Colored context cues can facilitate the ability to learn and to switch between multiple dynamical force fields

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Running Title: Explicit and implicit color cues about force fields
ABSTRACT

We tested the efficacy of color context cues during adaptation to dynamic force fields. Four groups of human subjects performed elbow flexion/extension movements to move a cursor between targets on a monitor while encountering a resistive (Vr) or assistive (Va) viscous force field. They performed two training sets of 256 trials daily, for 10 days. The monitor background color changed (red, green) every four successful trials, but provided different degrees of force-field context information to each group. Irrelevant-cue groups: the color changed every four trials, but one group encountered only the Va field and the other only the Vr field. Reliable-cue group: the force field alternated between Va and Vr each time the monitor changed color (Vr: red; Va: green). Unreliable-cue group: the force field changed between Va and Vr pseudo-randomly at each color change. All subjects made increasingly stereotyped movements over 10 training days. Reliable-cue subjects typically learned the association between color cues and fields and began to make predictive changes in motor output at each color change during the first day. Their performance continued to improve over the remaining days. Unreliable-cue subjects also improved their performance across training days, but developed a strategy of probing the nature of the field at each color change by emitting a default motor response and then adjusting their motor output in subsequent trials. These findings show that subjects can extract explicit and implicit information from color context cues during force-field adaptation.
INTRODUCTION

As subjects learn to compensate for an external force field that deviates their arm movements from their intended path, the kinematics (e.g. spatial path, velocity profile) of their original unperturbed movements are gradually restored (Brashers-Krug et al. 1996; Gandolfo et al. 1996; Shadmehr & Brashers-Krug, 1997; Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 1999). As adaptation progresses, compensation gradually shifts from a dependence on feedback-mediated error-correction mechanisms and increased co-contraction of muscles to reduce the perturbing impact of the field (Thoroughman & Shadmehr 1999; Milner, 2004; Milner & Franklin, 2005) to predictive changes in muscle activity that generate extra force components to counteract the effect of the field (Brashers-Krug et al. 1996; Gandolfo et al. 1996; Shadmehr & Brashers-Krug, 1997; Shadmehr & Mussa-Ivaldi, 1994; Krouchev & Kalaska, 2003; Thoroughman & Shadmehr, 1999; Milner, 2004; Milner & Franklin, 2005).

However, many studies have shown that subjects have difficulty adapting to two different force fields that are presented in sequential blocks of trials in the classic A-B-A learning paradigm. Typically, the learning of field B is initially impeded by the skill acquired during exposure to field A (anterograde interference), and the eventual adaptation to field B leads to an “unlearning” of skilled performance in field A (retrograde interference) (Karniel and Mussa Ivaldi, 2002; Shadmehr and Brashers-Krug, 1997; Shadmehr & Mussa-Ivaldi, 1994). Some evidence suggests that both types of interference can be minimized if a period of consolidation is permitted between exposures to the two fields (Brashers-Krug et al. 1996; Shadmehr and Brashers-Krug, 1997). However, the nature and even the existence of a consolidation process have been challenged (Caithness et al.)
The rate of learning and degree of interference may also be altered by the nature of the different motor skills being learned (Fukushi and Ashe 2003; Krakauer et al. 1999; Tong and Flanagan, 2003; Davidson et al. 2005; Imamizu et al. 2005).

Nevertheless, it is obvious that the motor system can learn, retain and recall many different motor skills. Moreover, many studies have demonstrated the slower acquisition but eventual benefits of learning multiple motor skills in interleaved practice schedules, the so-called “context interference effect” (Cunningham and Welch 1994; Del Rey, 1989; Hall and Magill, 1995; Roller et al. 2001; Shea and Kohl, 1990).

To learn multiple skills simultaneously during interleaved schedules, the motor system must in fact learn several different but associated skills. First, it must adapt neural circuits to acquire and retain each of the separate motor skills. It must also learn to recognize the current task context, that is, which skill is currently required, and it must learn how to switch between the different skills when the context changes. Theoretical studies suggest that these aspects of multi-skill learning would be facilitated if the motor system had an internal modular structure whereby different modules or “internal models” are preferentially assigned responsibility for different skills (Shadmehr and Brashers-Krug, 1997; Shadmehr & Mussa-Ivaldi, 1994, Wolpert and Kawato, 1998; Thoroughman & Shadmehr 1999; Imamizu et al. 2004; Wada et al. 2003; Wolpert and Kawato, 1998).

In this perspective, a critical step is to identify the current task conditions to determine which internal models should be modified to learn new skills or activated to recall previously acquired skills. According to the MOSAIC model (Wolpert and Kawato, 1998), this can be done in two ways. Sensory feedback during a movement could be used
to identify the properties of the environment and to determine responsibility based on the
error between the predicted and sensed outcome of the outgoing motor command
(“postdictive switching”; Milner & Franklin 2005; Imamizu et al. 2007). Alternatively,
prior knowledge provided by other sources of information (“context cues”) could be used
to identify the current task conditions and to switch responsibility between different
modules even before moving (“predictive switching”; Imamizu et al. 2007).

Context cues can influence the ability of subjects to learn multiple motor skills. For
example, different starting postures or positions of the arm can permit simultaneous
learning of different skills (Gandolfo et al 1996; Shadmehr & Mussa-Ivaldi, 1994;
Hwang et al. 2003, 2005; Richter et al. 2004; Shadmehr, 2004; Shadmehr & Moussavi,
2000), by providing prior knowledge about the environment that will be encountered
during a movement, or by associating different environments with different sets of
muscle activity patterns (Conditt et al. 1997; Hwang et al. 2003, 2005, 2006; Mussa-
Ivaldi and Shadmehr 1994; Richter et al. 2004; Shadmehr 2004; Woolley et al. 2007).

Other context cues have ranged from verbal instructions about the nature of the
perturbations and how to compensate for them (Imamizu et al. 2004, 2007) and graphic
representations of the impending perturbations (Osu et al. 2004) to more indirect cues
such as the serial order of movements in a sequence (Karniel and Mussa-Ivaldi, 2002;
Wainscott et al. 2005) and the shape of grasped objects (Cothros et al. 2008). The
effectiveness of these different context cues has proven equally diverse.

Another potential context cue is color. Several studies have reported that color cues do
not facilitate learning of multiple dynamical environments or visuomotor rotations
(Gandolfo et al. 1996; Gupta and Ashe 2007; Miall et al. 2004; Rao and Shadmehr 2001).
In contrast, Wada et al (2003) showed that subjects could learn over several days to make predictive compensations for assistive and resistive viscous fields applied in random order to elbow movements, when the fields were signaled by different monitor colors before each movement started. Osu et al (2004) found that color cues permit learning of opposing dynamical force fields during whole-arm movements. Krouchev and Kalaska (2003) reported that a monkey that was extensively trained to perform elbow movements in several different force fields associated with different monitor colors could immediately change its motor output each time the monitor changed color, in anticipation of the expected perturbation before it physically encountered the field. Finally, Ganguly and Carmena (2009) showed that monkeys can use color cues to learn to exert covert “brain” control over cursor motions via two different neuroprosthetic decoder algorithms, and to switch readily between them after learning.

The inability of subjects in some studies to use color cues to learn multiple skills is somewhat surprising, given that humans can readily learn many tasks based on color cues. We tested the ability of human subjects to use color cues in a simple motor adaptation task. We found that subjects can rapidly learn a reliable arbitrary association between different colors and force fields and make predictive adjustments to their motor output (predictive switching). Even when the association between colors and fields is unreliable, subjects can still extract useful implicit context information about the task from color changes, and develop a behavioral strategy that permits learning and postdictive switching between different motor skills. The results emphasize that the ability to switch between motor skills is also a skill that improves with practice. A preliminary report of this study has been presented (Addou et al. 2005).
METHODS

We tested 24 healthy right-handed subjects (16 males, 8 females; 15-43 years old). The subjects were naïve to the objectives of the task and participated in this study after they read and signed a consent form approved by the Institutional Research Ethics Committee.

Experimental Setup

The subjects sat in a chair and placed their right arm on a horizontal manipulandum (Fig. 1), with their upper arm abducted into the horizontal plane at shoulder height (~90° with respect to the trunk). The subjects made elbow flexion or extension movements from a central start position to move a cursor between targets displayed on a computer monitor positioned at eye level 0.75 m in front of them. The movements were sometimes perturbed by force fields generated by a single-axis torque motor (ShinMaywa, BB-51, Japan). Subjects received verbal instructions about how to perform the task, but no instructions about the nature of the force fields or the contextual relevance of the monitor colors. All procedures were developed during pilot studies with different subjects.

Behavioral trials

At the start of each trial, a horizontal 150° arc of 17 cm radius, a cursor and a start window appeared on the monitor. The cursor swept along the arc as a function of the subjects’ elbow angle. The start window was a white circle of 0.425 cm radius positioned centrally at the top of the arc. This corresponded to a starting elbow angle of 90° ± 5.74° with respect to the humerus. The subjects had to hold the cursor in the start window for a 500 ms Center hold time (CHT). At the end of CHT, the start window disappeared and a circular white movement target circle (1.7 cm radius) appeared to the left (-45°, flexion).
or right (+45°, extension) of the start window. The subjects had to rotate their elbow to
move the cursor into the target circle and hold it for a 200ms Target hold time (THT).

This task design placed priority on the predictive control of the initial phase of the
movements and less importance on endpoint stability. Control of the late phase of
movement, especially while in the target circle, will likely be strongly influenced by
feedback. While feedback processes are intimately involved in the acquisition of a motor
skill (Shadmehr et al. 2010; Todorov & Jordan 2002; Wagner and Smith 2008), we
focused on the parts of the task that are the most likely to be under the control of
predictive processes - the initial output forces and timing of the movement.

Movement duration was controlled to ensure that all subjects encountered velocity-
dependent force fields of similar magnitude. Movement duration was calculated as the
time interval between exit of the start window and entry of the target window. Subjects
were given knowledge of results about performance at the end of each trial: 1) Success: If
movement duration was 300-400ms and the cursor remained in the target for the THT,
the target circle appeared to “explode”, accompanied by a chime sound. 2) Slow: If
duration was >400ms, the color of the target changed from white to blue, accompanied by
a 0.5 sec low tone (150 Hz). 3) Fast: If duration was <300ms, the color of the target
changed from white to yellow, accompanied by a 0.5 sec high tone (1000 Hz).

The relationship between final target color, auditory tone and movement duration was
explained to the subjects before the experiment, and repeated when requested by the
subjects. They received no other verbal instructions about the task.

**Trial sequence**
All task sets involved multiple blocks of 4 successful trials, comprised of pairs of successive flexions and extensions. The orders of the pairs (FF/EE or EE/FF) varied pseudo-randomly between blocks and counterbalanced to ensure equal numbers of blocks of each order. If a trial was not a success, it was immediately repeated until the subject was successful. As a result, the total number of trials attempted in each block could exceed four, especially early in training.

**Force fields**

Subjects performed sets of trials in three force-field conditions. In the Null-field (N) condition, no external force field was encountered. In the Resistive-Viscous (Vr) condition, the torque motor applied a torque in the direction opposite to the direction of motion and proportional to the instantaneous velocity of elbow rotation ($V_r = 5.0 \text{ Nms/rad}$). In the Assistive-Viscous (Va) condition, a velocity-dependent torque was applied in the direction of motion. Because the Va field is inherently unstable, the gain of the field was smaller than the Vr field ($V_a = 1.2 \text{ Nms/rad}$). This Va-field gain required the subjects to apply a large transient active braking force in the direction opposite to the direction of movement to stop the elbow movement in the target window. It was challenging but learnable with practice, while avoiding undesirable long-term strategies such as extensive co-contraction of muscles to stiffen the elbow joint.

During Va- or Vr-fielded trials, the torque motor was not activated until the subjects entered the start window. The gain of the field gradually increased to full strength over 500ms while the subjects held their elbow stationary in the start window. This minimized abrupt perturbations of the elbow caused by instantaneous activation of the torque motor that could provide the subjects with proprioceptive cues about the nature of the
impending force field before the target window appeared. At the end of the THT of each 
fielded trial, the gain of the force field gradually decreased to zero over 400ms. Because 
viscous force fields are velocity-dependent, the potential perturbations prior to and after 
movement were relatively minor but pilot studies showed that these extra precautions 
effectively eliminated them. The subjects then actively returned their elbow to the central 
start position in the N field during a 1s inter-trial interval. Typically, the cursor was 
already stationary at the start position before the start window appeared to begin the next 
trial. As a result, Va or Vr fields were only encountered during the flexion or extension 
movements from the start window to the target windows.

**Context cues**

The subjects received context cues in the form of the background color of the monitor 
during each block of trials. Blocks of N-field trials were always signaled by a black 
monitor. Blocks of Vr- and Va-field trials were signaled by a red or green color. The 
color appeared at the start of each 4-trial block and changed at the end of the 4th 
successful trial in that block. The color remained unchanged during the return movements 
to the start window at the end of each trial in a 4-trial block even though they were made 
in an N-field. All subjects experienced the same visual cues. However, the utility of the 
red and green colors as context cues varied systematically in different groups of subjects.

**Experimental Protocol**

Subjects performed three sets of trials each day for ten non-consecutive daily sessions. 
Each daily session began with a set of 16 blocks (64 successful trials) of N-field trials 
signaled by a black monitor background. This baseline set allowed the subjects to re-
establish the desired timing of elbow movements across daily sessions. The subjects then performed two training sets of 64 blocks (256 successful trials each) during which the elbow movements were perturbed by either the Va or Vr fields.

Subjects were allowed to rest for several minutes after the N-field set and between the two Vr/Va-field sets. Subjects could also ask for a rest at any time during any trial set, but this happened very rarely. Subjects were divided into four groups of six subjects:

**Irrelevant context cues (IRC):** For these subjects, the color of the monitor alternated between red and green every 4 successful trials during the training set, but the field never changed. IRC-Va subjects encountered only the Va field and IRC-Vr subjects experienced only the Vr field in each training set. The red and green colors were irrelevant to these subjects, except as a cue that they were performing a training set.

**Reliable context cues (RC):** RC subjects encountered both the Va and Vr fields in their training sets. The monitor was always red during a 4-trial block of Vr-field trials and green during a block of Va-field trials. Monitor color and fields alternated in synchrony every 4 successful trials, yielding 32 blocks of trials in each field per training set.

**Unreliable context cues (URC):** During their training sets, URC subjects also encountered the Va and Vr fields and the monitor color changed every 4 successful trials. However, unlike RC subjects, there was only a 50% chance on average that a change in monitor color was accompanied by a change in applied field. As a result, the monitor color at the start of each 4-trial block provided unreliable information about the impending field. The block sequence was counterbalanced so that all four possible color/field combinations were presented with equal frequency in each trial set, as well as all possible combinations
of field change/no change at each block transition. This ensured that URC subjects also
experienced 32 4-trial blocks in each of the Va and Vr fields.

“Catch” trials: In intermittent trials during the training sets, the monitor remained red or
green but the torque motor was not activated, and the subjects unexpectedly encountered
an N field during the movement (“catch” trials; 16/256 trials per training set). Catch trials
occurred during only the first or the last trial of a 4-trial block, but never at both the first
and last trials in the same block. Catch trial sequence was fully counterbalanced for
position in a block (first, last), and direction of movement (flexion, extension) for all
subjects, as well as for field (Vr, Va) in RC and URC subjects. The first catch trial in
each training set was always presented after the subjects had performed several 4-trial
blocks of fielded trials. A catch trial could be completed successfully according to the
usual criteria, but if not, it was never repeated. Instead, it was replaced by a normally-
fielded trial that was repeated if necessary until performed successfully.

**Explicit and implicit information provided by the context cues**

The significance of the color cues was never explained to the subjects. However, because
of the very simple structure of the task, the color cues provided the subjects with explicit
and implicit context information that could be learned through repetition. A black
monitor color explicitly signaled the N-field. The red and green colors explicitly divided
each training set into blocks of 4 successful trials that were always presented in pairs of
flexions or extensions. For IRC subjects, this information was largely irrelevant because
they only encountered one field. In RC and URC subjects, Va and Vr fields only changed
at the start of a block of trials signaled by a change in monitor color. RC subjects only
experienced the red/Vr and green/Va pairings so they could learn that the colors provided
explicit predictive information about the field that would be encountered in each block. In contrast, in URC subjects, a change in monitor color only signaled the possibility of a change in field. Moreover, RC and URC subjects could learn that, with the exception of catch trials, the field encountered in the first trial after a color change would always be followed by a short sequence of trials in the same field until the monitor color changed. Finally, although catch trials were rare, all subjects could have learned that there was a low but finite probability of a catch trial in the first trial after the monitor color changed, and failing that, a possible catch trial a few successful trials later.

We did not use the opposite strategy in URC subjects of alternating Vr and Va fields every 4-trial block while randomly changing the monitor color. This would have provided a different visual environment than the other groups. More importantly, URC subjects could have acquired implicit knowledge of the block structure of the task to predict a change in the field every 4 successful trials, independent of the color cues.

**Data analysis**

Elbow joint angle was measured by a rotary position encoder in the manipulandum.

Angular position was sampled at 1 kHz for real-time torque control and stored at 200Hz for off-line analysis. Position signals were low-pass filtered (25Hz; 3rd order Butterworth filter). The velocity and acceleration signals were then estimated by differentiating the filtered position signals. The forces and torques applied by the subjects’ hand onto the handle of the manipulandum were measured by a 6-axis force/torque transducer (ATI Industrial Automation Inc Gamma series; Apex, NC), and stored at 200Hz.
Reaction time (RT): The time interval from the appearance of the target window on the monitor (GO) to the moment of movement onset (movement start, MS), estimated as the first of three consecutive 5-ms time intervals after the GO signal in which the velocity was significantly higher than the mean velocity during the 500ms prior to the GO signal.

Statistical significance of different factors on task performance was tested using ANOVA (Systat 9, Systat Software Inc, San Jose CA). The acceptable significance level was 5%. When sphericity was violated, the Greenhouse-Geisser correction was used.

RESULTS

Performance of representative single subjects

Specific examples of movement kinematics will be shown for extension movements. The results for flexion movements were similar and were included in all quantitative analyses.

Single-trial velocity curves and force profiles

IRC-Va and IRC-Vr subjects showed the usual progress of motor adaptation across the 10-day training period, with increasingly stereotyped velocity profiles in the Va and Vr fields respectively and in the N-field (Fig 2a,b,e,f). In the N-field, both representative subjects produced an initial accelerative force on the robot handle followed by a slightly smaller decelerative force in the opposite direction to halt the movement in the target window (Fig 2c, g). In their last training set in the Va field, the IRC-Va subject produced force output profiles with a smaller initial accelerative force in the direction of movement and a much larger decelerative force in the opposite direction (Fig 2d). In contrast, the IRC-Vr subject applied a large continuously-varying output force only in the direction of movement in the Vr field, without a decelerative reversal of forces (Fig 2h). In summary,
skilled performance in the N, Va and Vr fields required strikingly different output forces to produce movements with similar kinematics.

RC subjects encountered both the Va and Vr fields during their training sets, coupled predictably to green and red color cues. There was a high degree of inter-trial variability in the velocity curves during the first training set in the representative RC subject (Fig 3a,e). Note in particular the frequent high-velocity movements, endpoint overshoots and terminal oscillations in the Va field (Fig 3a) compared to the Vr field (Fig 3e). By the last training set, inter-trial variability was much smaller in both fields (Fig 3b,f), and the shape of the velocity curves was nearly identical in both fields and also to that in the N field (not shown). The inter-trial variability of the output forces also decreased considerably from the first training set (Fig 3c,g) to the last (Fig 3d,h). Unlike the velocity curves, however, the output forces clearly diverged towards two different patterns (Fig 3d,h). By the end of training, the RC subject could compensate for the two fields by generating two distinct patterns of output forces that resembled the behavior of the IRC-Va and IRC-Vr subjects in the corresponding force fields.

Comparable trends were seen in the representative URC subject. The inter-trial variability in velocity and force profiles decreased substantially from the first (Fig 4a,c,e,g) to the last training set (Fig 4b,d,f,h). The URC subject learned to generate different force output patterns that resulted in increasingly stereotypical elbow movements in the two fields, even though the color cues had no fixed relationship with the force fields.

Time course of improvements in performance across training sets

A trial was scored as an error if a subject did not move between the start and target circles within a 300-400ms movement-time interval or stay in the target for 200ms. Error rates
pooled across extension and flexion movements were high during the first training set in the RC subject (Fig 5a,b) and especially the URC subject (Fig.5e,f). However, they declined sharply in the second training set of the first daily session in the RC subject, and continued to decline at a slower rate across the remaining training sets (Fig. 5a,b). Error rates were greater at all times for the URC subject (Fig.5e,f). Error rates were modestly but systematically higher in the Va field than the Vr field for both subjects.

We quantified the velocity variability (Fig 5c,d,g,h) by calculating their norm, defined as the summed squared deviation of the velocity curve for each fielded trial at each 5ms interval, from the mean velocity curve of all baseline N-field trials collected across all 10 days for that subject. Mean velocity variability was calculated from all trials in each 4-trial block (solid squares) and training set (open squares), including successes and errors. For the RC subject, single-trial velocity variability decreased abruptly from the first to the second training set, especially in the Vr field, and continued to decrease gradually across training sets (Fig. 5c,d). Variability was somewhat higher in the Va field than in the Vr field throughout all training sets. Similar trends were also seen for the URC subject, although the decrease in velocity variability (Fig 5g,h) was more gradual and less extensive across sets and sessions than the RC subject.

*Mean velocity curves: use of explicit and implicit information provided by context cues*

Figures 6-8 show the mean velocity curves, averaged across all trials including successes and errors, for the representative subjects during extension movements in fielded and catch trials in the first training set (thick solid lines), the last training set (thin solid lines), and all baseline N-field trials (dashed lines).
Despite a considerable decrease in inter-trial velocity variability from the first to the last training set, the mean velocity curve of the IRC-Va subject in Va-field trials was similar to that of N-field trials throughout training (Fig 6a). The velocity curve of catch trials in the first or last trial of a 4-trial block during the first training set showed a truncated initial component followed by a second, delayed peak (Fig 6b,c, thick line). The initial truncated response showed that the subject was already adjusting their motor output to compensate for the Va field after only a few trials. The delayed peak likely represented a rapid feedback-mediated correction for the unexpected absence of the Va field. Similar catch-trial responses persisted during the last training session (Fig 6b,c, thin lines).

Corresponding results were seen in the IRC-Vr subject (Fig. 6d-f). Mean velocity curves during Vr-field trials were similar to those of N-field trials (Fig. 6d). When the subject encountered a catch trial, the movements were of high velocity during both the first and last training sets (Fig. 6e,f).

These results showed that the IRC subjects quickly began to anticipate and compensate for the Va and Vr fields after only a few trials in the first training set, and continued to improve with further training. The kinematics of fielded and catch trials did not change between monitor colors (data not shown). In contrast, the behavior of the representative RC and URC subjects was more complex.

During the first training set, movements of the RC subject showed slightly higher initial velocities and more asymmetric velocity curves on average in the Va- and Vr-field trials (Fig 7a,d, thick lines; c.f. Fig 3a,e) than in N-field trials (Fig 7a,d, dashed lines). By the last training set, mean velocity curves in the fielded trials (Fig 7a,d, thin lines) were essentially identical to that in N-field trials.
In the first training set, the RC subject made a high-velocity movement when a catch trial occurred in the first trial of a block after the monitor changed from green to red (Fig 7e, thick line). This showed that after experiencing only a few block transitions, the subject had already begun to associate a red monitor color with the Vr field. The peak velocity was even larger in catch trials in the last trial of a 4-trial block in the first training set (Fig 7f, thick line), indicating further short-term adaptation after performing three or more prior trials in the Vr field. In the last training set, the difference in the high-velocity movements between catch trials in the first and last trial of a red color-cued block were smaller (Fig 7e,f, thin lines), suggesting more consistent performance and less short-term adaptation during a block.

Catch-trial movements of the RC subject in the first trial of a block after the monitor changed from red to green during the first training set were slightly faster than in normal N-field trials and required a delayed corrective response (Fig 7b, thick line). This may have reflected an effect carried over from the preceding block of Vr-field trials. However, if the subject had not adjusted their motor output from the preceding Vr-field trials when the monitor color changed, they would have produced a very high-velocity movement (c.f. Fig 7f, thick line). Instead, the velocity profile showed that the subject was already learning the association between the green context cue and the Va field in the first training set, but their motor output was still not fully appropriate for the Va field.

Catch-trial movements in the last trial of a 4-trial block cued by a green monitor in the first training set (Fig 7c, thick line) were significantly slower than in catch trials in the first trial of the block (Fig 7b, thick line). This indicated considerable short-term adaptation after only three or more prior trials in the Va field. By the last training set,
catch-trial kinematics in the first and last trial of a 4-trial Va block were much more similar. This indicated that the subject had learned to associate the green context cue with the Va field and that their behavior had become more stereotyped.

All other RC subjects showed similar trends. Catch-trial results suggest that they learned the reliable association between color cues and force fields during the first training set and quickly began to use the cues to modify their motor output in anticipation of the expected force field at the start of each 4-trial block. In later training sets, the subjects generated increasingly stereotyped motor outputs to compensate for each field.

In the representative URC subject, the mean velocity profiles for Va- and Vr-field trials differed from each other in the first training set (Fig. 8a,d, thick lines). By the last training set, however, they were nearly identical (Fig. 8a,d, thin lines), showing that the subject had learned to make movements with stereotypical kinematics in the two fields after 10 days of training despite the unreliable context cues.

When the URC subject encountered a catch trial at the start of a Vr-field block in the first training set, the movements were too slow and required a delayed correction (Fig. 8e, thick line). This indicated that the URC subject had not begun to anticipate the onset of a Vr field block, unlike the RC subject (c.f. Fig. 7e). In contrast, when the catch trial occurred at the end of a Vr-field block in the first training set, the response was a high-velocity movement (Fig 8f, thick line), indicating a striking short-term learning effect of three or more prior Vr trials irrespective of the color of the context cue.

When the URC subject encountered a catch trial at the start of a Va block in the first training set, the mean movement velocity was slightly slower and of longer duration than during N-field trials (Fig. 8b, thick line). Catch trials at the end of a Va-field block in the
first training set showed an appropriate adjustment of motor output following 3 or more
Va trials (Fig 8c, thick line).

In the last training set, the catch-trial movements of the URC subject at the start of Va
and Vr blocks were nearly identical (Fig 8b,e, thin lines). This was strikingly different
from the RC subject (Fig 7b,e, thin lines). Like the RC subject however, catch trials at the
end of the blocks in the last training set resulted in very different movement kinematics
between the Va- and Vr-field blocks for the URC subject (Fig. 8c,f, thin lines).

The data in Fig. 8 were pooled across all blocks with either monitor color. When the data
are subdivided according to monitor color in each block, the results are similar (data not
shown). This indicated that the subject did not alter their motor output in any systematic
way as a function of the color of the unreliable context cue.

In URC subjects, the change in monitor color at the start of a trial block may or may not
be accompanied by a change in field. As a result, the subjects might have continued to
anticipate the same field encountered in the previous block. This raises the possibility that
the mean catch-trial velocity curves of the URC subject at the start of a block may be an
artifact of averaging motor responses appropriate for the two opposite fields.

To test this possibility, we separated the first trials of each 4-trial block according to the
field in the previous block, pooled across monitor colors (Fig 9). In the first training set,
there were clear differences in the movements depending on the combination of force
fields encountered at the transition between blocks that were usually consistent with a
carry-over of the motor response appropriate to the previous block of trials to the first
trial of the next block (Fig 9). This was particularly clear in the URC subject after they
had just completed a block of Va-field trials (Fig 9a-c, thick lines). If the next block
started with a catch trial, the movement was slower than in normal N-field trials (Fig 9a). If the first trial was another Va-field trial, the movement was slightly faster than in N-field trials (Fig 9b). Finally, if the first trial was a Vr-field trial, the movement was initially much slower than in N-field trials (Fig 9c) and even slower than in a catch trial (Fig 9a). This likely reflected the combined effect of a carry-over of the motor output response appropriate to a Va field and the presence of the Vr field.

The trends were similar in the first training set after completing a Vr block (Fig 9d-f, thick lines). If the first trial at the start of the next block was another Vr-field trial, the movement was only slightly slower than in normal N-field trials (Fig 9f), suggesting that their motor output was approximately appropriate for the Vr field. In contrast, when they encountered a Va-field trial, the movement had a very high peak velocity, presumably because a forceful Vr-appropriate motor output summed with the effect of the Va field (Fig 9e). The only exception were the few catch trials encountered right after the completion of a Vr-field block, whose mean velocity was similar to N-field trials in that particular training set in that subject (Fig 9d).

Overall, the behavior of the URC subject at the transition between blocks in the first training set suggested that they produced a motor output in the first trial after a monitor color change that was often similar to that in the immediately preceding block of trials. In contrast, the movement velocities of the URC subject were relatively constant across all the same combinations of transitions between blocks in the last training set (Fig 9a-f, thin lines). This suggests that by the end of training, this URC subject had developed a behavioral strategy to deal with their inability to predict the impending field at each block transition. Whenever the monitor changed color, they generated a default motor output to
probe the field. That default response resulted in movements that had fairly similar
kinematics in catch trials and were relatively resistant to the perturbing effects of Va- and
Vr fields (Fig 9a-f, thin lines). In subsequent trials, they adjusted their motor output
appropriately to compensate for the field in that block (Fig 8c,f). The large differences in
the kinematics of catch trials presented at the end of Va- and Vr-field blocks in the first
and last training set, that were similar to that seen in the RC subject, provided further
evidence that the URC subject did not compensate for the lack of reliable context cues
solely by stiffening the elbow joint to minimize the effects of the external fields.

Strikingly, every URC subject developed a similar strategy of probing the fields with a
default motor response whenever the monitor changed color, and then making the
appropriate adjustment in motor output for the remainder of the 4-trial block. The default
response emitted by most subjects was similar to that of the representative subject in Fig
8, 9. No subject adopted a strategy of generating a default response appropriate for the Vr
field. This is not surprising, since the resulting movement would have been extremely
vigorous should the subject have encountered a Va field.

As a result, in their last training set, the mean velocity profile of all URC subjects during
catch trials at the start of a block of Va- or Vr-field trials were fairly similar, and also
similar to their N-field velocity profiles (Fig 10c,f). In contrast, the mean catch-trial
velocities at the end of Va- and Vr-field blocks were quite different and showed that all
subjects had made the appropriate adjustment to the fields during the blocks (Fig 10c,f).
This was in striking contrast to the other groups, whose mean catch-trial velocity curves
were very different in the first trial of Va- and Vr-field blocks, very different from N-field trials, and showed little change in last-trial catch trials (Fig 10). The only exception
was the RC subjects, who showed a somewhat incomplete recall of the Vr-appropriate response in catch trials at the start of Vr-field blocks, and further adjustment during the rest of the block (Fig 10e). The probability of successful completion of catch trials also varied across fields and groups, and provided further evidence for a default strategy by URC subjects in the first trial of a block (see Supplemental Material).

The velocity profiles in normally-fielded trials in the last training set are also informative. They were very similar in the first trial and remaining trials of each block in each field for all four groups (Fig 11). In particular, the movements of URC subjects were only modestly perturbed whether they encountered a Va or Vr field in the first trial of a block, even though they could not predict what field they would encounter (Fig 11c,f).

The forces exerted by the subjects on the handle of the manipulandum provide more insight. The initial force output of the IRC-Va and IRC-Vr subjects in catch trials was appropriate to the Va and Vr field respectively, was followed by delayed corrective adjustments, and was identical for catch trials in the first and last trial of a block (Fig 12a,d). The initial force outputs of RC subjects were also field-appropriate (Fig 12b,e) and similar for catch trials in the first and last trials of Va-field blocks (Fig 12b). In Vr-field blocks, the forces in catch trials at the start of the block were not as large as at the end of the block, indicating further output adjustments still occurred during a Vr-field block in the last training set (Fig 12e; c.f. Fig 10e). In contrast, the output forces generated by URC subjects during catch trials at the start of Va- and Vr-field blocks were very similar, and nearly identical to those recorded during baseline N-field trials (Fig 12c,f), but showed field-appropriate adjustments at the end of a block (Fig 12c,f).
In normally-fielded trials, all groups generated force outputs that were field-appropriate, very similar in the first trial and the remaining trials of each block, and very different from baseline N-field trials (Fig 13). The only exception is that the initial part of the force profiles of URC subjects in the first trials of a block showed a small delay compared to later trials in the block. This is further evidence that URC subjects could not make a complete field-appropriate predictive adjustment to their initial motor output in the first trial of each block, but that they could make rapid adjustments to their output during the first trial, and then made appropriate predictive adjustments in later trials of each block.

**Measures of performance across training sets: Group data**

We used ANOVA to assess the effect of the main task factors (context cue color, force fields) on the error rates and velocity variability of all subjects in each group, across all trials (extension, flexion, successes, errors). RC and URC subjects did 32 4-trial blocks of both Va and Vr fields in each training set, whereas IRC-Va and IRC-Vr subjects did 64 blocks of only Va or Vr fields in each set. For these analyses, we used only the 32 blocks in each training set during which the monitor was green for IRC-Va subjects and red for IRC-Vr subjects, to compare equal numbers of trials with the same combination of field and context cue as in RC subjects. Comparison of the performance of IRC subjects in blocks with green and red monitor colors showed that there was no significant difference (p>0.05) for the main effect of color on both error rates (IRC-Va, $F_{1,5} = 0.104$; IRC-Vr, $F_{1,5} = 0.008$) and velocity variability (IRC-Va, $F_{1,5} = 0.031$; IRC-Vr, $F_{1,5} = 0.221$).

Similarly, monitor color had no significant effect on the velocity variability of URC subjects in either force field (Va, $F_{1,5} = 4.141$; Vr, $F_{1,5} = 3.478$), or on error rates in the Vr field ($F_{1,5} = 2.518$). The only significant effect of color was on the error rate in Va-field.
blocks in URC subjects ($F_{1,5} = 10.706$, $p=0.022$). Overall, these results suggest that the monitor color had little systematic effect on the performance of URC subjects, allowing us to pool the URC data recorded in a given field when the monitor was either color. In contrast, there was a highly significant color effect ($p<0.05$) on both error rates (color, $F_{1,10} = 15.234$; color-group interaction, $F_{1,10} = 17.807$) and velocity variability (color, $F_{1,10} = 10.960$; color-group interaction, $F_{1,10} = 7.945$) between RC and URC groups. This presumably reflected the difference in reliability of the color-field association between the two groups. To confirm this, further analyses were done with respect to force fields.

Most performance errors were due to failure to acquire the target within the 300-400ms movement time window. We calculated the mean error rate for consecutive sequences of 16 successful trials (i.e. four consecutive 4-trial blocks) in each field (Fig 14). Mean error rates (number of error trials per successful trial) decreased rapidly in the two training sets of the first daily session for all groups and declined more slowly across later training sets. Error rates were higher and decreased more slowly in the Va field (Fig 14a-c) than in the Vr field (Fig 14d-f). RC subjects showed slightly higher error rates in Va- and Vr-field blocks (Fig 14b,e) in early training sets compared to IRC-Va and IRC-Vr subjects (Fig 14a,d), but showed similar error rates in each field in later sets. In contrast, URC subjects showed systematically higher error rates than all other groups at all times in both fields (Fig 14c,f).

Similar trends were seen for velocity variability (Fig 15). IRC-Va, IRC-Va and RC subjects showed similar levels and time courses in reduction of variability across training sets. In contrast, URC subjects showed systematically higher velocity variability than the other groups in both fields (Fig 15,c,f).
We fit the learning curves to a double-exponential function of the form

\[ f(t) = c_1 \cdot e^{t/\tau_1} + c_2 \cdot e^{t/\tau_2} \]  

This analysis confirmed that the performance of RC subjects improved more rapidly than URC subjects during the first 1-2 training days (Fig 14, 15). Note that URC subjects showed almost no improvement in velocity variability in the Vr field after the first half of the first training set (Fig 15f). IRC-Va subjects adapted to the Va field somewhat more quickly than RC subjects (Fig 14ab; 15a,b) but the velocity variability of IRC-Vr subjects appeared to decline more slowly than RC subjects (Fig 15d,e). However, this was entirely due to one IRC-Vr subject who showed very high variability during the first two training days. The learning curve of the other 5 IRC-Vr subjects was significantly more rapid than the RC subjects (data not shown). Finally, examination of the learning curves at even higher block-by-block resolution showed that intra-day learning and inter-day forgetting was much more prominent in the first 2-3 training days than later days, and varied between subject groups and fields (see Supplemental Material).

All groups, including URC subjects, converged on the same low error rate during the N-field baseline sets of each training day, and showed a gradual decline in velocity variability, whose slope after the first 2-3 training days was similar to that in the Vr field (data not shown). This suggests that after the initial rapid adaptation of the subjects to the Va and Vr fields, they continued to show a general improvement in their ability to make stereotyped movements across all external field conditions in later training days.

The reductions in error rates and velocity variability were closely associated in all groups. The ‘learning curves” of the velocity variability of only the successful trials across
training sets formed nearly horizontal lines (data not shown). This showed that the
movement duration constraint imposed to define a successful trial required a movement
with a stereotyped velocity profile, and that all subjects became more skilled at producing
movements with the required kinematics across different field conditions with practice.

These qualitative differences were supported by statistical analysis of the mean error rate
and velocity variability in each training set. There was a significant main effect (p<0.05)
of Group on error rates when comparing RC and URC groups with IRC-Va in the Va
field (F_{2,15} = 6.573) and with IRC-Vr in the Vr field (F_{2,15} = 12.509), as well as a
significant effect of training set (Va, F_{19,285} = 73.845; Vr, F_{19,285} = 50.133) and Group-set
interactions (Va, F_{38,285} = 6.457; Vr, F_{38,285} = 4.173). In contrast, there was no significant
effect of Group on error rates between RC and IRC-Va alone in the Va field (F_{1,10} =
1.931) and between RC and IRC-Vr in the Vr field (F_{1,10} = 1.313). There were still
significant effects of training set (F_{19,190} = 25.140; F_{19,190} = 23.918, respectively) but no
significant Group-set interactions (F_{19,190} = 2.482; F_{19,190} = 2.192, respectively).

Similarly, there was a highly significant main effect of Group on velocity variability
between IRC-Vr, RC and URC groups in the Vr field (F_{2,15} = 10.024) as well as a
significant effect of training set (F_{19,285} = 21.293), but no significant Group-set interaction
(F_{38,285} = 0.523), and no main effect of Group between IRC-Vr and RC alone (F_{1,10} =
0.428) (Fig 14e). Finally, although there was a highly significant effect of training set for
IRC-Va, RC and URC groups in the Va field (F_{19,285} = 39.281) and a highly significant
interaction between Group and set (F_{38,285} = 2.352), there was no significant main effect
of Group (F_{2,15} = 1.980), despite the systematically higher velocity variability observed in
the Va field in URC subjects (Fig 15).
Error rates decreased significantly in N-field baseline sets across daily sessions ($F_{9,180} = 16.937$), but with no significant main effect of Group ($F_{3,20} = 1.284$) or significant Group-set interaction ($F_{27,180} = 0.998$). Velocity variability also decreased significantly during baseline sets across sessions ($F_{9,180} = 19.227$), with no significant difference between Groups ($F_{3,20} = 0.890$), and no significant Group-set interaction ($F_{27,180} = 1.228$). This indicates that any differences in performance among groups in the training sets cannot be due to inherently different levels of motor skill or motor learning per se.

**Use of explicit and implicit information provided by context cues: Group data**

The catch trial responses of RC subjects (Fig 7, 10) indicated that they quickly learned to use the explicit field-related information from the reliable context cues to make predictive adjustments to their motor output when the monitor color changed. However, this does not provide a precise measure of how well they switched between the two motor skills in the first trial of a 4-trial block, or whether their performance improved during the remaining trials in each block even in later training stages (e.g., Fig 10d). Furthermore, the systematically poorer performance of URC subjects was based on performance measures averaged over each 4-trial block. Was this poorer performance evident for all trials in each block, or was it primarily due to the inability of URC subjects to predict the nature of the impending field in the first trial after the monitor changed color? Was their poorer performance largely due to their strategy to emit a default response in the first trial after a color change, while their performance in the remaining trials of a block was more comparable to that of the other groups?

To assess these questions, we compared the data from the first trial position in each block with the remaining trials in each block (Fig 16,17). Data for the first trial position
included the first successful trial in the block as well as all error trials preceding the first
successful trial. These data were compared to the data from all subsequent trials needed
to complete a 4-trial block, including successful and error trials. Only Va- and Vr-fielded
trials were used; catch trials were not included.

IRC-Va and IRC-Vr subjects showed no difference in error rates (Fig 16a,d) or velocity
variability (Fig 17a,d) between the first trial position and the remaining trials of each
block at any stage in their training. This is to be expected since the distinction between
those trials is arbitrary for those subjects.

In contrast, RC subjects showed slightly higher error rates in the first trial position of a
block compared to the remaining trials when switching from Vr to Va (Fig 16b) and from
Va to Vr (Fig 16e), but only during the first 5-10 training sets. They also showed
modestly higher velocity variability in the first trial position of a block, especially Va
blocks (Fig 17b,e). These trends show that even though RC subjects quickly recognized
the field-predictive information provided by the color cues, their ability to minimize
anterograde interference to switch from one procedural skill to the other at each field
transition improved more gradually with practice over many training sets.

URC subjects showed the highest error rates (Fig 16c,f) and velocity variability (Fig
17c,f) in the first trial position of a block across all training sets. However, they also
showed the largest improvement in performance from the first trial position to all
subsequent trials for both field transitions throughout the entire training period. After
paying a penalty for the lack of reliable context cues at the start of each 4-trial block, the
performance of URC subjects during the remainder of each block was much closer to that
of the other groups.
These qualitative differences were supported by statistical analysis. ANOVA was performed on error rates and velocity variability between the first trial position and the remainder of the block in the Va field for IRC-Va, RC and URC groups and in the Vr field for IRC-Vr, RC and URC groups respectively.

For error rates in both the Va and Vr fields, there was a highly significant main effect of Group (Va, $F_{2,15} = 11.545$; Vr, $F_{2,15} = 28.050$), training set (Va, $F_{19,285} = 67.349$; Vr, $F_{19,285} = 58.439$) and trial position (Va, $F_{1,15} = 204.405$; Vr, $F_{1,15} = 470.629$). Importantly, there were also highly significant interactions between Group and set (Va, $F_{38,285} = 6.736$; Vr, $F_{38,285} = 5.631$) and between Group and trial position (Va, $F_{2,15} = 50.445$; Vr, $F_{2,15} = 84.397$). When the Va-field performance of only IRC-Va and RC was compared, there was no main effect of Group ($F_{1,10} = 2.820$) but there were significant main effects of training set ($F_{19,190} = 23.071$) and trial position ($F_{1,10} = 123.506$) and significant interactions between Group and trial position ($F_{1,10} = 22.874$) but not between Group and training set ($F_{19,190} = 2.891$). Comparing the performance of IRC-Vr and RC in the Vr field, there was no significant main effect of Group ($F_{1,10} = 2.380$), but there were significant main effects of training set ($F_{19,190} = 29.103$) and trial position ($F_{1,10} = 131.703$), and significant interactions between Group and training set ($F_{19,190} = 3.520$) and between Group and trial position ($F_{1,10} = 6.210$).

With respect to velocity variability, there were significant main effects of Group (Va, $F_{2,15} = 4.436$; Vr, $F_{2,15} = 14.007$), training set (Va, $F_{19,285} = 39.339$; Vr, $F_{19,285} = 24.371$) and trial position (Va, $F_{1,15} = 105.351$; Vr, $F_{1,15} = 17.466$), significant Group-training set ($F_{38,285} = 3.077$) and Group-trial position interactions ($F_{2,15} = 49.710$) in the Va field, and significant interactions for Group-trial position ($F_{2,15} = 11.419$) but not for Group-training...
set \( (F_{38,285} = 0.560) \) in the Vr field. When URC was removed, there was no significant main effect of Group \( (F_{1,10} = 0.007) \) but still a significant main effect of training set \( (F_{19,190} = 19.488) \) and trial position \( (F_{1,10} = 24.749) \) between IRC-Va and RC in the Va field, as well as a significant interaction for Group-trial position \( (F_{1,10} = 17.161) \) but not for Group-training set \( (F_{19,190} = 2.098) \). There was no main effect of Group between IRC-Vr and RC \( (F_{1,10} = 0.658) \) in the Vr field, a significant main effect of training set \( (F_{19,190} = 17.136) \), but no main effect of trial position \( (F_{1,10} = 1.668) \) and no significant interactions for either Group-training set \( (F_{19,190} = 0.447) \) or Group-trial position \( (F_{1,10} = 3.095) \).

In summary, the ANOVA results confirm that the URC subjects had higher error rates and velocity variability than the other Groups in the first trial position of each block. In contrast, the performance of RC subjects was much more similar overall to IRC-Va subjects in the Va field and to IRC-Vr subjects in the Vr field.

**DISCUSSION**

_The task required several kinds of motor skill acquisition_

This study involved several different kinds of motor skill acquisition. The first was the skill of performing elbow movements within the time constraints imposed by the task. This was evident even in the N–field baseline sets, in which all subjects showed increasingly stereotyped form and timing of their velocity profiles across the 10 daily sessions. All groups also had to learn the procedural skill of making movements with the same kinematics in one or both of the assistive Va field or resistive Vr field. All groups, including URC subjects, showed predictive changes in motor output consistent with the acquisition of “internal models” of the different dynamical environments (Shadmehr &

RC and URC subjects faced the further challenge of learning to perform the precisely timed movements in the two anti-correlated dynamic force-field conditions in an interleaved practice schedule of short 4-trial blocks. This required them to recall and switch rapidly between the two skills with little anterograde and retrograde interference. Finally, all groups had to learn to recognize the force-field environment in which they would perform movements in each trial block. This was trivial for IRC-Va and IRC-Vr subjects, for whom a black monitor signaled a baseline set in the N-field while a red/green monitor signaled a training set in only the Va or Vr field respectively. This was much more critical for RC and URC subjects for whom the force-field environment changed frequently during the training sets. Those subjects had to learn the contextual information provided by the red and green monitor colors on their own.

This last facet of the task, awareness and recognition of the behavioral relevance of the color context cues, may also involve more cognitive or declarative processes that are known to facilitate motor skill acquisition and performance (Krouchev & Kalaska 2003; Miall et al 2004; Osu et al 2004; Hwang et al 2006; Imamizu et al 2007, 2008; Hinder et al 2008; Werner & Bock 2007). This may involve neural circuits that are at least partially separate from those implicated in more procedural aspects of motor learning and performance (Willingham et al. 2002; Imamizu et al. 2008).

*Human subjects can use color context cues to learn two opposite motor skills simultaneously.*
For RC subjects, the red and green monitor colors provided reliable cues about the nature of the field to be presented in each block of the training set before they made a movement. They used this predictive context information effectively to learn, recall and switch predictively between the two motor skills required to compensate for the opposing viscous force fields, so that their performance in normally-fielded and catch trials in each field converged on those of IRC subjects after the first few training sets. To achieve that performance, the RC subjects had to learn simultaneously the same two opposing motor skills that were learned separately by the IRC-Va and IRC-Vr subjects, while switching between them in short blocks of trials and while performing only half as many successful trials in each field as the IRC subjects.

Furthermore, these different skills were learned at different rates. The acquisition of the procedural motor skills to compensate for the opposing force fields occurred over an extended period of time. This involved learning processes that occurred rapidly during a single 4-trial block in a given field and that dominated task performance during the initial training sets, as well as slower processes that spanned training sets and days (Smith et al. 2006). They recognized and began to use the explicit information about the force fields provided by the monitor colors to make predictive adjustments to their motor output after only a few presentations of the reliable color-field conjunctions in the first training set. Their ability to minimize anterograde and retrograde interference to recall and switch between skills in response to each color change continued to improve with practice over multiple training sets. Even after extensive practice in field switching at the end of the training period, the velocity variability of RC subjects was modestly higher in the first trial of a block than in subsequent trials. This is also evident in the small difference in
catch-trial velocities between the first and last trial of a 4-trial block in the Vr field in the
last training set. Of the three aspects of force-field compensation in this study, the ability
to switch between the appropriate motor skills in response to a change in context cue
color appeared to be learned more slowly than the recognition of the behavioral
significance of the context cues and the ability to compensate for the fields themselves.

URC subjects also displayed a substantial degree of adaptation to the two fields despite
the unreliable relation between context cues and force fields. To accomplish this multi-
skill learning, they appeared to use the implicit context information provided by the color
cues about the structure of the task. Specifically, the color cues divided the training set
into short 4-trial blocks during which only one field would be encountered. Moreover, a
change in monitor color signaled the possibility of a force field change in the upcoming
trial. However, the definitive sensory information that identified the nature of the field
could only be acquired by performing the first movement of the block, with the exception
of infrequent catch trials at the start of a block.

The behavior of the URC subjects suggested that they gradually recognized this implicit
information provided by the context cues and used it to develop a behavioral strategy
over several training sets. In early training sets, they often showed a carry-over of the
motor output from the previous block of trials into the first trial of the next block. By the
end of training, however, whenever the monitor changed color, all URC subjects probed
the nature of the field by emitting a default motor output in the first trial in a block. These
probing responses produced movements with fairly similar kinematics despite the large
differences in external forces the subjects encountered in Va- or Vr-field trials or N-field
catch trials. This may indicate a strategy of muscle co-contraction to stiffen the elbow
joint during the first trial after the monitor color change to minimize the perturbing effect of the unknown field. Alternatively, adaptive changes in reflex gains may have allowed more efficient use of feedback signals from the perturbation experienced early in the movement in the first trial after the color change to make rapid on-line changes in their motor output to compensate for the force field (Akazawa et al. 1983; Doemges & Rack 1992; Nicols et al. 1999; Franklin et al. 2007; Perrault et al. 2008; Pruszynski et al. 2009; Krutky et al. 2010; Shemmel et al. 2010). Whatever mechanism(s) they used is not critical to the objectives of this study, but it is clear that the kinematics of their movements in the first trial of a block at the end of training were perturbed much less than one would expect given the magnitude of the force fields. Nonetheless, the inability of the URC subjects to predict the nature of the field after a context cue color change resulted in significantly higher error rates and velocity variability in Va- and Vr-field trials in the first trials of each block compared to the other subject groups, which persisted across all 10 training days.

The initial default responses clearly allowed the URC subjects to identify the nature of the field in the current 4-trial block, since they all made appropriate changes in their motor output for the remaining trials in the block, resulting in lower error rates and velocity variability. Late in training, the performance of URC subjects in the last three trials of each block approached that of the other three groups, except for higher velocity variability in the Vr field. This is somewhat surprising, since the Vr field is inherently stable and generally easier to learn than the Va field.

The behavioral strategy used by URC subjects appears to be a striking example of “postdictive switching” between motor skills based on the difference between the
intended and sensed movement evoked by a motor output command (Milner & Franklin
2005; Imamizu et al. 2007a,b; Imamizu and Kawato, 2008).

Imamizu et al (2007) trained subjects to adapt to two opposite visuomotor rotations of
cursor motions during a wrist-finger pointing task in 8 directions. The opposing rotations
were applied in 10 alternating blocks of 120 trials in one training session. One group of
subjects received explicit verbal instructions about the rotations and how to correct for
them at the start of the training session, and at the start of each block of trials. A second
group received no explicit instructions and had to discover the nature of the perturbation
by performing hand movements and observing the resulting cursor motions. All subjects
showed large cursor motion errors at the start of each block and gradual improvement
during each block, as well as anterograde interference at the start of each block after each
transition between rotation conditions. However, like our RC subjects, their verbally-
instructed subjects showed evidence of predictive switching between motor skills in
response to the explicit verbal context cues and improved ability to reduce anterograde
interference and recall the appropriate motor skill with practice at each block transition.
Like our URC subjects, their uninstructed subjects were still able to learn the opposing
visuomotor rotations and to switch increasingly effectively between skills with practice
based on sensed errors in the first trials after a transition (“postdictive switching”).

Previous studies of color as a context cue for motor skill acquisition

The present findings are consistent with a study by Wada et al (2003). Although details of
the paradigms are quite different, Wada et al (2003) showed that subjects can learn to
compensate for rapidly alternating assistive and resistive force fields signaled by color
context cues across multiple training days. Also like the present study, they found that
subjects appeared to learn how to compensate for each field more quickly than to switch between the two motor skills at each color cue change. However, there were several notable differences in the two studies. First, Wada et al (2003) gave the subjects explicit verbal instructions about the meaning of the colors and the nature of the two opposing fields at the start of training. In contrast, our subjects received no explicit instructions about the color cues or force fields. Explicit knowledge and awareness of the nature of perturbations can facilitate learning (Osu et al. 2004; Hwang et al. 2006; Imamizu et al. 2007; Werner & Bock 2007). Second, the strengths of the Va and Vr fields in their study were substantially weaker (0.16 Nms/rad for both) than in the present study (Va: 1.2 Nms/rad; Vr: 5.0 Nms/rad). As a result, whereas Va fields are inherently unstable, the combined dynamics of the Va-field/arm/manipulandum system was stable in the Wada et al (2003) study and did not require the strong braking forces to slow down the movement that were produced by our subjects. The field strengths were sufficiently modest that Wada et al. (2003) could apply the opposite force field in their catch trials rather than a Null field, as was done here. Nevertheless, this still only produced a 10% difference in peak velocity between Vr- and Va-field catch trials. It is also not clear to what degree this small difference reflected the anticipatory motor adjustments of the subjects for each field, or the physical effects of the unexpectedly-applied opposite force fields themselves since the effect of the two factors will sum to enhance the difference in kinematics between the two sets of catch trials. These various factors suggest that the subjects in the Wada et al (2003) only had to make small adjustments in the magnitude of their net motor output force in the direction of movement in the two fields rather than having to master two opposing dynamical environments, as was the case in the present study.
Osu et al. (2004) also reported that subjects could learn to compensate for viscous curl fields that switched between opposite directions in short blocks of trials during whole-arm reaching movements when provided with complex visual cues that included the color of a border displayed on the monitor. Further tests showed that the color cue alone permitted the subjects to adapt to and switch between the two skills.

Imamizu and Kawato (2008) trained subjects in the same visuomotor rotation task with verbal instructions as Imamizu et al. (2007). The subjects then performed the task during fMRI recordings. While being scanned, some subjects received only color cues (the color of a central start window) that reliably signaled the direction of the visuomotor rotation (similar to our RC group) or color cues with no reliable relation to the direction of rotation (like our URC group). Consistent with our findings, the subjects that received reliable color cues progressively improved their ability to make predictive switches between the previously learned visuomotor rotations, while the subjects that received unreliable cues nevertheless showed progressive improvements in postdictive switching using sensed errors after a change in visuomotor rotation. Differences in the BOLD activation patterns between the two subject groups implicated separate brain circuits in the predictive versus postdictive switches (Imamizu and Kawato 2008).

Finally, Hinder et al. (2008) found that subjects could use color cues to distinguish between trials that required either a 30° CW or 60° CCW visuomotor dissociation between the direction of isometric forces and resultant cursor motions, presented in random order. Subjects that received reliable color cues reduced the magnitude of errors in the 60° CCW condition but not the 30° CW condition. This suggests that they could discriminate between the two task conditions using the color cues, but could not learn
both rotations during a single training period. In contrast, subjects that did not receive
color cues showed a reduction of errors in the 60° CCW condition but an increase in
directional errors in the 30° CW condition, suggesting a default strategy that migrated
toward the mean of the amplitudes of the two different rotations.

In contrast, several other studies have reported that colored context cues are largely
ineffective in facilitating multi-skill learning of dynamic force fields or visuomotor
dissociations (Gandolfo et al. 1996; Rao and Shadmehr, 2001; Miall et al. 2004; Gupta
and Ashe 2007). This raises the question why color context cues are effective in some
studies, such as the present, but ineffective in others.

One likely important factor is that our task comprised many short blocks of trials. This
gave the subjects many examples of color-field pairings to learn the nature of the
association and the different types of information provided by the context cues. It also
gave the RC and URC subjects many opportunities to practice switching between the two
skills over many days. This would not be the case in studies that used longer blocks of
trials or few exposures to context switches in a classic A-B-A task design during a single
training session (Gandolfo et al. 1996; Miall et al. 2004). Even within each block, our
subjects had to switch between the current field during movements to the targets and the
N-field during the return movements to the start position at the end of each trial.

Furthermore, our task design gave RC and URC subjects a few trials to practice each skill
within a block and required them to perform four successful trials before switching fields.
This allowed them to use errors from unsuccessful trials to adapt their motor output in
subsequent trials in the same field. As a result, both RC and URC subjects showed
substantial short-term learning during each trial block in early training sets. Other studies
did not appear to require successful performance before switching (Gandolfo et al. 1996; Miall et al. 2004; Rao & Shadmehr, 2001; Gupta and Ashe 2007). Wada et al (2003) also found that subjects learned to switch between two motor skills more effectively when they switched between them frequently in short blocks of trials rather than infrequently after longer blocks of continuous training in each field. At the other extreme, Osu et al (2004) reported that subjects could not adapt to opposite viscous curl fields that alternated between trials (c.f., Rao & Shadmehr, 2001; Gupta and Ashe 2007), even though they received explicit context cues. In contrast, subjects that performed short blocks of trials in each field adapted to both fields (Osu et al 2004). However, short trial blocks are not obligatory to learn how to switch predictively between different dynamic motor skills, provided that the subjects are given sufficient practice. Krouchev and Kalaska (2003) trained a monkey to perform elbow flexion-extension movements in 5 successive blocks of 48 trials, during each of which it was exposed to one of 5 different force fields that were reliably associated with a specific monitor color. After performing this task hundreds of time over many months, the monkey was then presented with a modified task in which they had to switch rapidly between Va- and Vr-perturbed movements in blocks of 8 trials, much like the present task. The monkey immediately showed a striking ability to switch predictively between the two anti-correlated motor skills, even though it had never been presented with that particular challenge in its prior training history (Krouchev and Kalaska 2003). Osu et al (2004) concluded that variable numbers of trials in each block of exposure to the opposing fields was critical for successful simultaneous adaptation. Wada et al (2003) likewise used variable-length blocks of trials. In contrast, our task required a fixed
number of four successful trials in each block. Nevertheless, a degree of variability was introduced by the fact that subjects in all groups performed variable numbers of unsuccessful trials in each trial block before completing four successful trials. However, the resulting degree of variability in the number of trials per block was greatest for URC subjects but their overall learning was the slowest of all four Groups.

Wada et al (2003) concluded that simultaneous learning of multiple dynamic skills can be facilitated if the color context cues are sufficiently clear and distinct and the force fields are readily distinguishable. In theory, those conditions would make it easier to acquire the putative “internal models” for each motor skill and to switch between them when given the appropriate contextual information (Wada et al. 2003; Wolpert and Kawato, 1998; Haruno et al. 2001; Imamizu et al. 2007a,b; Imamizu and Kawato, 2008, 2009).

Our findings support those conclusions. In our task, the color cues were easily detectable and prominent - the monitor background color on which the cursor and targets were presented. Furthermore, with the exception of catch trials, the subjects only experienced the black color associated with a Null field and green and red colors associated with the Va or Vr fields. In contrast, in studies in which color cues were ineffective, the color cues were more subtle changes in the color of the cursor or targets (Rao and Shadmehr, 2001) or less obviously associated with the task, such as the color of the ambient light in the room (Gandolfo et al 1996). Furthermore, in the Rao & Shadmehr (2001) study, the subjects experienced the different color cues during an initial familiarization session in a Null field before being exposed to the two opposing force fields. This might have further reduced their task relevance during the subsequent training period.
The relatively strong assistive and resistive viscous force fields applied in the direction of single-joint elbow movements in our study were also simple and easily discriminable. The same may not be the case for viscous curl fields applied perpendicular to the direction of reaching movements (Rao & Shadmehr, 2001; Gupta and Ashe 2007), especially if applied during movements in many different reaching directions (Gandolfo et al. 1996). The associated changes in motor output during the single-joint elbow movements in our study may also be simpler to learn than motor skills required to compensate for viscous curl fields during multi-joint reaching movements. Nevertheless, color context cues can facilitate the simultaneous adaptation to opposing viscous curl fields during whole-arm reaching movements in multiple directions in the appropriate task conditions (Osu et al. 2004).

Summary

This study showed that arbitrary colors can be very effective context cues to facilitate the simultaneous learning of two anti-correlated procedural motor skills. These findings also emphasize that switching between different motor skills is itself a motor skill that must be learned and has its own sets of conditions to facilitate that learning. The classic A-B-A task paradigm is which subjects perform lengthy blocks trials in each condition may optimize the learning of each skill within a block, but is sub-optimal for retention, recall and switching between each skill.

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**FIGURE LEGENDS**

**Figure 1**
Task apparatus. Subjects sat with their right arm abducted in the horizontal plane at shoulder level to rest their forearm on the handle of a torquable robotic manipulandum. They made flexion or extension movements of their elbow to displace a cursor on a monitor screen between a central starting target window and a target at either 45° to the left (flexion) or right (extension) of the central starting position. The background color of the monitor changed in different task conditions. During null (N)-field baseline trial sets, the monitor background color was black. During training sets, subjects made elbow movements against either a velocity-dependent resistive viscous (Vr) force field or an assistive viscous (Va) force field. The monitor background color alternated between red and green every block of four successful trials in the training sets. The utility of the monitor color as a context cue about the nature of the force field presented during each block of 4 trials differed for different groups of subjects. See text for details.

**Figure 2**
Single-trial velocity profiles (A, B, E, F) and force profiles (C, D, G, H) from a representative IRC-Va subject (A-D) and a representative IRC-Vr subject (E-H) during the final N-field baseline set (A, C, E, G) and the last training set (B, D, F, H). During the
training sets, the IRC-Va subject encountered only the Va field, while the IRC-Vr subject encountered only the Vr field. Data are shown only for elbow extension movements, and are aligned to the detected onset of movement within the start window (Reaction Time; time 0) after the appearance of the target window. All elbow-extension trials are shown, including successful trials and errors. Note the different force scales (C, D, G, H).

Figure 3

Single-trial velocity profiles (A, B, E, F) and force profiles (C, D, G, H) from a representative RC subject during the first training set (A, C, E, G) and the last training set (B, D, F, H). Trials were separated into blocks performed in the Va field (A-D) and Vr field (E-H). All elbow-extension trials are shown, including successful trials and errors. Note that the velocity and force traces are flat during the center-hold period prior to the onset of movements (time 0) after the appearance of the target windows. This indicates that the RC subject did not attempt to probe the nature of the impending force field by making small movements during the center-hold period.

Figure 4

Single-trial velocity profiles (A, B, E, F) and force profiles (C, D, G, H) from a representative URC subject during the first training set (A, C, E, G) and the last training set (B, D, F, H). Same format as Figure 3. Note that the velocity and force traces are flat during the center-hold period prior to the onset of movements (time 0) after the appearance of the target windows. This indicates that the URC subject did not attempt to probe the nature of the impending force field by making small movements during the center-hold period, either early in training or at the end of training.

Figure 5

Time course of improvement in performance of the representative RC subject (A-D) and URC subject (E-H) in the Va field (A, C, E, G) and Vr field (B, D, F, H), averaged for both extension and flexion movements, across all 20 training sets. The RC subject showed a progressive decrease in the error rate, calculated as the number of error trials per successful trial, across sets (A, B), and in the variability of the velocity profiles,
including both successful and error trials (C, D). Velocity variability was calculated for each 4-trial block (small squares) as well as for each training set (open squares; thin lines show s.d.). Both error rates and velocity variability of the URC subject were systematically higher and showed greater within- and across-set variability in both fields compared to the representative RC subject.

Figure 6
Mean velocity profiles for elbow extension movements made by the representative IRC-Va subject in Va-field trials (A-C) and the representative IRC-Vr subject in Vr-field trials (D-F), in the first training set (thick solid lines), the last training set (thin solid lines) and all baseline N-field sets (dashed lines). Mean velocity profiles were generated using all trials, including both successful and error trials. Separate mean velocity profiles were calculated for normally-fielded trials (A, D), and for catch trials presented in the first trial of a 4-trial block immediately after the change in the color of the context cue (B, E), or the last trial of a 4-trial block (C, F).

Figure 7
Mean velocity profiles of the representative RC subject in Va-field trial blocks (A-C) and Vr-field trial blocks (D-F), in the first training set (thick solid lines), the last training set (thin solid lines) and all baseline N-field sets (dashed lines). Same format as Figure 6.

Figure 8
Mean velocity profiles of the representative URC subject in Va-field trial blocks (A-C) and Vr-field trial blocks (D-F), in the first training set (thick solid lines), the last training set (thin solid lines) and in all baseline N-field sets (dashed lines). Same format as Figure 6.

Figure 9
Mean velocity profiles of the representative URC subject during the first trial after a change in color context cue in the first training set (thick solid lines), the last training set (thin solid lines), as well as the mean velocity curve averaged across all baseline N-field
sets (dashed lines). Trials are sorted according to the nature of the field encountered in
the first trial of a 4-trial block after completing a block of Va-field (A-C) or Vr-field (D-F) trials, including catch trials (A, D), Va-field trials (B, E) and Vr-field trials (C, F). In some cases, the field changed when the context cue color changed at the start of a 4-trial block (C, E) and in other cases the field did not change (B, F).

Figure 10
Mean velocity profiles in catch trials encountered in the first trial (thick solid lines) and the last trial (thin solid lines) of a 4-trial block of Va-field (A-C) and Vr-field (D-F) trials during the last training set, as well as the mean velocity curve averaged across all baseline N-field sets (dashed lines), for all subject groups.

Figure 11
Mean velocity profiles in normally-fielded trials in the first trial (thick solid lines) and the remaining trials (thin solid lines) of a 4-trial block of Va-field (A-C) and Vr-field (D-F) trials during the last training set, as well as the mean velocity curve averaged across all baseline N-field sets (dashed lines), for all subject groups.

Figure 12
Mean force profiles in the same catch trials in the last training set and in all baseline N-field sets shown in Figure 10. Same format as Figure 10.

Figure 13
Mean force profiles in the same normally-fielded trials in the last training set and in all baseline N-field sets shown in Figure 11. Same format as Figure 11.

Figure 14
The time course of changes in the error rate across training sets in Va-field trials (A-C) and Vr-field trials (D-F), for IRC-Va (A), IRC-Vr (D), RC (B, E) and URC (C, F) subjects. Each solid circle is the mean error rate for consecutive sequences of 16 successful trials (e.g. four consecutive 4-trial blocks) in the corresponding field. Solid
line – the best-fit two-exponent function for each distribution of data. The equation in each figure provides the parameters of the best-fit function.

Figure 15
The time course of changes in the velocity variability across training sets in Va-field trials (A-C) and Vr-field trials (D-F), for IRC-Va (A), IRC-Vr (D), RC (B, E) and URC (C, F) subjects. Each solid circle is the mean velocity variability for consecutive sequences of 16 successful trials and interspersed error trials (e.g. four consecutive 4-trial blocks) in the corresponding field. Solid line – the best-fit two-exponent function for each distribution of data. The equation in each figure provides the parameters of the best-fit function.

Figure 16
Mean error rates (number of error trials per successful trial) during the first trial of each 4-trial block (dashed lines) and during the remaining trials of each 4-trial block (solid lines), calculated for each training set in Va-field trials (A-C) and in Vr-field trials (D-F), for IRC-Va (A), IRC-Vr (D), RC (B, E) and URC (C, F) subjects.

Figure 17
Mean variability of velocity profiles during the first trial of each 4-trial block (dashed lines) and during the remaining trials of each 4-trial block (solid lines) calculated for each training set in Va-field trials (A-C) and in Vr-field trials (D-F), for IRC-Va (A), IRC-Vr (D), RC (B, E) and URC (C, F) subjects.
Figure 1. Setup
Velocity variability

Set number

Error rate

Set number

RC subject

Vr

Vr

URC subject
Fielded trials
First-trial catch trials
Last-trial catch trials

A) B) C)

V_{a}

RC subject

D) E) F)

V_{r}

Velocity (rad/s)

Time (ms)
Fielded trials  First-trial catch trials  Last-trial catch trials

Velocity (rad/s)

Va

A)

URC subject

B)

C)

--- all N
- 1st set
- last set

Velocity (rad/s)

Vr

D)

E)

F)

Time (ms)
Catch trials - Last training set

A) IRC_Va

B) RC

C) URC

D) IRC_Vr

E) RC

F) URC

Velocity (rad/s)

Time (ms)
Fielded trials - Last training set

IRC_Va

IRC_Vr

Vr
Catch trials - Last training set

A) IRC_Va
B) RC
C) URC

D) IRC_Vr
E) RC
F) URC

Force (N)

Time (ms)
Fielded trials - Last training set

**A)** IRC\_Va

**B)** RC

**C)** URC

**D)** IRC\_Vr

**E)** RC

**F)** URC

- IRC\_Va: 1st trial
- Trials 2-4
A) IRC_Va
\[ f(t) = 1.2e^{t/2.8} + 0.4e^{t/133.2} \]

B) RC
\[ f(t) = 1.6e^{t/3.1} + 0.6e^{t/107.1} \]

C) URC
\[ f(t) = 2.3e^{t/4.3} + 0.8e^{t/128.4} \]

D) IRC_Vr
\[ f(t) = 0.4e^{t/8.3} + 0.2e^{t/206.7} \]

E) RC
\[ f(t) = 1.1e^{t/4.3} + 0.2e^{t/197.1} \]

F) URC
\[ f(t) = 1.2e^{t/7.1} + 0.3e^{t/227.5} \]
Velocity variability

\[ f(t) = 3.7e^{t/2.9} + 5.4e^{t/13.077} \]

\[ f(t) = 4.2e^{t/5.9} + 5.0e^{t/171.51} \]

\[ f(t) = 4.4e^{t/9.4} + 6.2e^{t/845.2} \]

\[ f(t) = 2.9e^{t/11.3} + 4.0e^{t/1002.2} \]

\[ f(t) = 3.7e^{t/4.3} + 4.2e^{t/-33687.0} \]

\[ f(t) = 5.5e^{t/1.0} + 5.0e^{t/6260.7} \]