

# Context-Dependent Anticipation of Different Task Dynamics: Rapid Recall of Appropriate Motor Skills Using Visual Cues

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**Krouchev, Nedialko I. and John F. Kalaska.** Context-dependent anticipation of different task dynamics: rapid recall of appropriate motor skills using visual cues. *J Neurophysiol* 89: 1165–1175, 2003; 10.1152/jn.00779.2002. Recent studies have reported that human subjects show varying degrees of ability to use contextual cues to recall the motor skills required to compensate for different dynamic external force fields during arm movements. In particular, the subjects showed little or no ability to use color cues to adjust motor outputs in anticipation of the perturbing fields after limited periods of training that were sufficient to learn to compensate for the fields themselves. This is unexpected since humans and monkeys can use color cues to perform a wide range of visuomotor tasks. Here we show that a monkey with extensive practice compensating for viscous fields in an elbow-movement task can use associated color cues to adjust motor output in anticipation of an impending field before physically encountering it.

## INTRODUCTION

Normal unperturbed arm movements are characterized by stereotypical kinematic features such as approximately bell-shaped velocity profiles and straight handpaths between targets (Gandolfo et al. 1996; Morasso 1981; Shadmehr and Mussa-Ivaldi 1994). When the arm encounters an external force field, movement kinematics are perturbed, resulting in deviations from the stereotypical kinematics (Gottlieb et al. 1989; Jansen-Osmann et al. 2002; Shadmehr and Brashers-Krug 1997; Shadmehr and Mussa-Ivaldi 1994). With practice, however, subjects usually learn to compensate for the effects of the field to minimize the perturbation, suggesting that the motor system is attempting to restore the stereotypical kinematics seen in unperturbed movements (Gottlieb et al. 1989; Jansen-Osmann et al. 2002; Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 1999, 2000).

In everyday life, the motor system learns to compensate for a wide range of task dynamics, and skilled subjects can switch rapidly between the different control strategies needed to cope with each situation (Gandolfo et al. 1996; Shadmehr and Mussa-Ivaldi 1994). An important question relates to the nature of the signals that are used to recall different motor skills. Two likely sources are proprioceptive and visual signals about sensed errors when the field is encountered. However, a further intriguing question is to what degree these expert circuits can

be activated by contextual cues or central cognitive processes before actually encountering the task environment and so prior to the arrival of any performance-error signals? Is vision of a tool or any other knowledge of the nature of an impending motor task sufficient to activate the appropriate circuitry underlying the skill?

Several recent studies have addressed this question and suggest that the rate of learning of the ability to recall learned motor skills in response to contextual cues can vary widely (Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002; Rao and Shadmehr 2001). Cohn et al. (2000) showed that subjects can rapidly learn to emit appropriate motor outputs in contexts associated either with or without perceptual illusions of self-rotation. Gandolfo et al. (1996) trained subjects to compensate for clockwise or counter-clockwise viscous curl fields during reaching movements, while holding their arm in a different posture for each field. Once learned, the subjects could rapidly recall and switch between the two opposing motor skills simply by changing arm posture. In contrast, subjects could not learn an association between the two force fields and two different color cues or two thumb positions in the same time period. Similarly, Rao and Shadmehr (2001) reported that subjects could rapidly learn to recall the motor skills required for the two opposing viscous curl fields in response to spatial cues in two different locations but not to cues of two different colors in the same location. Finally, Karniel and Mussa-Ivaldi (2002) trained subjects to perform random movement sequences in one of the two opposing curl fields separately in two successive days. On the third day, the subjects attempted to perform movement sequences while the two curl fields alternated after each movement. The subjects showed no evidence that they were able to switch rapidly between the two skills required to compensate for the alternating force fields. These studies showed that subjects could learn rapidly to use some contextual cues (arm posture, stimulus location) to recall motor skills, but not others (color, sequence order), within the limited time period necessary to learn the procedural skill itself. The failure to use color cues in those task conditions is particularly surprising since color is commonly used as an instructional cue in a wide range of behavioral tasks. Although the authors of those studies did not draw any such conclusion, the convergence of results may leave the impression that the motor system may

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have a limited ability to learn arbitrary associations between color context cues and certain procedural skills such as compensation for different external force fields.

Here we present evidence that a monkey that had extensive prior training in a task in which it had adapted to different external force fields associated with different color cues can rapidly change its motor output on cue before actually physically encountering the associated field. The results show that the CNS can learn to use arbitrary contextual color cues to recall a simple motor skill given enough behaviorally significant practice.

## METHODS

The results presented here were collected from a rhesus monkey that had been extensively trained over a period of several months to perform single-degree-of-freedom elbow movements that could be perturbed by externally generated force fields, using either the left or the right arm.

### *Experimental setup*

The monkey's arm was placed in a single-joint robotic torquable manipulandum (Kyowa, 25 N.m sustained, 50 N.m peak) positioned beside a primate chair. The height of the chair was adjusted so that the upper arm of the monkey was abducted into the horizontal plane approximately 90 deg with respect to the trunk. The animal performed elbow flexions/extension in the horizontal plane to move a cursor between targets presented on a computer monitor positioned at eye level 0.5 m in front of the monkey. The primate chair could be placed on either side of the manipulandum so that the monkey could perform the task with either arm.

### *Experimental protocol*

**BEHAVIORAL TRIALS.** During each trial, the monkey viewed a horizontal 150 deg arc of 17-cm radius, presented on the computer monitor, and a cursor that swept along the arc as a function of the angular position of the monkey's arm. This plotting scale permitted a 1:1 representation of the displacement of the actual (physical) limb. At the beginning of each trial, the screen was cleared; the arc and cursor appeared, and a circle of 1.7-cm radius (corresponding to an angular precision of  $\pm 5.74$  deg) was displayed centrally at the top of the arc (0 deg) as a start target-window. This corresponded to a starting elbow angle of 90 deg of the forearm with respect to the humerus, so that at the start position, the forearm was pointing forward. Within an allowed period of 3,000 ms, the monkey had to position the cursor in this target and remain in it for a 600-ms hold period. After the latter elapsed, the start target disappeared and a circular movement target (1.7-cm radius) was presented at either the +45 or -45 deg position. At this point the monkey had 5,500 ms to complete a flexion/extension movement into the specified target. A minimum reaction (RT) and movement time (MT) of 150 and 200 ms, respectively, were imposed to prevent anticipatory movements initiated before actual targets appeared. An upper-bound restriction on RT of 1,000 ms was imposed to ensure that the monkey attended to the task and made the movements promptly. Note that with the lengthy upper-bound limit on MT, the movements were essentially self-paced, therefore yielding "natural" trajectories and velocity profiles. The vast majority of movements were completed well within a 1,000-ms duration. If the monkey failed to complete a trial successfully, it was immediately repeated.

### *Force fields*

The monkey made the elbow flexion/extension (F/E) movements under a variety of dynamic field conditions. There was a baseline null

field (N) condition in which the movements were done without perturbing torque. A set of different force-field conditions was also implemented, featuring assistive (-) or resistive (+) fields proportional to velocity (viscous, V), position (elastic, E), as well as their linear combinations. Each force field was associated with a different monitor background color that signaled the nature of the field throughout each trial. This information would potentially allow the monkey to anticipate the nature of the impending force field before it was actually experienced in each trial.

### *Prior experience*

Before doing the behavioral study described here, the monkey participated in a neural recording study of primary motor cortex (MI). For this purpose, it was initially trained to make the F/E movements without a perturbing force field. It was then trained over a period of many months to perform a task in which different fields were presented in sequential blocks of 48 trials each. Different monitor background colors [N: black, V+: dark red, V-: bright (pinkish) red, E+: blue, VE+: magenta] signaled the nature of the field throughout each block of 48 trials. The color associations were kept constant for the whole period of about 12 mo, and the monkey learned all field conditions in parallel through extensive practice. The monkey learned the task first using its right arm and practiced for about 6 mo; then a transfer to the left arm was achieved within a relatively short time. Neural recordings were subsequently made over many weeks in MI of each hemisphere.

### *Behavioral test of context-dependent recall of motor skills*

At the end of this lengthy neural recording experiment (results to be reported elsewhere), and motivated by the recent reports of limited learning of context-dependent recall of motor skills (Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002; Rao and Shadmehr 2001), we decided to assess the ability of the monkey to adjust its motor output in anticipation of a cued change in the external force field. To this end, we tested it in the following modified cued-recall task using only two of the fields and associated color cues with which it was already very familiar.

Each run consisted of 384 trials in the pair (V+, V-) of anti-correlated viscous fields, each field presented in alternating blocks of eight trials (4 movements in each of the 2 possible directions). At the start of each block, the monitor changed color (dark red or bright red) to signal the nature of the field for the impending block of eight trials (V+ or V-, respectively) and remained that color until the trials were successfully completed. These were the same field-color associations with which the monkey had extensive prior experience. Initially, target directions (F/E) were randomized in a balanced design within each block of trials. In later runs, only the initial direction (at the start of each block) was randomized. The blocks were subdivided into two series of movements to the same target—the first four trials were in one direction, while the next four targets were in the opposite direction. This was done to facilitate assessing the evolution of performance within blocks and to eliminate the risk of confounding the interference between different movement directions. Since this change had no significant effect on overall performance, the results were pooled across all runs.

There were 384 successful trials (48 blocks of movements) in each run. Interspersed among these fielded trials were "catch trials" in which the monitor background color (dark red, bright red) signaled a V+ or V- field, respectively, but an N field was presented instead. Catch trials occurred at either the first or the last trial in a block. Twenty-four catch trials were programmed into each run on a blocked basis to balance all three task factors: field, movement direction, and trial position in the block (first/last). Catch trial occurrences were randomized through a factorial design to happen about every two blocks.

The V+ or V- field was active only during the actual movement phase of the trial. It was turned on at the end of the start hold period of each trial, i.e., at the same time as the movement target was presented and just before the monkey initiated its movement. As a result, the monkey could not use proprioceptive cues during the start hold period to determine forward control strategies in either regular or catch trials. At the end of each fielded trial, the torque motor was turned off and the monkey returned to the central start position in the N field condition. At the end of each run of 48 alternating blocks of fielded trials, the monkey made 32 N-field trials that gave a measure of baseline performance without perturbing fields. A black monitor background signaled these baseline trials, as had been done during the monkey's previous training and neural-recording experience.

Only 24 catch trials were presented in each run of the cued-recall paradigm regardless of their outcome, i.e., whether they were successful or not. Unlike baseline N-field trials or trials with a viscous field, a catch trial was not repeated if the monkey failed to complete it successfully. This was done to avoid anticipation by the monkey of a repeated catch-trial perturbation after an error and consequent alteration of response kinematics.

To further try to prevent the monkey from adopting an anomalous "default" strategy in anticipation of catch trials, practice sessions with the same task structure but without catch trials were intermixed with the cued-recall paradigm sessions on a given day, and on some days the monkey was never presented runs of the cued-recall paradigm with catch trials. Nevertheless, over the period of several sessions of data collection with the paradigm, the monkey began to show signs of recognition that some of the runs contained catch trials and began to alter its behavior in the runs in which it detected the perturbations (see RESULTS). We terminated the study at that point, after 15 complete runs of the cued-recall paradigm with embedded catch trials.

Data analysis

BEHAVIORAL MEASUREMENTS. Measurement devices incorporated in the robotic manipulandum were as follows. Manipulandum angle was measured by a rotary position encoder (Heidenhain ROD 456) with a resolution of 40 pulses/deg and a 50x 12.5-kHz hardware interpolator for resolution enhancement ≤2,000 pulses/deg. Manipulandum net torque was measured by a piezoelectric torque sensor (ShinMaywa DPM 711). Tangential linear acceleration at the cursor-related tip of the handle was measured using a low-frequency filtered accelerometer (Wilcoxon 799LF, 500 mV/g). Data were sampled at 1 kHz for manipulandum control and at 200 Hz for monkey performance analysis. Analog signals were digitized using 12-bit AD/DA converters (nominal precision of 0.02%).

The maximum pulse frequency of the position encoder limits detecting velocities much higher than 300 deg/s (approximately 5 rad/s). Typical movement velocity profiles peaked well below 3 rad/s and had frequency contents well below the 1 Hz range. Hence low-pass filtering of position signals at 25 Hz (3rd-order Butterworth filter) was justified and applied to increase the signal-to-noise ratio. The velocity signal was then computed by differentiating the position.

TABLE 1. Numbers of trials in each task condition, from 15 runs of the cued-recall task

Movement Direction	Total	Null	Fielded		Catch			
			V+	V-	V+	V-		
Total	6,271	480	2,733	2,704	175			179
Flexion	3,123	248	1,352	1,343	89			91
					45	Last	44	45
Extension	3,148	232	1,381	1,361	86			88
					43	Last	43	44

Values are number of trials. V+, resistive viscous field; V-, assistive viscous field.

Performance criteria

For all behavioral analyses, data were aligned to the actual moment of exit from the start-window (RT).

Measures to quantify the monkey's trial-by-trial performance were defined by unique kinematic landmarks or by integration of data over the entire movement. The former included the value of the peak velocity during a given movement and the moment in time this peak occurred  $X = (V_{max}, T_{max})$ . The latter included the norm, calculated as the sum of squared differences between the velocity profile in a fielded trial and the mean velocity profile of N-field baseline trials in that run, sampled at 200 Hz.

Statistical analysis

A multivariate analysis of variance (MANOVA) on the data pairs X assessed the monkey's performance in different task conditions. Its core (standard) method is canonical decomposition analysis (CDA). MANOVA (results computed using SPSS Systat 9 or MathWorks Matlab Statistics toolbox were essentially identical) gives the canonical variable (CV), which represents the data in the optimal (linearly) transformed space, i.e., the projections of cluster centers onto the direction of best separation, and hence, the significance level of differences in the intra-group means. Pair-wise comparisons of two groups at a time were done for all three groups of N-fielded trials: 1) Baseline N-field; 2) N-fielded trials as catch within the "V+" condition; 3) N-fielded trials as catch within the "V-" condition; as well as between fielded trials and the catch trials embedded in the fielded blocks.

RESULTS

Data set

The data presented are from 15 runs of the paradigm collected over several weeks. Table 1 provides a summary of the number of trials of each type. The monkey used only its left arm in this behavioral study.

Qualitative description of performance

Figure 1 illustrates the monkey's performance in flexion movements on a single-trial basis for two runs. Figure 1A shows the very first run in the paradigm, and Fig. 1B shows results from one of the last runs. The velocity profiles of catch trials (b, d, thick and thin solid lines), were visibly different from the corresponding fielded trials (a, dashed lines in d), and from the null-field baseline (c, dotted lines in d). Movements were slower and of longer duration in V- catch trials, while they were faster and of shorter duration in V+ catch trials, with respect to the movements observed in the N-field baseline. In particular, the initial phase of the velocity curves in V- catch

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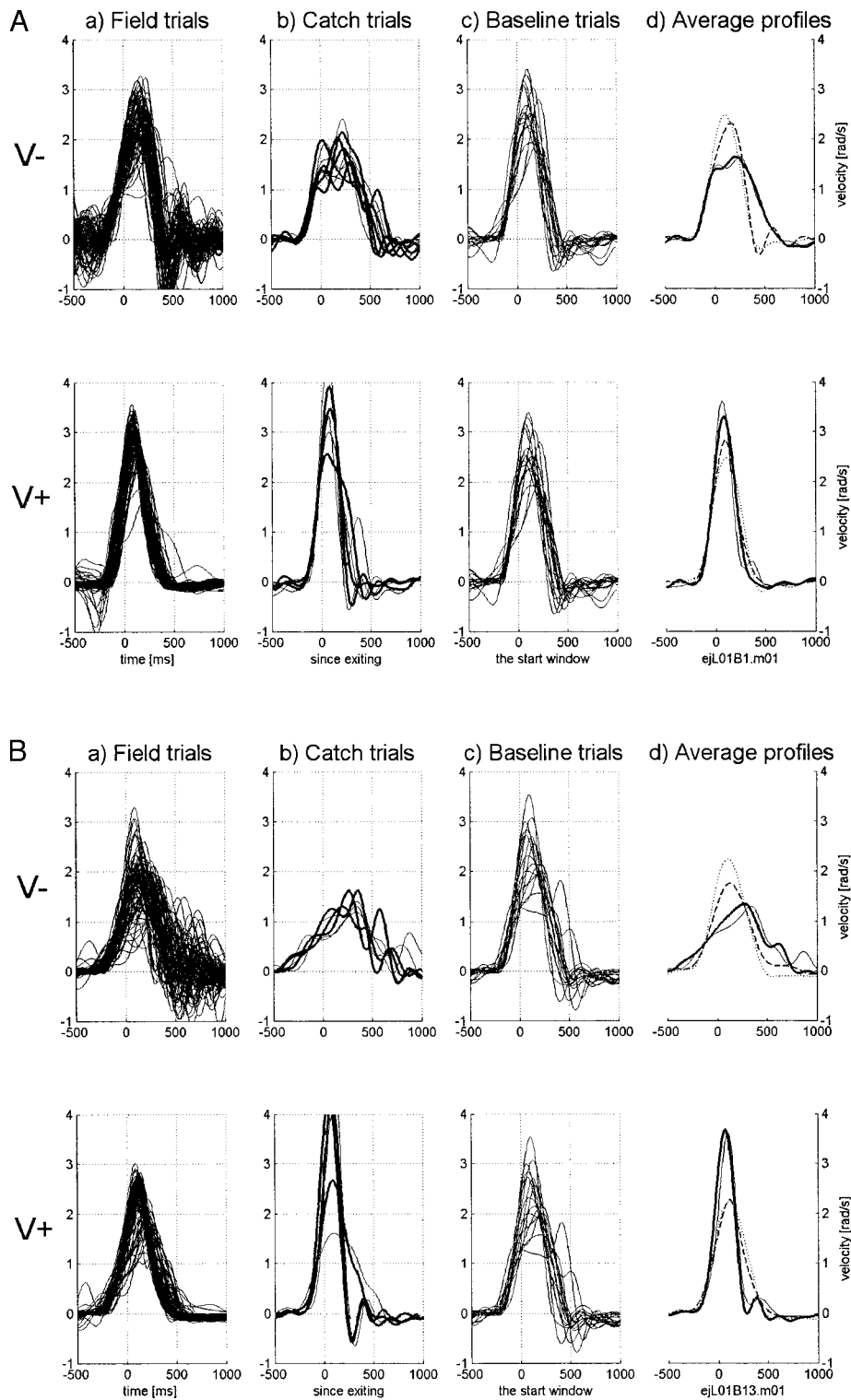


FIG. 1. The monkey's performance on an individual-trial basis for 2 left-arm runs. *A*: the very first run in the cued-recall paradigm: *top row*: velocity profiles in the  $V^-$  condition: *a*: fielded trials; *b*: catch trials; *c*: N-baseline trials; *d*: average profiles as follows: first-trial and last-trial catch trials—thick and thin solid lines; fielded trials—dashed lines; null-field baseline—dotted lines. *Bottom row*: velocity profiles in the  $V^+$  condition. *B*: a later run—same format as *A*.

trials was identical to that in fielded trials and N-field baseline trials but abruptly plateaued at about the time of peak acceleration (Fig. 1*Ad*), followed by a delayed second velocity peak. This indicates that when the monkey was anticipating the  $V^-$  field in a given trial, it emitted a truncated agonist output to initiate the movement and then let the assistive  $V^-$  field provide the rest of the torque necessary to complete the movement. When this was not encountered in catch trials, a delayed

correction was made to reach the target. Furthermore, the  $V^+$  and  $V^-$  catch trials were strikingly different from each other even though all of them were performed in an identical physical environment (N-field). Finally, when the catch trials were presented as either the first or the last trial in a block of  $V^+$  or  $V^-$ , the movement kinematics appeared to be similar (Fig. 1: *b*, *d*, thick and thin solid lines). No carryover effect from the previous block of fielded trials (such as observed with naive

human subjects) seems to be present on switching monitor background colors and force fields, even though the color cues that were used for the monkey had only a hue difference (dark or bright red) as detailed in METHODS.

It is noteworthy that the monkey exhibited the effects reported here in its very first encounter of the cued-recall task in which fields changed every eight trials (Fig. 1A). In all its prior experience, fields had changed far less frequently (blocks of 48 trials) and there was little incentive for the monkey to use the color background on a trial-by-trial basis to adjust its motor output. Nevertheless, as soon as it was confronted with a new task structure in which previously learned fields changed far more frequently than in its prior experience, it immediately manifested an ability to use the contextual cue (monitor background color) to scale its motor output appropriately at each occurrence of a color change. As we collected behavioral data from the monkey over a few weeks, we also noted a gradual change in overall performance in this task. Movement kinematics became more variable in all field conditions; behavioral reaction times began to lengthen, and there was a slowing of movements in the V- field (Fig. 1B). We suspect that despite efforts to avoid it, the monkey soon recognized that when it was performing this cued-recall task, it would occasionally receive unexpected catch-trial perturbations and it became more hesitant to initiate movements. Nevertheless, its performance in catch trials continued to show striking evidence of the use of context cues to adjust motor output in anticipation of the signaled viscous fields (Fig. 1B). Eventually, the monkey began to show signs of agitation and lack of willingness to perform when confronted with this task and we ended the study after 15 experimental runs.

#### Statistical analysis: catch trials

Figures 2 and 3 present scatter plots and results of the MANOVA of the data pairs  $X = (V_x, T_x)$  described above for different trial types in all 15 left-armed runs the paradigm.

Figure 2 compares the kinematics of catch trials to baseline N-field trials pooled across all runs of the task. Clearly, the distribution of points from catch trials in the V+ condition (+) was very different from those in the V- condition (○). At the same time, both catch-trial conditions differed substantially from regular N-field trials (●). The peak velocities of V+ catch trials were greater and occurred earlier than in baseline N-field trials, whereas the peak velocities of V- catch trials were lower and later, even though all of these movements were performed in the same null field. The only difference was the color of the monitor background according to the block in which each trial occurred. Thick symbols and boxes represent the computed means and confidence intervals for each cluster of data. Pair-wise comparisons of two groups at a time were done for all three groups of N-fielded trials: 1) baseline N-field, 2) N-fielded trials as catch within the "V+" condition, and 3) N-fielded trials as catch within the "V-" condition. Cluster mean differences were all highly statistically significant ( $P < 0.00001$ , MANOVA, computed using SPSS Systat 9 or the MathWorks Matlab R12 Statistics toolbox with identical results) for both flexion and extension movements.

Figure 3 (left 4 plots, A–D) compares the cluster means and confidence intervals for the kinematics of catch trials to corresponding fielded trials pooled across all runs of the task. The

points representing catch trials were again very different from those within the fielded conditions. Differences in cluster means were all highly statistically significant ( $P < 0.00001$ , MANOVA for both fielded types and both movement directions).

These analyses were based on only two landmarks of the velocity curve—peak velocity and time of peak velocity. The analysis was repeated using the peak acceleration and time of peak acceleration, with similar results—statistically significantly greater peak accelerations in the V+ field catch trials and lower peak accelerations in the V- field ( $P < 0.00001$ , MANOVA; data not shown). We also calculated the norm (i.e., the length, computed through inner vector products) of the deviations of each single-trial velocity curve relative to the mean velocity curve of movements in the baseline N-field trials. The distributions of the norms of the catch-trial velocity curves were once again significantly different from the distributions of the norms of the N-field trials [ $P < 0.00001$ , analysis of variance (ANOVA)]. This showed that the overall shape of the velocity curves in catch trials was significantly different from that in N-field trials for both movement directions in both fields.

Figure 3 (right 4 plots, E–H) compares the cluster means and confidence intervals of the kinematics of first-trial catch trials to last-trial catch trials pooled across all runs of the task. First-trial and last-trial catch trials were strikingly similar [ $p(H_0) > 0.1$ , MANOVA] in the V+ flexion movements (Fig. 3G). The results were quite similar for the V+ extension movements [Fig. 3H;  $p(H_0) > 0.1$ , MANOVA], as well as for the V- extension movements [Fig. 3E;  $p(H_0) > 0.1$ , MANOVA]. The flexion movements in the V- condition seemed to show additional fine tuning of kinematics, which occurred within the block (Fig. 3E;  $p(H_0) < 0.001$ , MANOVA). This latter finding may be another secondary consequence of the monkey's gradual change in performance with repeated exposure to the cued-recall task with catch trials.

#### Statistical analysis: noncatch trials

Another way to assess the monkey's ability to use the context cues is to compare the kinematics of movements in the first trial of a block in which the signaled field was presented appropriately (i.e., noncatch trials). If the monkey failed to use the color cue to scale its motor output in the trial immediately after a transition between anti-correlated viscous fields, its movement kinematics would potentially be even more perturbed than in N-field catch trials. Instead, the monkey's movement kinematics were very consistent for a given movement, irrespective of its position in a block of trials in a given field. Figure 4 shows such an analysis for the data accumulated in the run illustrated in Fig. 1B. As can be seen, the mean velocity profiles for flexion movements occurring as first-trial fielded trials, last-trial fielded trials, and at all intervening positions in the block were very similar. Cluster analysis of the value and timing of the peak velocities of all trials showed no significant difference for the three groups of trials for both flexion and extension trials in that run ( $P > 0.1$ , MANOVA). Comparison of the mean velocity curves of first-trial and last-trial fielded trials showed no systematic differences across all 15 runs (Fig.

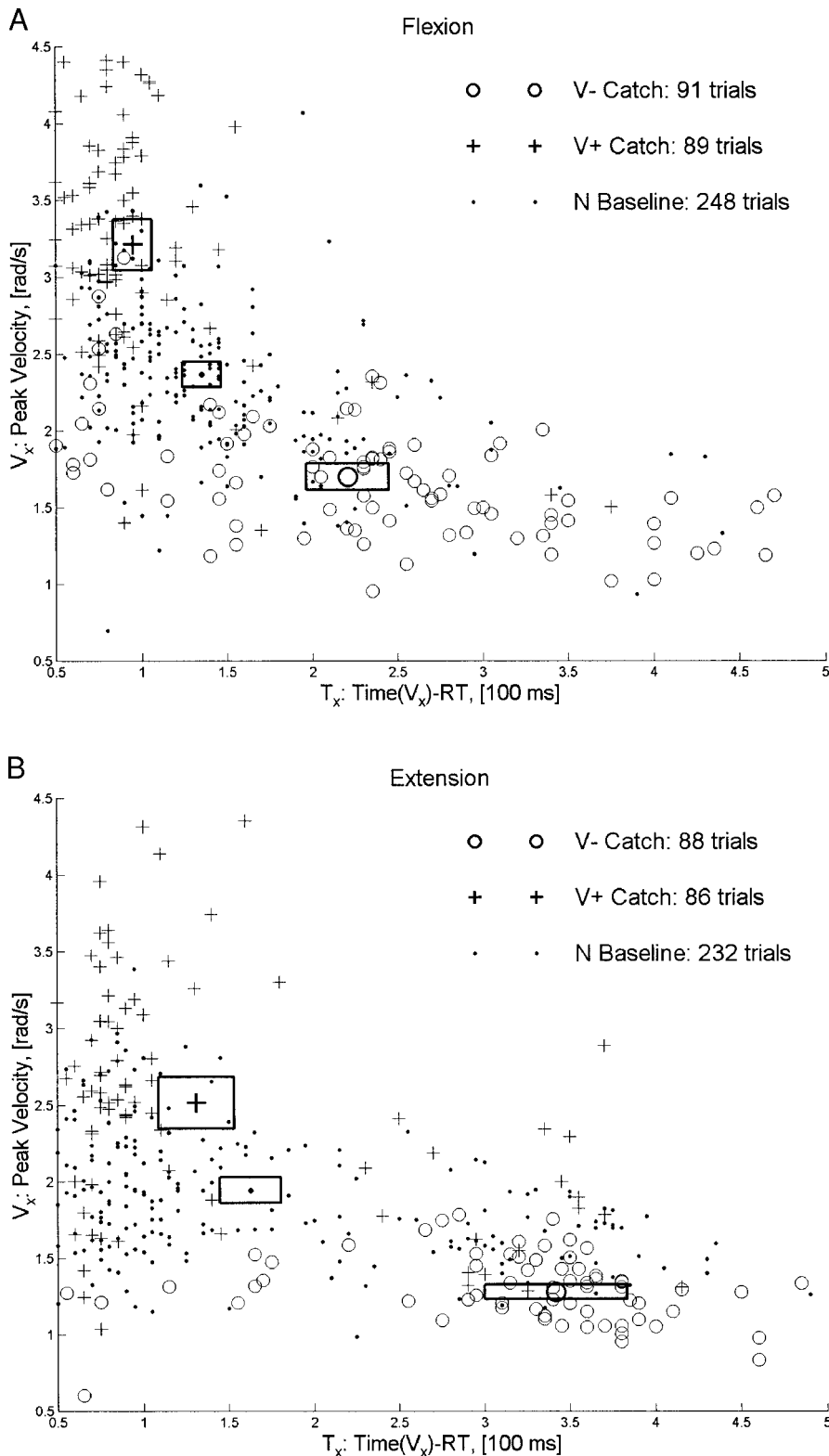


FIG. 2. Scatter plots and results of the multivariate analysis of variance (MANOVA) of the statistics  $X = (V_x, T_x)$  from 15 left-arm runs for catch trials versus baseline N-field trials. Each catch trial in the V- condition is represented by an open circle ( $\circ$ ) at coordinates  $(V_x, T_x)$ ; trials in the V+ condition are represented by plus signs (+); trials in the N-baseline condition are represented by a dot ( $\cdot$ ). Thick variants of the above 3 symbols represent the mean value of the statistics for each of the conditions of interest. The boxes surrounding the mean points are a graphical representation of the confidence intervals (CI) on the computed means. A: flexion movement; B: extension movement.

4). Finally, cluster analysis of the value and timing of peak velocities of first-trial and last-trial fielded trials likewise showed no significant differences for flexion movements in either V+ or V- fields and for extension movements in V- field ( $P > 0.1$ , MANOVA). Extension movements in the V+ field showed a small but statistically significant decrease in

peak velocity from 1.85 to 1.76 rad/s ( $P = 0.004$ , MANOVA). These results all show that the monkey adjusted its motor output in the first trial after a field transition in such a way as to produce a movement whose kinematics was largely indistinguishable from similar movements made later on in a block of trials in the same field.

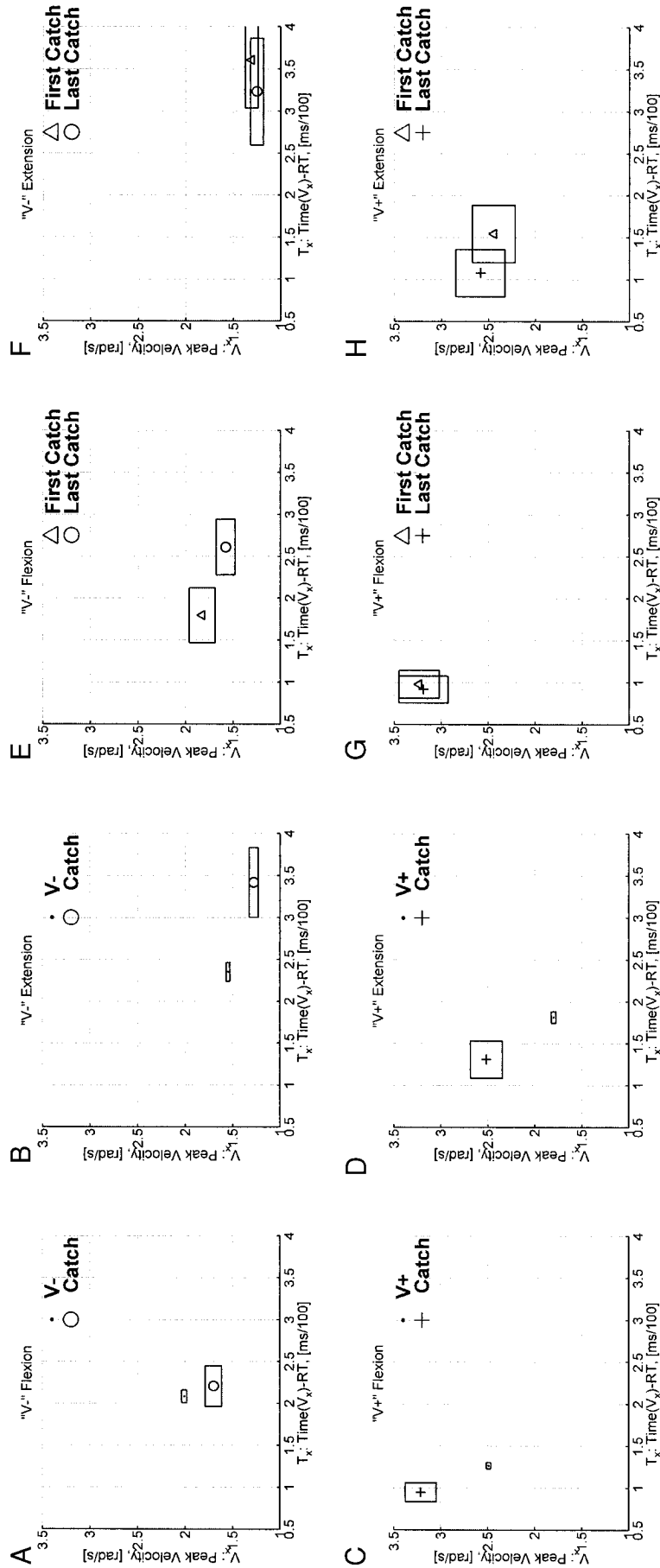


FIG. 3. (A–D) Box plots of the summary statistics [cluster means and CI for the distribution of  $X = (V_x, T_x)$ ] from 15 left-arm runs for catch trials versus fielded trials. A, B: flexion and extension movements in the V– condition. As in Fig. 2, thick variants of symbols represent the mean value of the statistics for the catch trial conditions of interest—an open circle (○) for V– and a plus sign (+) for V+. Rectangular boxes represent the confidence intervals on the computed means. The mean from fielded trials is represented by a thick dot (•). C, D: flexion and extension movements in the V+ condition. E–H: box plots of the summary statistics for the distributions of  $X = (V_x, T_x)$  from 15 left-arm runs for first versus last catch trials. E, F: flexion and extension movements in the V– condition. G, H: flexion and extension movements in the V+ condition. The mean from first catch trials is represented by an upward triangle (△), while the means from last catch trials follow the convention established in (A–D) above.

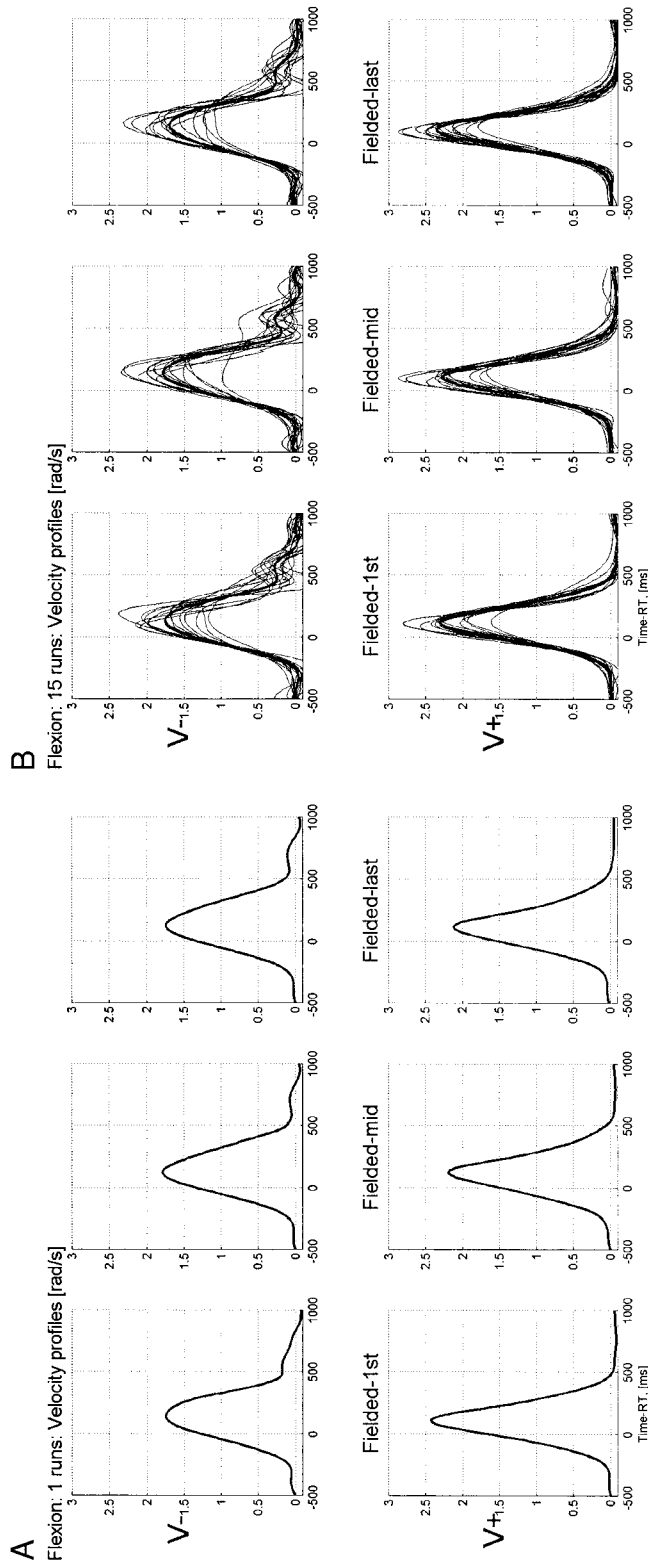


FIG. 4. Kinematics of fielded trials at different sequential locations in a block. *A*: 1 run (data from Fig. 1*B*) of the paradigm: *top row*: average velocity profiles in the  $V -$  condition; *a*) first trials in each block; *b*) middle trials (2nd through 7th) in each block; *c*) last trials in each block; *bottom row*: velocity profiles in the  $V +$  condition. *B*: the grand mean (thick solid lines) and average velocity profiles from each of the 15 left-arm runs (thin solid lines) presented in the same format as *A*.



### Adaptation versus recall

A subject is usually considered to be fully adapted to a perturbing force field when their movement kinematics are identical to that seen in the absence of perturbation. By that standard, the monkey's performance showed a good level of adaptation in the V+ field, but less so in the V- field despite many months of practice (Fig. 1). In particular, by the time we tested the monkey in this cued-recall task, there were consistent terminal oscillations at the end of movement in the V- field. We attribute this in part to the difficulty of fully compensating for this unstable assisting field, and in part to the cumulative effect of the microlesions made by many dozens of microelectrode penetrations in the contralateral (*right*) MI of that monkey during the neural recording experiments that preceded this behavioral study. Furthermore, the fairly generous tolerances for timing and endpoint precision permitted in the task meant that these movements were still considered successful and were rewarded, providing the monkey with no motivation to show more stereotypical kinematics across field conditions. However, the goal of this particular behavioral study was not to assess the quality or limits of adaptation across different field conditions. Instead, it was designed to assess the ability of the monkey to use contextual cues to adjust its motor output in anticipation of the dynamics of a perturbing field. The monkey's performance showed compelling evidence of context-dependent predictive adjustments of motor output irrespective of the level of adaptation itself.

### DISCUSSION

When catch trials were presented at the end of a block, the kinematics of movement deviated from those of movements in the corresponding fielded trials and also from that seen in the null-field baseline. This so-called "after-effect" (Gandolfo et al. 1996; Shadmehr and Mussa-Ivaldi 1994), after unexpected removal of the perturbing field, is evidence that the monkey was attempting to compensate for the expected perturbation by generating specific output forces to counterbalance each field, rather than using a default strategy such as coactivation to stiffen one or more joints. The direction of the after-effects in this study, speeding up when expecting to encounter the resistive V+ field and slowing down when expecting the assistive V- field, are consistent with the former control strategy.

The major finding of this study was that when catch trials were presented in the first trial of a block, the after-effect observed in that trial was consistent with the *anticipated* field associated with the background color presented in that trial. It was *inconsistent* with the field presented in the last trial of the previous block. In all four cases catch trials that were presented as first in a block resulted in speeding up of the movements at the beginning of a V+ block and slowing down for V- blocks. Furthermore, in three cases (of a total of 4), there was no statistically significant difference in kinematics between catch trials presented as either first or last of a block. This suggests that in these three situations, the monkey made a complete switch between the two motor skills, with no significant change in performance resulting from the fielded trials intervening between the first and the last of a block. Even in the fourth case (V-, flexion) the first-trial after-effects were significant and consistent. There was a further minor but significant slowing

down possibly due to further fine-tuning of adaptation during the fielded trials of the block, which may be functionally significant or which may merely be an epiphenomenon resulting from undesired changes in the monkey's performance with repeated exposure to the cued-recall task.

These findings in the catch trials were further corroborated by analysis of the kinematics of appropriately fielded trials at different sequential locations in a block. In particular, the kinematics of movements in the first trial of a block, after a transition between anti-correlated viscous fields, were very similar to that of fielded trials at all other later sequential locations in that block. This provided further evidence that the monkey made an abrupt transition in motor output planning in anticipation of the change in task dynamics signaled by the color cue, before physically encountering the field and receiving any subsequent performance-error feedback.

These results support the hypothesis that the monkey does switch motor output strategies in response to the arbitrary visual stimuli. The latter had acquired consistent behavioral salience over the course of extensive training.

Extensive prior experience was undoubtedly the major factor contributing to the present findings. In other studies that had found less evidence of context-dependent learning or recall, the subjects' performance was assessed over the course of only one or a few daily sessions (Gandolfo et al. 1996; Karniel and Mussa-Ivaldi 2002; Rao and Shadmehr 2001). In contrast, before testing the monkey in the cued-recall task described here, it had performed many tens of thousands of trials in the same V+ and V- fields while viewing the same two associated monitor background colors. However, these field-color pairings were embedded in a different paradigm in which the monkey performed blocks of 48 movements in N, V+, V-, E+, and VE+ fields, each associated with a different monitor color. In that task, the monkey made movements in a given field for several minutes before it changed. It is all the more significant therefore that the monkey showed the ability to use the color cues to adjust motor outputs the very first time it encountered the cued-recall task in which the fields alternated rapidly. It had had no previous experience with that particular task environment yet it used the cues to adjust motor outputs on a trial-by-trial basis. The complexity of the motor skills in the different studies may also be a significant factor. In the other studies, subjects experienced an unusual viscous curl field that perturbed the arm sideways, while performing whole-arm reaching movements in many different directions. This required complex adaptive changes in the already complex dynamics of whole-arm movements (Bhushan and Shadmehr 1999; Thoroughman and Shadmehr 1999, 2000). In the present study, in contrast, the monkey dealt with a viscous field that acted only in the direction of movement during flexion/extension of a single joint. Nevertheless, all the subjects in the other studies mastered the complex procedural skill of compensating for the external fields. Where they differed was in the rate at which they learned the association between different contextual cues and the corresponding procedural skills. That latter rate was in turn likely influenced by factors related to the nature of the contextual cues and the complexity or degree of arbitrariness of the association.

For instance, Cohn et al. (2000) found that subjects could rapidly learn to emit the correct motor outputs for reaching movements depending on whether or not visual inputs evoked

powerful illusions of self-rotation. Gandolfo et al. (1996) showed that subjects could also quickly learn and recall two different procedural skills in two different arm postures, likely because the context cue (arm posture) was an integral part of each procedural skill. In contrast, they could not learn to associate two thumb positions or two colors of room illumination with two opposite viscous curl fields at the same rate over the course of 1 day's training. Similarly Rao and Shadmehr (2001) found that subjects could not learn to associate two different movement target colors with two opposing directions of viscous curl fields over the course of several hundred training trials, yet could learn to recall the two motor skills in response to spatial cues located in opposite sides of the movement target in the same time frame. The latter contextual cues may have been easier to learn because their location relative to the target may have provided easily recognizable implicit information about the directionality of the impending perturbations compared with the small and nonspatial color cues. The physical salience of the cues may also be a contributing factor. It may be easier to recognize and learn a color-field association when the entire monitor background changes color, rather than just a small target spot.

The subjects in Karniel and Mussa-Ivaldi (2002) were evidently given no independent external sensory cues about the alternating field context in which they had to rapidly perform the movements of their final session. It may have been quite difficult for them to recognize and adapt (synchronize) themselves to the underlying structure of the task (alternating directions of curl between successive trials) while paying attention to a random sequence of movements in different directions of the two-dimensional (2D) plane, even though they had already learned to compensate for the two fields in earlier sessions. Nevertheless, given enough practice, they may have eventually succeeded in this challenging combined (procedural and nonprocedural) task (Karniel and Mussa-Ivaldi 2002).

In summary, all of the human studies involved two simultaneous learning processes—the procedural learning required to deal with different physical environments and the nonprocedural learning required to recognize and associate contextual cues with the different procedural skills. The latter may show a much slower learning rate than the former. The results of all these and the present studies show that failure to demonstrate a learned association with arbitrarily chosen cues as soon as the procedural skill is acquired does not preclude the eventual acquisition of the related associative knowledge. This second learning process may require much more practice and a behaviorally significant task.

The findings of the present study are not surprising; indeed, the opposite findings would have been far more surprising. Furthermore, the goal of this study was not to disprove the earlier studies and we do not interpret the present results in that manner. On the contrary, this study draws attention to the issue of the different types of learning and different learning rates involved in such tasks, and its results should dispel any impression that may have arisen from the convergence of results in those studies that the motor system cannot learn arbitrary associations between color cues and compensatory skills for task dynamics. Clearly, such associations are learnable given enough time and the appropriate task conditions. Moreover, it is entirely likely that one can design tasks in which naïve subjects could learn to recognize and begin to

apply the behavioral significance of contextual cues before they master the associated procedural skills, thereby facilitating the procedural learning process.

Finally, although not designed to address this specific issue, the results provide circumstantial evidence concerning the underlying computational architecture of the motor system. Behavioral and modeling studies suggest that these procedural motor skills are acquired by adaptive control systems that capture the relationship between the desired motions and the required forces or muscular activity in different external environments. These adaptive systems are often referred to as “internal models” (Bhushan and Shadmehr 1999; Doya et al. 2002; Flanagan et al. 1999; Ghahramani and Wolpert 1997; Haruno et al. 2002; Kawato 1999; Wolpert and Kawato 1998; Wolpert et al. 1995). The ability of the motor system to rapidly recall different motor skills raises further important questions about the computational architecture of the putative internal models. For instance, is there one single omnibus system that learns to deal with a wide range of dynamics (monolithic structure) or multiple subsystems that each become expert in a limited range of dynamic conditions (modular structure) (Doya et al. 2002; Flanagan et al. 1999; Ghahramani and Wolpert 1997; Haruno et al. 2002; Karniel and Mussa-Ivaldi 2002; Kawato 1999; Wolpert and Kawato 1998)? This study appears to present evidence consistent with a modular control structure that would subvert the rapid switching of motor skills. However it does not necessarily reject a monolithic structure with a capacity for multiple re-parameterization (Jansen-Osmann et al. 2002). Extensive behaviorally relevant training may put in place or tune circuitry to implement “on demand” rapid recalibration of control circuits.

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