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Visual Cues Signaling Object Grasp Reduce Interference in Motor Learning

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Cothros N, Wong J, Gribble PL. Visual cues signaling object grasp reduce interference in motor learning. *J Neurophysiol* 102: 2112–2120, 2009. First published August 5, 2009; doi:10.1152/jn.00493.2009. Recent motor learning studies show that human subjects and nonhuman primates form neural representations of novel mechanical environments and associated forces. Whereas proficient adaptation is seen for a single force field, when faced with multiple novel force environments, movement performance and in particular the ability to switch between different force environments declines. It is difficult to reconcile these findings with the notion that primates can proficiently switch between multiple motor skills. Conceivably, particular kinds of sensory, cognitive, or perceptual contextual cues are required. This study examined the effect of visual feedback on motor learning, in particular, cues that simulated interaction with a virtual object. A robot arm was used to deliver novel patterns of forces (force fields) to the limb during reaching movements. We tested the possibility that subjects transition more easily between novel forces and their sudden absence when they are accompanied by visual cues that relate to object grasp. We used a virtual display system to present subjects with different kinds of visual feedback during reaching, including illusory feedback, indicating grasp of a virtual object during reaching in the force field, and object release in the absence of forces. Throughout the experiment, subjects in fact maintained grasp of the robot. We found that, indeed, the most effective visual cues were those associating the force field with grasp of the virtual object and the absence of the force field with release of the object. Our findings show more broadly that specific visual cues can protect motor skills from interference.

INTRODUCTION

An impressive feature of the human motor system is its ability to execute different skilled movements as the situation warrants. In the laboratory, motor learning has been explored by studying how subjects form neural representations of novel forces. In a typical experiment, subjects reach to visual targets while grasping a robotic device that applies a novel pattern of forces (force field) to the hand. Evidence of motor learning has been reported using this method both in behavior, in subjects' ability to offset the forces and restore straight reach trajectories (Conditt et al. 1997; Gandolfo et al. 1996; Shadmehr and Mussa-Ivaldi 1994), and in neurophysiological measurements, for example in altered patterns of neural activity in motor regions of the brain (Brashers-Krug et al. 1996; Gandolfo et al. 2000; Gribble and Scott 2002; Li et al. 2001).

Recent studies have shown that force field learning is hindered when subjects are required to transition between different force fields (Brashers-Krug et al. 1996; Caithness et al. 2004; Cothros et al. 2008; Davidson and Wolpert 2004; Shadmehr and Brashers-Krug 1997) or switch between reaching in a force field and a null field, in which no forces are applied (Caithness et al. 2004; Cothros et al. 2006b; Thoroughman and Shadmehr 1999). Difficulties that arise because of learning multiple skills have been attributed to interference effects (for review, see Wixted 2004), which are thought to arise because of persisting neural representations of previously learned motor skills (Cothros et al. 2006a; Muellbacher et al. 2002; Richardson et al. 2006). Another recent view is that switching between multiple motor skills may be problematic because of contextual retrieval effects (Krakauer et al. 2005).

Whether or not difficulties in switching between motor skills are caused by interference effects from persisting representations of previous skills or by retrieval effects, proficient switching is likely dependent on sensory, perceptual, and/or cognitive cues that signal required changes in neural control signals for movement (Cothros et al. 2006b; Gandolfo et al. 1996; Hwang et al. 2006; Imamizu et al. 2007; Osu et al. 2004; Wada et al. 2003). Without informative contextual cues, it is conceivable that previously learned motor behavior persists, leading to errors when a new task requires a change in motor behavior (Conditt et al. 1997; Gandolfo et al. 1996; Goodbody and Wolpert 1998; Malfait et al. 2005; Mattar and Ostry 2007; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994; Tong et al. 2002). The search for cues that reduce interference in force field learning has yielded mixed findings (Gandolfo et al. 1996; Krouchev and Kalaska 2003; Osu et al. 2004; Wada et al. 2003). Building on recent studies that have suggested that force field learning is akin to learning to manipulate a novel object (Cothros et al. 2006b; Kluzik et al. 2008; Lackner and DiZio 2005), this study considers more focused cues, specifically visual cues that relate to object grasp.

Here we asked subjects to learn to move in a force field and switch between this field and a null field. All visual feedback was provided through a computer-generated display. We show that a purely visual simulation of grasping and releasing an object reduced interference and facilitated skilled reaching in the two mechanical environments, even though in all cases subjects in fact maintained grasp of the robot arm. Associating the force and null fields with other visual cues had no effect.

METHODS

Subjects

A total of 44 right-handed subjects between the ages of 18 and 32 yr (mean, 21.5 yr) participated in the study. The 44 subjects were divided into equal groups of 11 for random assignment to four experimental conditions. All subjects gave their written informed consent before participation. All subjects reported normal or corrected vision and no history of neurological or musculoskeletal disorder. All procedures were approved by The University of Western Ontario Research Ethics Board.

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Apparatus

Subjects grasped the handle of an InMotion robotic manipulandum (Interactive Motion Technologies, Cambridge, MA). The right arm was supported by a custom-made air sled, which expelled compressed air beneath the sled. The air sled minimized friction and fatigue by supporting the arm against gravity. The subject's arm and the manipulandum were beneath a mirror, which reflected images projected by a computer controlled LCD screen. Visual targets were projected that appeared to lie in the same plane as the hand. In addition, computer-generated visual representations of the subject's arm and the robotic device were displayed in real time. The virtual image of the subject's arm consisted of two narrow rectangles, corresponding to the upper and lower arm segments, which were hinged together at a point corresponding to the elbow (Fig. 1*A*). For each subject, the lengths of these segments were matched to those of the subject's actual arm segments. The subject's arm was positioned such that the virtual arm was superimposed on the arm's actual position and the virtual arm mirrored the movements of the subject's unseen arm. The projected visual representation of the manipulandum either mimicked the movement of its real counterpart (Fig. 1*B*) or remained stationary in a "docked" position at the top of the screen (Fig. 1*A*), depending on the experimental condition.

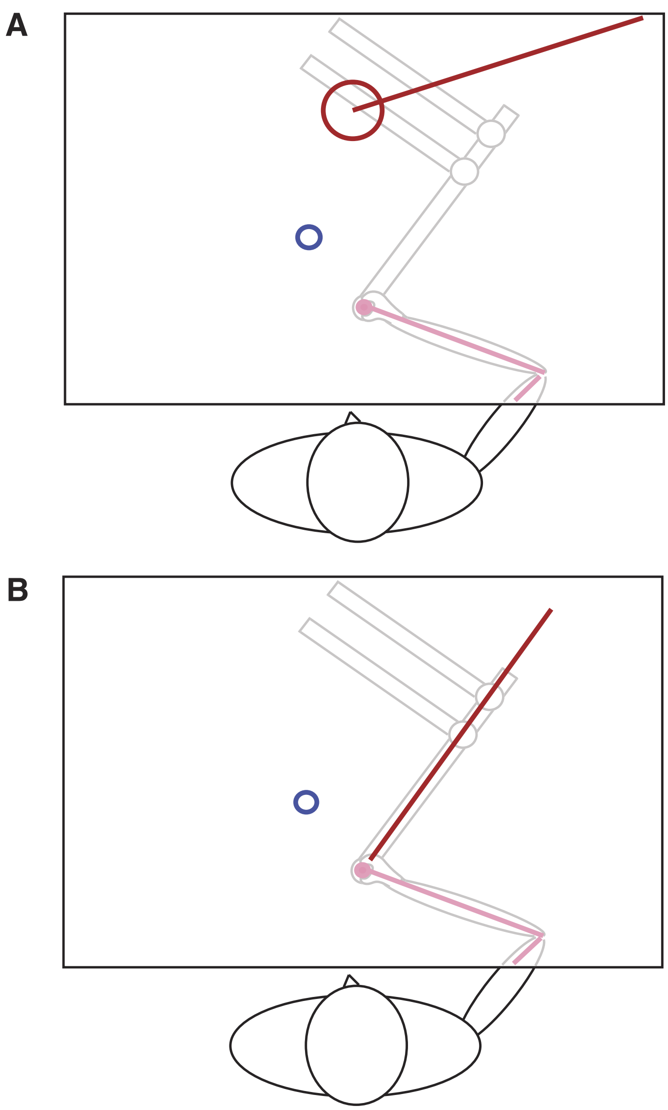

FIG. 1. Experimental setup. The subject's view of their arm was blocked by a mirror. They were presented with a virtual display of their arm and the robot linkage. In some experimental conditions, the robot appeared to be "docked," disconnected from the subject's arm. In other conditions, the subject appeared to be grasping the robot. In all cases, the subject was in fact grasping the handle of the robot.

The manipulandum was programmed to generate forces at the handle. The magnitude of the force vector varied with the velocity of the hand. The direction of the force vector was perpendicular to the instantaneous direction of hand movement. The force field was thus a counterclockwise (CCW) curl field described by the following equation

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = b \begin{bmatrix} 0 & d \\ -d & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}$$

where F_x and F_y are robot-generated forces along the left-right and forward-backward axes, respectively, and $\dot{x}$ and $\dot{y}$ are instantaneous hand velocities: $b = 25$ Ns/m and $d = +1.0$. Forces were zero when the robot was held still and reached their maximum at peak hand tangential velocity. The robot was controlled using custom software running under the RT Linux operating system on a Pentium 4 CPU.

Procedure

Subjects alternated between blocks of trials in which they reached in a force field intended to perturb movement and a null field in which no forces were applied. This required subjects to both adapt to the force field and adjust accordingly to its sudden absence. All visual feedback was provided through the computer-generated display. Because the motor experience of subjects was held constant (subjects in all conditions grasped the robot handle, regardless of the visual display), differences arising between groups could be attributed only to differences in visual feedback.

After the subject was properly positioned, the handle of the manipulandum was placed in the subject's hand by the experimenter, in a central start position 25 cm from the subject's sternum, along the midline. Each trial was marked by the appearance of a target (measuring 24 mm in diameter, in 1 of 8 positions around the circumference of a circle 10 cm in diameter). Subjects were required to reach to the targets within a time window of 200–300 ms. When subjects reached a target in >300 ms, the target turned green; when subjects reached a target in <200 ms, it turned red. If a target was reached within the prescribed range of time, the target turned blue. Subjects were instructed to come to a full and complete stop after reaching each target. Targets were presented in a pseudorandom order such that each cycle of eight targets included all eight locations.

The reaching task was repeated across four phases: A1, B1, A2, and B2 (Fig. 2). Subjects were first familiarized with the null field (A1), in which the manipulandum applied no forces, and then trained in the force field (B1) and underwent further testing in the null (A2) and force fields (B2). Subjects were randomly assigned to one of four groups: one experimental group and three control groups. The groups differed only in terms of the visual feedback presented to them (Fig. 2).

Catch trials, in which the robot forces were unexpectedly turned off, were randomly interspersed within the force field trials (B1 and B2). Phase B1 contained 12 catch trials, scattered throughout the block. Phase B2 contained three catch trials. During these catch trials, the force field was suddenly and unexpectedly removed. The extent of learning was measured not only by observing changes in perpendicular distance (PD) but also by observing performance during these catch trials. Catch trials show that adaptation to a force field entails learning to precisely counteract the force field. The steadily increasing magnitude of after-effects is an index of motor learning (Shadmehr and Mussa-Ivaldi 1994).

Subjects in the experimental group were presented with visual cues that associated the force field with grasp of the virtual object and the null field with release of the object. When the force field was in effect (phases B1 and B2), the object appeared to be connected to the cursor

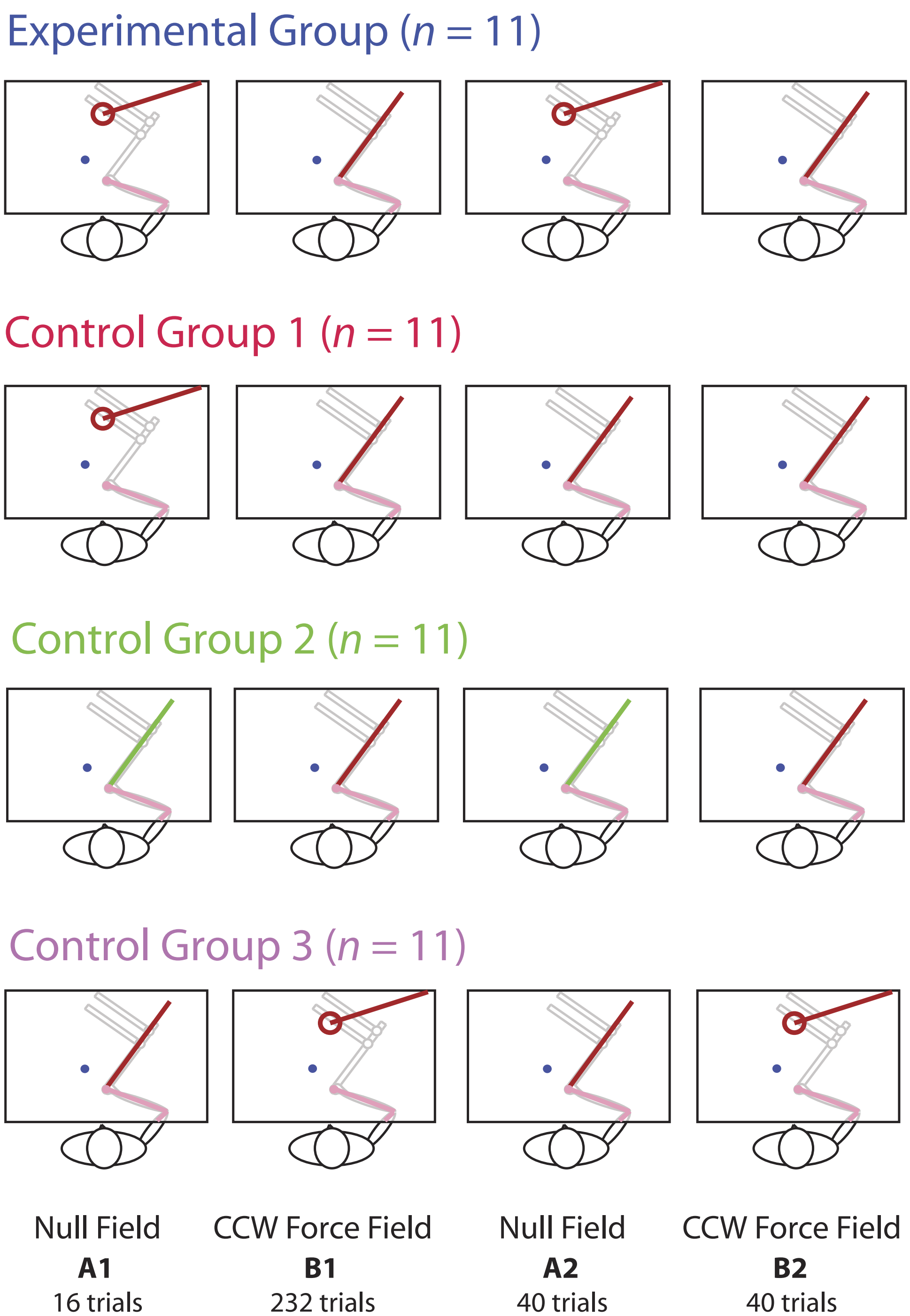

FIG. 2. Experimental design. For the experimental group, the virtual display indicated grasp of the robot when subjects moved in a force field (FF), and the robot appeared to be in a stationary "docked" position when subjects reached in a null field (NF). Note in all cases, subjects were in fact grasping the robot handle. For control group 1, the virtual display indicated grasp of the robot in the FF (B1), subsequent NF (A2), and 2nd FF (B2) trials. For control group 2, the virtual display always indicated grasp of the robot, but a color cue was associated with FF (robot appeared green) or NF (robot appeared red) trials. For control group 3, the pairing of grasped/docked and FF/NF was reversed from that for the experimental group.

(and thus the hand). During the phases in which the null field was in effect (A1 and A2), the object appeared to be detached from the hand and remained stationary at the edge of the screen, in a "docked" position. This was designed as a purely visual homolog of the haptic experience of subjects who release the manipulandum from their grasp between force field training sessions, as in the study reported by Cothros et al. (2006b).

Specifically, at the end of A1, the experimenter instructed subjects in the experimental group to move the handle of the manipulandum forward, to the edge of the workspace, and to let go of it, and return their own arm to the center of the workspace. Once the subject released the robot at the edge of the workspace, the experimenter triggered the visual display software so that the projected image of the virtual robot remained stationary in the "docked" position. The experimenter then indicated to the subject that they were to grasp another object, and unbeknownst to the subject, moved the robot handle back into the subject's grasp (even though the virtual image of the robot remained stationary, in the docked position). At the end of A1, the experimenter instructed subjects to release their grasp of the handle, and to reach back to the edge of the workspace, to retrieve the manipulandum again. Unbeknownst to the subject, the experimenter returned the robot to the docked position, and the subject grasped it again. At the end of B2 the same procedure was repeated. Note that throughout the experiment, vision of the subject's arm and the robot arm was blocked by an opaque curtain.

Subjects in control groups 1 and 2 were presented with more static visual cues, in which the display system showed the virtual object perpetually attached to the hand. Whereas subjects in control group 1 were given verbal instructions about "docking" the robot in the first block of trials (A1), for the remaining blocks (B1, A2, B2), subjects in control groups 1 and 2 were simply instructed to grasp the robot handle and move to the visual targets. For subjects in control group 1, the object was depicted as being attached to the hand in all phases except the first. The sensory experience of these subjects was meant to emulate those of subjects who experience static visual and grasp-related cues, as in Cothros et al. (2006b). To rule out the possibility that any variation in visual cues could bestow a benefit on subjects, in control group 2, the virtual object was seen to be attached to the hand in all four phases, and its color changed depending on the force field—green during the null field (phases A1 and A2) and red during the force field (phases B1 and B2). Like the experimental group, these subjects were thus provided with an opportunity to associate the two mechanical environments with specific visual cues, although these were designed to be more arbitrary changes in the visual display.

In control group 3, subjects were presented with the same visual cues as the experimental group; however, the order of the cues was reversed. Verbal cues about "docking" the robot were the same as for the experimental group, just associated in a converse fashion with the force field and null field. During the null field, the object appeared to be attached to the hand. When the force field was in effect, the subjects were presented with a paradoxical cue: the object appeared to be detached from the hand. The meaning of these cues was thus changed, whereas the salience arguably remained constant. It was predicted that the experimental group would show reduced movement curvature at the outset of phases A2 and B2, during re-exposure to the null and force fields, relative to the remaining groups.

Data analysis

The positions, velocities, and applied forces at the handle of the manipulandum were sampled at a rate of 200 Hz and stored on a computer. For each movement trial, PD was computed. PD is the maximum orthogonal deviation of the hand path from a straight line connecting the start position and the target. It is a measure of movement curvature and thus reflects a subject's skill in compensating for a force field (Malfait et al. 2005; Mattar and Gribble 2005; Shadmehr and Brashers-Krug 1997; Thoroughman and Shadmehr 1999). As this skill increases, PD decreases. To perform control tests of other features of movement trajectories, we also computed time from movement onset to maximum perpendicular distance, peak tangential velocity, and peak rate of acceleration (jerk) (see *Control tests*).

Mean values of the dependent variables described above were computed over successive windows of eight movements, such that each mean comprised all eight target directions. These means excluded catch trials. Effects of the type of visual display on movement curvature were tested using a split-plot ANOVA in which two factors were included: a within-subjects factor corresponding to movement training (blocks of 8 movements) and a between-subjects factor corresponding to the type of visual display shown to the subjects (experimental group vs. control groups 1, 2, and 3). Tukey post hoc tests were used to test differences between individual means. In all cases in which statistical tests resulted in a failure to reject the null hypothesis (i.e., no significant difference), we conducted power analyses to rule out the possibility that small but systematic differences were not detected because of low statistical power (e.g., because of high variance). In all cases except one (in which power was 0.67), we found that statistical power (the probability of detecting a difference assuming it exists) was >0.75. Data analyses were conducted using custom software written in Matlab (The Mathworks, Natick, MA).

RESULTS

Initial force field learning

All subjects were able to adapt to the force field when it was first presented in phase B1 (Fig. 3). Initially, movements were skewed in the direction of the force field. Mean PD over the first eight movements in phase B1 was significantly higher than in the previous eight movements in phase A1 when no perturbing forces were applied [$F(1,26) = 363.5$, $P < 0.001$]. With practice, subjects reduced movement, curvature and PD decreased throughout phase B1. Mean PD over the last eight movements in phase B1 was significantly lower than mean PD over the first eight movements in phase B1 [$F(1,26) = 201.8$, $P < 0.001$]. Table 1 shows a list of PD means and SD.

Catch trial data also showed that adaptation to the force fields took place. As subjects practiced reaching in the force field, a reduction in curvature in their movements was accompanied by an increase in the size of after-effects when the force field was unexpectedly removed during catch trials. For all groups, mean PD during the last catch trial in phase B1 was higher than mean PD of the first catch trial [$F(1,48) = 90.3$, $P < 0.001$]. A list of PD values during catch trials is shown in Table 2.

The four subject groups did not differ in terms of their adaptation to the force field in phase B1. No statistically significant differences were observed between groups in mean PD over the first eight movements [$F(3,34) = 0.65$, $P = 0.59$] or last eight movements in phase B1 [$F(3,34) = 1.9$, $P = 0.16$]. Similarly, there were no statistically significant differences between groups in mean PD in the first null field [phase A1; $F(3,34) = 0.50$, $P = 0.57$]. Mean PD of the first catch trial in phase B1 did not differ significantly between groups [$F(3,17) = 2.1$, $P = 0.14$]. Mean PD over the the last catch trial in phase B1 also did not differ significantly between groups [$F(3,17) = 0.6$, $P = 0.66$]. Taken together, these results show that there were no preexisting differences between the groups in their ability to reach to targets in straight lines in either a null field or force field.

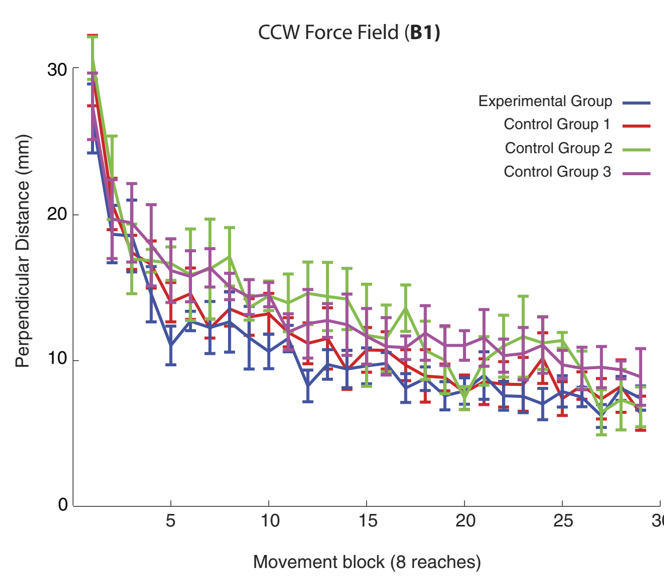

FIG. 3. Learning curves for the first FF block (B1). Individual data points represent mean trajectory curvature averaged over 8 reaches. Vertical bars indicate SE.

TABLE 1. *Mean perpendicular distance (mm) for null field movements and for initial and final performance in each force field, for subjects in all groups*

		Experimental Group		Control 1		Control 2		Control 3	
Force Field	Movements	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Null (A1)	1–16	2.4	2.3	4.1	2.4	3.9	4.8	2.2	3.5
CCW (B1)	Initial 8	26.3	5.5	28.1	4.9	25.2	4.9	25.8	4.1
	Final 8	6.9	2.0	7.3	3.3	9.6	2.9	9.7	3.5
Null (A2)	Initial 8	−18.8	4.3	−25.5	4.1	−27.2	6.2	−28.8	8.1
	Final 8	−5.6	1.0	−8.1	3.0	−7.6	3.3	−5.8	2.3
CCW (B2)	Initial 8	12.9	3.3	20.4	3.3	21.4	3.7	24.0	1.8
	Final 8	7.5	2.5	9.3	2.9	11.6	4.1	10.5	4.0

Values are mean and SD. CCW, counterclockwise.

Subsequent exposure to the null field

After adaptation to the force field in phase B1, subjects showed deficits in their performance when faced with the null field a second time in phase A2 (Fig. 4). Movement trajectories were once again curved, but in the opposite direction [the clockwise (CW) direction] of the preceding force field. Mean PD over the first eight movements in phase A2 was significantly more curved in the CW direction than for phase A1, when subjects encountered the null field for the first time [$F(1,26) = 286.6$, $P < 0.001$]. Subjects thus showed difficulty reaching in straight lines in the null field (phase A2) despite showing skilled performance in this task previously (phase A1). With further practice, movement curvature decreased. Mean PD over the last eight movements in phase A2 was smaller than at the beginning of phase A2, over the first eight movements; this was the case for all groups [$F(1,26) = 120.7$, $P < 0.001$].

Importantly, the degree to which movements showed curvature at the beginning of phase A2 varied between groups. The experimental group showed less movement curvature over the first eight movements in phase A2 than control groups 1, 2, and 3 [$F(1,26) = 177.0$, $P < 0.001$]. The three control groups did not differ significantly from one another in this regard, showing similar amounts of movement curvature over the first eight movements in phase A2 [$F(2,24) = 0.58$, $P = 0.60$, not significant]. By the end of phase A2, all groups reached similar levels of performance, with no significant differences in mean PD over the last eight movements [$F(3,34) = 2.2$, $P = 0.11$, not significant, power = 0.67]. We also performed tests based on the first individual movement in A2, and the results are similar. The mean PD for the first movement in A2 for the experimental group was significantly lower than mean PD for the first movement in A2 for control groups 1, 2, and 3 [$F(1,26) = 259.99$, $P < 0.001$], and mean PD for the first movement in A2 for control groups 1, 2, and 3 did not differ [$F(2,24) = 1.11$, $P > 0.35$]. Figure 5*A* shows representative hand trajectories taken from one subject in each group for their first movement in block A2.

Retraining in the force field

When faced with the CCW force field a second time, in phase B2, re-adaptation was observed (Fig. 6). Re-exposure to the force field resulted in curved trajectories, and these straightened with practice. Mean PD over the last eight movements in phase B2 was significantly lower than mean PD over the first eight movements in phase B2 [$F(1,26) = 35.5$, $P < 0.001$]. A list of PD values is shown in Table 1. Catch trial data also showed that adaptation to the force field in phase B2 took place. Mean PD for the last catch trial in phase B2 was higher than mean PD of the first catch trial in phase B2, again indicating adaptation to the force field [$F(1,48) = 29.3$, $P < 0.001$].

Despite having previous experience in the force field (in B1), the extent of movement curvature at the outset of phase B2 was significantly greater for the three control groups than at the end of phase B1 (the last episode of force field training). For control groups 1, 2, and 3, mean PD over the first eight trials in phase B2 was higher than mean PD over the last eight trials in phase B1 [$F(1,26) = 88.7$, $P < 0.001$]. In addition, mean PD for the first movement in B2 for control groups 1, 2, and 3 was significantly higher than mean PD over the last eight trials in B1 [$F(1,26) = 81.69$, $P < 0.001$]. Importantly, for the experimental group, mean PD over the first eight trials in phase B2 was significantly smaller than for the three control groups [$F(1,26) = 126.3$, $P < 0.001$]. Likewise, mean PD for the first movement in B2 for the experimental group was significantly smaller than mean PD of the first movement in B2 for the three control groups [$F(1,26) = 167.45$, $P < 0.001$]. Figure 5*B* shows representative hand trajectories taken from one subject in each group for their first movement in block B2.

TABLE 2. *Mean perpendicular distance (mm) for catch-trials in phases B1 and B2, for subjects in all groups*

		Experimental Group		Control 1		Control 2		Control 3	
Force Field	Movements	Mean	SD	Mean	SD	Mean	SD	Mean	SD
CCW (B1)	First	−16.3	5.6	−12.1	8.2	−14.4	4.4	−6.5	5.3
	Last	−30.9	8.8	−33.9	11.3	−37.2	10.3	−38.2	9.4
CCW (B2)	First	−19.6	11.3	−18.2	8.5	−20.0	10.1	−19.3	5.3
	Last	−28.5	12.5	−35.8	13.6	−28.3	8.5	−21.9	1.4

Values are means and SD. CCW, counterclockwise.

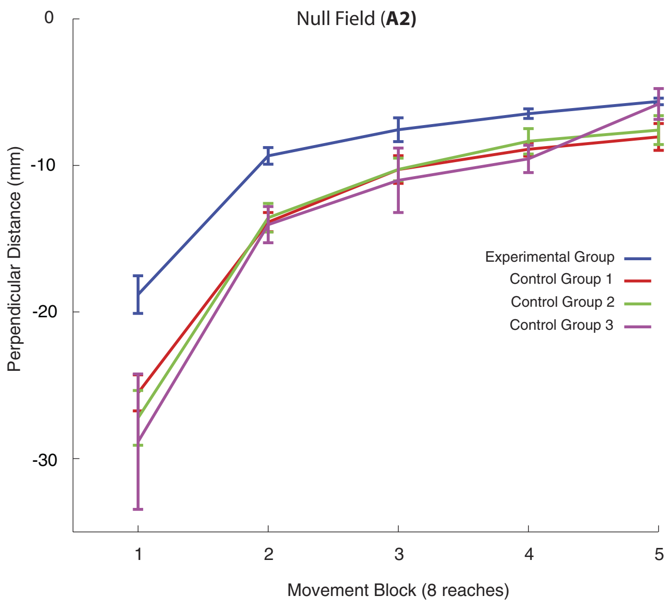

FIG. 4. Mean trajectory curvature in the second NF block (A2), just after completing FF learning (B1). Individual data points represent mean trajectory curvature for the 1st 5 movements in A2, averaged over subjects. Vertical bars indicate SE.

Additionally, their performance did not differ significantly from that at the end of phase B1, when the force field was last experienced. Although subjects in the experimental group showed some curvature in their movements when reintroduced to the force field, differences between mean PD over the first eight trials in phase B2 and the last eight trials in phase B1 were not statistically significant [$F(1,26) = 0.10$, $P > 0.75$].

Control tests

Because the force field used in phases B1 and B2 was velocity dependent, the magnitude of perturbing forces applied to the hand is obviously affected by movement speed. It is thus important to rule out the possibility that the experimental group's reduced movement curvature in phases A2 and B2 could be attributed to simply moving more slowly (and hence experiencing reduced perturbing forces). We tested mean peak tangential velocity in the first eight movements in phases B2 [$F(3,34) = 0.65$, $P = 0.59$, not significant] and A2 [$F(3,34) = 0.64$, $P = 0.60$, not significant] and found no differences between groups. Similarly, no evidence was found that the experimental group's markedly different movement curvature was caused by alterations in the basic shape of movement trajectories. Over the first eight movements in phases A2 [$F(3,34) = 0.07$, $P = 0.98$, not significant] and B2 [$F(3,34) = 1.2$, $P = 0.34$, not significant], the mean time needed to reach peak PD did not differ significantly between groups. Finally, to assess trajectory smoothness, we computed mean jerk. Jerk is the rate of change of acceleration and has been used to characterize movement smoothness and the basic ability to move the limb in a smooth, coordinated fashion (Cothros et al. 2006a; Flash and Hogan 1985). Over the first eight movements in phases A2 [$F(3,34) = 0.75$, $P = 0.53$, not significant] and B2 [$F(3,34) = 0.12$, $P = 0.95$, not significant], the groups did not differ significantly in mean jerk (rate of change of acceleration). It is therefore unlikely that the experimental group's performance was the result of changes in the basic ability to move the arm.

DISCUSSION

The findings presented here suggest that visual cues and in particular those that signal interaction with grasped objects are an important part of protecting newly learned motor skills from interference. Only visual cues associating the CCW force field with grasp of a virtual object reduced interference when switching between the force field and a null field and back to the force field a second time. Relative to control groups 1, 2, and 3, the experimental group showed less movement curvature during phases A2 (~30% less curvature) and B2 (~40% less curvature). These findings are notable because subjects grasped the handle of the robot during all phases and therefore any differences in the sensory experience of grasping and releasing the object were strictly confined to the visual domain.

It is perhaps not surprising that subjects in control group 1 experienced more difficulty in switching between null field and force field movements, because these subjects received no appreciable changes in context from one phase to the next (apart from experiencing the changes in forces themselves). Like control group 1, control groups 2 and 3 showed worse performance during phases A2 and B2 than the experimental group. This is a notable finding, given that these two groups did in fact receive changing visual cues. Thus not just any visual cue facilitated proficient switching between null field and force field movements. Rather, only visual cues that associated the force field with the presence of the virtual object and the null

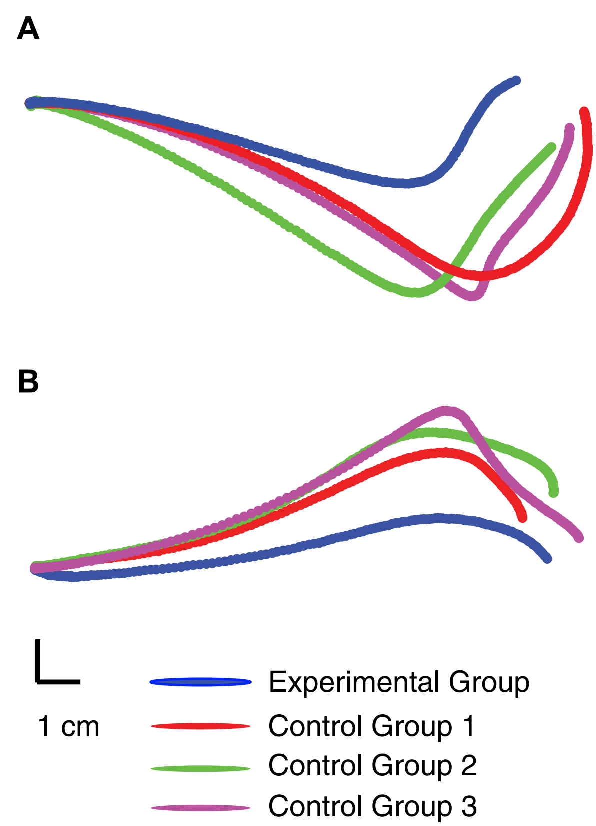

FIG. 5. Representative hand trajectories of individual subjects for their 1st movement in block A2 (*A*) and B2 (*B*).

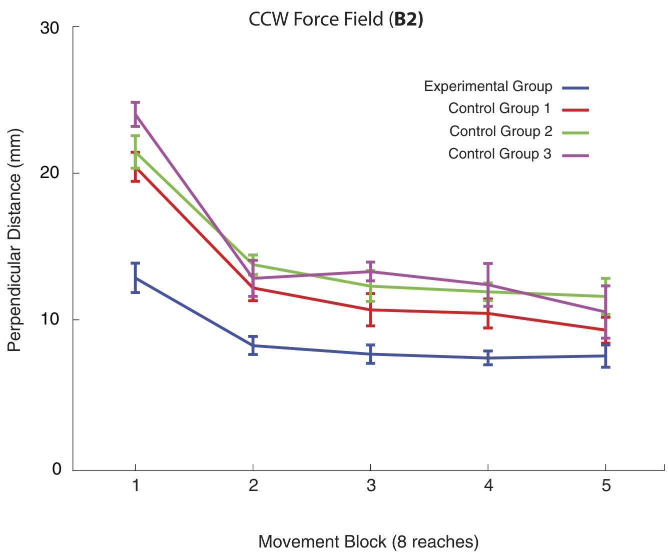

FIG. 6. Mean trajectory curvature in the second FF block (B2), just after completing NF trials (A2). Individual data points represent mean trajectory curvature for the 1st 5 movements in B2, averaged over subjects. Vertical bars indicate SE.

field with the absence of that object, as in the experimental group, facilitated skilled switching. Interestingly, the effectiveness of object-based visual cues provided to the experimental group is sensitive to how they are associated with force and null fields. The poor performance of control group 3, which was presented with the same cues as the experimental group but with the order reversed, showed that the advantages these cues confer on subjects is not of a general nature, but rather, highly constrained by their pattern of presentation and perhaps their meaning.

Previous studies have shown that force field learning shows limited transfer to reaches in free space, in which the robotic device is released—this seems to some extent to guard previous learning from interference (Cothros et al. 2006b; Kluzik et al. 2008; Lackner and DiZio 2005). The experimental group's reduced after-effects in phase A2 and improved performance in phase B2 mirror these findings. This is compelling not only because it lends further support to the idea that force field learning is related to learning the behavior of a novel object, but also because, in this study, the visual cue that signaled grasp and release of the manipulandum was illusory—grasp was in fact maintained in all conditions. The implication is that the illusory visual cues were effective warning signs of a change in context that required a different set of neural control signals for movement, but only when they associated the force field with grasp of an object and the null field with release of the object, as if subjects were reaching in free space.

Similarly, Davidson et al. (2005) examined force field learning in the context of differing cutaneous cues, associated with different robots that applied loads either to the hand or to the arm segments themselves. They tested whether subjects could retain learning when forces were applied to the hand after subsequently experiencing the opposing field applied to the arm (or vice versa) or whether retrograde interference would be observed. Despite very different cutaneous inputs that were directly related to the movement task, subjects displayed complete interference between opposing fields. Their results suggest that loads applied to the arm and hand are not represented independently by the sensorimotor system, and more generally, that cutaneous cues on their own are not sufficient to promote the learning of independent internal models.

These findings support the idea that interference arises in part from a lack of informative sensory/perceptual cues. How interference occurs is not entirely clear, although previous studies have put forward a number of ideas (Bock 2003; Brashers-Krug et al. 1996; Caithness et al. 2004; Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002; Krakauer and Shadmehr 2006; Krakauer et al. 2005; Magill and Hall 1990; Mattar and Ostry 2007; Overduin et al. 2006; Shadmehr and Brashers-Krug 1997; Tong and Flanagan 2003; Tong et al. 2002; Wada et al. 2003). Motor learning entails learning to predict the consequences of movement, in this case, forming progressively more accurate predictions of how a mechanical environment like a force field affects movement (Brashers-Krug et al. 1996; Conditt et al. 1997; Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 1999). Presumably the contextual cues experienced by subjects in the experimental group enabled them to more accurately predict the consequences of their actions, thus reducing interference from phase B1 to phase A2 and likewise from phase A2 to phase B2. This scheme has been proposed more formally in a recent computational model of motor learning called modular selection and identification for control, or MOSAIC (Haruno et al. 2001; Wolpert and Kawato 1998). In the model, multiple internal models relating task demands to neural control signals for movement may be combined in a weighted fashion, depending partly on signals related to task context, and in particular, on predictions of the outcome of a set of candidate internal models. Although our study does not by any means represent a test of the MOSAIC model, our results are nevertheless consistent with the idea that sensory and/or cognitive signals related to task context are used by the nervous system to select appropriate control signals for different mechanical environments.

Krakauer et al. (1999) proposed that two motor tasks should not interfere if they are learned in different coordinate frames. The authors concluded that forming new neural representations of the dynamics of the arm, which likely occurs in an intrinsic coordinate system, does not interfere with learning to compensate for altered visual feedback, which likely occurs in an extrinsic coordinate system. These results may be relevant to the present findings. Perhaps by associating the force field with an external object, subjects in the experimental group engaged an extrinsic, object-based coordinate system, reducing interference with learning that took place in the null field phases, during which an intrinsic coordinate system was more heavily recruited. This is consistent with a recent study that showed that novel dynamics can be learned in a mixture of the two coordinate frames (Ahmed et al. 2008). However, this conflicts with previous research suggesting that velocity-dependent force fields are learned in an intrinsic coordinate system (Gandolfo et al. 1996; Malfait et al. 2005; Shadmehr and Moussavi 2000; Shadmehr and Mussa-Ivaldi 1994). Moreover, it may be the case that dynamics are represented in extrinsic, object-based coordinates only with the benefit of extensive experience (Ahmed et al. 2008). If object-based visual cues engage a different coordinate system, this would be expected to change how learning generalizes across space. Researchers may wish to explore this possibility in the future by repeating the present experiment using a force field that produces varying patterns of forces across space, like those used by Shadmehr and Mussa-Ivaldi (1994) and Malfait et al. (2005).

Context as a mechanism to prevent or promote forgetting has been explored in other research areas. Studies using classical conditioning, in which the organism under study learns to generate a response to a once neutral stimulus, have shown that "reminder stimuli," which are particular to the training context, can facilitate forgetting of the conditioned response, even when it is well learned (Dudai 2004, 2006). These findings were considered by Lewis (1979), who proposed that stored, inactive memories can be made active and modifiable by a return to the training context. In this experiment, it was possible that the static contextual cues presented to control groups 1 and 2 maintained motor memories in an active, modifiable state, preventing their consolidation.

In summary, the findings presented here provide new evidence in support of the idea that the learning of multiple motor skills is partly determined by context, and also that the range of contextual cues that effectively promotes retention of, and thus proficient switching between, motor skills is quite narrow. Our results support the idea that force field learning is akin to learning to manipulate an object and, accordingly, only (visual) contextual cues that associated the force field with an object guarded against interference. Strikingly, these visual cues conferred a benefit on subjects even without extensive training and without associating the force and null fields with different arm postures, effectors, or motor tasks (Conditt et al. 1997; Gandolfo et al. 1996; Hwang et al. 2006; Krouchev and Kalaska 2003; Shadmehr and Mussa-Ivaldi 1994; Tong et al. 2002).

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