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RESEARCH NOTE

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Interference between velocity-dependent and position-dependent force-fields indicates that tasks depending on different kinematic parameters compete for motor working memory

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Abstract Humans demonstrate motor learning when exposed to changes in the dynamics of movement or changes in the visuomotor map. However, when two opposing dynamic transformations are learned in succession, the memory of the first is overwritten by learning of the second; the same is true for two opposing visuomotor rotations. This retrograde interference is not seen for all combinations of transformations, however. When a dynamic transformation is learned subsequent to a visuomotor rotation, the presence or absence of interference appears to depend crucially on the structure of the dynamic task: a force-field dependent on the position of the hand produces interference, whereas an inertial load applied lateral to the hand does not. To explain these results, it has been hypothesized that two transformations can be learned without interference if they depend on two different kinematic parameters of movement (such as position and velocity of the hand). Here we demonstrate, contrary to this hypothesis, interference between a dynamic transformation that depends on the position of the hand and one that depends on its velocity. However, the interference was found to be incomplete, supporting the view that the ability to retain motor memories for different tasks depends on the degree to which their representations conflict in working memory.

Keywords Motor control · Motor learning · Dynamics · Sequential adaptation · Interference

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Introduction

Our ability to rapidly learn and recall a single motor task stands in sharp distinction to our inability to learn two related, but different, motor tasks when they are presented in rapid succession. After a single exposure to a novel motor task, performance on the task exceeds that of novices even after a gap of several months (Brashers-Krug et al 1996; Gandolfo et al 1996; Wigmore et al 2002). However, exposure to a second motor task soon after the first can return performance on the first to novice levels. Learning the second task effectively extinguishes memory of the first, a phenomenon known as retrograde interference. Similarly, performance on the second task may be disrupted by the memory of the first: this is known as anterograde interference (Baddeley 1986, 1992; Brashers-Krug et al 1996).

These interference effects have been convincingly demonstrated in a number of studies in which subjects adapt to perturbations applied during reaching movements. When a dynamic perturbation, such as a state-dependent force field, or a visuomotor perturbation, such as a rotation of visual feedback, is first imposed it causes errors in movement trajectory and timing; with experience an internal model of the perturbation is acquired and errors decrease (Shadmehr and Mussa-Ivaldi 1994; Imamizu et al 1995; Gandolfo et al 1996; Goodbody and Wolpert 1998; Sainburg et al 1999). When two velocity-dependent rotary force-fields are experienced in succession, both of equal magnitude but acting in opposite directions, initial performance in the second force-field is worse than initial performance in the first, an example of anterograde interference. If subjects are subsequently retested in the first force-field, performance is no better than on first exposure, an example of retrograde interference (Brashers-Krug et al 1996). These interference effects have also been observed between two equal and opposite rotations of visual feedback (Krakauer et al 1999; Wigmore et al 2002), and between inertial loads applied at equal distances medially and laterally to the hand (Krakauer et al 1999). However, when the two perturbations are not directly opposite to each other retention is sometimes observed. Krakauer et al (1999) found that adaptation to an inertial load did not interfere with retention of a visual rotation, and proposed that adaptation to changes in limb dynamics occurs independently of adaptation to changes in hand kinematics. However, Tong et al (2002) showed that retrograde interference did occur when the inertial load was replaced by a position-dependent force-field, another type of dynamic transformation. To explain these apparently conflicting results they proposed that two perturbations can be learned independently if they depend on different kinematic parameters of movement (such as hand position and acceleration). This proposal is attractive because sensorimotor transformations encountered in everyday life can often be distinguished on the basis of the kinematic parameter upon which they depend. For example, the resistive force felt by the arm during a swimming stroke is proportional to its velocity, whereas the force experienced when lifting an object is proportional to its acceleration. Moreover, neural signals correlated with position, velocity and/or acceleration are ubiquitous in primates in both the central and peripheral nervous system (Cheney and Preston 1976; Johnson and Ebner 2000).

A previous study has sought to address this kinematic-parameter hypothesis (Bock 2003) in a visuomotor learning paradigm. Bock (2003) examined anterograde interference between two different visual perturbations: one in which hand position determined the cursor position (in a left–right or up–down reversal) and one in which hand position determined the cursor velocity.

Interference was observed between these two visual perturbations, and Bock (2003) interpreted this as evidence against the kinematic-parameter hypothesis. However, it should be noted that both of these visual distortions are, in fact, dependent on the same kinematic parameter of movement—the position of the hand. The difference between the two perturbations is how the hand position affects the cursor movement. The kinematic-parameter hypothesis was proposed to account for the results of studies in which the perturbations depended on different kinematic parameters of the hand, such as the hand's position, velocity or acceleration. Therefore, this previous study, while important in its own right, does not constitute a test of the kinematic-parameter hypothesis. In the present study we directly test the kinematic-parameter hypothesis by examining interactions between two dynamic perturbations that depend on different kinematic parameters of movement: a position-dependent and a velocity-dependent force-field. If the hypothesis is correct, no interference should be seen when these two fields are learned in close temporal proximity.

Materials and methods

After providing written informed consent, 24 right-handed subjects (12 male, 12 female, aged 18–40) participated in the experiment at the Institute of Neurology in London. The experimental protocol was approved by a local ethics committee. While seated, subjects grasped with their right hand a robotic manipulandum (Phantom Haptic Interface 3.0, Sensable Devices, MA, USA) which could be moved freely in three dimensions. Subjects made movements to virtual targets located in a horizontal plane. The targets and position of the hand were represented as virtual spheres using a three-dimensional stereoscopic system (Fig. 1a; for full details of the set-up see Goodbody and Wolpert 1998); subjects could not see their hand or arm. The spheres repre-

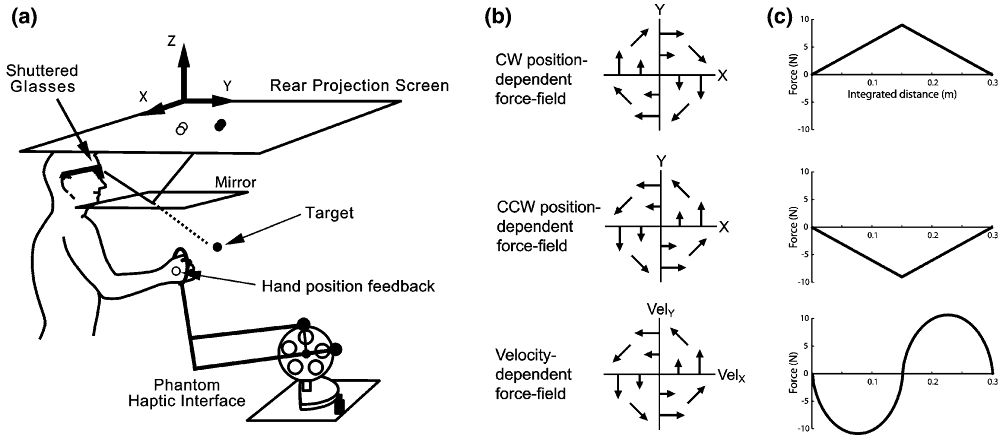

Fig. 1a–c **a** The experimental apparatus. Looking down at the mirror through field sequential glasses, the subject sees virtual representations of the hand and the target. The Phantom Haptic Interface generates state-dependent forces on the hand. **b** Schematic vector-field representations of the force-fields over the horizontal workspace. The *arrows* show the direction and magnitude of the force applied to the hand as a function of the position or velocity of the hand. **c** The force applied to the hand as a function of the integrated distance travelled during a simulated out-and-back movement to a target, for each force-field. The simulated movement consists of minimum-jerk trajectories (Flash and Hogan 1985) from the starting position to the target and back to the starting position

senting targets (green) and the sphere showing the position of the hand (white) were 1 cm in radius. The three-dimensional force exerted by the manipulandum on the hand was servo-controlled at 1 kHz in order to create force-fields in the horizontal plane.

Subjects made out-and-back movements to eight targets arranged radially at a distance of 15 cm from a central starting position 20 cm below shoulder level and in the subject's midsagittal plane. Targets were presented one at a time in a counter-clockwise sequence; a cycle was defined as a set of eight successive trials, one to each target. Subjects were instructed to move their hand out to the target and back to the starting position in a single quick continuous motion. An auditory and visual signal was given 450 ms after the start of the movement (defined as the first time the distance of the hand from the starting position exceeded 2 cm) and subjects were instructed to time each movement so that they arrived back at the starting position coincident with this signal.

Subjects were randomly assigned to one of four groups of equal size ($n=6$). All subjects were first familiarised with the apparatus and task by making three cycles of movements during which no force-field was applied. Over the following two days subjects then completed between one and three sessions of 30 cycles under a variety of force-fields, according to the schedule shown in Table 1. Session 1 was completed immediately following the familiarisation period, session 2 followed 5 min after completion of the first, and session 3 took place on the following day, at least 18 h after the start of the first session. Within each session, subjects were given a brief (1 min) rest period every five cycles to prevent fatigue.

Under the position-dependent rotary force-fields, the manipulandum applied a force at the hand proportional to the displacement of the hand away from the starting position and directed perpendicular to the hand displacement vector (Tong et al 2002). The following equation was used to compute the force applied:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k_\mathrm{p} \begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix},$$

Where x and y are the coordinates of the hand in the horizontal plane relative to the starting position, F_x and F_y are forces acting in the horizontal plane, and k_p equals 60 N/m. Two opposite position-dependent force-fields were used, varying only in their sign, such that the force acted to move the hand either clockwise (θ equals $-90°$) or counter-clockwise (θ equals $+90°$) about the start position; in Table 1 these transformations are denoted "CW Position" and "CCW Position" respectively. Vector-field representations of these force-fields are shown in Fig. 1b (top and centre). The forces these fields would produce during a simulated out-and-back movement are shown in Fig. 1c (top and centre).

Table 1 Experimental conditions

Group	Day 1		Day 2
	Session 1	Session 2	Session 3
Group 1	CW Position		CW Position
Group 2	CW Position	CCW Position	CW Position
Group 3	CW Position	Velocity	CW Position
Group 4	Velocity		

Under the velocity-dependent force-field, the force applied was proportional to the velocity of the hand and directed perpendicular to the hand velocity vector (Brashers-Krug et al 1996), according to the following equation:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k_v \begin{bmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix},$$

Where $\dot{x}$ and $\dot{y}$ are the components of the velocity of the hand in the horizontal plane, k_v equals 10 Ns/m, and θ equals $+90°$. The sign of the transformation was such that a movement outward from the start position produced a force that tended to move the hand counter-clockwise (Fig.1b and c, bottom). This transformation is denoted "Velocity" in Table 1. The magnitudes of the position-dependent and velocity-dependent force-fields were chosen so that the peak force experienced during a movement was similar for both fields. The means of the peak force (across the subjects) in session 1 in the position-dependent and velocity-dependent fields were 9.55 and 9.29 N respectively, with no significant difference between subject means ($F_{(1,22)}=0.44$; $P=0.52$).

The position of the hand was recorded at 200 Hz using the encoders of the robot. To measure performance we calculated the average absolute perpendicular distance between the hand path (for all points more than 2 cm from the start position) and the straight line connecting the starting and target positions, measured in the horizontal plane. Thus a straight-line movement to the target and back would result in zero error for that movement, and any deviation from a straight line increased the error score irrespective of the direction of the deviation. We used the average distance rather than the integrated distance because the average distance measures perturbations to the hand path independently of the overall timing of the movement, whereas an error score equal to the integrated distance would be biased against movements that took longer to complete.

Previous studies have used a variety of different measures to assess performance under dynamic and visuomotor perturbations, including the directional error at peak outward velocity, the correlation between the perturbed hand path and a previously-recorded unperturbed hand path to the same target, the normalized length of the hand path, and the normalized area enclosed by the hand path. We chose as our error measure the absolute perpendicular distance between the hand path and a straight line because this measure is insensitive to total movement time, takes into account the position of the target, and reflects errors throughout the entire movement.

Following the procedure used by Krakauer et al (1999) and Tong et al (2002) we assessed initial performance in a session for each subject by calculating the mean error score over movements in the second and third cycles, and final performance by calculating the mean error over movements in the last two cycles of the session. Within-group and between-group comparisons of performance were made using analysis of variance (ANOVA) on these measures. Where statistically significant between-group differences were found, post hoc comparisons were performed according to Fisher's least significant difference procedure for three means.

Results

On two successive days, three groups of subjects (1, 2, and 3) made reaching movements in a position-dependent rotary force-field. The solid lines in Fig. 2a–c show the mean performance of each group of subjects during their first session in the force-field. Initially the force-field caused subjects to make large deviations from a straight-line path, but over the course of the session subjects adapted to the perturbation and errors substantially decreased. The average mean perpendicular deviation across subjects fell from 2.22 cm (SE = 0.12 cm) in cycles 2 and 3 to 1.06 cm (SE = 0.05 cm) in cycles 29 and 30, and this decrease was statistically significant ($P < 0.05$) for all three groups.

In order to obtain a measure of retention of force-field learning in the absence of further learning, subjects in group 1 performed no further training on day 1. On returning the next day they completed another session of movements in the same position-dependent field they had previously experienced. Mean performance in this session is shown by the dashed line in Fig. 2a. These subjects showed considerable retention of the previous day's learning: their average error over cycles 2 and 3 ($M = 1.13$ cm, SE = 0.09 cm) was significantly less ($F_{(1,5)} = 56.1$; $P < 0.001$) than over the same cycles of the first session ($M = 2.32$ cm, SE = 0.24 cm) and was not significantly different ($F_{(1,5)} = 2.67$; $P = 0.16$) from their error over the last two cycles of the first session ($M = 0.97$ cm, SE = 0.06 cm).

Subjects in group 2 underwent the same training protocol as group 1, except that they were exposed to a second session of force-field training 5 min after the end of the first session on day 1. This second position-dependent force-field produced forces equal and opposite to those produced by the previously-learned field. The dashed line in Fig. 2b shows the performance of this group when retested in the original force-field on day 2. Their initial performance on day 2 ($M = 2.09$ cm, SE = 0.22 cm) was substantially impaired compared to the initial day 2 performance of group 1 subjects who had not experienced the opposing force-field (overall effect of group: $F_{(2,15)} = 6.31$, $P = 0.01$; post hoc comparison of groups 1 and 2: $F_{(1,10)} = 15.7$, $P = 0.0027$) and was not significantly different ($F_{(1,5)} = 0.75$; $P = 0.43$) from their performance over the same cycles in the first session ($M = 1.83$ cm, SE = 0.16 cm). This demonstrates complete retrograde interference between the two opposing position-dependent force-fields.

In order to test the hypothesis that perturbations which depend on different kinematic parameters of movement can be learned independently, subjects in group 3 completed the same experimental protocol as those in group 2, except that the force-field experienced during the second session of day 1 was velocity-dependent. The dashed line in Fig. 2c shows their performance

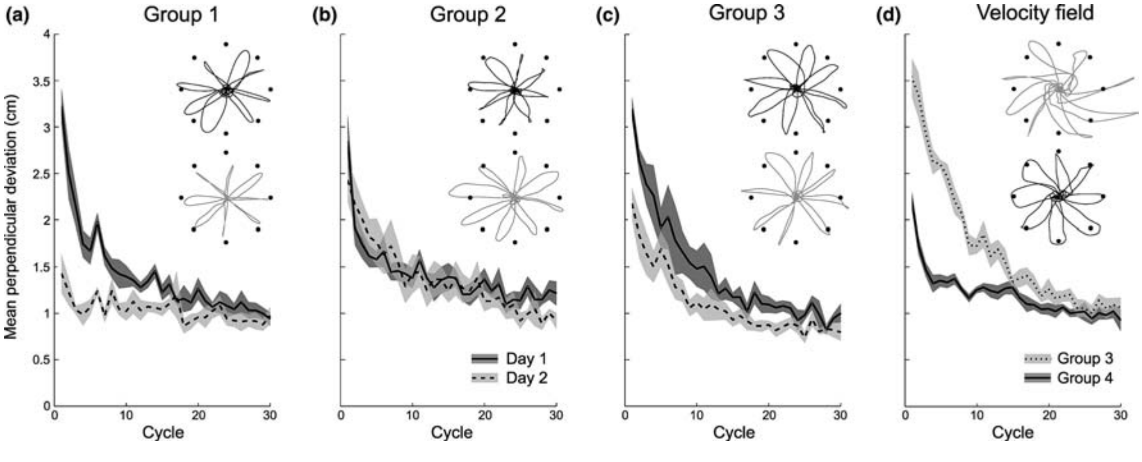

Fig. 2a–d Adaptation to the force-fields. *Curves* show the mean perpendicular deviation from a straight line as a function of cycle. The height of the *grey area* represents ±1 SE. *Insets* show for each group a typical subject's hand paths corresponding to the second cycle of each curve (the *grey tones* of the paths match those of the corresponding learning curves). **a**–**c** Performance in the clockwise position-dependent force-field in the first session on day 1 (*solid lines*) and on day 2 (*dashed lines*). **a** Results from subjects in group 1, who were only exposed to the clockwise position-dependent field on day 1. **b** Results from subjects in group 2, who completed a second session on day 1 during which they adapted to a counter-clockwise position-dependent field. **c** Results from subjects in group 3 for whom the second session on day 1 consisted of adaptation to a velocity-dependent force-field. **d** Performance in the velocity-dependent force-field. Subjects in group 3 (*dotted line*) adapted to the velocity-dependent field 5 min after completing a session of 30 cycles in the clockwise position-dependent field. Subjects in group 4 (*solid line*) had not been exposed to any force-field prior to the velocity-dependent field

when retested in the original position-dependent field the next day. Initial performance of this group on day 2 ($M = 1.74$ cm, SE = 0.23 cm) was significantly worse than the initial day 2 performance of group 1 (post hoc comparison, $F_{(1,10)} = 5.99$; $P = 0.034$) and not significantly different from the initial day 2 performance of group 2 (post-hoc comparison, $F_{(1,10)} = 1.19$; $P = 0.30$). These results clearly show that adaptation to the velocity-dependent force-field produced substantial retrograde interference on recall of the previously-learned position-dependent force-field. However, the subjects in group 3 did show reliably better ($F_{(1,5)} = 23.1$; $P = 0.0049$) initial performance on day 2 than in the first session of day 1 ($M = 2.51$ cm, SE = 0.15 cm), suggesting that adaptation to a velocity-dependent force field, unlike an opposing position-dependent field, did not entirely erase previous learning. This difference in retention of learning between groups 2 and 3 was confirmed by a significant ANOVA interaction term between day and group for these subjects ($F_{(1,10)} = 9.06$; $P = 0.013$).

In addition to retrograde interference, previous studies have also demonstrated anterograde interference between opposing perturbations, in other words an impairment in learning a second perturbation when it is experienced after adaptation to an opposite perturbation (Brashers-Krug et al 1996; Caithness et al 2004). Figure 2d shows the mean performance of group 3 subjects in the velocity-dependent force-field (dotted line) along with performance of subjects in group 4 (solid line), who experienced the same force-field without previous exposure to the position-dependent field. Initial performance of group 3 ($M = 3.14$ cm, SE = 0.19 cm) was significantly worse ($F_{(1,10)} = 55.5$; $P < 0.001$) than initial performance of group 4 ($M = 1.61$ cm, SE = 0.08 cm) demonstrating a substantial anterograde effect from the previously-learned position-dependent force-field on adaptation to a velocity-dependent field. Similar anterograde effects have been shown when adapting to opposing position-dependent force fields (Caithness et al 2004). Performances of both groups improved over the course of the session in the velocity-dependent field ($F_{(1,5)} > 57.6$; $P < 0.001$) and there was no significant difference in final performance between the two groups ($F_{(1,10)} = 0.74$; $P = 0.41$). Similarly, performance of group 2 in the second position-dependent field was initially poor ($M = 3.69$ cm, SE = 0.21 cm; data not shown) but improved substantially over the course of the session ($F_{(1,5)} = 29.6$; $P = 0.0028$; final performance: M = 1.86 cm, SE = 0.21 cm).

Discussion

Humans adapt their motor output to compensate for perturbations in the visual and motor environment. Re-adaptation to a previously experienced perturbation is often very rapid, suggesting that the memory of the previous learning has been stored and is now being recalled. However, the ability to store and recall multiple adaptations is limited, and interference effects are observed. Consistent with previous results from studies of dynamic learning, in this study we have demonstrated that once a subject has adapted to a position-dependent force-field this learning is retained for at least 24 h (Caithness et al 2004). Also in agreement with previous findings we have shown that adaptation to an opposite position-dependent force-field results in complete retrograde interference, returning performance on the original force-field to novice levels (Caithness et al 2004). In general, whether interference is observed between two perturbations depends crucially on their structure. Tong et al (2002) proposed that perturbations which depend on different parameters of movement can be learned without interference. However, contrary to this hypothesis, in this study we have demonstrated substantial interference, both retrograde and anterograde, when adaptation to a position-dependent force-field is followed by adaptation to a velocity-dependent force-field.

Bock (2003) found interference between two visuomotor tasks which depended on the same parameter, hand position, but determined different kinematic parameters of a cursor, its position or velocity. In contrast, in the current study we have observed interference between two perturbations that depend on different kinematic parameters of movement (hand position and hand velocity) but determine the same dynamic parameter: force on the hand. This result is inconsistent with the kinematic-parameter hypothesis. Despite the differences between these studies, our findings in dynamic learning may well be consistent with the conclusions of this previous study, that “the magnitude of interference between two successive adaptation sessions depends on the overlap of the involved neural structures” (Bock 2003).

It has been suggested that the observed patterns of interference between dynamic tasks and visuomotor rotations could be explained in terms of the coordinate systems in which the perturbations are learned (Krakauer et al 1999). Some types of learning generalize (and are therefore believed to be represented) in extrinsic coordinates, such as Cartesian space, whereas other perturbations generalize in intrinsic coordinates, such as joint space. The hypothesis is that perturbations which are represented either both in extrinsic or both in intrinsic space will interfere, whereas an extrinsic and an intrinsic perturbation can be learned independently of each other. Visual rotations are known to be learned in extrinsic coordinates related to the position of the arm in space (Krakauer et al 2000). The fact that they do not interfere with inertial loads (Krakauer et al 1999) would suggest, under this hypothesis, that the latter are learned in intrinsic coordinates related to the sensors and muscles of the arm (Sainburg et al 1999). Velocity-dependent force-fields are also known to be learned in intrinsic coordinates (Shadmehr and Mussa-Ivaldi 1994; Gandolfo et al 1996). If position-dependent force-fields are learned in extrinsic coordinates then the interference observed here would conflict with the hypothesis. If position-dependent force-fields are learned in intrinsic coordinates then the interference seen in Tong et al (2002) would conflict with the hypothesis. Therefore, the hypothesis that extrinsically-represented and intrinsically-represented transformations are learned independently cannot account for all the data.

One difference between the current study and that of Krakauer et al (1999) is that we provided visual feedback of the hand position during the dynamic learning, whereas they withheld it. A previous study (Tong et al 2002) examined visual feedback during dynamic learning and its role in interference with a visuomotor task. Interference was found to be independent of the presence or absence of visual feedback during the dynamic task, suggesting that visual feedback is not an important factor in these interference studies.

Although the retrograde interference we have shown between velocity-fields and position-fields is substantial, some retention of learning of the original force-field was observed. It is apparent that learning of a velocity-dependent field does not entirely erase previous learning of a position-dependent field, unlike learning of an opposing position-dependent field. Similarly, adaptation to a position-dependent field produces only partial retrograde interference on retention of a visual rotation (Tong et al 2002), while an opposing visual rotation produces complete interference (Krakauer et al 1999; Wigmore et al 2002). After adaptation to a visuomotor transformation, only partial transfer of learning is seen to a new initial arm posture (Baraduc and Wolpert 2002); this finding suggests that adaptation does not occur at the level of endpoint kinematics, but rather may reflect changes at the level of the motor command specifying joint dynamics or muscle activations. If this is the case, it may be that the amount of interference between two perturbations depends upon the extent to which the required adjustments to this motor command conflict, with complete interference only when the required motor adjustments are exactly opposite. The visual rotation used by Tong et al (2002) and the velocity-dependent field used in this study both require adjustments to the motor command that, if the perturbation were switched off, would send the hand clockwise of the target on the outward movement. In contrast, the adjustment learned during adaptation to the position-dependent force-field used in both studies is such that it would send the hand counter-clockwise of the target, thus the motor adjustments strongly conflict and interference is observed. The inertial load used by Krakauer et al (1999) did not appear to have a strong rotary consequence on the hand path and so the observed absence of interference with visuomotor learning may occur because there is little conflict between the adjustments to the motor command required for each task. A strong prediction of this motor-adjustment hypothesis is that there should be little or no interference between any two perturbations (whether dynamic or visuomotor) that require uncorrelated motor adjustments and facilitation for perturbations that require similar motor adjustments (Bock et al 2001; Wigmore et al 2002).

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