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# The Synergistic Organization of Muscle Recruitment Constrains Visuomotor Adaptation

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**de Rudy A, Hinder MR, Woolley DG, Carson RG.** The synergistic organization of muscle recruitment constrains visuomotor adaptation. *J Neurophysiol* 101: 2263–2269, 2009. First published February 18, 2009; doi:10.1152/jn.90898.2008. Reaching to visual targets engages the nervous system in a series of transformations between sensory information and motor commands. That which remains to be determined is the extent to which the processes that mediate sensorimotor adaptation to novel environments engage neural circuits that represent the required movement in joint-based or muscle-based coordinate systems. We sought to establish the contribution of these alternative representations to the process of visuomotor adaptation. To do so we applied a visuomotor rotation during a center-out isometric torque production task that involved flexion/extension and supination/pronation at the elbow-joint complex. In separate sessions, distinct half-quadrant rotations (i.e., 45°) were applied such that adaptation could be achieved either by only rescaling the individual joint torques (i.e., the visual target and torque target remained in the same quadrant) or by additionally requiring torque reversal at a contributing joint (i.e., the visual target and torque target were in different quadrants). Analysis of the time course of directional errors revealed that the degree of adaptation was lower (by ~20%) when reversals in the direction of joint torques were required. It has been established previously that in this task space, a transition between supination and pronation requires the engagement of a different set of muscle synergists, whereas in a transition between flexion and extension no such change is required. The additional observation that the initial level of adaptation was lower and the subsequent aftereffects were smaller, for trials that involved a pronation–supination transition than for those that involved a flexion–extension transition, supports the conclusion that the process of adaptation engaged, at least in part, neural circuits that represent the required motor output in a muscle-based coordinate system.

## INTRODUCTION

Reaching to visual targets engages the nervous system in a series of sensorimotor transformations that relate target and hand position information to an operational goal, a desired movement, and the joint torques and muscular activity required to produce it (Shadmehr and Wise 2005). The respective roles played by these various transformations in the course of visuomotor adaptation remain to be adequately resolved. Adaptation to prismatic goggles involves sensory recalibration (visual and/or proprioceptive) (Harris 1965), although the presence of task-specific effects suggests that part of the adaptation also

occurs at subsequent stages (Simani et al. 2007; Sober and Sabes 2003; Welch et al. 1974). Results obtained during exposure to superimposed force fields provide evidence that adaptation occurs at least in part via levels of neural processing in which the task is represented in muscle- or joint-based coordinate systems (e.g., Gandolfo et al. 1996). Successful generalization to an unpracticed area of the workspace has for instance been found repeatedly when the mapping between joint torque and displacement, as opposed to the mapping between endpoint force and displacement, is maintained (Ghez et al. 2000; Malfait et al. 2002; Shadmehr and Massaoui 2000; Shadmehr and Mussa-Ivaldi 1994). The organization of muscle recruitment that underlies the production of joint torques (Cheung et al. 2005; d'Avella et al. 2003; Windhorst et al. 1991) also constitutes a possible basis for the remapping of motor commands to sensory feedback that is necessary for visuomotor adaptation to occur. It is therefore not clear whether the processes that mediate sensorimotor adaptation engage neural circuits that represent the required movement in joint-based and/or in muscle-based coordinate systems. Here, we present an experiment designed to assess the extent to which the adaptive process is constrained 1) by a joint-based reference frame and 2) by the presence of synergies that coordinate the muscles engaged in the production of the joint torques dictated by the task.

We applied a visuomotor rotation during a center-out isometric torque production task that involved the acquisition of radial targets with two degrees of freedom (df) at the elbow-joint complex: flexion–extension (FE) and supination–pronation (SP) (Fig. 1). In separate sessions, distinct half-quadrant rotations (i.e., 45°) were imposed such that adaptation could be achieved either by only rescaling the individual joint torques (i.e., the visual target and torque target remained in the same quadrant; condition SAME, Fig. 2) or by additionally requiring torque reversal at a contributing joint (i.e., the visual target and torque target were in different quadrants; condition DIFF, Fig. 2). Assuming that the extra requirement of torque reversal at a contributing joint would increase the complexity of a joint-based adaptation, we expected lower adaptation for this latter condition.

To differentiate the influence of a joint-based coordinate system from that of a muscle-based coordinate system, we made strategic use of the stereotypic patterns of muscle activation associated with the generation of joint torques in this task space that have been documented extensively (e.g., Buchanan et al. 1989; Jamison and Caldwell 1993; Sergio and

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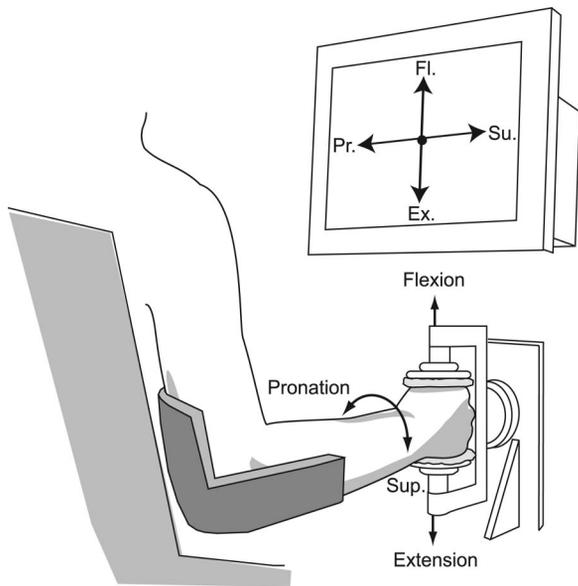


FIG. 1. Experimental apparatus.

Ostry 1994; Zuylen et al. 1988). The synergies expressed in this context reflect the requirement that the recruitment of muscles that have a selective mechanical action in one df (i.e., monofunctional muscles) be coordinated with that of muscles that have a simultaneous action in both dfs (i.e., bifunctional muscles). For example, biceps brachii (BB) and pronator teres (PT) have significant moment arms both for flexion and supination and for flexion and pronation, respectively (Murray et al. 1995). Accordingly, the activation of these muscles scales in proportion to the combined (i.e., 2 df) levels of torque required (Barry et al. 2005a,b; Buchanan et al. 1989; Cnockaert et al. 1975; de Rugy et al. 2008; Jamison and Caldwell 1993; Sergio and Ostry 1994; Shemmell et al. 2005a,b). These

muscles, however, are also engaged in combination with the main elbow extensor (i.e., triceps brachii [TB]) to generate pure supination and pure pronation, respectively (Buchanan et al. 1989; Ettema et al. 2005; Zuylen et al. 1988). The superposition of either flexion or extension torque on pure supination or pronation (i.e., condition DIFF/FE, Fig. 2) thus may not require the recruitment of additional muscles and could, in principle, be achieved by simply rescaling the respective contributions of muscles that are already engaged. In contrast, the generation of pure flexion and pure extension torques principally involves monofunctional muscles (i.e., brachialis [BRA] and brachioradialis [BRD]) for pure flexion and TB for pure extension (e.g., Sergio and Ostry 1994; Zuylen et al. 1988). In this instance, the superposition of either supination or pronation torques on pure flexion or extension (i.e., condition DIFF/SP, Fig. 2) requires the recruitment of muscles that have moment arms in the additional degree of freedom. This may be characterized as a transition to an alternative muscle synergy. The present study was designed to assess whether in such circumstances the rate and extent of visuomotor adaptation are lower than those in cases in which the imposition of a novel environment may not necessitate the use of a different muscle synergy.

## METHODS

### Subjects

Twelve subjects (eight male and four female, ages 23–42 yr) volunteered for this experiment. A second group of eight subjects was included for a control experiment described in the following text. All subjects were right-handed with normal or corrected-to-normal vision. Participants were naïve to the purpose of the experiment. They all gave informed consent prior to experiment, which was approved by the local ethics committee and conformed to the Declaration of Helsinki.

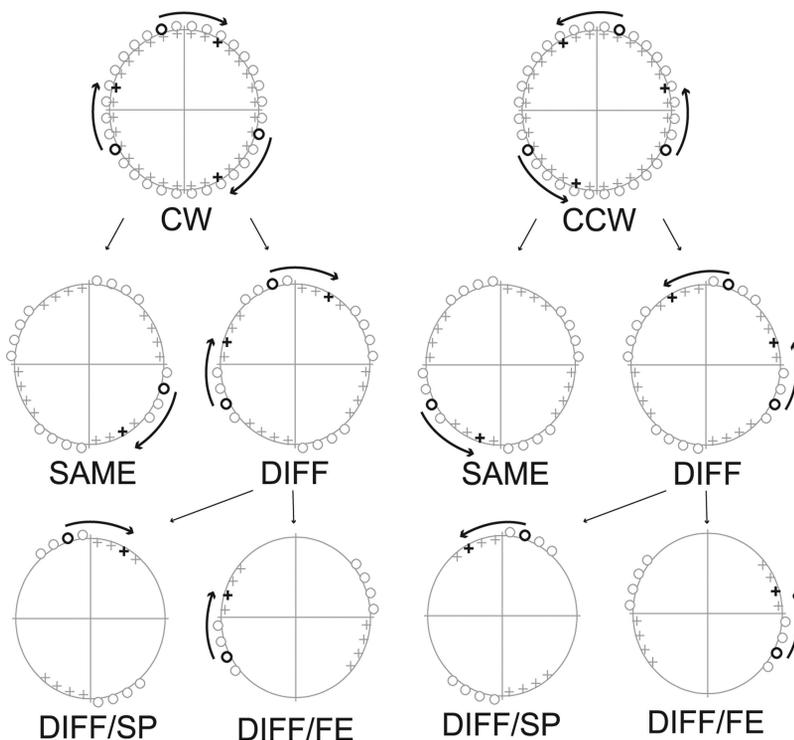


FIG. 2. Position of visual targets (circles) and rotated torque targets (crosses) during the TRAINING block for the clockwise (CW: left-hand diagrams) and counterclockwise (CCW: right-hand diagrams) visuomotor rotation. Visual and motor targets are slightly displaced from the circle for ease of viewing. *Middle diagrams*: trials from CW and CCW (*top diagrams*) are separated into quadrant conditions SAME and DIFF (*bottom diagrams*) according to whether the visual target and its corresponding rotated torque target belong to the same or different quadrants, respectively. *Bottom diagrams*: trials from DIFF are separated into condition DIFF/FE and DIFF/SP according to whether the rotation between the visual target and its corresponding torque target involved a transition between flexion and extension or a transition between supination and pronation, respectively. The visual and corresponding torque targets of a few example trials (one per separated condition) are displayed in black, with arrows indicating the corresponding visuomotor rotation.

### General experimental procedure

The setup was similar to that described in detail in previous reports (Hinder et al. 2007, 2008; Woolley et al. 2007). Subjects sat 65 cm from a computer display positioned at eye level. The right arm was placed in a padded brace with the elbow flexed at 90° and the forearm in neutral position, midway between pronation and supination (see Fig. 1). Subjects grasped an instrumented vertical cylindrical handle, with pads positioned above and below to minimize movements of the hand. A 6 df force/torque transducer (Delta ATI, Industrial Automation Systems, Sterling Heights, MI) was used to record flexion/extension and pronation/supination torques at 2 kHz.

Real-time visual feedback of the flexion–extension (vertical axis) and pronation–supination (horizontal axis) torques was represented on the visual display by a cursor. Visual feedback in the absence of visuomotor rotation corresponded to flexion and extension moving the cursor up and down along the vertical axis and supination and pronation moving the cursor right and left along the horizontal axis, respectively. The vertical and horizontal axes were not displayed on the screen. A low level of torque (i.e., no more than 10–20% of subjects' maximum torque capacity) was necessary to acquire targets, thus reducing the possibility of fatigue. This level of torque was identical across all subjects.

Each trial began with the cursor positioned in the center of the display, which was calibrated to zero torque along both axes (arm relaxed) prior to testing. A tone sounded on presentation of the target to indicate the start of the trial. Subjects were instructed to move the cursor from the start position over the target as fast as possible. When the cursor was moved into the target zone (i.e.,  $\pm 5\%$  of the torque requirements) and held there for 100 ms a second tone signaled target acquisition. At this time the subject relaxed and the cursor returned to the start position. Each trial lasted for 7 s, with the target appearing randomly within the first 2 s and a minimum of 5 s allowed to acquire the target. Although targets were typically acquired within 1 s of movement initiation, this was not the case in the initial part of the adaptation when the visuomotor rotation was first introduced. The large time allowance was therefore necessary to ensure target acquisition at all stages of the experiment.

Subjects completed two experimental sessions (clockwise [CW] and counterclockwise [CCW]), each comprising three separate blocks (PRE, TRAINING, POST) of trials. One of 32 radial visual targets was presented on each trial, with targets evenly distributed (11.25° intervals) around the start position (Fig. 2). Each block consisted of five consecutive sets of 32 trials (i.e., one per target, presented in a randomized order), giving rise to a total of 160 trials per block. The PRE and POST blocks incorporated visual feedback of the cursor position that was veridical (i.e., the cursor moved according to the direction indicated, Fig. 1), whereas the TRAINING block involved visual feedback that was rotated by 45° (either CW or CCW). The aim of the PRE block was to familiarize subjects with the manipulandum and to provide a baseline measure of performance. The TRAINING and POST blocks were used to assess the time course of the adaptation and any associated aftereffects. The two experimental sessions, CW and CCW, were performed on different days, interspaced by a minimum of 5 days. The order of sessions was counterbalanced across subjects.

### Data reduction and analysis

The accuracy of the feedforward commands was determined by the initial directional error, calculated as the averaged difference between the direction of the target from the initial cursor position and the direction of the cursor from the initial cursor position, in a 10-ms window centered at 100 ms after movement onset. Movement onset was determined using the algorithm proposed in Teasdale et al. (1993). By convention, positive errors are those that are opposite to the visuomotor rotation applied in the TRAINING block.

Baseline performance was calculated for each subject and session as the mean directional error obtained for the final 2 trials to each

target (i.e., 64 trials) in the PRE block. To adjust for small intersubject differences in baseline directional biases (Ghilardi et al. 1995), the directional error of trials performed in the TRAINING and POST blocks was corrected by subtracting the bias obtained during baseline performance.

Trials from visuomotor rotations CW and CCW were separated into quadrant conditions SAME and DIFF according to whether the visual target and its corresponding rotated torque target belonged to the same quadrant or to a different quadrant, respectively (Fig. 2). Within each visuomotor rotation and quadrant condition, the time course of adaptation was assessed using the mean directional error obtained over successive cycles of eight trials (giving rise to 10 cycles). Note that the resulting time courses of adaptation for conditions SAME and DIFF were each calculated on the basis of only half of the targets. A time course of adaptation that was representative of all visual and motor targets was obtained for each quadrant condition by averaging values from the two visuomotor rotations (CW and CCW). Trials from condition DIFF were further separated into conditions DIFF/FE and DIFF/SP according to whether the rotation between the visual target and its corresponding torque target involved a transition between flexion and extension or a transition between supination and pronation, respectively (Fig. 2, *bottom diagrams*). Trials from conditions DIFF/FE and DIFF/SP were similarly separated in 10 cycles and averaged over the two visuomotor rotations (CW and CCW).

A two-way repeated-measures ANOVA (2 quadrants  $\times$  10 cycles) was conducted on data obtained for the TRAINING and POST blocks. For statistically significant effects the proportion of total variability attributable to the factor concerned was reported as the value of partial eta-squared ( $\eta^2$ ) (see Pierce et al. 2004 for information about partial  $\eta^2$  measures). Pairwise comparisons between quadrant conditions were also conducted separately for each cycle when a significant main effect was obtained. The significance level was set to  $P < 0.05$ , with corrections for multiple comparisons (modified Bonferroni test) conducted as necessary following Keppel (1991).

### Control experiment

A control experiment was conducted on eight subjects, with movement of the cursor produced by isometric force generated at the wrist instead of isometric force generated at the elbow-joint complex. This control experiment was designed to test for a potential influence of an external reference frame. If an external reference frame has an influence on visuomotor adaptation in our task, this influence should similarly apply whether the task is performed with the elbow or with the wrist. In the wrist system, however, the mechanical actions of the constituent muscles are not as clearly aligned along the flexion–extension and radial–ulnar deviation axes (e.g., Hoffman and Strick 1999), and variations in the level of activation of the muscles across these two degrees of freedom are more gradual than those associated with the elbow complex. Specifically, the sharp boundary that exists between supination and pronation in terms of the set of muscle synergists involved with the elbow has no equivalent with the wrist. Therefore the control experiment performed with the wrist should isolate a potential effect of external reference frame in the task investigated.

The position of the participants' body, arm, and forearm was similar to that of the main experiment (Fig. 1). Instead of grasping the handle to exert FE and SP force at the elbow, the participants' forearm was fixed to the frame of the apparatus while their hand was clamped in alignment with the forearm and mechanically linked to the force transducer. Visual feedback in the absence of visuomotor rotation was aligned with the degrees of freedom of the wrist, with wrist flexion and extension moving the cursor left and right along the horizontal axis and radial and ulnar deviations moving the cursor up and down along the vertical axis, respectively. The protocol was similar to that of the main experiment except that one experimental session only (CW) was conducted. Data were similarly analyzed and separated into quadrant

conditions SAME and DIFF. Trials from condition DIFF were further separated into conditions DIFF/Horizontal and DIFF/Vertical according to whether the rotation between the visual target and its corresponding force target involved a transition that crossed the horizontal axis or the vertical axis, respectively. In terms of an external reference frame, DIFF/Horizontal and DIFF/Vertical involved transitions similar to those for conditions DIFF/FE and DIFF/SP of the main experiment.

## RESULTS

### *Adaptation is attenuated when torque reversal in a contributing degree of freedom is required*

As Fig. 3 illustrates, there was less adaptation to the visuomotor rotation for trials in which visual targets and their corresponding rotated torque targets were located in different quadrants (condition DIFF, which involved a reversal of the direction of torque in a contributing df), compared with trials in which they were located in the same quadrant (condition SAME). The two-way repeated-measures ANOVA (2 quadrants  $\times$  10 cycles) conducted on the directional error obtained during the TRAINING block revealed a large effect for cycle [ $F(9,99) = 82.58, P < 0.001, \eta^2 = 0.88$ ], for quadrant [ $F(1,11) = 20.12, P = 0.001, \eta^2 = 0.65$ ], and a significant interaction between these factors [ $F(9,99) = 2.05, P = 0.041, \eta^2 = 0.16$ ]. Pairwise comparisons revealed that directional error was reliably lower for condition SAME than that for DIFF for all but cycles 1, 2, and 7 (Table 1). The difference of  $5.7^\circ$  between the mean directional errors obtained for condition SAME and DIFF on the last cycle represents 20.6% of the total adaptation obtained for the condition SAME (i.e.,  $27.7^\circ$  difference between mean error in the first and last cycles). The final directional error obtained on the last cycle for condition DIFF ( $14.3^\circ$ ) was 1.66-fold that obtained for condition SAME ( $8.6^\circ$ ).

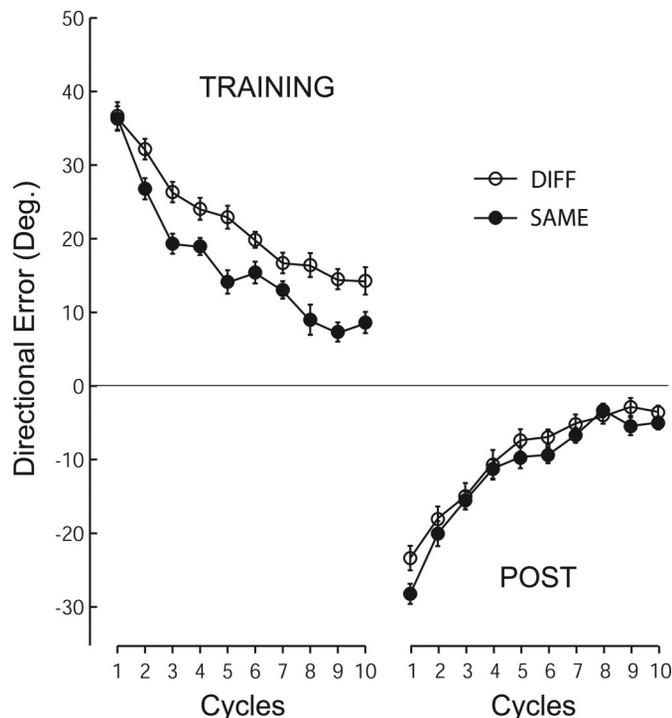


FIG. 3. Time course of the adaptation indicated by directional error (mean  $\pm$  SE) presented per cycle for quadrant conditions SAME (filled circles) and DIFF (open circles), for the TRAINING and POST blocks.

The two-way repeated-measures ANOVA conducted for the POST block revealed a large effect for the cycle [ $F(9,99) = 71.03, P < 0.001, \eta^2 = 0.86$ ] and an effect for the quadrant [ $F(1,11) = 4.83, P = 0.049, \eta^2 = 0.30$ ]. No interaction was observed and pairwise comparisons revealed no further significant differences (Table 1). The overall difference between directional errors obtained in conditions SAME and DIFF was  $1.8^\circ$ . The substantial difference between adaptations for the two quadrant conditions in the TRAINING block was therefore incompletely represented in the aftereffects obtained for the conditions SAME and DIFF.

### *Adaptation is attenuated when a different muscle synergy is engaged*

When the data from condition DIFF were separated according to whether the adaptation required engagement of a different set of muscle synergists (i.e., DIFF/SP) or not (i.e., DIFF/FE), Fig. 4 illustrates that adaptation during the TRAINING block was lower (i.e., higher directional errors) for the former condition than that for the latter [ $F(1,11) = 12.65, P = 0.004, \eta^2 = 0.52$ ]. Although directional errors for conditions DIFF/SP and DIFF/FE are both different from that of condition SAME [ $F(1,11) = 28.69, P < 0.001, \eta^2 = 0.72$  and  $F(1,11) = 10.29, P = 0.008, \eta^2 = 0.48$ , respectively], the magnitude of the effect corresponding to the contrast between DIFF/SP and SAME is larger, as indicated by the higher  $\eta^2$  value. Table 1 also indicates that the cycles for which differences between conditions DIFF/SP and SAME were obtained (comp. 3, Table 1) match those noted for the comparison of the conditions DIFF and SAME (comp. 1, Table 1). When the equivalent comparison was conducted for the differences between DIFF/FE and SAME (comp. 4, Table 1), the correspondence was present in only four of seven cycles.

Concerning the POST block, Fig. 4 illustrates that there were smaller aftereffects (i.e., lower absolute directional errors) for condition DIFF/SP than for conditions DIFF/FE [ $F(1,11) = 5.03, P = 0.046, \eta^2 = 0.31$ ] and SAME [ $F(1,11) = 8.12, P = 0.016, \eta^2 = 0.42$ ]. Conditions DIFF/FE and SAME, however, did not differ reliably [ $F(1,11) = 0.02, P = 0.88$ ]. It was only for the contrast between the conditions SAME and DIFF/SP therefore that the difference in the initial degree of adaptation was also expressed in terms of the magnitude of the aftereffect. This vagary serves to highlight the need for caution in relation to the interpretation of aftereffects. In that aftereffects also reflect retention, the constraints on their time course may differ somewhat from the factors that impinge on the rate of initial adaptation.

### *Effects described earlier were not observed in the control experiment performed with the wrist*

Inspection of Fig. 5 reveals that adaptation to the visuomotor rotation was unaffected by quadrant conditions. The two-way repeated-measures ANOVA (2 quadrants  $\times$  10 cycles) conducted on the directional error obtained during the TRAINING block and the POST block did not reveal any significant differences between conditions SAME and DIFF [all  $F(1,7) < 0.28$ , and  $P > 0.610$ ]. When the data from condition DIFF were separated according to whether they involved crossings of the horizontal or crossings of the vertical axis, conditions

TABLE 1. Results of the planned comparisons of means conducted for each cycle between directional errors produced in conditions SAME, DIFF, DIFF/SP, and DIFF/FE, for both TRAINING and POST blocks

Block	Comp.	Cycle									
		1	2	3	4	5	6	7	8	9	10
TRAINING	1	0.035	5.12	19.18**	13.91**	12.86**	7.15*	2.72	10.24*	17.85**	7.58*
	2	0.270	1.99	3.96	0.40	3.57	8.24*	1.85	0.32	1.68	1.01
	3	0.490	4.70	15.51**	10.34*	15.05**	16.18**	5.76	12.64**	18.58**	9.78*
	4	0.000	4.99	7.55*	14.89**	5.59	1.08	0.19	13.79**	14.81**	4.92
POST	1	5.035	1.00	0.10	0.07	2.54	5.71	1.54	0.14	3.14	0.98
	2	4.710	2.66	10.11*	2.58	2.98	0.09	2.41	0.01	1.75	0.26
	3	7.400*	3.57	3.68	2.48	5.17	2.07	1.68	0.02	2.59	3.53

The four pairs of conditions compared are as follows: Comp. 1: SAME versus DIFF; Comp. 2: DIFF/SP versus DIFF/FE; Comp. 3: SAME versus DIFF/SP; Comp. 4: SAME versus DIFF/FE. *F* values of the planned comparisons are presented separately for each cycle. \* $P < 0.05$ , \*\* $P < 0.01$ .

DIFF/Horizontal and DIFF/Vertical did not differ reliably from each other nor from condition SAME, neither in the TRAINING block nor in the POST block [all  $F(1,7) < 3.58$ , and  $P > 0.10$ ].

## DISCUSSION

In the present study, we assessed the extent to which the process of visuomotor adaptation is constrained by the presence of synergies that coordinate the muscles engaged in the production of the joint torques. We applied a rotation in the context of a carefully configured visual and motor workspace such that adaptation could be achieved either by rescaling the torques applied in the two constituent degrees of freedom (pronation–supination; flexion–extension) or by additionally requiring a reversal in the direction of the applied torque (e.g., from pronation to supination) in one of the degrees of freedom. The time course of directional errors obtained following the

imposition of the rotation revealed that the degree of adaptation was substantially lower (by ~20%) for the latter case. Furthermore, most of this difference, and its representation in the aftereffect subsequently expressed, could be attributed to a condition in which the adaptation is likely to have required the implementation of a different muscle synergy, rather than a rescaling of the respective contributions of the muscles engaged in the initial condition.

Our results indicate that at least part of the process of visuomotor adaptation occurs at a level of the CNS that represents the task in terms of specific patterns of joint torques. Converging evidence is provided by studies demonstrating that prism adaptation acquired during throwing of balls is specific to the movement involved (overhand or underhand) (Martin et al. 1996) or to the inertia of the arm (Fernandez-Ruiz et al. 2000). For reaching movements, Kitazawa et al. (1997) established that the adaptation is also specific to movement velocity:

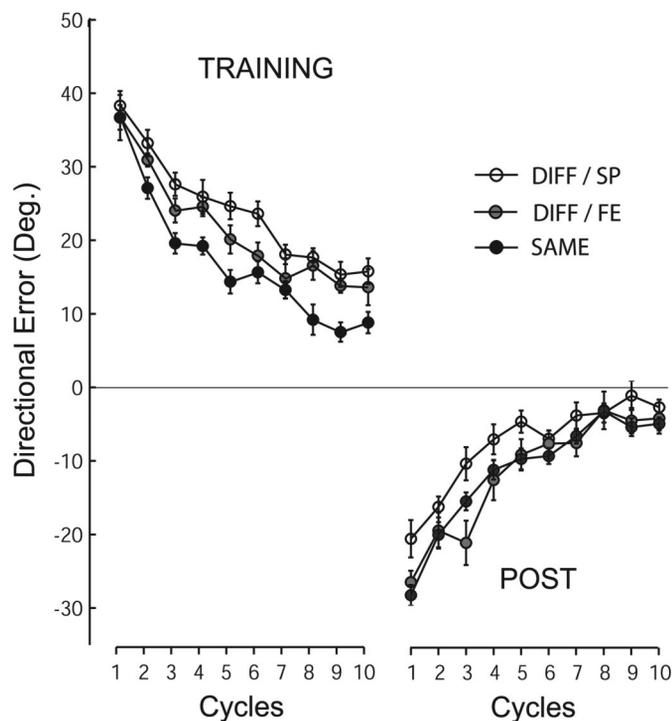


FIG. 4. Time course of the adaptation indicated by directional error (mean  $\pm$  SE) presented per cycle for quadrant conditions SAME (black circles), DIFF/SP (open circles), and DIFF/FE (gray circles), for the TRAINING and POST blocks.

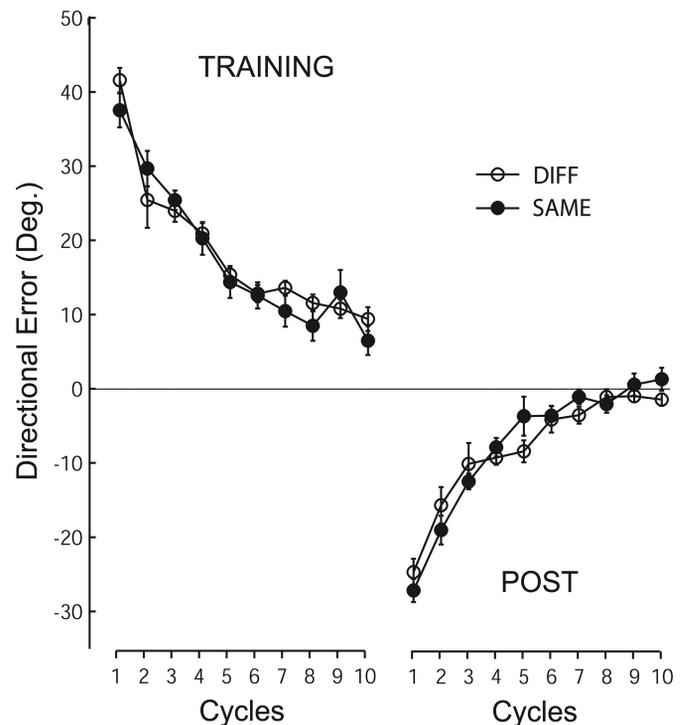


FIG. 5. Time course of the adaptation obtained for the control experiment performed with the wrist. Directional error (mean  $\pm$  SE) is presented per cycle for quadrant conditions SAME (black circles) and DIFF (open circles), for the TRAINING and POST blocks.

the aftereffect was maximal at the practiced velocity and decreased with deviations from that velocity. Baraduc and Wolpert (2002) showed that the degree of adaptation was sensitive to a change in the initial posture that affected the trajectory of the arm as it was defined in joint space, while not altering the endpoint trajectory. Results obtained during adaptation to superimposed force fields also provide a strong case that adaptation occurs at least in part via levels of neural processing in which the task is represented in muscle- or joint-based coordinate systems. For example, Gandolfo et al. (1996) found that aftereffects were specific to the grip and posture used to hold a manipulandum that applied a force field. This specific manipulation modified the joint torque as well as the muscle activity required to produce the movement, but not the force experienced at the end effector. Successful generalization to an unpracticed area of the workspace has also been found repeatedly when the mapping between joint torque and displacement, as opposed to the mapping between endpoint force and displacement, is maintained (Ghez et al. 2000; Malfait et al. 2002; Shadmehr and Massaoui 2000; Shadmehr and Mussa-Ivaldi 1994).

Although consistent with the results of the foregoing studies, our research goes further in revealing that there are specific constraints on the process of adaptation that do not pertain to posture, joint kinematics, and/or the magnitude of the underlying joint torques. Indeed, in the variants of our task, these factors were maintained constant throughout. The key factor that was varied was the requirement for a reversal in the direction of the applied torque in one of the degrees of freedom (e.g., from pronation to supination) following imposition of the rotation. The observation that less adaptation was obtained when a torque reversal was required could conceivably be attributed to a perturbation of an intuitive mapping between the direction of the applied torque and the displacement of the end effector (i.e., the cursor) in visual space. To the degree that pure flexion–extension and pure supination–pronation corresponded initially to vertical and the horizontal displacement of the cursor, discrimination of the required torques may have been facilitated. This direct mapping would no longer have applied following the rotation. Although an influence of the external reference frame represents a plausible alternative explanation of our results, the observation that most of the differences in the extent of the adaptation between conditions could be attributed to the requirement that a different synergy be engaged suggests that these constraints have as their basis neural circuits that represent the required motor output in a muscle-based coordinate system. Furthermore, any potential influence of an external reference frame should similarly apply when the same task is performed with another joint, as was the case when the wrist was used in our control experiment. None of the effects of the different quadrant conditions obtained in the main experiment, however, was observed in the control experiment when the task was performed with the wrist. This result therefore rules out the alternative explanation in terms of an external reference frame and reinforces our interpretation in terms of a muscle-based coordinate system.

Although we did not record muscle activity, our experiment was motivated by prior characterization of the patterns of recruitment that are manifested during the generation of torque in this task context (Barry et al. 2005a,b; Buchanan et al. 1989; Cnockaert et al. 1975; de Rugy et al. 2008; Ettema et al. 2005;

Gielen et al. 1988; Jamison and Caldwell 1993; Sergio and Ostry 1994; Shemmell et al. 2005a,b; Zuylen et al. 1988). The patterns of muscle activation are sufficiently stereotypic to permit the inference that the transition between flexion and extension around pure supination or pronation did not require the recruitment of additional muscles, but rather was achieved by rescaling the respective contributions of muscles that were already engaged. The transition between supination and pronation around pure flexion and pure extension, in contrast, is likely to have required the recruitment of additional muscles that were not engaged when the same visual targets were acquired before the visuomotor rotation was imposed. The lower adaptation obtained for the latter condition thus suggests that the synergistic organization of muscle recruitment imposes a significant constraint on visuomotor adaptation. The protocol used in the present study, however, does not permit identification of the specific processes mediating the selection, modulation, and/or combination of muscle synergies that may be implicated in the expression of this constraint. This constitutes an important challenge for future research.

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#### GRANTS

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