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A dissociation between visual and motor workspace inhibits generalization of visuomotor adaptation across the limbs

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Abstract

We have previously shown that the pattern of interlimb transfer following visuomotor adaptation depends on whether the two arms share task-space at a given workspace location: When the two arms adapted to a novel visuomotor rotation in unshared, lateral workspaces, transfer of movement direction information occurred symmetrically (i.e., from dominant to nondominant arm, and vice versa). When the two arms shared the same task-space, however, transfer of the same information became asymmetric (i.e., only from dominant to nondominant arm). In the present study, I investigated the effect of a conflict between visual and proprioceptive information of *task-space* on the pattern of interlimb transfer, by dissociating visual and motor workspaces. I hypothesized that the pattern of interlimb transfer would be determined by the way the motor control system uses available sensory information, and predicted that depending on whether the system relied more on vision or proprioception, transfer would occur either symmetrically or asymmetrically. Surprisingly, the results indicated that despite substantial adaptation to a novel visuomotor rotation, no transfer occurred across the arms when the visual and motor workspaces were dissociated in space. Based on this finding, I suggest that when a conflict exists between visual and proprioceptive information with respect to the sharing of the given task-space by the two arms, it interferes with executive decisions made by the motor control system in determining hand dominance at a given workspace, which results in a lack of transfer across the arms.

Keywords

Reaching movement; Motor Learning; Motor Control; Inter-limb; Inter-manual; Workspace

Introduction

Visuomotor adaptation has been extensively studied to understand how the central nervous system integrates sensory information from different sources (e.g., vision, proprioception) in a novel environment that requires a remapping of visual-motor space. Studies investigating visuomotor adaptation typically alter the relationship between vision and proprioception by rotating and/or translating a visual display of either the hand or the target (e.g., Roby-Brami and Burnod 1995; Redding and Wallace 1996; Goodbody and Wolpert 1999; Wang and Sainburg 2005) or by providing a proprioceptive perturbation to the moving arm (e.g., Pipereit et al. 2006; Bernier et al. 2007), and investigate how such manipulations affect performance measures, such as movement accuracy. Findings from these studies are somewhat discrepant, in that some observed the prevalence of visual information (Redding and Wallace 1996; Mon-Williams et al. 1997; Goodbody and Wolpert 1999), while others indicated a balanced, and weighted, role of vision and proprioception in determining the altered hand-target relationship

(Rossetti et al. 1995; van Beers et al. 1999; Sarlegna and Sainburg 2006), or even a dynamic relationship between the two modalities that may be context dependent (van Beers et al. 2002). It has also been suggested that these two sensory modalities contribute differentially to the control of different features of reaching movement (e.g., planning direction vs. amplitude, Sainburg et al. 2003) or to the identification of different aspects of movement (e.g., evaluating spatial layout vs. dynamical component of movement, Boy et al. 2005).

We recently conducted a series of studies to understand how a novel visuomotor transform obtained through an adaptation process generalizes across different effectors (Sainburg and Wang 2002; Wang and Sainburg 2003, 2004, 2006a, b, 2007a). In these studies, we investigated the pattern of interlimb transfer following adaptation to novel visuomotor rotations, and showed that different features of movement transfer in different directions (e.g., direction information only transfers from the nondominant to the dominant arm, and final position information only from the dominant to the nondominant arm at a shared midline workspace). Findings from these studies also indicated that the pattern of interlimb transfer depends on whether the two arms share task-space at a given workspace. That is, when the two arms learn the task at unshared, lateral workspaces, initial direction information transfers in both directions (i.e., direction information transfers from the nondominant to the dominant arm, and vice versa), whereas when both arms learn the task at a shared workspace (midline and lateral), transfer of direction information occurs asymmetrically, such that it only transfers in one direction at a given workspace location. Based on these findings, we suggested that during interlimb transfer, the motor control system may selectively facilitate or inhibit the access of each arm controller to the information obtained during prior adaptation with the other arm, thereby reducing redundant, and competing, solutions (i.e., both arms being available to perform the task in a given workspace) when the task-space is *shared* by both arms (Wang and Sainburg 2006b, 2007a).

In the present study, I investigate the effect of visual-motor dissociation of task-space on the pattern of interlimb transfer. I provided a visuomotor dissociation by translating the visual display of task-space, such that the workspace visually appeared to be shared by the two arms on midline while each arm actually adapted to a novel visuomotor rotation only in its ipsilateral workspace, and vice versa. By creating this visual-motor conflict, I was interested in determining whether the motor control system would rely more on visual information, proprioceptive information, or mixture of both, in determining the pattern of interlimb transfer. Different predictions are available depending on the amount of contribution each type of information makes. First of all, it is possible that visual, as opposed to proprioceptive, information plays a crucial role in determining the pattern of interlimb transfer, as suggested in some visuomotor adaptation studies (Redding and Wallace 1996; Mon-Williams et al. 1997; Goodbody and Wolpert 1999). If the central nervous system relied more on visual information, it would perceive the situation, and determine the access of each arm controller to opposite arm information, based on whether the task-space visually appears to be shared by the two arms. In that case, one can expect that when the two arms appeared to share the task-space while they did not physically share it, the pattern of interlimb transfer would be the same as that observed when both arms actually shared the workspace in our previous study (i.e., asymmetrical transfer of initial direction information). When the two arms appeared to perform the task in their ipsilateral workspaces while they did share it physically, its pattern would resemble that observed in our study in which the arms did not share the workspace (i.e., symmetrical transfer). In contrast, if the system relied more on proprioceptive information, the results would be opposite. It is also plausible that the contribution of each type of information will be weighted in a certain way (Rossetti et al. 1995; van Beers et al. 1999; Sarlegna and Sainburg 2006), or alternatively, that such an incongruency between the two types of information will result in no transfer of movement information at all. Indeed, it has been shown that when the two arms experienced opposing directions of visuomotor rotation tasks (i.e.,

dominant arm experienced counterclockwise rotation, nondominant arm clockwise), neither facilitative nor detrimental transfer occurred across the arms, likely due to the fact that the two types of visuomotor transforms obtained were incompatible (Wang and Sainburg 2003).

Materials and Methods

Subjects

Subjects were 28 neurologically intact right-handed adults (14 female, 14 male), aged from 18 to 30 years old. Subjects were recruited from the university community and were paid for their participation. Informed consent was obtained prior to participation. Right handedness was assessed using the 10-item version of the Edinburgh inventory (Oldfield 1971).

Apparatus

Subjects sat facing a table with either the right or left arm supported over a horizontal surface, positioned just below shoulder height, by a friction-less air jet system (Fig. 1A). A start circle, target, and cursor representing the index-finger position were displayed on a horizontal, back-projection screen positioned above the arm (Fig. 1B). A mirror, positioned parallel and below this screen, reflected the visual display, so as to give the illusion that the display was in the same horizontal plane as the fingertip. Calibration of the display ensured that this projection was veridical. Position and orientation of each limb segment was sampled at 103 Hz using the Flock of Birds® (Ascension-Technology, Burlington, VT) magnetic 6-DOF movement recording system. The position of the following three bony landmarks was digitized using a stylus rigidly attached to a FOB sensor: 1) index finger tip, 2) the lateral epicondyle of the humerus, and 3) the acromion, directly posterior to the acromio-clavicular joint. This sensor was then attached to a rigid upper arm cuff. Another FOB sensor was attached to a rigid forearm support. Thus, the position of the body landmarks relative to these sensors remained constant throughout the experiment, and these positions were computed by our custom software as sensor data were received from the Flock of Birds®. For more detailed information, see Sainburg and Wang (2002).

Experimental Design

In the present study, I attempted to have the experimental design the same as that used in our previous studies (e.g., Sainburg and Wang 2002; Wang and Sainburg 2004, 2006a, b). Thus, the visuomotor rotation task employed in this study (i.e., the degree of visual rotation, the number of target directions, target size, etc.) was identical to that used in our previous studies, except for the fact that visual and motor task-spaces were dissociated in the present study. The number of performance trials experienced by the subjects was also identical in all these studies (i.e., 192 trials per block, total four blocks of performance).

As illustrated in Figure 1C, the starting circle (1.5 cm in diameter) and targets (2 cm in diameter; 13 cm away from the starting position) were presented either in midline or 45 cm laterally from midline. When they were presented in midline, subjects physically performed the task laterally, such that each arm learned the task in its ipsilateral workspace (fig. 1C, left). In contrast, when they were presented laterally, subjects shared the task-space with both arms in midline (fig. 1C, right). Prior to movement, one of eight targets, presented in a pseudorandom sequence, was displayed on the horizontal tabletop. Subjects were asked to move the finger from the starting circle to the target using a single, ballistic motion in response to an auditory 'go' signal. During the movement, visual feedback was provided by a screen cursor. At the end of each trial, knowledge of results was provided in the form of a circle indicating the final location of the index finger tip and by points awarded for spatial accuracy (2D distance between the target and the final finger position): 1 point for accuracy <4 cm, 3 points for accuracy <2 cm, and 10 points for accuracy <1 cm. Points, displayed on the target once the reaching movement was

completed, were only provided to keep the participants motivated, and did not carry any monetary value. Accumulated points were also visible on the upper edge of the screen. No points were given for movements that took longer than 400 msec, regardless of accuracy. In order to examine adaptation to visuomotor rotations, the position of the cursor was rotated 30° counterclockwise (CCW) relative to the start circle.

In this study, half the subjects performed the task in the visually shared task-space condition, while the other half performed the task in the physically shared task-space condition. The experiment consisted of two sessions: baseline (no visual rotation) and exposure (visual rotation) sessions. Subjects performed two blocks of trials in each session: one block with each arm. In each task-space group, half the subjects performed with the left arm first and then the right arm (group LR), while the other half performed with the right arm first and then the left arm (group RL). Each block comprised 192 trials, divided into 24 cycles, with each cycle containing all eight of the targets consecutively. A 10 min break was given between each block of trials. Each group consisted of seven subjects. The number of subjects was determined by a power analysis (power of .80 for two-tailed alpha of .05) using our previous data (Sainburg and Wang 2002; Wang and Sainburg 2004, 2006a, b). Subjects were not informed about the CCW rotation employed during the exposure session.

Data Analysis

Two measures of performance were calculated: hand-path direction error at peak tangential arm acceleration ($A_{\max}$) and velocity ($V_{\max}$). Both direction errors were used because the former mainly reflects a feedforward control process, while the latter can reflect a feedback-mediated control process as well. Direction errors were calculated as the angular difference between the vectors defined by the target and by the hand-path position at movement start and at $V_{\max}$ or $A_{\max}$.

A mixed-design ANOVA was conducted with task-space (visually shared, physically shared) and group (LR, RL) as between-subject factors, and arm (left, right) and epoch (1~12) as within-subject factors, to examine the main effects of, and the interaction effects among, these factors. Because the purpose of this study was to examine the effect of initial training with one arm on subsequent performance with the other arm, I was most interested in post-hoc pair-wise comparisons using Tukey's test, which were made between naïve performance and performance following prior adaptation with the other arm (referred to as "opposite arm" hereafter) for the dominant-and nondominant-arm blocks under each of the four task-space by arm combinations (visually shared/L, visually shared/R, physically shared/L, physically shared/R). This effect of opposite arm adaptation was only assessed for the first epoch (mean of cycles 1 and 2) in order to focus on the extent of initial information transfer. Pair-wise comparisons at the first epoch were of primary interest, because previous studies have frequently shown substantial effects of initial training on the very first trials of the subsequent testing session (e.g., Krakauer et al. 1999; Sainburg and Wang 2002; Wang and Sainburg 2003). An effect size, a difference between naïve performance and the performance following opposite arm adaptation in the first epoch, divided by their pooled standard deviation, was also computed to determine if the difference was nearly significant in case the P value did not reach the significance level of .05.

To make a further comparison between the two performance conditions, a line of approximation was also constructed for each condition by finding a nonlinear logarithmic regression line. The slope, which represented the rate of learning throughout the course of adaptation, and the intercept, which represented the amplitude of errors in the beginning of adaptation, for this regression equation were obtained from each subject for each condition, and they were subjected to an independent t-test, as another post hoc test.

Results

Figure 2A shows typical hand-paths of representative subjects during the final phase of the baseline session, and during the initial and final phases of the adaptation session. These hand-paths are shown for the right arm only, and the left arm performances are similar to these. Upon first exposure to the visuomotor rotation, hand-paths during naïve performance (grey lines) are initially directed approximately 20~30° CCW to the target, as expected (column 2). During the performance following opposite arm adaptation (black lines), the effect of opposite arm adaptation, reflected by the differences in accuracy between the two sets of hand-paths (column 3), appears to be minimal. Such a trend was observed in all four task-space by arm conditions (visually shared/L, visually shared/R, physically shared/L, physically shared/R). Following adaptation to the visuomotor rotation, hand-paths in all performance conditions are directed relatively straight to the target and become substantially more accurate (column 4).

As stated above, a visual examination of hand-paths indicated a minimal effect of opposite-arm adaptation on subsequent performance with the other arm. To confirm this, I calculated direction error at $V_{\max}$ and at $A_{\max}$, which were subjected to a statistical analysis (only direction error at $V_{\max}$ was illustrated in Fig. 2B, because the performances were almost identical between these two direction measures). The mixed-factor ANOVA revealed a significant three-way interaction between group (LR, RL), epoch (1~12) and arm (L, R) for both direction errors ($P < .01$), which indicated that for the left arm, changes in performance across epochs were not different between the LR and RL groups. For the right arm, however, these changes were different between the two groups, in that the RL group reached the final adaptation level faster than the LR group. The final adaptation level was not different between the two groups. A significant two-way interaction between task-space and arm was also found for both direction errors ($P < .01$, indicating that the right arm performed better in the physically shared (i.e., midline) task-space condition than in the visually shared (i.e., lateral) task-space condition, although the performance was similar between the two conditions for the left arm.

To examine the extent of initial information transfer following opposite arm training, which was of main interest in this study, I made post hoc pair-wise comparisons using Tukey's test between naïve performance and performance following opposite arm adaptation (i.e., between group LR and group RL) at the first epoch for each arm, under each of the four task-space by arm combinations (visually shared/L, visually shared/R, physically shared/L, physically shared/R). Surprisingly, the results showed that despite a substantial improvement observed from the first to the last epoch of performance in every condition ($P < .001$), the performance following opposite arm training was not statistically different from naïve performance in any condition. The largest difference was observed for the comparison between the two left arm performance conditions for direction error at $V_{\max}$, in which the P value was .26, and the effect size was .47. This indicates that upon initial exposure to the visual rotation, neither the left nor the right arm benefited from opposite arm training, regardless of the task-space conditions.

Since the pair-wise comparisons using Tukey's test did not show a significant difference between the two performance conditions (i.e., between group LR and group RL) at the first epoch, I conducted a further analysis by finding a nonlinear logarithmic regression line for each arm performance. The slope, which represented the rate of learning throughout the course of adaptation, and the intercept, which represented the amplitude of errors in the beginning of adaptation, of the regression equation obtained from each subject for each arm were subjected to independent t-tests. As illustrated in figure 2B, the nonlinear curves were quite similar between the two performance conditions, and the slopes and the intercepts were not statistically different between the two performance conditions under any of the four task-space by arm combinations. The difference in these curves appear to be the largest for the left arm in the visually shared task-space in terms of direction error at $A_{\max}$ (not shown in figure 2), although

it was not statistically significant (naïve performance: $Y = 20.71 - 4.03 \ln(X)$, performance following opposite arm adaptation: $Y = 20.15 - 2.15 \ln(X)$; $P = .8$ for intercept, $P = .09$ for slope).

In fact, a close examination of these curves reveals some performance differences between the two performance conditions with the left arm in the visually shared condition and with the right arm in the physically shared condition, as shown in figure 2B. The direction of potential transfer in the comparisons, however, is opposite to what was originally expected, in that direction errors in naïve performance were actually smaller than those in the performance following opposite arm adaptation. This indicates that visual-motor dissociation of task-space might even cause interference in interlimb transfer.

Discussion

In the present study, I investigated how visual-motor dissociation of task-space would influence the transfer pattern of movement information obtained during a visuomotor rotation task from one arm to the other arm. I predicted that if the motor control system relied more on visual information of the task-space, symmetrical transfer of initial direction information (i.e., transfer from the left to the right arm, and vice versa), as demonstrated in our previous study (Wang and Sainburg 2006b), would occur when the task-space was visually unshared by the two arms (but physically shared in the current experiment). In contrast, if the system relied more on proprioceptive information, I predicted that the transfer of direction information would be asymmetric (i.e., transfer from the left to the right arm only) in the same task-space condition. The current data demonstrated that despite a substantial adaptation to the rotation by the end of the training session, the performance following opposite arm training did not differ from naïve performance, either at the first epoch (reflecting the extent of initial information transfer) or in terms of adaptation rate, thus indicating no transfer of direction information at all. This finding is quite surprising, considering that unambiguous positive transfer of direction information was observed in all our previous studies (Sainburg and Wang 2002; Wang and Sainburg 2004, 2006a, b) in which the experimental paradigm was almost identical to that used in the current study (i.e., same rotation task, same target directions, equal number of trials, equal or smaller number of subjects (six or seven subjects per condition in previous studies; seven in the present study), etc.).

The current study is somewhat similar to a recent study conducted by Woolley et al. (2007), who showed that two opposing visuomotor rotations could be learned in separated workspace regions. Their finding may indicate that two different visuomotor transforms associated with different workspace regions are independently represented in the nervous system, thus allowing dual adaptation to the opposing rotations to occur. This finding seems to be in agreement with the current finding, to suggest that the way a novel visuomotor transform is associated with a region of workspace in which the transform is learned plays an important role in determining the pattern, or characteristics, of visuomotor adaptation.

In our recent series of interlimb transfer studies, we demonstrated that initial direction information of reaching movement transfers asymmetrically when both arms learn a visuomotor rotation task in a shared workspace (Sainburg and Wang 2002; Wang and Sainburg 2004, 2006a, 2007a), whereas it transfers symmetrically when the task-space is separated for the two arms (Wang and Sainburg 2006b). Based on these findings, we suggested that asymmetries in interlimb transfer might result from a cognitive processing that involves a competition between available solutions, when task-space is shared by both arms. That is, when the two arms perform a visuomotor task in a shared workspace, the motor control system is provided with redundant solutions (i.e., two arms being available to perform the task in a given workspace), and has to decide which arm to use based on the current state of the system and

task conditions, such as accuracy and timing constraints (e.g., Fitts 1954), biomechanical considerations (e.g., Uno et al. 1989; Bagesteiro and Sainburg 2002) and comfort (e.g., Zhang and Rosenbaum 2007). During this process, competition arises between the alternative solutions, which include the two arms, and the executive system might selectively facilitate or inhibit the access of each arm controller to opposite-arm information, depending on task requirements for control of such factors as dynamic efficiency and limb impedance (Sainburg 2002), thereby reducing redundant (and competing) solutions when the task-space is *shared* by both arms. According to this idea, asymmetry in transfer occurs because the two arm controllers are differentially proficient for controlling different features of movement (i.e., dominant arm for controlling movement trajectory, nondominant arm for specifying final limb posture; Sainburg and Kalakanis 2000; Bagesteiro and Sainburg 2003; Wang and Sainburg 2007b), and the motor control system determines the direction of information flow depending on the compatibility between task requirements and arm proficiency. Thus, when the left arm performs a visuomotor adaptation task in a left workspace location following initial training with the right arm in a right workspace location, for example, the motor control system allows the nondominant controller to access all of the available information obtained during the right arm training, as indicated by a transfer of direction information from the right to the left arm (Wang and Sainburg 2006b), probably because the left arm is performing the task in a workspace in which the control system considers using this arm as a more affordable solution, as compared with using the right arm (Bryden & Roy, 2006; Gabbard & Helbig, 2004; Gabbard & Rabb, 2000). Such access would not be allowed if the left arm was performing the task in a workspace location shared by both arms, as observed in our previous studies (Sainburg and Wang 2002; Wang and Sainburg 2007a), because the control system would perceive using the right arm as a more viable option for controlling this type of information (i.e., trajectory control) in the given task-space. This idea of competitive processes that may occur between the two arm controllers during interlimb transfer is in agreement with a recent notion that animal solutions to the response-selection problem are achieved by a competition between available actions, requiring inhibition of the less competitive, alternative solutions (e.g., Cisek, 2007; Prescott, Redgrave, & Gurney, 1999; Reddi, Asrress, Carpenter, 2003; Roe, Busmeyer, & Townsend, 2001; Usher & McClelland, 2001).

The current finding, that visual-motor dissociation of task-space results in the lack of interlimb transfer, may be explained by this same idea. Using the example mentioned above, when the left arm performed the visuomotor task in a left workspace following the right arm training in a right workspace in the current study, the left arm visually shared the same, midline task-space with the right arm, although the actual task-space was not physically shared. This might develop a conflicting situation, because based on the visual information of the task-space condition, the left arm controller would not be given access to the direction information obtained during the initial training with the right arm, whereas based on the proprioceptive information, it would. It is, thus, speculated that a conflict between visual and proprioceptive information with respect to the sharing of the given task-space by the two arms may cause an interference in executive decision-making processes of the motor control system for determining hand dominance, or for selecting a more affordable solution, at a given workspace, which results in a lack of transfer across the arms.

The current finding may also be interpreted in such a way that the lack of interlimb transfer associated with the visual-motor dissociation of task-space is attributed to the development of two internal representations of the effector-environment relationship, one based on the visual information and the other on the proprioceptive information, that conflict with each other. It seems plausible that the motor control system is provided with these two internal representations, and that when the system perceives the discrepancy, or incongruency, between the two representations, it does not utilize the available information obtained during initial training with the opposite arm, and rather behaves as if it is performing the task for the very

first time (i.e., naïve performance). This is analogous to a finding reported in our previous study, that when the two arms experienced opposing directions of visuomotor rotation tasks (i.e., dominant arm experienced counterclockwise rotation, nondominant arm clockwise), neither facilitative nor detrimental transfer occurred across the arms, likely due to the fact that the two types of visuomotor transforms obtained were incompatible (Wang and Sainburg 2003). Similarly, Galea et al. (2007) recently reported that a concurrent adaptation to two opposing force fields with one arm transferred positively to improve subsequent performance of the same task with other arm across an intrinsic coordinative system, whereas across an extrinsic coordinative system, neither positive nor negative transfer was observed, probably because the information to be transferred was not useful (i.e., incompatible). This interpretation of the current finding also appears to be somewhat consistent with an idea recently proposed by Hwang et al. (2006), which states that two internal models are formed during adaptation to novel dynamics, one based on proprioception and the other on vision, and that performance is a sum of these two internal models. Especially given that the planning of reaches to visual and proprioceptive targets may involve distinct sensorimotor transformations (Bernier et al. 2007), it seems plausible that a conflict between these two types of internal representations may pose a serious computation problem to the motor control system. Collectively, these findings suggest that when the motor control system is provided with conflicting information from visual and proprioceptive sensors with respect to the sharing of a given task-space by the two arms, it may make an executive decision to disregard the available information obtained during opposite arm training, likely to avoid movement errors based on invalid sensory information.

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Figure 1.

Experimental setup. **A** Top view: the positions of the Flock of Birds sensors are shown. **B** Side view: subjects were seated in a dentist-type chair with the arm supported by an air jet system that removed the effects of friction on arm movement. Targets and the cursor representing finger position were back-projected on a screen placed above the arm. A mirror placed below this screen reflected the image, such that the projection was perceived in the plane of the arm. **C** Visually shared task-space condition: in this condition, targets were presented at the same locations for both arms, while each arm performed the task in its ipsilateral workspace. **D** Physically shared task-space condition: in this condition, the two arms performed the task in the same midline workspace, while the targets were presented laterally.

Figure 2.

A. Hand-paths of right arm performance from representative subjects. Each column shows hand-paths of eight consecutive trials during the final phase of the baseline session (column 1), during the initial phase of naive performance (column 2), during the performance following opposite arm adaptation (column 3, black lines; gray lines are the same as those in column 2, shown here for comparison purposes), and during the final phase of the adaptation session (column 4). B. Mean performance measures of direction errors at peak velocity. Every data point shown on X axis represents the average of 16 consecutive trials (epoch) across all subjects (mean $\pm$ SE). DA represents dominant arm, whereas NDA represents nondominant arm. Performance measures for naive performance (open circles) and performance following opposite arm adaptation (filled circles) are shown separately. Gray lines represent nonlinear logarithmic curve fits for naive performance, while black lines represent those for the performance following opposite arm adaptation (OAA).