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J Neurophysiol 104:382-390, 2010. First published 19 May 2010; doi:10.1152/jn.01058.2009

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Motor Memory and Local Minimization of Error and Effort, Not Global Optimization, Determine Motor Behavior

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Submitted 4 December 2009; accepted in final form 12 May 2010

Ganesh G, Haruno M, Kawato M, Burdet E. Motor memory and local minimization of error and effort, not global optimization, determine motor behavior. *J Neurophysiol* 104: 382–390, 2010. First published May 19, 2010; doi:10.1152/jn.01058.2009. Many real life tasks that require impedance control to minimize motion error are characterized by multiple solutions where the task can be performed either by co-contracting muscle groups, which requires a large effort, or, conversely, by relaxing muscles. However, human motor optimization studies have focused on tasks that are always satisfied by increasing impedance and that are characterized by a single error-effort optimum. To investigate motor optimization in the presence of multiple solutions and hence optima, we introduce a novel paradigm that enables us to let subjects repetitively (but inconspicuously) use different solutions and observe how exploration of multiple solutions affect their motor behavior. The results show that the behavior is largely influenced by motor memory with subjects tending to involuntarily repeat a recent suboptimal task-satisfying solution even after sufficient experience of the optimal solution. This suggests that the CNS does not optimize co-activation tasks globally but determines the motor behavior in a tradeoff of motor memory, error, and effort minimization.

INTRODUCTION

Motor planning and execution have been modeled as the optimization of a cost function involving physiological and task variables such as motion smoothness (Flash and Hogan 1985; Uno et al. 1989), task error (Burdet and Milner 1998; Harris and Wolpert 1998), effort (Todorov and Jordan 2002), or a combination of error and effort (Emken et al. 2007; Franklin et al. 2008; Miyamoto et al. 2004; O'Sullivan et al. 2009). However, tasks used in motor control experiments such as reaching movements (Morasso 1981; Osu et al. 2003; Uno et al. 1989), force field learning (Burdet et al. 2001; Shadmehr and Mussa-Ivaldi 1994), and movements through via-points (Flash and Hogan 1985; Uno et al. 1989) are limited in their ability to differentiate effort from error minimization (O'Sullivan et al. 2009): Noise and thus error generally increase monotonically with motor command (Jones et al. 2002; Osu et al. 2004), such that error and effort are in one-to-one relationship. These tasks thus feature a single optimum of error and effort in which optimization has been computed using linear optimal control (Todorov and Jordan 2002) or nonlinear optimization with constraints (Biess et al. 2007) or by gradient descent (Franklin et al. 2008). Suboptimality has been examined with respect to incomplete convergence to the unique optimum (Izawa et al. 2008) but never in a paradigm with distinct multiple optima.

In contrast, many real life tasks requiring muscle co-activation control are characterized by multiple solutions and hence distinct optima of error and effort. To prevent spilling water from a glass due to a force disturbance, one can either stiffen one's arm to reduce the amplitude of its movement (i.e., a strategy requiring large muscle activations and effort) or conversely relax the arm (requiring less effort), leading to a larger movement but low hand acceleration. Considering a multi-joint task involving both arms, the stability of a bicycle while riding downhill on a bumpy road (detailed explanations and modeling are provided as supplementary information[1]) can be maintained by keeping the handle bar stiffness either below or above a certain range of values in which there is resonance and the cycle becomes unstable. Note that in both these tasks an increase of muscle co-activation can lead to increasing task noise. Tasks with multiple muscular solutions can also lead to drastic changes in movement kinematics (Todorov and Jordan 1998; Zhang and Rosenbaum 2008).

To systematically investigate how humans deal with such co-activation tasks characterized by multiple muscular solutions, while avoiding confounds connected with multi-joint tasks (such as monitoring and control of multiple muscles and designing of experiment with low inter subject variability), we introduce a simple and well-controlled paradigm inspired by the glass of water example. Traditionally, robotic interfaces have been used in motor control experiments to provide force fields for the subject to adapt force or mechanical impedance (Burdet et al. 2001; Shadmehr and Mussa-Ivaldi 1994). While these experiments investigated interaction as function of subject position, velocity, or force, our paradigm enables interaction as a function of subject muscle activation (and hence joint impedance). However, using force perturbations would require complex subject specific fine tuning of the working environment. To avoid these complications, we utilize a strategy of muscle activity [electromyography (EMG)] mediated position perturbation that helps us provide a well controlled multisolution environment to observe subject behavior. While it is generally assumed that stiffening the joints attenuates perturbations, this paradigm enables us to study for the first time a task that can be fulfilled by lowering of impedance to reduce noise. The paradigm enabled us to let subjects repetitively (but inconspicuously) take different solutions, requiring different effort and observe how this affects their motor behavior.

While task error and effort costs have been the popular variables used to model motor optimization, the results of our study suggest that motor memory is an additional and major determinant of motor behavior. Subjects were observed to

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[1] The online version of this article contains supplemental data.

involuntarily repeat recent task-satisfying muscle activations with little regard to minimization of effort.

METHODS

Subjects and task

Twenty naive healthy right-handed subjects (aged 22–40 yr, 18 males) without known pathology performed three experiments in two environments (Table 1). The experiments were conducted according to the principles in the Declaration of Helsinki. The experiments were approved by the ethics committee at Imperial College, and the subjects gave informed consent prior to performing them.

The subjects stood in an upright posture and had their forearm fixed to the wrist manipulandum (Fig. 1*A*). The manipulandum imposed sinusoidal perturbations of varying frequencies between 4 and 6.5 Hz in the flexion-extension direction, in steps of 0.25 Hz presented for 10 s each. The chosen frequencies prevented subjects from using reciprocal activation (unpublished information) of their muscles for posture control. The subjects had to thus control the co-activation of their muscles (and hence effort) to maintain wrist movement within a target amplitude of ±3° (Fig. 1*B*). EMG was recorded from the wrist muscles throughout the experiment (Fig. 1*C*) and, unknown to the subject, was used to control the manipulandum and apply a perturbation on the wrist such that the subject had two distinct co-activation levels to satisfy the task.

The co-contraction task with multiple solutions (*environment 1*) is described in Fig. 1, *A–D*. The darker areas in Fig. 1, *D* and *E,* indicate the regions where the task is satisfied, i.e., where the wrist angle amplitude is within the target. At each frequency, the subjects could co-activate strongly and be in the *high region* requiring large effort or relax co-activation and use the *low region* requiring less effort (Fig. 1*E*). The subjects were expected to realize this by exploration during the numerous trials. Each subject worked in either *environment 1* or *environment 2.*

Muscle co-activation

When a subject co-activates his wrist in a fixed posture muscle activity (EMG) across flexors and extensors of the wrist co-vary, and thus the subject co-activation can be reliably estimated from the activation of a single pair of antagonist muscles. EMG signals were thus recorded from two wrist muscles: flexi-carpi radialis (FCR) and extensor-carpi radialis brevis (ECRB). After electrode placement for each muscle was determined using functional movements, the area was cleansed with alcohol and abrasive gel (Nuprep, DO Weaver). Electrode paste (Biotach, GE Marquette Medical Systems) was applied onto the EMG electrodes (Delsys Biotech), and the electrodes were fixed to the subject's skin with tape. A ground electrode was fixed to the ankle of the subject. The EMG signals were amplified using a Delsys EMG amplifier (BAGNOLI 16), before being fed into the manipulandum computer through a National Instruments data acquisition card (NI 6221). The collected EMGs were rectified and smoothed with a moving average of 500 ms. The smoothed EMG signals from the two muscles were scaled to equate the amplified values and added to estimate the subject co-activation. The maximum value of the co-activation a subject could generate was termed as the maximum voluntary co-activation (MVCA).

Environments and control

In the experiment, the manipulandum motor (and hence the subject wrist) was controlled to follow reference sinusoidal trajectories of different frequencies and amplitudes using a PID algorithm implemented in the National Instruments LabVIEW Real Time 8.5.1 environment. The frequencies were varied between 6.5 and 4 Hz over a period of 110 s (Fig. 1*E*), while the amplitude of the perturbation was determined by a predefined multi-solution *environment mapping* between frequency, current subject co-activation (in % MVCA) and disturbance amplitude (Fig. 1*D*). High gains of the PID controller ensured that the desired trajectory was tracked strictly without any significant decrease of the movement amplitude due to mechanical stiffening of the subject wrist. This allowed us to choose customized environments to benefit the study; i.e., environments (like Fig. 1*D*) with two distinct co-activation levels (solutions) that satisfy the task goal.

This control strategy provided two benefits: *1*) although the system was position controlled and stable, the continuous change of wrist amplitude with change of co-activation induced a behavior similar to a system under force perturbations. This is important for the study of impedance changes; *2*) it enabled us to set up a custom co-activation-amplitude relation (Fig. 1*D*) for the subject to explore. Setup of a similar environment with force perturbations would prerequisite joint impedance measurements for every subject at different muscle activations, perturbation frequencies, and amplitudes.

The sinusoidal movement amplitude *A,* which is a function of coactivation in %MVCA (κ) and disturbance frequency (ν) in *environment 1* is shown in Fig. 1*D,* is defined by

TABLE 1. *Summary of experiments*

Experiment	Description
Environment 1 (5 subjects, 4 males)	- 1 training trial - 1 set of 3 free trials - 1 set of three forced trials - 1 set of 3 free trials - 1 set of three forced trials - 1 set of 3 free trials
Environment 2 (tapering) (10 subjects, 9 males)	- 1 training trial - 1 set of 3 free trials - 1 set of three forced trials - 1 set of 3 free trials - 1 set of three forced trials - 1 set of 3 free trials
Subsidiary experiment (in Environment 2) (5 male subjects)	- 3 free trials with increasing frequency - 1 free trial with decreasing frequency, (3rd and 4th) trials with sudden change in disturbance frequency.

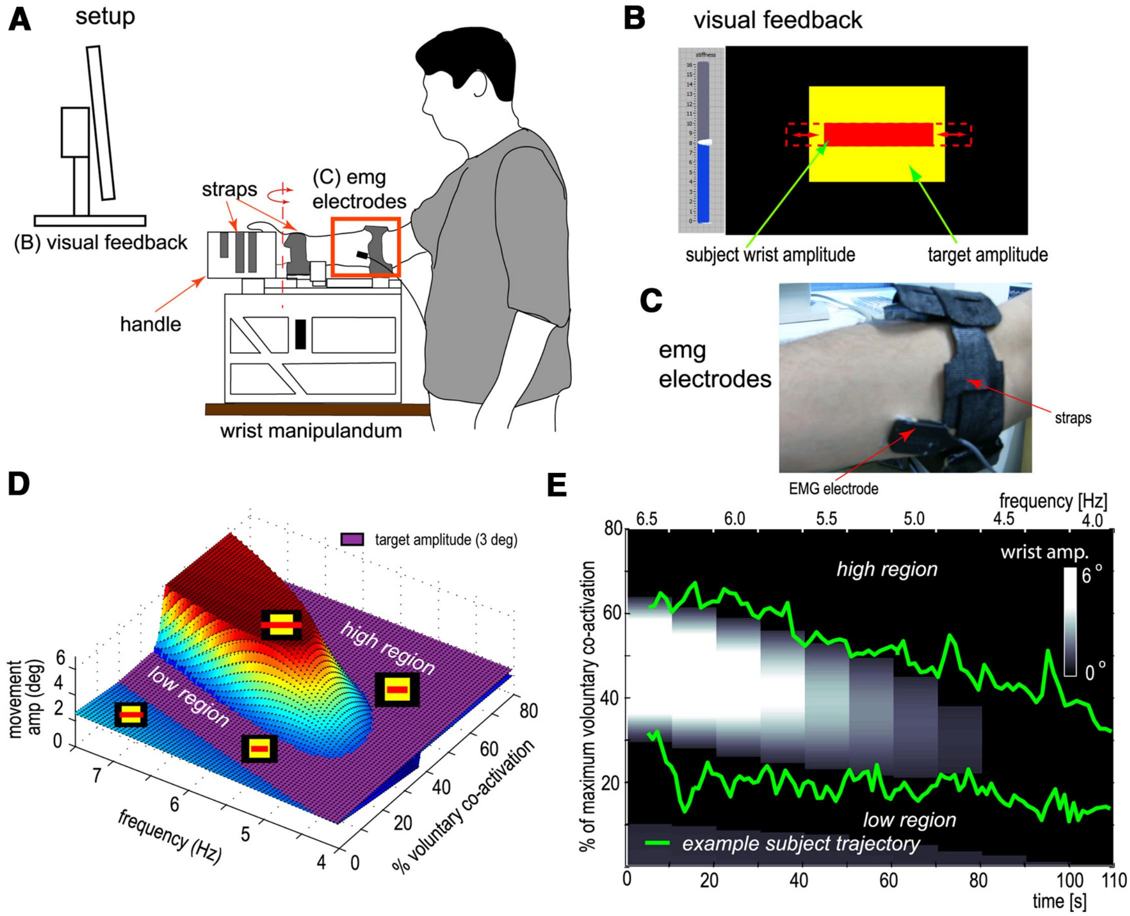

FIG. 1. Experimental setup. The subject stood with the arm comfortably fixed to a wrist manipulandum (*A*), which imposed sinusoidal perturbations to the wrist. The subject received visual feedback of the wrist amplitude in the form of a red bar (*B*) and had to maintain it within a target. The electromyographic (EMG) signals from the flexi-carpi radialis (FCR) and extensor-carpi radialis brevis (ECRB) muscles (*C*) determined the subject co-activation and modified the red bar width according to the function of *D* where the target width (3°) is represented by the violet plane such that any co-activation level below the violet plane would satisfy the task. The 2 dimensional gray scale representation of *D* is plotted against time in *E*. The subject could co-activate to use either the low or high (co-activation) region (darker regions in *D* and *E*) to satisfy the task and keep the red bar inside the yellow target (*B*). In *forced trials*, the subject got an additional feedback of his co-activation (blue bar in *B*) for the 1st 5 s of the trial.

$$
\begin{aligned}
A(\kappa, \mathrm{v}) &= \frac{(21-\kappa)^2}{400} + \frac{2(\mathrm{v}-4)}{5} \quad \text{if } |\kappa - 5\mathrm{x}| > p/2 \\
&= \frac{16\mathrm{z}(\kappa - x)^4}{p^4} - \frac{8\mathrm{z}(\kappa - x)^2}{p^2} + z + \frac{(20-\kappa)^2}{400} \\
&\qquad + \frac{2(\mathrm{v}-4)}{5} \quad \text{if } |\kappa - 5x| > p/2 \qquad (1)
\end{aligned}
$$

where

$$
\begin{aligned}
z &= 2.0(\mathrm{v}-4)^2\,; \quad p = 8 \quad \text{if } \mathrm{v} > 4 \\
&= 0 \qquad\qquad\quad ; \quad p = 4 \quad \text{if } v < 4
\end{aligned}
$$

and

$$x = 1.6(\mathrm{v} - 2.5) + 5.8$$

Further

$$
\begin{aligned}
&\mathrm{A}(\kappa, \mathrm{v}) = \mathrm{A}(\kappa, \mathrm{v}) - 0.06(\kappa - 8.5) \\
&\mathrm{A}(\kappa, \mathrm{v}) = 1.6 - 0.005(-14\mathrm{v} + 8\kappa - 13) \quad \text{if } 7\kappa > 16\mathrm{v} + 12
\end{aligned}
$$

For the second experiment, a tapering environment (like in Fig. 3) was defined by

$$
\begin{aligned}
A(\kappa, \mathrm{v}) &= \frac{4.62(100-\kappa)^2}{20000} + \frac{4.62(\mathrm{v}-4)}{5} \qquad \text{if } 8|\kappa - 5\mathrm{x}| > 75z \\
&= \frac{5.97(\kappa - 5x)^4}{10000z^3} - \frac{10.92(\kappa - 5x)^2}{100z} + z + \frac{4.62(100-\kappa)^2}{20000} \\
&\qquad + \frac{4.62(\mathrm{v}-4)}{5} \quad \text{if } 8|\kappa - 5\kappa| \le 75z \qquad (2)
\end{aligned}
$$

where

$$z = 0.8(\mathrm{v} - 4)$$

and

$$x = 2.8(\mathrm{v} - 4) + 2.7$$

Further

$$
\begin{aligned}
&A(\kappa, \mathrm{v}) = A(\kappa, \mathrm{v}) - 0.092(\kappa - 7.5) \quad \text{if } \kappa > 7.5 \\
&A(\kappa, \mathrm{v}) = 3.23 - 0.25\big[3.23 - A(\kappa, \mathrm{v})\big] \quad \text{if } A(\kappa, \mathrm{v}) < 3.23 \text{ and} \\
&\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \kappa > 14\mathrm{v} - 43.5
\end{aligned}
$$

The parameters of the environments were adjusted to achieve the following salient features. *1*) The environment is characterized by clear and distinct minima while maintaining the width of the high and low regions approximately similar. This was important to ensure that the subjects do not have a larger margin of safety in either region. *2*) The surface of the mapping from co-activation to perturbation amplitude (i.e., *Eq. 1* and *2*) are smooth with nonzero slope, such that co-activation change is always accompanied by a change in wrist amplitude. *3*) The minimum wrist amplitude (Fig. 4*A*) is similar in the *low* and *high regions* and is equal in the parts that the subject trajectories lie in (Fig. 4*A*). This ensures that the error cost is similar for the subject in both *regions*. *4*) The gradient sign is same in both the low and high regions such that in both regions the movement amplitude decreases as muscle co-activation increases. This makes interpretation of subject behavior intuitive.

The only free parameter, the maximum wrist amplitude allowed in the experiment, was adjusted so as to avoid discomfort at the highest frequency. All the subjects could perform in the environment immediately in the very first trial. The paradigm did not need learning. The subjects were able to maintain the wrist amplitude inside the target value during most of the duration (i.e., in 91 ± 6.6%; mean ± SD) already in their very first trial.

Trial types

The subjects performed a series of trials in which they received perturbation of frequencies decreasing in steps of 0.25 Hz from 6.5 Hz down to 4 Hz (Fig. 1*E*). Each frequency lasted for 10 s. This gave rise to a *co-activation trajectory* (green traces in Fig. 1*E*) in each trial that we use to analyze the behavior of each subject.

The subjects performed two types of trials: *free trials*, performed with the aid of visual feedback of the wrist movement amplitude, and *forced trials* in which additional feedback of the co-activation level (the blue bar in Fig. 1*B*) was provided in the first 5 s of the trial, during which the subjects had to maintain a target co-activation level. A target level of 30% of the MVCA let them start the trial in the low region and one of 70% MVCA in the high region. Note that the co-activation feedback was switched off after the first 5 s, and the remaining part of the trial was pursued similar to a free trial.

After a training trial in which frequencies were reversed, i.e., presented in increasing order, the subjects performed five alternating sets of three free and three forced trials (starting with a set of 3 free trials).

Visual feedback

The graphical user interface was also implemented in the LabVIEW environment. The wrist movement amplitude was measured using a position encoder (Hengsler RI58-O/5000AS.41RB), smoothed using a 500 ms moving average, and used (with a scaling factor of 1 cm/°) to adjust the length of a red bar (Fig. 1*B*), which the subjects had to keep inside the 3° target, i.e., the yellow band in Fig. 1*B*.

Protocol of experiments

The experiment for each subject followed the following sequence.

EMG CALIBRATION. EMG calibration is required because the baseline and maximum EMG activities change within subjects due to positioning of electrodes, skin properties, subject strength, and external noise. In addition, the baseline EMG activity (EMG activity when the subject is at rest) changes with the frequency of vibration of hand.

Between the experiment frequencies of 4 and 6.5 Hz, the baseline EMG activity was found to vary linearly and with a maximum of change of <10% MVCA. To reduce this difference and normalize to subject strength, the experiment started with a calibration procedure.

The subject wrist was vibrated with a 3° amplitude sinusoidal signal of 5.25 Hz frequency, corresponding to the middle of the frequency range during the main trials. EMG was recorded when the subject relaxed completely, defining m_0, and when he co-activated his muscles maximally, defining $m_{\max}$. These values were used to calibrate the function of *Eq. 1* or *2* according to the subject capabilities as follows

$$\kappa(t) = \frac{m(t) - m_0}{m_{\max} - m_0} \cdot 100$$

where $m(t)$ is the instantaneous subject co-activation and $\kappa(t)$ the normalized % of MVCA, which was used to compute the perturbation amplitude using *Eq 1* or *2*.

CALIBRATION TESTING. To check that the subject can comfortably perform the experiment, the same (3°, 5.25 Hz) sinusoidal perturbation was applied while the subject was asked to maintain his or her wrist co-coactivation level for 5 s each at 20, 40, 60, and 80% of his/her MVCA. The subjects were aided in this task by a visual feedback of their co-activation level. The ability to maintain these co-activation levels indicated a successful calibration.

TRAINING TRIAL. The experiment started with a training session where the subjects experienced perturbations with frequency increasing from 4 to 6.5 Hz, in steps of 0.25 Hz with each frequency step lasting 10 s. This session helped the subjects experience the system and the task.

EXPERIMENT TRIALS. The training was followed by five alternating sets of three *forced* or *free* trials each, starting with a set of free trials. In each trial, the subjects experienced the same set of frequencies as in the training trial, but in a decreasing sequence. Five subjects experienced the first environment while 10 worked in the second environment.

Subsidiary experiment

A separate subsidiary experiment was conducted with five subjects to evaluate properties of the mapping learnt by the subjects. The experiment aimed at evaluating if the memory was a time course of muscle activations, or a mapping between muscle activation and frequency, and investigated how and if the memory related behavior is robust to sudden changes in disturbance frequency. The five subjects performed four free trials in *environment 2*. The disturbance frequency increased in the first three trials from 4 to 6.5 Hz while it decreased from 6.5 to 4 Hz in the fourth trial. In addition, in the third and fourth trials the disturbance frequency suddenly changed to a previous value in the last ten seconds (Fig. 4*B*).

Data analysis

The intra set deviation in the co-activation trajectories was calculated by subtracting the mean set trajectory from each of the subject trial trajectory and collecting the data points through the trial time over 20 subjects. The SD of this collection was used to show that subjects followed similar trajectories in all trials of a same set.

The co-activation difference plots of Figs. 2*B* and 3*B* were produced by subtracting the individual time points of each set trajectory by the corresponding time point of the next set trajectory. The absolute values of this subtraction (*environment 1*: 5 subjects x 11 time points = 55 data points; *environment 2*: 110 data points) were then collected and the mean (total bar height) and SD (error bar) plotted. Paired *t*-test between the data points gave the significance of the set differences. In addition, the data points (55 in *environment 1* and 110 in *environment 2*) were also subdivided into three categories according to whether the subtracted time points of the two sets corresponded to the same, in-between, or different regions. The mean of each of the categories was shown in different colors to give a quantitative measure of how the set differences corresponded to the provided environment.

To quantify trajectory differences in the subsidiary experiment (Fig. 4*B*), the co-activation values corresponding to the same disturbance frequency in the third and fourth trials were subtracted for each of the

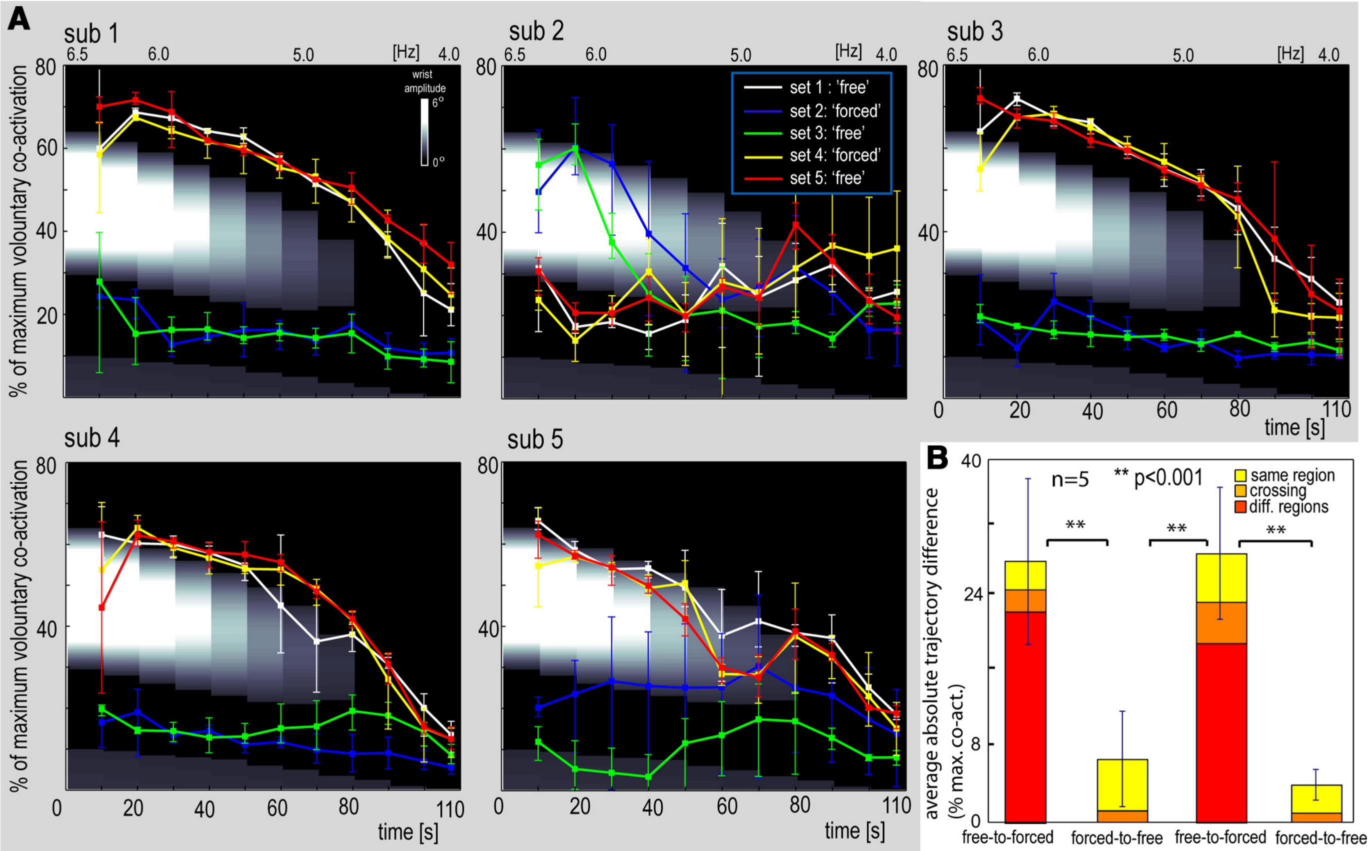

FIG. 2. Trajectories that 5 subjects used to perform the task described in Fig. 1. *A*: traces represent the average trajectories over 10 s and 3 trials, and the maximum and minimum (error bars) over the 3 trials of each set. After the 1st set of 3 free trials (white trace), the subjects were forced (blue) into the region other than what they take in the 1st set, following which they make another set of free trials (green). They were then forced back into the 1st region (yellow) and then let free again (red) in the last set (detailed plots available as Supplementary information). The average absolute co-activation difference between consecutive set trajectories (*B*) were plotted for the subjects when the consecutive trajectories lie in the same (yellow) or different regions (red) and when either one or both trajectories are crossing between regions (orange). The error bars show SD over the entire trial. The difference between consecutive forced and free sets (*2nd* and *4th columns*) is obviously lower (with $P < 0.001$) than that between the free and next forced set to the other region (*1st* and *3rd columns*), while the 2 tall and 2 short columns were equal in height (with $P > 0.70$ and $P > 0.16$, respectively). The shorter columns have no red and are mainly yellow, indicating that for all the subjects, every free set was in the same region as the previous forced set. Note that the 2nd subject showed a tendency to jump regions in the forced condition.

five subjects. This data (5 subjects × 12 points = 60 data points) were collected, and a *t*-test was performed to determine difference from zero. A similar procedure was used to determine the co-activation difference between two occurrences of a disturbance frequency in the same trial (orange lines in Fig. 4*B*). The difference of co-activation value for the five subjects (5 subjects × 2 trials = 10 data points) were collected and analyzed using a *t*-test as before.

RESULTS

No global optimization

In our experiments, subjects could keep their wrist joint angle within the target while it was perturbed, either by co-contracting, or conversely by relaxing their muscles. The perturbation frequency was varied, which gave rise to *trajectories* of the co-contraction level as a function of the time. The results from five subjects performing this task in *environment 1* of Fig. 1 are shown in Fig. 2*A* (detailed results are available in the supplementary figures). The three trajectories performed by each subject in the same set were very similar, with a mean intra-set SD of <4.75% of the MVCA and are thus represented by the *mean set trajectory*.

The subjects started the experiment with a set of free trials (white traces of Fig. 2*A*). When forced to start in the other region (blue trace in Fig. 2*A*), all subjects adopted a new trajectory. In the next three free trials (green trace), the subjects followed a trajectory similar to the one in the forced trials (as shown by the absence of red in *column 2* of Fig. 2*B*), with little difference (~7% of MVCA) between the set trajectories (*B*). After being forced back to the initial region (yellow trace), the subjects again followed the forced trajectory in all the subsequent free trials (red trace).

By repeatedly letting a subject start in the low region, his or her CNS was given the opportunity to explore the global minimum where the task could be achieved with less effort. After this exposure, the subsequent three free trials followed the same trajectory as the forced trials, indicating that the CNS realized the new trajectory. However, when forced back to the local minimum of the high region, the subject similarly followed the new, nonoptimal forced trajectories. This behavior was consistent in all of the subjects tested (Figs. 2*A* and 3*A* and Supplementary Fig. S1 and S2). The CNS clearly did not consider the global minimum for adapting the motor behavior. Even after having experienced the low region, subsequent free

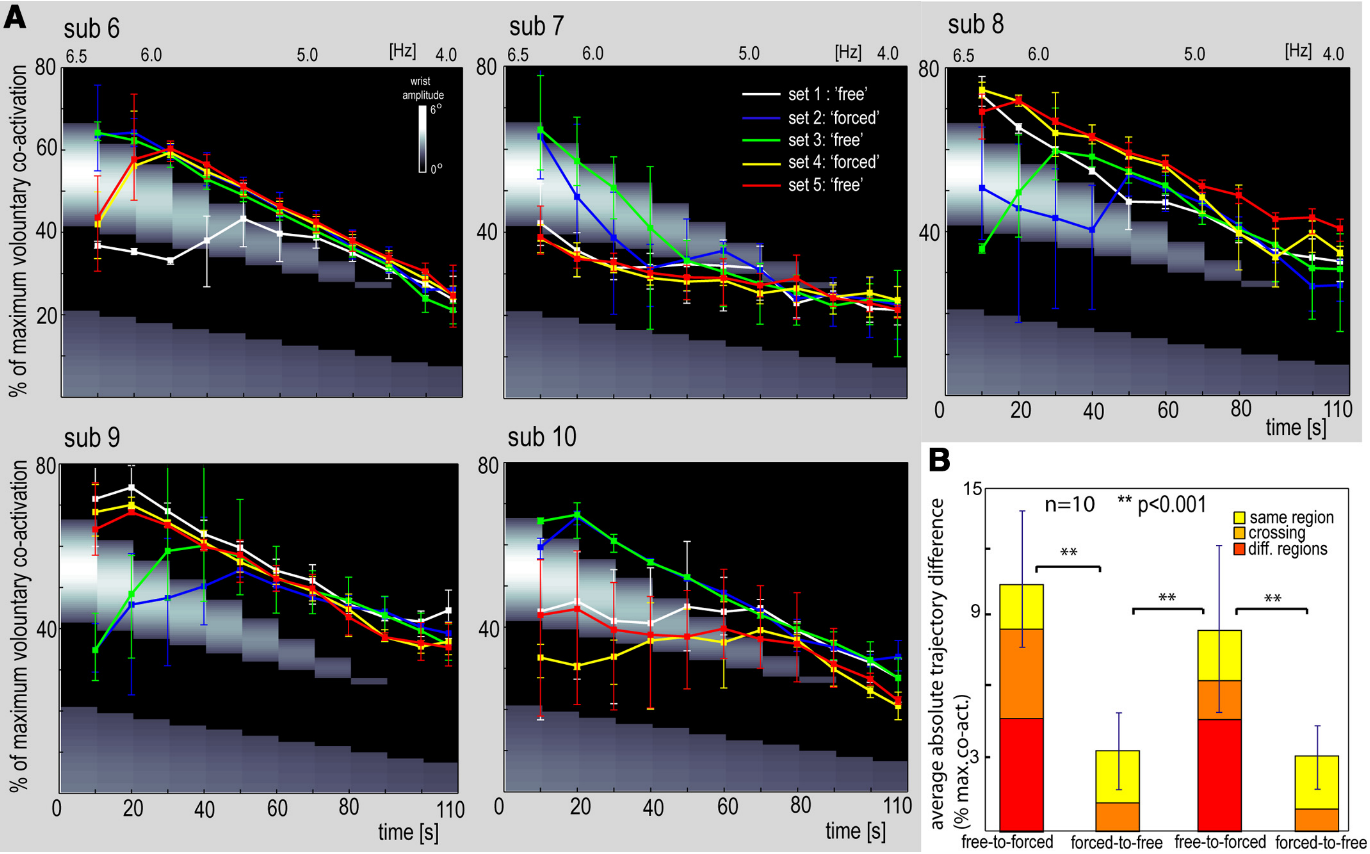

FIG. 3. Motor memory in forced trials. Ten subjects performed in environment 2 with tapering intermediate band, of which 5 representative subjects are shown in *A*. The trajectory differences (*B*) are plotted similar to Fig. 2*B*. Compared with the 1st experiment, a large part of the tall columns is orange as 4 of the 5 subjects jumped across the regions in the forced trial to converge to the previous free trials.

trials were not performed in the low region which costs less effort.

Evidence of motor memory

In all subjects, a strong tendency was observed to perform free trials with a similar trajectory as they had chosen in the preceding forced trials (as shown by the short *columns 2* and *4* of Fig. 2*B*). If this corresponds to an effect of *motor memory*, one could expect that the free trials also influence the subsequent forced trials. However, such a tendency was observed only in one of the five subjects (Fig. 2*A, 2nd panel*), whose forced trajectories, after the initial forced period, converged to the previously performed free trajectories.

The large co-activation difference between the high and low regions of the environment of Fig. 1 might have prevented this tendency to express itself in the other four subjects. To test this eventuality, 10 new subjects performed a second experiment with a similar protocol but using *environment 2* in which the co-activation difference between the high and low regions slowly decreased with time. We refer to this as a tapering environment (Fig. 3). All these subjects again performed free trials similar to the previous forced trials (Fig. 3*A* and Supplementary Fig. S2), but, importantly, a similar tendency was now also observed in the forced trials. The subjects initially used a different region when forced to do so (red sections of *columns 1* and *3* in Fig. 3*A*) but converged with time to the previous free trials (yellow sections of *columns 2* and *4*), jumping over the narrower intermediate region (orange sections of the columns in Fig. 3*B*) to do so.

In the first set of free trials (white traces in Fig. 3*A*), 5 of the 10 subjects adopted the low region while the others used the high region. Depending on the region selected in the first free trials, the succeeding forced trials showed a tendency to follow the previous free trials, jumping between regions to do so (three jump to the low while seven toward high region). The next free trials then followed the forced trials, again jumping between the regions at the same frequency as the forced trials.

When the subjects jump between regions, the error and effort (when jump is from low to high region) is high. However, they repeated the jump in the forced trials and then in *all* the three free trials that follow. Even though the subjects saw their error increasing during the jumps, they were still compelled to repeat the same behavior in all the trials with jumps taking place at about the same frequency each time.

These observations indicate the presence of a *motor memory*. This major determinant of motor behavior could even over-weigh the error-effort cost if it was not large as was demonstrated by the second experiment.

Local optimization

To interpret the way subjects performed the wrist muscles co-contraction task, we assume that they tried to minimize a generic cost function of error and effort of the form

$$V(e, u) = \varepsilon(e) + \mu(|u|) \tag{3}$$

where ε and μ are any positive, monotonically increasing functions representing the *error and effort costs*, respectively, e is the task error and $u = (u_1, \ldots, u_n)$ the activation of the n muscles involved in the task. While the effort cost is larger in the high region than in the low region (Fig. 1*E*), the error cost is similar in both of these regions (see *Experiment and control*). Therefore for any cost of the form given by *Eq. 3,* the high region represents a local minimum while the low region represents the global minimum of the cost function. The new paradigm introduced in this paper is thus characterized by clear and controllable multiple optima of the error-effort cost.

While global optimization was not observed, all 15 subjects in these two experiments showed evidence of *local optimization* of effort. As the task requirement did not specify any particular amplitude below the target amplitude, error cost may be considered to be constant within the high or low region where the amplitude is within the target level. Proving local minimization in this case is trivial, as all the subjects showed a decrease of co-activation in the high region as the trial proceeds, even when maintaining the same high level would have satisfied the task.

However, the subjects may have tried to minimize their wrist movement amplitude even once inside the target. In this case, a more detailed proof of local minimization is required that we show for the second environment that has more subjects to analyze. Figure 4A shows the constant wrist movement amplitude contours for the second environment. Except during inter-region jumps, throughout each trial, all the subjects used trajectories between the theoretical error optimal (red) trajectory and effort optimal (blue) trajectory (Fig. 4*A* and Supplementary Fig. S2), indicating that they minimize both error and effort. Furthermore, note that in both the high and low regions, where the task is satisfied, the contours have a slope of −0.118%/s. Thus at any time point, while a negative trajectory slope would decrease the co-activation, a slope smaller than −0.118%/s would increase the wrist amplitude. The average slope over all the trials across subjects (excluding the 1st 30 s to avoid the inter region jump) was found to be −0.252%/s and significantly smaller than the contour slope of −0.118%/s ($P <$ 0.002). This means first that the subjects decreased the wrist co-activation level, and hence effort, as keeping the same level would still keep the red bar inside the yellow target. Second, this means that they decreased the co-activation level, even if this meant to increase the movement amplitude.

Subsidiary experiment

Finally, in the subsidiary experiment the subjects adopted the same region in the third and fourth trials even when the disturbance frequency was reversed ($P = 0.35$). When the disturbance frequency was changed abruptly (red arrow) in the last 10 s of the (3rd and 4th) trials, the subjects revert back to the co-activation level ($P = 0.78$) that they had used with the gradual frequency change (orange lines) even when the current co-activation would have satisfied the task.

Conclusion

Contrary to common intuition, the observations from the preceding two environments indicated that vibratory disturbances did not necessarily lead to a high co-contraction in subjects (with around half of the tested subjects took the low region in their 1st free trials). When forced to do so, subjects adopted a trajectory that did not minimize effort, even having previously realized a lower effort trajectory. The effort difference being large between the two trajectories (~40% MVC in *environment 1*), this behavior was not due to the inability of the CNS to distinguish the two effort costs. The behavior seems to originate from some motor memory, which compels the CNS to follow a previous motor activation pattern even if it was not globally optimal. However, co-activation could be relaxed along a chosen trajectory yielding local minimization of effort.

While motor memory was shown to be present in every (forced or free) movement, it was not always prevalent over error and effort. The memory effect could be overweighed if the error and effort cost is high as illustrated by the experiment

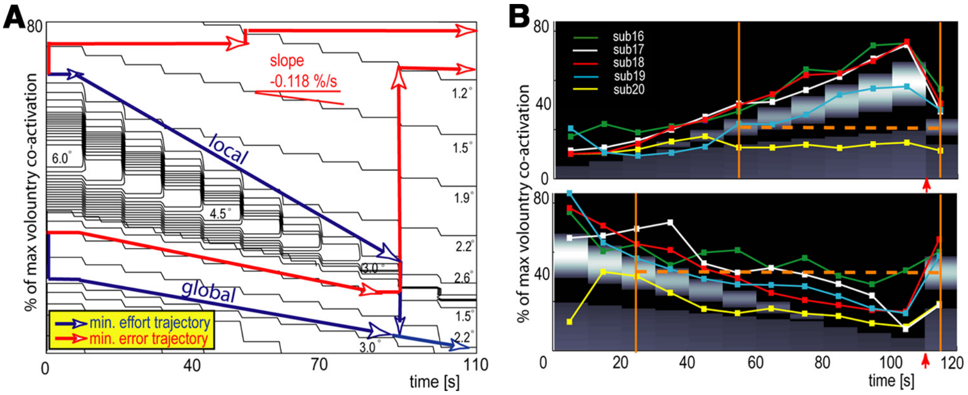

FIG. 4. Evidence of local optimization (*A*) and of the memorized mapping (*B*). The wrist amplitude contour map of the environment in *A* shows the similar depth of the 2 regions in which the task is satisfied. In these regions, the wrist amplitude decreases as the co-activation increases and follows a slope of −0.118%/s. Schematics of the (theoretical) optimum error minimization (red line) vs. pure energy minimization (blue line) have been plotted. All subject trajectories from second environment were within the blue and red traces and have a slope less than the contours, i.e., −0.118%/s, thus showing local optimization of effort by subjects. To check the nature of task mapping (*B*), 5 subjects (different color traces) performed 3 trials with perturbations of increasing frequencies (*top* shows the 3rd trial) followed by a trial with decreasing frequencies (*bottom*). The subjects adopted the same region in the 2 trials with similar trajectories ($P = 0.35$). When the disturbance frequency was changed abruptly (red arrow) in the last 10 seconds of the (3rd and 4th) trials, the subjects revert back to the co-activation level ($P = 0.78$) that they had used with the gradual frequency change (orange lines). This shows the presence of a mapping between disturbance frequency and co-activation. The trajectories are plotted as in Fig. 2*A*.

of Fig. 2 and conversely the memory could over-weigh the error- effort cost (jumping behavior of Fig. 3). Thus it seems that motor memory, error and effort together determine the subject behavior.

DISCUSSION

Study of optimization in motor control has typically focused on tasks involving a single optimum, perhaps because of a belief that the human CNS can always converge to the optimal solution with sufficient experience. However, many motor tasks are characterized by multiple optima, and the convergence to optimal muscle activation patterns may be very difficult due to complex dynamics of the musculoskeletal system. In this context, our experiments enabled a systematic investigation of optimization in tasks with multiple optima.

The first main observation from the experimental results is that the realization of the global optimum (in terms of being able to independently track it) is not sufficient to adopt it. Even in our simple one joint paradigm, when the subjects were forced away from a realized global optimum, they kept the forced nonoptimal trajectory in the following free trials instead of going back to the optimal trajectory that they had previously performed.

This behavior seems to originate from some unconscious memory of the muscle activations that prevents immediate change of activation patterns in consecutive trials. We used a qualitative questionnaire to examine what the subjects believed they were doing. When asked if they had any particular behavioral strategy during the task, 8 of the 10 subjects (who performed in *environment 2*) replied that they had none and only tried to keep their wrist movement inside the target as much as possible. The two other subjects replied that they tried to maintain a constant co-activation level once they saw the task was being satisfied though their co-activation level varied over time similar to the other subjects. Seven of the subjects confirmed that they had no difficulty starting at a given level in the forced trials, whereas three replied that they found the first forced trial difficult and the subsequent ones easier, which would correspond well to the formation of a memory in the first forced trial and its use in subsequent trials. In summary, the subjects seemed to believe that they performed a visual feedback task and were completely unaware of the repetitive pattern in their behavior. This pointed to the fact that this behavior was not an assimilation of distinct discrete choices by the subjects.

In psychology, memory is defined as an organism's ability to store, retain, and recall information, and information pertaining to muscle activations is referred to as motor memory. Motor memory has been examined extensively (Adams and Dijkstra 1968; Stamm and Kelso 1978; Stelmach and Kelso 1975) as a conscious recollection process but not as an unconscious process that can interfere with behavior. While motor pattern retention effects were presented in recent studies (Muller and Sternad 2004; Quaney et al. 2003), our study shows for the first time through a multi-solution task that motor memory can impede optimality of motor behaviors.

The subsidiary experiment examined how this motor memory works. As one can see in Fig. 4*B,* the subjects adopted a similar level of co-contraction as they had used previously, when the frequencies were reversed or changed suddenly (even when the current level would have satisfied the task). This indicated that the observed behavior cannot be attributed to memory of instructions given to the subject (like in the forced trials) but originates from a mapping between motor activation and disturbance frequency.

However, these results were obtained with an essentially isometric task. Although in the bicycle and water in cup examples (in INTRODUCTION), the perturbations are in the null space of the movement and thus essentially isometric, in other real situations, the dynamics of the body will also interact with these perturbations and may also provide additional feedback that is absent in our setup. Therefore while it is not completely clear how the observed effects would translate to movement tasks, our results show an example where the variables commonly presumed to determine motor behavior (error and effort being the most popular) do not capture human behavior completely. In relatively common multi-solution tasks involving muscle co-activation, motor memory may be an important factor that significantly influences motor optimization.

On the other hand motor memory and local optimization may also be affecting movement tasks. This is illustrated in sports by the catastrophic evolution of the high jump style. After years of adaptation, by the 1960s, the "straddle" style of high jump was considered to be most efficient until a self-styled athlete called Dick Fosbury introduced the "Fosbury flop," a radically new style that can be shown to be more effort efficient than the straddle (Dopena 1980). Although this crude example may have involved other logistical factors, it shows that even after years of exploration, we may not be performing tasks optimally. The large kinematic differences between the straddle and the Fosbury flop gives some indication of how difficult it can be to converge from a sub-optimal local optimum (like straddle) to the global optimum (like that of the Fosbury flop).

Therefore instead of attempting global optimization, the CNS may rather remember any task satisfying solution and use it to solve the task. This behavior corresponds to the *motor memory* observed in our results, where even after previous exposure to the *optimal* solution, the CNS followed the recent sub-optimal solution. The muscle activations can however be locally optimized (Franklin et al. 2008).

Although our study did not check for retention effects over days, we checked to confirm that a chosen sub-optimal solution did not change even with continuous environment exposure of ~1 h. Considering that consolidation is known to occur in much shorter time periods (Smith et al. 2006), this suggests the importance of training "correct" motor behaviors in rehabilitation and physical education.

While the CNS can automatically optimize tasks locally, global optimization of effort and error may require a conscious effort by the individual or an external influence as in the forced behavior of our experiment. A teaching signal or reference like that of Fosbury may be required to make the CNS realize a globally optimal behavior. The competitive advantage of optimal behaviors may explain why the human brain is equipped with explicit networks for imitation learning (Rizolatti and Craighero 2004). Imitation behavior may help humans achieve gross convergence to globally optimal solutions realized by experienced individuals, while local optimization of newly adopted behaviors in regard of error and effort would automatically arise with repeated practice (Franklin et al. 2008; Izawa et al. 2008).

ACKNOWLEDGMENTS

The authors thank Dr. A. Melendez for helping in the development and setup of the wrist manipulandum.

GRANTS

This research was supported by the Strategic Research Program for Brain Sciences (SRPBS) Japan and by the EU grant FP7-ICT-2007-3 VIACTORS.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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