) between the target and the final hand position: 1 point for accuracy <4 cm, 3 points for accuracy <2 cm, and 10 points for accuracy <1 cm. No points were given for movements that took >400 ms.

There were two subject groups in each of the first two experiments (six subjects per group in experiment 1, four in experiment 2; each subject participated in only one experiment). In experiment 1, one subject group used the left arm during the preunilateral session and the right arm during the postunilateral session (Fig. 1C) and the other group vice versa (Fig. 1D). In experiment 2, one subject group used the left arm and the other group the right arm during the postunilateral session. The last experiment consisted of only one subject group (four subjects) who performed the task with the left arm first. Table 1 summarizes these conditions.

Data analysis

We calculated three measures of performance in this study: hand-path direction error at peak velocity ($V_{\text{max}}$) and at peak acceleration ($A_{\text{max}}$) and final position error. Direction error was calculated as the angular difference between the vectors defined by the target and by the hand-path position at movement start and at $V_{\text{max}}$ or at $A_{\text{max}}$. Final position error was calculated as the 2D distance between the center of the target and the index finger at movement termination [defined as the first minimum (<5% maximum tangential hand velocity) following the peak in tangential hand velocity].

In experiments 1 and 2, repeated-measures ANOVAs were conducted to examine the main effects of, and the interaction effects among, the three following variables: group (left arm first, right arm first), session (preunilateral, bilateral, postunilateral in experiment 1; bilateral and postunilateral in experiment 2), and epoch (1–12). An epoch is the mean of two consecutive cycles; 24 cycles in each session were reorganized into 12 epochs for the purpose of data reduction in statistical analyses. In experiment 3, a repeated-measures ANOVA was conducted to examine the main effects of, and the interaction effects between, session and epoch. The alpha level was set at 0.05 for statistical significance in all experiments.

Following the ANOVAs, because the main purpose of this study was to examine the effect of initial training on subsequent performance (i.e., the effect of unilateral adaption on bilateral adaptation and vice versa), we were most interested in post hoc pairwise comparisons using paired or independent $t$-test (for within-subject and between-subject comparisons, respectively), with an alpha level of 0.05. These pairwise comparisons were made mostly among the performances of three adaptation sessions at the first epoch, defined as the mean of cycles 1 and 2, or among those at the last epoch, defined as the mean of cycles 23 and 24 (e.g., right arm performance at the first epoch during the preunilateral session vs. that during the bilateral session, or during the bilateral session vs. that during the postunilateral session, which reflects the effect of unilateral adaption on bilateral adaption and that of bilateral adaption on subsequent unilateral adaption, respectively). The comparisons at the first epoch were made to assess the amount of immediate transfer from initial training to subsequent performance, whereas those at the last epoch were made to compare the final level of adaption across sessions.

Results

Experiment 1

Figure 2 shows typical hand paths from our representative subjects during the preunilateral, bilateral, and postunilateral adaptation sessions. Black lines represent the hand paths from the first eight consecutive trials during the given adaptation session, whereas gray lines represent those from the last eight consecutive trials during the same session. As expected, these paths (black lines) are initially directed CCW to the target, with a large “hook” at the end of motion that reflects an error correction. Following adaptation to the visual rotation, these movements (gray lines) become relatively straight and substantially more accurate. The effect of preunilateral training on bilateral adaptation seems to rely largely on which arm was used in the preunilateral session because the left-arm performance during the bilateral session (row 1, column 2, black line) does not appear to be better than that observed during the preunilateral session (row 1, column 1, black line), whereas a substantial improvement is observed from the preunilateral to the bilateral session in the right arm performance (row 2, column 1 vs. column 2, black lines). It is also noticeable that regardless of the arm used in the preunilateral session, unilateral training with one arm (column 1) did not facilitate opposite arm performance during the bilateral session (column 3), especially when compared with the naïve performance with the same arm observed in the other subject group [e.g., left-arm performance during bilateral adaptation (column 3, row 2, black line) compared with left-arm performance during preunilateral adaptation (column 1, row 1, black line)]. These
observations are also illustrated in Fig. 3, which shows the mean values (±SE) of direction errors at \( V_{\text{max}} \) across subjects. When the same-arm performances between the bilateral and postunilateral sessions are compared (Fig. 2, column 3 vs. column 4), a substantial and facilitative transfer effect is observed from the bilateral to the postunilateral performances. In fact, the initial phase of the postunilateral session (column 4, black lines) was already quite similar to that observed during the final phase of the same session (column 4, gray lines). The changes in the left-arm performance from the bilateral to the postunilateral session, in which the subjects performed the preunilateral task with their right arm (Fig. 2, row 2), appear most interesting because the performance in the initial phase of the postunilateral session (column 4, row 2, black line) was substantially better than that observed in the final phase of the bilateral session (column 3, row 2, gray line). This may indicate that learning of this novel visuomotor transform occurred without an improvement in performance during the bilateral session. In fact, this left-arm performance during the bilateral session was even worse than that of naïve performance with the left arm, as observed in the other group of subjects (see Fig. 3, column 3, row 2). This appears to reflect an interference effect of bilateral performance, such as that previously reported for more complex movements (Diedrichsen et al. 2001). (Thin lines shown in column 3 of this figure represent the naïve, preunilateral performance with the same arm of the other group of subjects. For example, the thin line shown in column 3, row 2 is the same as the line shown in column 1, row 1. These lines are included in this column for comparison purposes.)

To quantify these effects across subjects, we calculated three performance measures: direction error at \( V_{\text{max}} \), direction error at \( A_{\text{max}} \), final position error. Because all three measures showed the same pattern of results, we will restrict our analysis to the measure of direction error at \( V_{\text{max}} \) in the following section.

Repeated-measures ANOVA revealed a significant three-way interaction effect (group/adaptation session/epoch; \( P < 0.01 \)), indicating that the difference among the three adaptation sessions in terms of performance changes across epochs also varied depending on the group of subjects. Thus we performed pairwise comparisons among the performances of three adaptation sessions at the first epoch, to assess the amount of immediate transfer from initial training to subsequent performance, as well as among those at the last epoch, to compare the final level of adaptation across sessions. We made these comparisons within each subject group separately because we were primarily interested in testing the effect of preunilateral adaptation on subsequent bilateral adaptation, as well as the effect of bilateral adaptation on postunilateral adaptation, in each group.

Pairwise comparisons among the adaptation sessions at the first epoch and at the last epoch are illustrated in Fig. 3 (column...
5) for the two subject groups (rows 1 and 2) and for the left arm and right arm separately (mean ± SE of direction error at the first and last epochs represented by the top and bottom of each bar, respectively). As reflected by the horizontal lines shown in this figure, many pairwise comparisons were significant (P < 0.05) at both the first epoch and the last epoch. With regard to the effect of preunilateral adaptation on bilateral adaptation within the same arm, unilateral training with the right arm facilitated the same-arm performance during the bilateral session, which was reflected by an immediate improvement in performance (Fig. 3, column 5, row 2, left panel, indicated by a horizontal line on top) and also by the final adaptation level that was not statistically different from that observed during the preunilateral session (indicated by the absence of a horizontal line at the bottom). Preunilateral training with the left arm, however, had a differential effect on bilateral adaptation, in that whereas the performance at the first epoch during the bilateral session was significantly better than that during the unilateral session (Fig. 3, column 5, row 1, left panel, indicated by a horizontal line on top), the performance at the last epoch never reached the final adaptation level achieved in the preunilateral session (indicated by a horizontal line at the bottom, P < 0.01).

The amount of transfer occurring from the preunilateral to bilateral sessions is confounded by the amount of learning that occurred during the preunilateral session. Thus we also normalized our direction measures and calculated the amount of transfer in such a way that the amount of change in performance from the first epoch of the preunilateral performance to the first epoch of the same-arm performance during the bilateral session was compared with that from the first to the last epoch of the same-arm performance during the preunilateral session. The results indicated that the amount of transfer from the unilateral to bilateral sessions was significantly different between the left and right arms (22% vs. 68% improvement for the left and right arms, respectively; P < 0.01).

With regard to the effect of preunilateral adaptation on bilateral adaptation across the two arms, preunilateral training with the right arm appeared to negatively influence left-arm performance during the bilateral session, indicated by a significant detriment in performance at both the first and the last epochs (P < 0.01, Fig. 3, column 5, row 2, right panel, black bar) compared with the same-arm performance during a preunilateral session (white bar). (White bars shown in the right panels of column 5 correspond to thin lines shown in column 3.) In the other subject group, preunilateral training with the left arm had neither a facilitative nor a detrimental effect on bilateral adaptation with the right arm. However, this asymmetrical effect on left-arm performance during bilateral movements may reflect bilateral interference and may not be related to previous unilateral performance. Our second experiment addresses this hypothesis by assessing initial bilateral adaptation, without prior unilateral adaptation.
Finally, with regard to the effect of bilateral adaptation on postunilateral performance within the same arm, bilateral adaptation significantly facilitated the subsequent unilateral performance in both subject groups, as indicated by a large difference between the bilateral and postunilateral performances at the first epoch (Fig. 3, column 5, right panels, black vs. gray bars). Most interesting is the substantial improvement in the left-arm performances observed in Fig. 3 (row 2): subjects in this group—whose performance was very poor—performed the task with their left arm for the very first time in the bilateral session; when they performed the same task with only the left arm in the subsequent session, their performance at the first epoch (column 5, row 2, right panel, top of gray bar) was substantially better than that at the last epoch observed during the bilateral session (bottom of black bar, $P < 0.0001$). The amount of transfer, calculated using normalized direction measures, was substantially larger for the left arm compared with that for the right arm (210 vs. 94% improvement for the left and right arms, respectively). In this case, the amount of change in performance from the first epoch of the bilateral performance to the first epoch of the same-arm performance during the postunilateral session was compared with that from the first to the last epoch of the same-arm performance during the bilateral session for each arm. This may indicate, as pointed out earlier, that learning has occurred despite the absence of a visible improvement in performance, or bilateral interference, during the bilateral session. This point was further tested in experiments 2 and 3.

**Experiment 2**

The main purpose of this experiment was to determine whether the substantial improvement in performance observed in the beginning of the postunilateral session in experiment 1 was primarily due to the preceding bilateral adaptation or due to a combined effect of bilateral and preunilateral adaptations. In addition, we could directly assess whether the apparent interference in performance with the left arm was a direct effect of bilateral conditions or whether it was related to the previous unilateral performance experience. We were particularly interested in further examining whether transfer of learning—from bilateral to unilateral conditions—could occur with the left arm, when improvements in performance were not observed during the initial bilateral training (i.e., a poor performance at the last epoch during the bilateral session, followed by immediate improvements in performance at the first epoch during the postunilateral session, Fig. 3, row 2, left-arm performances). The experimental paradigm was the same as that in experiment 1, except that the subjects experienced only a bilateral and a postunilateral session.

The results from this experiment, illustrated in Fig. 4, are similar to those observed in experiment 1. Bilateral adaptation significantly facilitated the subsequent unilateral performance in all subject groups, as indicated by a large difference between the bilateral and postunilateral performances at the first epoch (Fig. 4, columns 2 and 3). A repeated-measures ANOVA revealed a significant two-way interaction not only between group and epoch ($P < 0.05$), but also between session and...
epoch ($P < 0.001$). Pairwise comparisons indicated that the difference between bilateral and unilateral performances at the first epoch (column 4) was significant in both subject groups, as indicated by horizontal lines on top ($P < 0.01$).

With regard to the improvement in the left-arm performances reported in experiment 1, from the bilateral to the postunilateral session (Fig. 3, row 2), a similar trend was also observed in this experiment, in that the mean direction error at the first epoch during the postunilateral session was smaller than that at the last epoch during the bilateral session (Fig. 4, row 2, column 4; compare between the bottom of the black bar and the top of the gray bar). Although this difference was not statistically significant, the amount of transfer, calculated using normalized direction measures, was still substantially larger for the left arm compared with that for the right arm (185 vs. 120% improvement for the left and right arms, respectively).

**Experiment 3**

In this experiment, we examined the retrograde effect of bilateral performance on unilateral adaptation, by having the subjects perform the task with the same arm during both the pre- and postunilateral sessions. We were particularly interested in examining this effect in a specific condition that was used in experiment 1: a condition in which subjects performed the task with their left arm during the preunilateral session (Fig. 3, row 1). In this condition, despite a substantial improvement in performance with the left arm in the preunilateral session (column 1), the same-arm performance during the bilateral session (column 2) was very poor in the beginning and did not improve much at all throughout the session. Thus we tested in this experiment the effect of poor performance with the left arm during the bilateral session on the retention of the novel visuomotor transform obtained during the initial training with the same arm.

The data obtained during the preunilateral and bilateral sessions reported in experiment 1 were successfully replicated in this experiment, as illustrated in Fig. 5 (columns 1–3). That is, the left-arm performance showed nearly complete adaptation during the preunilateral session, but became poor and showed no improvement during the subsequent bilateral session (i.e., no significant improvement from the first to the last epoch of the bilateral session, $P > 0.05$). Surprisingly, however, the same-arm performance at the first epoch during the postunilateral session (column 4) was substantially better than that at the last epoch during the bilateral session ($P < 0.0001$) and was not significantly different from that observed at the last epoch of the preunilateral session ($P > 0.05$, indicated by the absence of a horizontal line between the white and gray bars at the bottom of column 5). Our normalized direction measures indicated 118% improvement in performance at the first epoch of the postunilateral session compared with the amount of learning that occurred during the preunilateral session and 309% improvement compared with that occurring during the bilateral session with the same arm. These data clearly indicate a complete retention of the novel visuomotor transform obtained during the preunilateral training, without being disrupted by a poor performance during the bilateral condition.

**DISCUSSION**

Bilateral movements are generally thought to recruit unique neural processes (e.g., Brinkman 1981, 1984; Swinnen 2002; Wiesendanger and Serrien 2004) based on the findings from lesion and/or imaging studies, which indicate the motor cortices (i.e., supplementary motor, premotor, primary motor area) as the neural correlates most responsible for bilateral coordination (Brinkman 1981, 1984; Donchin et al. 2002; Sadato et al. 1997). For example, Sadato and colleagues (1997) measured regional cerebral blood flow and positron emission tomography to show an increased activation level in the supplementary motor area (SMA) and premotor cortex during bilateral movement, whereas Donchin et al. (2002) reported the activities of individual neurons in the primary motor cortex (M1) and SMA that varied between bilateral and unilateral movements. However, it has also been shown that the single neurons in these brain regions are activated similarly during a complex reaching and grasping behavior using the hands either bilaterally or unilaterally (Kazennikov et al. 1999). Although these findings suggest that the aforementioned brain regions are somehow involved in controlling bilateral actions to a certain extent, it still remains uncertain whether their involvement in bilateral control reflects the recruitment of a neural circuitry that is totally independent of that underlying unilateral movements or whether these regions are rather involved in coordinating synergistically the same neural circuitry that is recruited to control unilateral movements. The former hypoth-

![Fig. 5](http://jn.physiology.org) Mean performance measures of direction error at $V_{\text{max}}$ in experiment 3. Columns 1–4: every data point in each epoch represents the mean of 16 consecutive trials averaged across all subjects (mean ± SE). Column 5: this graph provides a summary of data shown in columns 1, 2, and 4 for statistical comparisons. White bar represents performance shown in column 1; black bar, performance in column 2; and gray bar, performance in column 4.
esi is partly supported by a recent study (Nozaki et al. 2006), in which the authors investigated the pattern of generalization following adaptation to novel dynamic conditions between unilateral and bilateral training conditions and reported a limited amount of generalization between these two types of movements. These findings suggested that bilateral movements might recruit circuits that do not simply act to synchronize the controllers for each limb but, instead, recruit synergies that uniquely coordinate the movements of two arms together.

It is plausible that the amount of generalization between bilateral and unilateral movements may vary, depending on the nature of the task used. Based on behavioral research, some investigators argued that visuomotor and dynamic adaptations are not represented independently in the nervous system (Tong et al. 2002), whereas others suggested that they are subserved by distinct neural processes (Krakauer et al. 1999). Findings from our interlimb transfer studies provide support to the latter idea by showing that the pattern of interlimb transfer changes substantially depending on whether a visuomotor or a dynamic task is learned (Sainburg and Wang 2002; Wang and Sainburg 2004). Although not much, some data from imaging studies are also available on this matter (Diedrichsen et al. 2005; Ghilardi et al. 2000; Rabe et al. 2009). However, they are not in agreement with each other. Although Diedrichsen et al. (2005) reported a large overlap of neural activations in the cerebellum and motor cortex during visuomotor and dynamic adaptation tasks, thus suggesting that the kinematics and dynamics of reaching are not computed in separate neural entities, Rabe and colleagues (2009) found that the atrophy of distinct cerebellar areas in patients with cerebellar degeneration correlated with impairment in two different tasks (i.e., visuomotor and dynamic), based on which they concluded that adaptation to the two different tasks is processed independently and relies on different cerebellar structures. Findings from a transcranial magnetic stimulation (TMS) study (Richardson et al. 2006) appear to be consistent more with the latter argument because it demonstrated that a disruption of M1 by TMS impairs dynamic adaptation, whereas visuomotor adaptation is known to involve the posterior parietal cortex more than M1 (Ghilardi et al. 2000).

Thus considering the possibility that visuomotor and dynamic transformations might be subserved by distinct neural mechanisms (Krakauer et al. 1999; Wang and Sainburg 2004), we questioned in the present study that the amount of generalization between bilateral and unilateral movements might be different, depending on the nature of sensorimotor transformation involved in a given motor task. Indeed, the present study, in which generalization of visuomotor adaptation was tested, demonstrated that the postunilateral performances undoubtedly benefited from the prior bilateral training, sometimes despite the presence of interference effects observed during the bilateral sessions. The extent of transfer from the bilateral to postunilateral sessions during the right arm performances was nearly complete and that during the left-arm performances was even greater. These findings indicate that the motor control system was able to use the novel visuomotor transform obtained during the bilateral session to immediately facilitate the subsequent unilateral performances, thus suggesting a substantial overlap, at least in the neural processes that underlie visuomotor transformations between bilateral and unilateral conditions.

These findings are consistent with the idea that movement planning and execution involve a multistage process, in which the kinematics of movement are first planned and later transformed into commands that correspond to the forces required to carry out the motion (e.g., Ghez et al. 1989; Jordan and Rumelhart 1992; Kawato et al. 1988; Krakauer et al. 2000). According to this idea, visuomotor transformations are thought to occur upstream to dynamic transformations (e.g., Ghez et al. 1991; Kawato et al. 1988; Sainburg 2002). It is also thought that adaptation to novel dynamic conditions requires modifications in the latter process, whereas visuomotor adaptation requires modifications in the former process (e.g., Ghez et al. 2000; Sainburg et al. 2003). Therefore it seems reasonable that visuomotor adaptations might occur independently of the effectors that are used during a given motor task, whereas dynamic adaptations are more directly associated with the specific effectors used during the task. This idea leads to a prediction that the extent of generalization between bilateral and unilateral conditions that involve different effectors may depend on the nature of sensorimotor adaptation in question, which is supported by our current findings and those reported by Nozaki et al. (2006). These findings collectively suggest that downstream to the visuomotor transformation process, bilateral synergies might be recruited during the dynamic transformation process, during which effector-specific neural commands associated with the forces to carry out a motion are determined. This argument, however, must be interpreted with caution because it is based on an assumption that the extent of generalization between bilateral and unilateral conditions observed in the current study is substantially greater than that reported in the study by Nozaki et al. (2006). A single study in which the generalization of visuomotor and dynamic adaptation between bilateral and unilateral movements is compared under the same experimental conditions may be needed to determine this.

The current findings are also consistent with previous studies, suggesting that visuomotor and dynamic adaptations involve distinct neural processes (Krakauer et al. 1999; Wang and Sainburg 2004). Krakauer and colleagues (1999) revealed that adaptations to a rotated visual display and a novel inertial dynamics do not interfere with each other and also that consolidation of the two learning conditions occur in parallel. Wang and Sainburg (2004) further demonstrated that the direction of movement information transferred across the arms following dynamic adaptation is opposite to that following visuomotor adaptation (Sainburg and Wang 2002), thus indicating that the pattern of interlimb transfer depends on the nature of the underlying sensorimotor transform. These findings are in agreement with other findings, which demonstrated that generalization of visuomotor adaptation within the same arm occurs best along extrinsic coordinates (Krakauer et al. 2000; Wolpert et al. 1995), whereas dynamic adaptation generalizes along intrinsic coordinates (Malfait et al. 2002; Sainburg et al. 1999; Shadmehr and Moussa-Ivaldi 1994). Other studies also indicated that when visual and proprioceptive data about the initial limb configuration are dissociated prior to movement, individuals rely more heavily on visual information to plan the direction and distance of hand motion, whereas they rely more on proprioceptive information to transform the kinematic plan into the neural commands associated with specific forces required to carry out the movement (Baghesteiro
vided (i.e., we provided visual perturbation to both arms) in two studies, which include the way perturbations were provided to some differences in experimental paradigms between the observed in the study by Nozaki et al. (2006) may be attributed to a possibility that visual attention was given more to the performance of the right, thus dominant, arm, rather than learning per se. These findings thus indicate that learning can occur despite the absence of improvement in performance and are in agreement with our current finding. It appears that bilateral performance during the visuomotor adaptation task had an effect similar to that of a concurrent secondary task, probably by forcing participants to divide their attention to the two arms.

With regard to the effect of bilateral training, our data indicate its differential effect for the two arms. The bilateral training with the left arm caused a retrograde interference effect: the initial training with the left arm had no positive effect on the same-arm performance during the bilateral session, which was reflected by a lack of improvement in performance throughout the session despite a better performance in the beginning, compared with the naive preunilateral performance (experiments 1 and 3). On the other hand, the bilateral training did not have a substantial retrograde interference effect on the initial learning with the right arm, reflected by improved performance with the right arm from the beginning of the bilateral session, compared with the same-arm naive performance. This indicates that the unilateral training with the right arm had a facilitative effect on the same-arm performance during the bilateral adaptation, with minimal bilateral interference. This differential effect of bilateral training may be attributed to a possibility that visual attention was given more to the performance of the right, thus dominant, arm, rather than its counterpart, during the bilateral session. Previous studies indicated that attention plays an important role in adapting to novel sensorimotor transformations (Ingram et al. 2000; Redding et al. 1992; Taylor and Thoroughman 2007). The fact that no differential effect of bilateral training on the two arms was observed in the study by Nozaki et al. (2006) may be attributed to some differences in experimental paradigms between the two studies, which include the way perturbations were provided (i.e., we provided visual perturbation to both arms simultaneously during bilateral conditions, whereas they provided dynamic perturbation to the left arm only) and the number of targets used for reaching (i.e., we had eight different target directions, whereas they had only one target direction). The experimental paradigm used in their study probably minimized the need to divide attention between the arms. Since we did not control for the distribution of attention in this experiment, further research is necessary to confirm this idea.

Our finding that the bilateral interference selectively influenced the left-arm performance may also be related to our hemispheric lateralization idea. We have previously argued that the dominant and nondominant hemisphere/limb systems are differentially specialized, such that the dominant system is specialized for controlling limb and task dynamics that mainly involve feedforward control mechanisms, whereas the nondominant system has a special role in sensory feedback-mediated error-correction mechanisms (Bagesteiro and Sainburg 2003). More recently, we also suggested that each system is specialized for stabilizing different aspects of task performance (Wang and Sainburg 2007). In that study, we demonstrated that the dominant arm performance is more stable and accurate when the starting point of reaching movement, and thus initial limb configuration, remains the same across different task conditions, whereas that of the nondominant arm is more stable when the target location, and thus final limb posture, remains invariant. Interestingly, the findings from the dominant arm performance appear to be more consistent with a forward dynamic control model of reaching movement, which suggests that the motor control system relies heavily on the accurate estimate of initial limb configuration to specify the dynamic variables associated with a desired movement trajectory in a predictive manner (Kawato 1999; Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995), whereas the findings from the nondominant performance are more consistent with earlier versions of the equilibrium point control model, which posits that the CNS specifies a final limb configuration by manipulating motor neuron threshold (Bizzi et al. 1982; Latash 1992). These findings collectively indicate that the dominant and nondominant systems may use different motor control mechanisms and also that, because the nondominant system relies more on sensory feedback-mediated mechanisms to control final position accuracy, it may be more susceptible to certain external factors that occur during performance, such as the requirement to move both arms simultaneously (and the possible division of visual attention because of that).

**GRANTS**

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