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RESEARCH ARTICLE

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Are there distinct neural representations of object and limb dynamics?

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Abstract In recent studies of human motor learning, subjects learned to move the arm while grasping a robotic device that applied novel patterns of forces to the hand. Here, we examined the generality of force field learning. We tested the idea that contextual cues associated with grasping a novel object promote the acquisition and use of a distinct internal model, associated with that object. Subjects learned to produce point-to-point arm movements to targets in a horizontal plane while grasping a robotic linkage that applied either a velocity-dependent counter-clockwise or clockwise force field to the hand. Following adaptation, subjects let go of the robot and were asked to generate the same movements in free space. Small but reliable after-effects were observed during the first eight movements in free space, however, these after-effects were significantly smaller than those observed for control subjects who moved the robot in a null field. No reduction in retention was observed when subjects subsequently returned to the force field after moving in free space. In contrast, controls who reached with the robot in a NF showed much poorer retention when returning to a force field. These findings are consistent with the idea that contextual cues associated with grasping a novel object may promote the acquisition of a distinct internal model of the dynamics of the object, separate from internal models used to control limb dynamics alone.

Keywords Human motor learning · Multi-joint arm movement · Internal model · Force field adaptation · Limb dynamics

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Introduction

A remarkable feature of the primate motor system is its ability to generate skilled movements under a wide variety of environmental conditions. It has been proposed that a neural representation of the motor effectors and the environment is developed when learning to adjust the control of the arm to suit new mechanical requirements (Shadmehr and Mussa-Ivaldi 1994; Flanagan and Wing 1997; Conditt and Mussa-Ivaldi 1999; Kawato 1999; Gandolfo et al. 2000; Gribble and Scott 2002). This compensatory adjustment is referred to as motor learning and the corresponding neural representations have been referred to as internal models (Kawato 1999).

Motor learning has been explored extensively by observing human subjects adapting to novel dynamics produced by robotic devices that are grasped in the hand (Shadmehr and Mussa-Ivaldi 1994; Conditt et al. 1997; Gandolfo et al. 2000; Bays et al. 2005; Malfait et al. 2005; Mattar and Gribble 2005). It has been proposed that this kind of motor learning is based on internal models of dynamics (Shadmehr and Mussa-Ivaldi 1994). In these studies and those like them, however, it is important to recognize that the novel dynamics are transmitted through devices that are grasped in the hand (for exceptions, see Lackner and Dizio 1994; Sainburg et al. 1999). Here, we explore the idea that when subjects learn to compensate for the perturbing effects of novel force fields produced by such devices, they are learning something specific about the grasped object. Under this framework, when the nervous system is confronted with a novel force field, sensory cues associated with grasping the novel object in the hand promote the formation of a distinct internal model corresponding to the object, without modifying existing neural representations used to control the limb on its own.

We tested this possibility directly by assessing transfer of adaptation between force field learning using a robot, and the same movements of the limb in free space, produced without grasping the robot. Human subjects were instructed to reach to targets while grasping the end of a robotic linkage which applied velocity-dependent rotational forces to the hand. After subjects adapted to the perturbing effects of the forces they were instructed to generate the same reaching movements without the robot (and thus in the absence of forces). Performance of these subjects was compared with that of a control group, who also underwent force field learning but subsequently generated movements while still grasping the robot in a null field.

If learning results in a change to an internal model of movement dynamics including limb and robot together, movements subsequently produced in free space would result in transfer of learning, and would be indicated by large after-effects. Similarly, after moving in free space for a period of time and returning to the force field, transfer of reaching in free space and a reduction in retention would be expected, and would be indicated by a reduction in performance in the force field. In contrast, if learning consists of the acquisition of a distinct internal model corresponding to the dynamics of the robot, no transfer and thus no after-effects would be expected when subjects let go of the robot and produce movements in free space. Similarly, no reduction in retention, and thus no reduction in performance would be observed when subjects subsequently return to the force field after reaching in free space.

Materials and methods

Subjects

A total of 21 right-handed subjects (12 males, 9 females) between the ages of 15 and 28 years (mean 22.4 years) participated in the experiments described here. All subjects reported normal or corrected vision, no history of neurological, or musculoskeletal disorder and gave their written informed consent before participation. All procedures were approved by the University of Western Ontario Research Ethics Board.

Apparatus

Subjects grasped the end of the InMotion2 robotic device (Interactive Motion Technologies) with their right arm abducted at the shoulder and supported by a custom fabricated air-sled placed under the upper arm (Mattar and Gribble 2005). The wrist was immobilized using an orthotic splint. By moving the robot in a horizontal plane subjects guided the motion of a cursor to a series of visual targets, which were back-projected using a computer controlled LCD projector onto a screen suspended 20 cm above the hand and reflected into view by a semi-silvered mirror positioned 10 cm below the screen. This resulted in the perception of virtual targets floating in the plane of the subject's hand.

The robot was programmed to apply forces to the hand during reaching movements to targets. Forces were velocity-dependent and were applied perpendicular to the instantaneous direction of hand movement, in a clockwise (CW) or counterclockwise (CCW) direction according to the following equation:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k \begin{bmatrix} 0 & d \\ -d & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \qquad (1)$$

where F_x and F_y are robot generated forces in the left/right and forward/backward direction, respectively, $\dot{x}$ and $\dot{y}$ are hand velocities, $k = 25$ Ns/m, and $d = +1.0$ (CW) or -1.0 (CCW). Thus forces applied by the robot were zero at movement start and movement end, and reached a maximum at peak hand tangential velocity. Robot forces were controlled using custom software running under the RT Linux operating system on a Pentium 4 CPU. Robot handle positions, velocities and applied forces were sampled at 200 Hz and stored on a digital computer for analysis.

During trials in which subjects let go of the robot and moved the limb in free space, a magnetic motion tracker, flock of birds (Ascension Technologies) attached to the hand was used to track motion of the limb. Hand position was sampled at 100 Hz and stored on digital computer for analysis. Trials in which subjects grasped the robot were used to verify the correspondence between robot positions and flock of birds position (see Results).

Experimental task

Subjects were instructed to move quickly and accurately between a central start target (corresponding to shoulder and elbow joint angles of 45° and 90°) and eight targets spaced equally around the circumference of a circle. Targets were 24 mm in diameter and were located 10 cm away from the central start location. Subjects were asked to complete each movement within a timing window of 200–300 ms. Feedback about movement time was given on each trial by changing the color of the target.

Subjects were randomly assigned to one of four groups (Table 1). Following a brief period of familiarization with the robot and the speed requirements of the task, all subjects performed a block of 16 movements (B1) while grasping the robot in a null field (no forces).

Table 1 Subject groups and experimental design

	B1 (16)	B2 (16)	B3 (192)	B4 (40)	B5 (40)	B6 (40)
G1 $N=6$	NF	FS	CW FF		FS	CW FF
G2 $N=5$	NF	FS	CW FF		NF	CW FF
G3 $N=5$	NF	FS	CCW FF		FS	CCW FF
G4 $N=5$	NF	FS	CCW FF		NF	CCW FF

The flock of birds sensor was activated during this block in order to verify the correspondence between flock of birds and robot positions (see below). All subjects then let go of the robot and performed a block of 16 movements in free space (B2); the flock of birds sensor was used to record hand positions. Subjects then performed a block of 192 movements in a CW or CCW force field (B3). The flock of birds sensor was not activated during this block, and positions were recorded using the robot. A series of 12 randomly occurring catch-trials in which the force field was unexpectedly turned off were also used to assess the degree of adaptation during learning. A second block of 40 movements were then collected in the same force field (B4), with the flock of birds sensor activated. This allowed us to re-test the correspondence between flock of birds and robot position data for movements in which the robot motors were active (see below). Three catch-trials were used in B4.

Following force field learning, subjects performed a block of 40 movements (B5) in free space or while grasping the robot in a null field. The flock of birds sensor was activated during this block and recorded hand positions. Subjects who let go of the robot and reached in free space were instructed to curl their fingers into a fist so as to mimic the grasp of the robot handle, and to produce movements at the same speed as the previous block of movements in which the robot was grasped. Finally all subjects then performed a final block of 40 movements (B6) while grasping the robot in a CW or CCW force field. Block B6 contained three catch-trials.

Data analysis

Performance on each trial was characterized by a measure of movement curvature defined as the maximum perpendicular distance from a line segment between start and target locations (Shadmehr and Brashers-Krug 1997; Thoroughman and Shadmehr 1999; Malfait et al. 2005; Mattar and Gribble 2005). Other similar measures such as angular error and path length yielded qualitatively similar results. Individual curvature scores were collapsed across bins of eight movements, and differences between group means were tested using analysis of variance (ANOVA) and Tukey post hoc tests. Data analyses were carried out using custom software routines in Matlab (The Mathworks).

Results

Figure 1a shows mean performance across subjects who learned a CW force field and then reached in free space (G1, see Table 1), and subjects who reached in a null field with the robot after force field learning (G2). A split-plot ANOVA was used to test for differences in movement curvature between G1 and G2 over the six experimental blocks. No differences between were present during the first block of 16 movements in a null field (B1, $P > 0.05$), during the second block of 16 movements in free space (B2, $P > 0.05$), or during the third and fourth blocks of movements in the CW force field (B3, B4, $P > 0.05$). When subjects in G2 then reached with the robot in a null field (B5), they showed large after-effects in a direction opposite the initial perturbing effects of the force field. The mean of the first eight movements in null field for G2 was significantly different than the mean of the last eight movements in the CW force field ($P < 0.01$, see Fig. 1b), and was also significantly different than the mean of the last eight movements in the null field prior to force field learning (B1; $P < 0.05$). In contrast, a smaller but nevertheless statistically reliable after-effect was observed for subjects in G1, who let go of the robot and reached in free space. Mean curvature over the first eight movements in B5 was significantly larger than the last eight movements in B4 for the same subjects ($P < 0.01$), but was significantly smaller than the after-effect (B5) of subjects in G2 who reached with the robot in a null field ($P < 0.01$). In addition the mean curvature of the first eight movements in free space was significantly different than the last eight movements made in free space, prior to force field learning (B2; $P < 0.05$).

Similarly, when subjects returned to the CW force field (B6), subjects in G1 who let go of the robot in B5 and reached in free space showed significantly greater retention of the CW forces than subjects in G2 who maintained a grip on the robot in B5. Mean curvature for the first eight movements in B6 was significantly smaller for subjects in G1 than for those in G2 ($P < 0.01$). Moreover, performance of subjects who let go of the robot in B5, when returning to the CW force field in B6, was not different than their performance in the last few trials of the CW force field (B4). Mean curvature for subjects in G1 for the first eight movements in B6 was not significantly different than for the last eight movements in B4 ($P > 0.05$). In contrast mean curvature for subjects in G2 who maintained a grip on the robot in B5 was significantly greater for the first eight movements in B6 compared to the last eight movements in B4 ($P < 0.01$).

To explore the nature of the after-effect observed in B5 when subjects reach in free space, we tested two additional groups of subjects who trained on an opposite (CCW) force field. If the after-effect is indeed related to previous training, its direction should be opposite when the direction of forces is opposite. In contrast if the small after-effect is due to some non-specific aspect

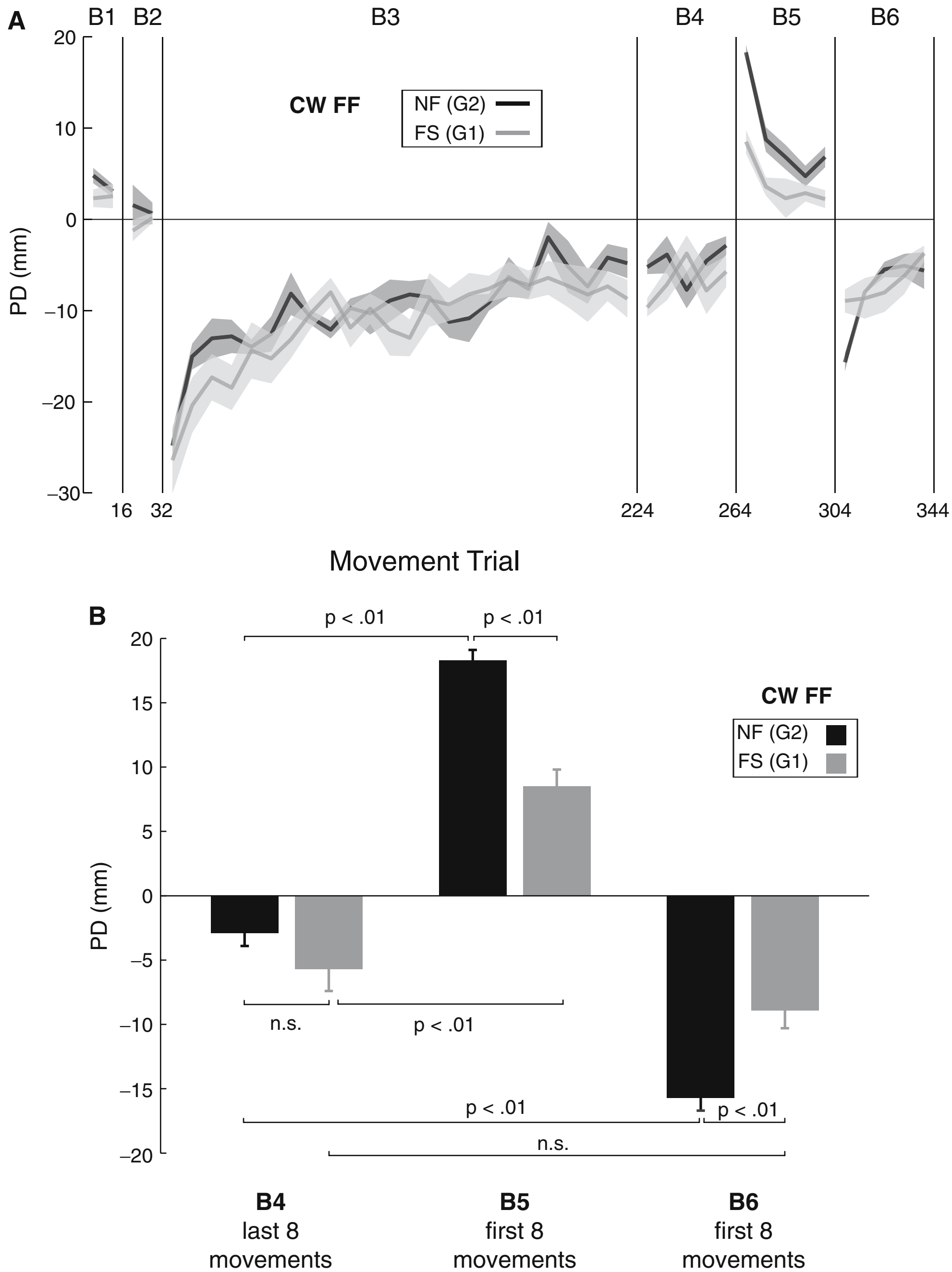

Fig. 1 **a** Movement curvature for subjects who performed reaching movements in free space after CW force field learning (*gray*) and control subjects who performed the same movements while grasping the robot in a null field (*black*). Means of eight consecutive movements are plotted; *shaded regions* indicate one standard error of the mean. **b** Mean curvature for subjects reaching in free space and subjects reaching in a null field, for the last eight movements in the CW force field (B4), first eight movements in free space or null field (B5), and first eight movements when returning to the CW force field (B6). *Vertical bars* indicate one standard error of the mean

of letting go of the robot (e.g. some effect of the reduced inertia on the limb), it may remain the same.

Figure 2a shows the results for groups G3 and G4, who trained in a CCW force field. In general, the same pattern of results was observed as for subjects who trained with CW forces. The same statistical tests described above for the subjects who learned CW forces were conducted, and the results of all tests were the same. Importantly, the small after-effect was again observed in B5, and for subjects who learned a CCW force field, the direction of the after-effect changed. This suggests the after-effect is not a non-specific result of letting go of the robot, but instead is a reflection of the previously learned forces.

Catch-trial performance

Performance on catch-trials was examined as another way of assessing the degree of adaptation during learning, and as a way of assessing retention of force field adaptation as subjects returned to the force field after reaching either in free space or in a null field. Large curvature on catch-trials indicates that subjects are ac-

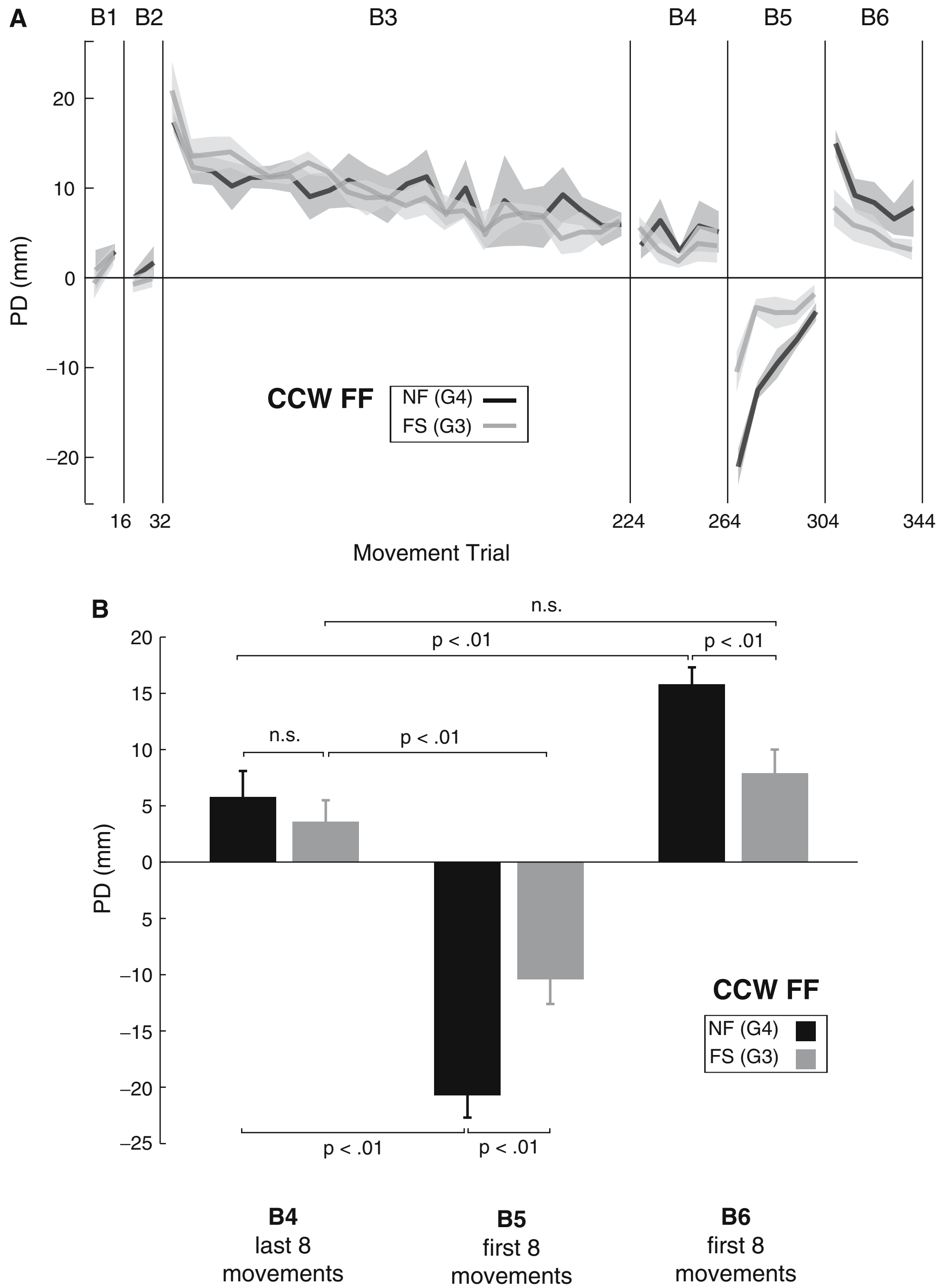

Fig. 2 **a** Movement curvature for subjects who performed reaching movements in free space after CCW force field learning (*gray*) and control subjects who performed the same movements while grasping the robot in a null field (*black*). Means of eight consecutive movements are plotted; *shaded regions* indicate one standard error of the mean. **b** Mean curvature for subjects reaching in free space and subjects reaching in a null field, for the last eight movements in the CCW force field (B4), first eight movements in free space or null field (B5), and first eight movements when returning to the CCW force field (B6). *Vertical bars* indicate one standard error of the mean

tively compensating for forces; low curvature on catch-trials would indicate that subjects are no longer compensating for the forces.

Split-plot ANOVA was used to test for differences in mean curvature across subject groups and movement blocks. Figure 3a shows mean catch-trial performance for subjects in groups G1 and G2 who learned a CW force field. At the beginning of learning (block B3), movement curvature for the first catch-trial was close to zero, indicating little adaptation had taken place at that time. No differences were observed between movement curvature on the first catch-trial in B3 for subjects in groups G1 compared to G2 ($P > 0.05$). By the end of training, curvature on catch-trials was significantly higher, indicating adaptation to the forces. For both subjects in groups G1 and G2, the mean curvature for the last catch-trial in B4 was significantly larger than for the first catch-trial in B4 ($P < 0.01$ in both cases). The magnitude of curvature on catch-trials at the end of block B4 was the same for subjects in groups G1 and G2 ($P > 0.05$).

When returning to the force field (B6) after subjects had either reached in free space (group G1) or reached while grasping the robot in a null field (group G2), a

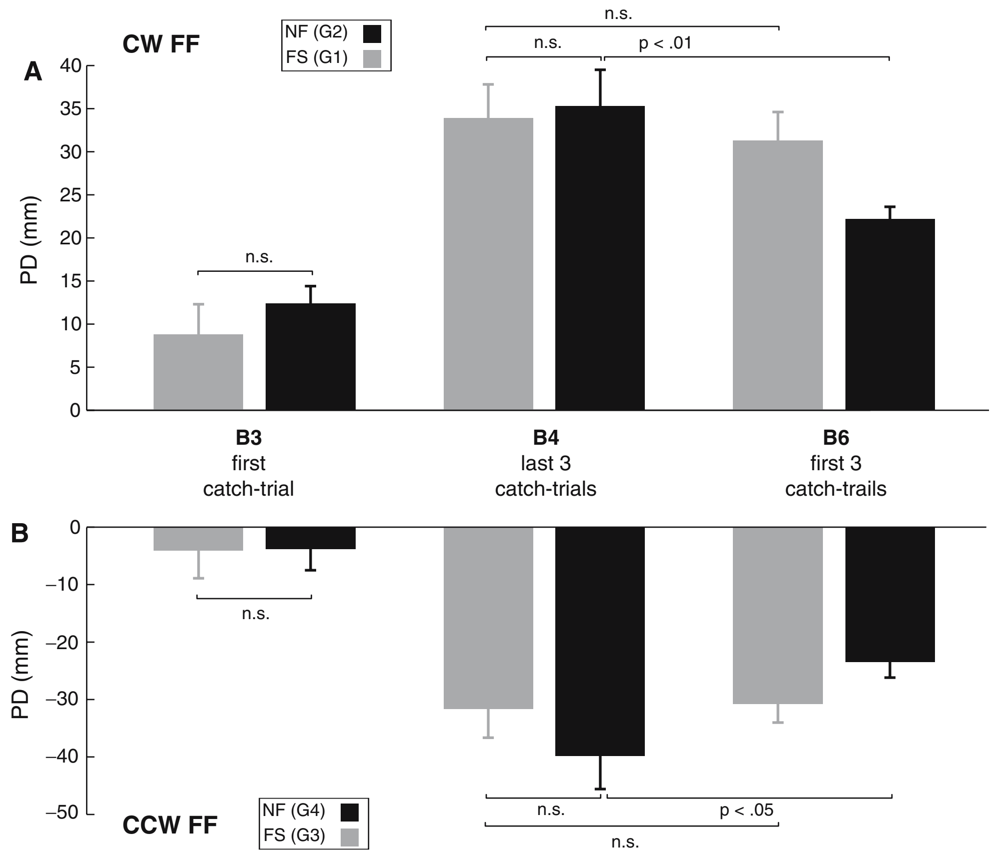

Fig. 3 **a** Performance on null field catch-trials for subjects who were trained in a CW force field in blocks B3 and B4. Mean curvature for the first catch-trial in B3 (beginning of training), last 3 catch-trials in B4 (end of training) and first 3 catch-trials in B6, after returning to the CW force field after having either reached in free space (subjects in group G1) or after reaching with the robot in a null field (G2). *Vertical bars* indicate one standard error of the mean. **b** Catch-trial performance for CCW force field training

different pattern of catch-trial performance was observed. For subjects in G1 who reached in free space in B5, the magnitude of curvature on catch-trials was the same as at the end of learning, in B4. This indicates retention of the CW force field learning. For subjects in G1, no difference was observed between the mean catch-trial at the end of B4 and the first catch-trial at the beginning of B6 ($P > 0.05$). In contrast, for subjects who were reaching while grasping the robot in a null field in B5, the magnitude of curvature on catch-trials when returning to the force field in B6 was significantly reduced. This indicates poorer retention of the CW forces after having reaching in a null field. For subjects in G2 who grasped the robot in B5 and reaching in a null field, the mean magnitude of curvature on the catch-trial at the beginning of B6 was significantly smaller than at the end of B4 ($P < 0.01$).

The same pattern of results was observed for subjects in G3 and G4 who trained in a CCW force field (Fig. 3b). The results of all statistical tests were the same as for subjects who trained with CW forces.

Control tests

It should be noted that the free space condition is accompanied by a sudden reduction in inertia due to the absence of the robot (the effective mass of the robot's endpoint is roughly 400 g). It is possible that this inertial reduction may cause a systematic bias in movement curvature. To control for this possibility, we compared performance of subjects in block B1, in which they moved in a NF while grasping the robot, and B2, in which they let go of the robot and reached in free space. For each group, a paired-samples *t* test was used to test differences in mean curvature in B1 and B2. For all four groups tested (G1–G4), no significant differences were observed between the mean movement curvature in B1 and in B2 ($P > 0.05$ in all cases). Moreover, if a reduction in inertia affects movement curvature, the resulting change should be constant in its direction and magnitude. Figures 1 and 2 both show that during B5 the direction of the small after-effects in free space vary with the direction of previous FF learning (see Figs. 1, 2).

It is possible that changes in movement curvature observed when subjects let go of the robot and reached in free space (B5) may have been due to differences in movement speed. To test this possibility we compared mean peak tangential velocity of movements in which subjects reached in free space, to mean peak tangential velocity for those controls who reached while grasping the robot in a NF (G1 vs. G2 and G3 vs. G4). Independent samples *t* tests showed no significant differences between mean peak tangential velocity in the first eight trials of B5 between G1 and G2 (mean = 0.3314 m/s, SE = 0.0153 m/s and mean = 0.3691 m/s, SE = 0.0473 m/s, respectively,

$P > 0.05$) or between G3 and G4 (mean = 0.3375 m/s, SE = 0.0606 m/s and mean = 0.3703 m/s, SE = 0.0190 m/s, respectively, $P > 0.05$).

Finally, we tested the possibility that recorded positions (and thus measures of movement curvature) recorded using the flock of birds system, which is based on electromagnetics, may have been distorted due to the nearby presence of the robotic linkage, which has many metal parts. To test this we compared mean curvature measurements computed using robot positions to those computed using flock of birds positions in block B1, in which both systems were actively recording data. For each of the four subject groups (G1–G4) we used paired-samples t tests to compare mean curvature in B1 computed using robot positions to those computed using flock of birds positions. In all cases no significant differences were observed between robot-based and flock of birds curvature measurements ($P > 0.05$ in all cases).

The possibility also exists that measurements using the flock of birds system may have been distorted specifically during those movements in which the robot was actively producing forces, due to increased electromagnetic radiation from the robot motors. To test for this possibility we compared mean curvature measurements based on robot positions to those based on flock of birds positions, during block B4, in which both systems were actively recording position data, and during which the robot was actively producing forces. We used paired-samples t tests to compare mean curvature in B4 using robot-based measurements to those based on flock of birds positions. For each of the four subject groups, no significant differences were observed between robot-based and flock of birds curvature measurements ($P > 0.05$ in all cases).

Discussion

Here we tested the idea that the sensory and motor cues associated with grasping a novel object in the hand would promote the acquisition of a new internal model of dynamics of the object, without disrupting the existing internal model used to control the limb alone.

When subjects who were trained in a CW or CCW force field let go of the robot and reached to targets in free space, we observed significantly reduced after-effects compared to controls who performed movements while still grasping the robot in a null field. Nevertheless, after-effects were still present, indicating some degree of carryover of force field learning to free space reaching. In contrast, when subjects who reached in free space subsequently returned to the force field, no significant change in performance was observed. This indicates that subjects who reached in free space did not suffer any loss in retention. In contrast, subjects who reached in a null field while grasping the robot showed significant reductions in performance when subsequently returning to the force field, indicating a lesser degree of retention as a result of moving in a null field. Performance on catch-trials showed a similar pattern: full retention of force field adaptation for subjects that reached in free space, and significant decreases in retention for subjects who reached in a null field while still grasping the robot.

These results are not compatible with a scheme in which a single neural representation of movement dynamics incorporating the limb and robot together, is modified as a result of learning. If this were the case, performance of subjects who reached in free space after learning a novel force field should be the same as for subjects who reached in a null field. The present results are consistent with a framework in which force field learning is based on the acquisition of a new internal model of object dynamics, distinct from that already in existence for controlling the limb. Indeed, it has been shown that stereotyped patterns of muscle activation associated with compensating for interaction torques due to limb dynamics are particularly resistant to adaptation, even after several hundred training trials (Koshland et al. 2000; Debicki and Gribble 2004; Debicki and Gribble 2005).

Grasping an object with the hand may be a powerful contextual cue that aids in the acquisition of a distinct model of object dynamics. The myriad changes in somatosensory, proprioceptive and haptic information associated with grasping the robot handle may represent a powerful contextual cue that allows the motor system to switch, to a greater extent, between different models of dynamics. In addition the sensory consequences of the sudden decrease in inertia associated with letting go of the robot handle may also play a similar role. When control subjects moved in a null field while still grasping the robot handle, the absence of these changes may have resulted in a persistence of the most recent model of dynamics, namely that associated with the recently learned forces (Mattar and Ostry 2005).

Previous work on retention of force field learning suggests that subjects who adapted to novel force fields showed significant retention many months after initial training (Shadmehr and Brashers-Krug 1997). Presumably, the many contextual cues associated with the experimental task, including the grasp of the hand around the robot, were sufficient to promote the recall of the previously learned force field. Moreover, both normal and amnesic subjects showed after-effects related to the previously learned force field when they returned to reach with a robot several hours following initial training (Shadmehr et al. 1998).

A recent study of motor learning using a robotic device to deliver forces to the limb suggests that the sensory cues associated with internal model acquisition may not be limited to the hand. Subjects who learned to move in a novel force field while grasping a handle showed complete transfer of learning when they released their grasp and the load was applied to the arm segments directly (Davidson et al. 2005). This suggests that when the load was applied to the hand or to the arm segments directly, the same neural representation of the load was used to control movement. The sensory signals associated with the robotic exoskeleton pressing against the skin, were likely sufficient cues to promote the use of the same internal model of dynamics. In the present study the sudden absence of any sensory cues related to the force field presumably acted as a strong contextual cue.

Different kinds of contextual cues may have differing effects on the ability of the motor system to switch between models of dynamics. Changes in limb posture, but not other cues less related to the motor requirements of the task, have been shown to promote a reduction in interference when learning to move in different force environments (Gandolfo et al. 1996). The nature of training may also affect the ability to acquire multiple representations of dynamics. Training schemes in which different force fields were presented in random order were better at promoting the acquisition of multiple models of dynamics than those in which forces were presented in consecutive blocks or in regularly alternating trials (Karniel and Mussa-Ivaldi 2002; Osu et al. 2004). Monkeys that were trained for several months using color cues associated with different force fields were able to successfully alternate between tasks with little or no loss in performance (Krouchev and Kalaska 2003).

Patterns of grip force adjustments during object manipulation tasks suggest that the motor system is capable of rapidly compensating for the inertial effects of grasped objects (Flanagan and Wing 1997). It has been proposed that this ability is based on distinct neural representations of object dynamics that are used to predict load forces of moved objects. These predictions presumably enable the nervous system to produce appropriate grip forces in parallel with limb movement commands, avoiding the problems associated with sensory feedback delays (Wolpert and Flanagan 2001). A more recent study of grip force modulation during object manipulation is consistent with the idea that the motor system is capable of acquiring distinct neural representations of grasped objects. Subjects first lifted two objects that looked the same but had different masses. As in previous studies, with practice, subjects predictively scaled grip forces to match load forces associated with object motion. When subsequently asked to lift both objects when stacked on top of each other, subjects were able to scale grip force appropriately for the sum of the load forces. This is consistent with the idea that two distinct neural representations of the two objects were combined in order to estimate the load forces associated with the combined object (Davidson and Wolpert 2004).

We have shown here that subjects who returned to a force field after having reached in free space were able to fully retain their previous learning without retroactive interference from free space reaching. This is clearly consistent with the view that a model of robot dynamics, distinct from the existing model of limb dynamics, is acquired during training. However, when first letting go of the robot and reaching in free space, after-effects related to the previous training, although significantly smaller than those of controls, were still present. This indicates that some (reduced) aspect of training is carried forward even when subjects are no longer grasping the robot. This observation is not inconsistent with the idea that a separate model of robot dynamics is acquired during learning. In a recently proposed scheme for motor learning that is based on multiple representations of dynamics it is suggested that multiple internal models, each based on different previously acquired sensory-motor learning experiences, may be combined in a continuous fashion for a given motor task (Kawato 1999; Haruno et al. 2001). The output of existing representations of dynamics may be combined in a weighted fashion depending partly on signals related to task context. In the experiments described here the major change in contextual cue from block B4 to B5 was that subjects no longer grasped the robot handle. However, many other contextual cues remained the same for the subject—e.g. the movement targets, the arm posture, the movement speed, and the overall task requirements and goals. The results presented here are consistent with a view in which the grasp of the robot handle is one of many potential contextual cues that are capable of differently weighting neural representations of limb dynamics and distinct neural representations of object dynamics.

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