Learning a Novel Myoelectric-Controlled Interface Task

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Radhakrishnan SM, Baker SN, Jackson A. Learning a novel myoelectric-controlled interface task. J Neurophysiol 100: 2397–2408, 2008. First published July 30, 2008; doi:10.1152/jn.90614.2008. Control of myoelectric prostheses and brain–machine interfaces requires learning abstract neuromotor transformations. To investigate the mechanisms underlying this ability, we trained subjects to move a two-dimensional cursor using a myoelectric-controlled interface. With the upper limb immobilized, an electromyogram from multiple hand and arm muscles moved the cursor in directions that were either intuitive or nonintuitive and with high or low variability. We found that subjects could learn even nonintuitive arrangements to a high level of performance. Muscle-tuning functions were cosine shaped and modulated so as to reduce cursor variability. Subjects exhibited an additional preference for using hand muscles over arm muscles, which resulted from a greater capacity of these to form novel, task-specific synergies. In a second experiment, nonvisual feedback from the hand was degraded with amplitude- and frequency-modulated vibration. Although vibration impaired task performance, it did not affect the rate at which learning occurred. We therefore conclude that the motor system can acquire internal models of novel, abstract neuromotor mappings even in the absence of overt movements or accurate proprioceptive signals, but that the distal motor system may be better suited to provide flexible control signals for neuromotor prostheses than structures related to the arm.

INTRODUCTION

The field of neuromotor prosthetics aims to restore function to patients lacking normal motor output by using signals derived directly from the nervous system to control external devices (e.g., computer cursors or prosthetic limbs). In the case of high spinal cord injury control signals must be derived directly from the brain, for example, by extracellular recording of action potentials in the cortex. A common implementation of a brain-controlled interface (BCI) involves decoding the firing rate of multiple neurons in arm areas of motor cortex to obtain a two- (2-D) or three-dimensional (3-D) cursor position (Carmena et al. 2003; Hochberg et al. 2006; Serruya et al. 2002; Taylor et al. 2002). Conceptually, the approach has evolved from experimental paradigms aimed at elucidating neural coding of normal arm movements (Paninski et al. 2004; Schwartz et al. 1988), with decoding being the inverse of this process. A large body of literature is now devoted to applying decoding algorithms of increasing sophistication to neural data (e.g., Kulkarni and Paninski 2008; Santhanam et al. 2006; Wu et al. 2006). However, BCI control remains slow and inaccurate in comparison to natural movements, with errors corrected only by visual feedback. Considerable improvements are required if these devices are to have real clinical application.

An alternative to the “biomimetic decoding” approach is suggested by operant conditioning experiments in which animals are trained to volitionally modulate cell activity under biofeedback conditions (Fetz 1969; Gage et al. 2006). Fetz and Finocchio (1975) found that motor cortical cells and upper-limb muscles that were normally coactivated could be readily dissociated. The brain’s remarkable flexibility to learn novel neuromotor mappings is further demonstrated by the recovery of function that follows surgical crossing of forelimb motor nerves (Brinkman et al. 1983). This plasticity is exploited by myoelectric prostheses in which control of distal joints is assumed by the proximal muscles of amputees. Such devices have achieved widespread clinical use (Esquenazi 2004; Parker et al. 2006), although the degree of control is limited and may be improved if distal motor nerves can be reinnervated into proximal muscles (Kuiken et al. 2007; Miller et al. 2008).

Since decoding strategies derived from neural coding of natural movements may be inappropriate after sensory inputs to motor cortex have been disrupted, cortical plasticity is likely to play an essential role in any successful BCI implementation. Changes in cell-tuning properties during BCI use have been reported (Carmena et al. 2003; Taylor et al. 2002) and, in principle, could supplant biomimetic decoding altogether. Instead of the BCI decoding appropriate movements for natural patterns of neural activity, subjects might be able to volitionally modify these neural patterns to produce the desired outcome. In other words, the motor system would learn an inverse model of the BCI transformation to enable feedforward control (Kawato 1999). Given the apparent flexibility of the motor system to learn new neuromotor mappings, it is reasonable to ask why BCI control remains relatively poor and whether this situation can be improved.

Despite the long history of studies demonstrating adaptation to novel visuomotor conditions (Held and Hein 1958; Mosier et al. 2005; Roby-Brami and Burnod 1995; Southall 1962; Welch 1978), the degree to which the motor system can learn inverse models of abstract neuromotor transformations may be limited, particularly if visual feedback is not associated with a corresponding movement of the body. On the other hand, biomimetic BCI strategies that aim to decode arm position or velocity may not be optimal for exploiting motor-learning mechanisms (Fetz 2007). One further possibility is that the lack of proprioceptive feedback impairs learning in BCI paradigms. Recent computational theories have emphasized the importance of sensory feedback for motor control (Scott 2004; Todorov and Jordan 2002) and its absence has been proposed as an explanation for poor BCI performance (Abbott 2006; Fagg et al. 2007). However, although proprioception is necessary for normal movement (Rothwell et al. 1982;...
Sanes et al. (1985), its role in learning inverse models of sensorimotor transformations is less clear. Comparisons of visuomotor adaptation in normal and deafferented subjects have often yielded ambiguous results (Bard et al. 1995; Bernier et al. 2006; Guédon et al. 1998; Ingram et al. 2000). Using wrist vibration, Pipereit et al. (2006) distinguished adaptation to mechanical perturbations (which required accurate proprioceptive input) from visual perturbations (which did not). However, it is not obvious what role should be expected for proprioception in learning the abstract neuromotor mappings involved in operating a BCI.

This study was designed to address these questions using a novel myoelectric-controlled interface (MCI) in which electromyogram (EMG) activity from multiple hand and arm muscles was mapped onto a 2-D cursor space. Since the firing rates of some motor cortex neurons are consistently related to EMG over a wide range of motor tasks (Holdefer and Miller 2002; Jackson et al. 2007; Pohlmeier et al. 2007) the MCI task provides an approximate emulation of a BCI with which to test key ideas in healthy subjects without the need for invasive recordings (Tian and He 2003). In a further experiment, the role of sensory and proprioceptive feedback in learning MCI transformations was tested by applying unpredictable vibration to the hand.

**METHODS**

**Subjects**

Experiments were performed on 22 healthy subjects (experiment A: 10; experiment B: 12) aged between 21 and 40 yr. All gave informed consent according to procedures approved by the local ethics committee.

**Behavioral task**

Subjects were seated with their right hand inside a tight-fitting glove attached palm-down to a horizontal board fixed to the armrest of the chair. The right elbow, forearm, and wrist were immobilized with cushioned restraints. A computer screen in front of the subject displayed two circles representing a (yellow) cursor and a (red) target. Subjects controlled the cursor position by making isotonic contractions of right arm and hand muscles (see following text); the task was to maintain the cursor overlapping with the target until a new target appeared. The experiment used a variant of the “center-out” task. Each trial began with the target at a central origin for a random hold-time between 1 and 2 s whereupon the cursor reappeared at one of 12 peripheral locations. Once the cursor had been held at the peripheral target for 1 s, the target returned to the origin and a new trial was initiated (Fig. 1A). Peripheral target locations were equally spaced around a circle at 70% of the distance from the origin to the edge of the screen (target and cursor radii were 14% on the same scale). Targets were presented in pseudorandom order such that each location occurred once in a block of 12 consecutive trials.

**Myoelectric control algorithms**

Cursor position was determined on-line by deriving control signals from EMG recorded with surface electrodes placed over arm and hand muscles. EMG was first amplified (gain 1–10K) and high-pass filtered at 30 Hz (Neurolog NL824/820, Digitimer) before sampling at 5 kHz (PCI-6071E, National Instruments). The MCI algorithm was implemented in real time by custom Delphi (Borland) software running in Windows XP on a Pentium PC. Control signals were obtained from rectified EMG by continuously averaging over the preceding 2,000 sample points (i.e., convolution with a rectangular window of width 400 ms; Fig. 2A). At the start of the experiment, subjects were informed of the specific movements that activated each recorded muscle and were instructed to produce comfortable levels of contraction, which they would be able to repeat many times without fatigue (typically corresponding to between 2 and 20% of maximum voluntary contraction [MVC]). Control signals were scaled from 0 (rest) to 100% (comfortable level of contraction) and combined such that each of six muscles moved the cursor along uniformly spaced directions of action (DoAs), with the 100% level corresponding to the distance to the screen edge. Thus the 2-D cursor position was determined by the sum of six vectors aligned along the DoAs with magnitudes determined by six control signals. Relaxing the hand and arm brought the cursor back to the origin of the center of the screen.

**Experiment A**

For experiment A, EMG was recorded from eight muscles (Table 1), of which six were used to control the cursor. Two types of control algorithm were compared, designated “intuitive” and “nonintuitive.” During intuitive control, muscles acted along DoAs that were consistent with their action on the limb in that posture. For example, with the palm of the right hand down, first dorsal interosseous (FDI) acts to abduct the index finger to the left; thus this muscle moved the cursor to the left on the screen. The complete set of muscle DoAs is shown in Fig. 1B; this arrangement was used for all subjects in experiment A. During nonintuitive control, six of the eight muscles recorded were selected at random to act along uniformly spaced DoAs (Fig. 1C). A different nonintuitive arrangement was selected randomly for each subject. For half of the nonintuitive arrangements, DoAs pointed toward the six targets that were in between the original directions (i.e., offset by 30°, as in the example in Fig. 1C). This was done to avoid biasing arrangements in favor of particular targets and to minimize generic task features that could be learned across sets. Subjects performed 192 intuitive and nonintuitive trials in continuous sets of each type. The order of intuitive and nonintuitive sets was counterbalanced across subjects. A third set was performed in which the arrangement of muscle DoAs was selected in the same way as the “nonintuitive” set. In this case, however, the variability of three of the control signals (every other direction, as shown in Fig. 1D) was increased by shortening the length of the smoothing window to 1,000

![Fig. 1. The myoelectric-controlled interface (MCI) task. A: subjects were required to move a computer cursor (shown in light gray but yellow on the screen) to a peripheral target (dark gray but red on screen) for 1 s before returning to the origin. B: arrangement of muscle actions during “intuitive” control in experiment A. Muscles acted on the cursor in directions that were consistent with their action on the limb. C: typical arrangement of muscle actions in “nonintuitive” control. Muscles acting on the cursor in each direction were selected at random from the set of recorded muscles. D: typical arrangement of muscle actions during the “added variability” set of trials. The variability in 3 of 6 directions (circled) was increased by halving the length of the smoothing window used to derive control signals from the rectified electromyogram (EMG).](http://jn.physiology.org/...)

**FIG. 1. The myoelectric-controlled interface (MCI) task.** A: subjects were required to move a computer cursor (shown in light gray but yellow on the screen) to a peripheral target (dark gray but red on screen) for 1 s before returning to the origin. B: arrangement of muscle actions during “intuitive” control in experiment A. Muscles acted on the cursor in directions that were consistent with their action on the limb. C: typical arrangement of muscle actions in “nonintuitive” control. Muscles acting on the cursor in each direction were selected at random from the set of recorded muscles. D: typical arrangement of muscle actions during the “added variability” set of trials. The variability in 3 of 6 directions (circled) was increased by halving the length of the smoothing window used to derive control signals from the rectified electromyogram (EMG).
sample points (200 ms). The set of 192 “added variability” trials was performed after the intuitive and nonintuitive sets.

**Experiment B**

In experiment B, three sets of 96 trials were performed using different, randomly selected “nonintuitive” control arrangements. During one of these sets, the hand and wrist were vibrated using a linear motor (V201/3, Ling Dynamic Systems) placed below the board to which the subject’s gloved hand was attached. The board was vibrated with a base frequency of 50 Hz. The vibration signal was amplitude- and frequency-modulated with independent low-pass filtered (cutoff 0.5 Hz) white noise (with resulting coefficients of variation [CVs] for instantaneous frequency and amplitude of 0.2). The purpose of vibration was to introduce unpredictable noise into the sensory feedback from the hand. A second set was performed without vibration for comparison and, in the third set, vibration was applied only for the second half (i.e., trials 49–96). The order of these three sets was counterbalanced across subjects. To maximize the effect of forearm vibration on task performance, only hand and wrist muscles (not arm muscles) were used to control the cursor during experiment B (Table 1).

**Data analysis**

Figure 2B shows the vertical cursor position for two complete trials. Performance of the task was quantified on a trial-by-trial basis by the movement time, defined as the interval between the appearance of the peripheral target and the beginning of the continuous 1-s hold period at that target.

**Table 1. Muscles used for MCI operation**

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Abbreviation</th>
<th>Group</th>
<th>Action</th>
<th>Experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biceps</td>
<td>Bic</td>
<td>Arm</td>
<td>Elbow flexion</td>
<td>A</td>
</tr>
<tr>
<td>Triceps</td>
<td>Tric</td>
<td>Arm</td>
<td>Elbow extension</td>
<td>A</td>
</tr>
<tr>
<td>Deltoid</td>
<td>Delt</td>
<td>Arm</td>
<td>Shoulder abduction</td>
<td>A</td>
</tr>
<tr>
<td>Flexor carpi ulnaris</td>
<td>FCU</td>
<td>Wrist</td>
<td>Wrist flexion</td>
<td>A, B</td>
</tr>
<tr>
<td>Extensor carpi radialis</td>
<td>ECR</td>
<td>Wrist</td>
<td>Wrist extension</td>
<td>A, B</td>
</tr>
<tr>
<td>First dorsal interosseus</td>
<td>FDI</td>
<td>Hand</td>
<td>Index finger abduction</td>
<td>A, B</td>
</tr>
<tr>
<td>Abductor pollicis brevis</td>
<td>APB</td>
<td>Hand</td>
<td>Thumb abduction</td>
<td>A, B</td>
</tr>
<tr>
<td>Abductor digitii minimi</td>
<td>ADM</td>
<td>Hand</td>
<td>Little finger abduction</td>
<td>A, B</td>
</tr>
<tr>
<td>Abductor pollicis longus</td>
<td>APL</td>
<td>Hand</td>
<td>Lateral thumb movement</td>
<td>B</td>
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</table>

In experiment A, eight arm, wrist, and hand muscles were recorded of which six were used for cursor control. In experiment B, only wrist and hand muscles were used and an additional muscle (APL) was included.

**RESULTS**

**Experiment A**

LEARNING INTUITIVE AND NONINTUITIVE CONTROL ALGORITHMS. The first question we addressed was whether subjects could learn to control the computer cursor using signals derived from hand and arm muscle EMG. In all cases the subject’s performance at
the task improved during each set of trials. Figure 3A shows trajectories (from the peripheral target appearing to the cursor first overlapping the target) for the first and last 12 trials of a set using a “nonintuitive” arrangement of muscle DoAs. When initially presented with this task, the subject’s performance was poor because the subject had no knowledge of the isometric contractions required to move the cursor in each direction. In addition, certain combinations of muscles required to reach some targets were unnatural. Therefore the cursor followed a meandering trajectory to the peripheral targets and the subject had difficulty holding the cursor within target for the required time. However, by the end of this 192-trial set movements to some targets were unnatural. Therefore the cursor followed a poor because the subject had no knowledge of the isometric contractions required to move the cursor in each direction. In addition, certain combinations of muscles required to reach some targets were unnatural. Therefore the cursor followed a meandering trajectory to the peripheral targets and the subject had difficulty holding the cursor within target for the required time. However, by the end of this 192-trial set movements to some targets were unnatural. Therefore the cursor followed a broad, with individual muscles active over a range of target directions (the DoAs are as in Fig. 1C). Tuning functions tended to be predictive, feedforward control of the cursor. Figure 3B plots the movement time (the time from appearance of a peripheral target to the beginning of the successful hold period) for each trial in the nonintuitive set. The data for this subject were fitted with an exponential curve with movement times halving every 66 trials.

Figure 3C compares learning of “intuitive” control arrangements (in which muscles move the cursor in approximately the same direction as they act on the particular joint) with “nonintuitive” arrangements (where DoAs for muscles are randomized). In this plot, average movement times over blocks of 12 consecutive trials (encompassing one target in each direction) have been combined across all 10 subjects. It is apparent that “intuitive” control was significantly easier than “nonintuitive” control during the first block of trials, with average (±SE) movement times of 7 ± 1 and 22 ± 3 s, respectively (a ratio of 1:3; \( P = 0.0001 \), paired \( t \)-test). This difference between intuitive and nonintuitive movement times remained statistically significant, but decreased as the subjects learned the control algorithm. By the last block, the average movement time was 2.0 ± 0.4 s for intuitive and 3.5 ± 0.5 s for nonintuitive arrangements (a ratio of 1:1.8; \( P = 0.02 \), paired \( t \)-test). Furthermore, the asymptotic levels approached by the exponential fits shown in Fig. 3C were not significantly different (2.4 ± 0.5 s for intuitive and 3.1 ± 0.6 s for nonintuitive arrangements; ratio 1:1.3). This diminishing difference between intuitive and nonintuitive algorithms suggests that, with practice, subjects can compensate effectively for nonintuitive control algorithms.

**MUSCLE TUNING FUNCTIONS.** To investigate the contribution of each muscle to cursor movements we calculated tuning curves based on the average control signal during the 1-s hold period for each target direction. Figure 4 shows tuning curves for a single subject over the entire set of nonintuitive control trials (the DoAs are as in Fig. 1C). Tuning functions tended to be broad, with individual muscles active over a range of target directions on either side of the DoA. In addition, muscles not involved in control of the cursor often showed substantial activation for some directions (e.g., ECR in Fig. 4). This presumably resulted from cocontraction with other muscles that were used for control.

Figure 5A shows tuning curves for the instantaneous level of control signals 500 ms after the peripheral target appeared. For this analysis, the 192 trials in each set were divided into four consecutive groups of 48 trials to show how tuning patterns evolved during learning. To combine across muscles and subjects, curves were aligned to the DoA before averaging. For the intuitive set, the average tuning curve was peaked around the DoA from the first group of trials onward. Therefore even during the early stages of learning, subjects were correctly able to predict the required muscle combinations soon after the appearance of the peripheral target. By contrast, during nonintuitive control this pattern emerged only as learning progressed. Over the first group of trials (1–48; blue line), the tuning function at 500 ms after target appearance was flat because subjects could not predict the appropriate com-

![Figure 3](http://jn.physiology.org/)

**FIG. 3.** Motor learning during MCI operation. A: trajectories of the cursor center to each of the 12 targets before and after learning the nonintuitive MCI arrangement shown in Fig. 1C. Small circles indicate position of cursor 500 ms after target appearance. B: movement time for each individual trial plotted for a single subject learning the nonintuitive arrangement. C: mean movement time over blocks of 12 consecutive trials averaged across all subjects for intuitive and nonintuitive MCI arrangements. Bars indicate SE.
bination of muscles to activate. However, by the third quarter of trials (97–144; red line) a peak around the DoA appeared, consistent with the development of feedforward cursor control.

Figure 5B shows average tuning curves compiled from the level of control signals during the peripheral hold period (i.e., once the target had been acquired). There was little difference between intuitive and nonintuitive arrangements (although since movement times were longer in the nonintuitive arrangement subjects took more time to produce this pattern on each trial). However, during the nonintuitive set there was a slight trend for the overall level of muscle activation to decrease during learning. This was true both for targets aligned to the DoA and in the opposite direction. In other words, subjects’
overall muscle use decreased as performance improved, reflecting more efficient control, since less activity of muscles acting toward the target was required to overcome the effect of muscles acting away from the target.

**TUNING FUNCTIONS AND MINIMIZATION OF MOVEMENT VARIANCE.** The tuning curves shown in Fig. 5 were well described by cosine functions, as also previously reported for natural movements (Hoffman and Strick 1999). Cosine tuning is not a straightforward consequence of the control algorithm we used; had subjects acquired targets using only the one or two muscles acting toward each location the tuning functions would have been much narrower. However, Harris and Wolpert (1998)) suggested that the motor system aims to minimize the variance of end position in the presence of signal-dependent motor noise and a strategy in which effort is divided among several muscles may be less susceptible to noise than if a single muscle produces the entire force (Haruno and Wolpert 2005; Todorov 2002).

To explore this further we analyzed the third set of “added variability” trials in experiment A. In this set, the variability of some muscles was artificially increased by shortening the smoothing window used to derive the control signal from rectified EMG. The principle of minimum variance predicts an optimal strategy in which the contribution of multiple effectors is scaled according to the noise in each signal so high-variability muscles should contribute less to cursor control. Figure 6A compares average tuning functions for the control signals derived with low and high variability. These tuning

![Fig. 6](http://jn.physiology.org/)

**FIG. 6.** Effect of variability and muscle group on tuning functions. A: mean hold period tuning functions for low (400-ms smoothing window) and high (200-ms smoothing window) variability control signals for all trials in the “added variability” set in experiment A. Bars indicate SE. Solid and dashed lines indicate best-fit cosine functions for low- and high-variability data, respectively. B: mean contribution of low- and high-variability control signals over all targets, averaged across muscles and subjects. P value calculated by treating each muscle in each subject as a single observation. C and D: similar plots comparing hand and arm muscles (see Table 1) during nonintuitive control. E and F: similar plots comparing those hand and arm muscles that did not move the cursor during nonintuitive control. Since there was no DoA associated with these muscles, tuning functions were aligned to the target direction eliciting maximum activation before averaging. Bars indicate SE throughout.
functions were calculated from the hold period activity and combined across all trials in the set. Both curves are cosine-shaped but low-variability muscles were used to a greater extent than high-variability muscles, consistent with the predictions of a minimum variance strategy. Expressed as a percentage of the distance to the screen edge, the mean (±SE) contribution of high-variability muscles for each target was 29 ± 2%, compared with 37 ± 3% for low-variability muscles (Fig. 6B; P = 0.05, unpaired t-test).

COMPARISON BETWEEN ARM AND HAND MUSCLES. Figure 6C compares hold period tuning curves during nonintuitive control for muscles categorized as acting on the hand and arm (see Table 1). Again, both curves are cosine-shaped, but the amplitudes differed significantly. Across all targets, arm muscles contributed a mean (±SE) control signal of 29 ± 3% compared with 40 ± 2% for hand muscles (Fig. 6D; P = 0.01, unpaired t-test). Thus although subjects could modulate the activity of all muscle groups to control the cursor, there was a preference for using distal muscles. Several possible explanations for this were examined further.

Metabolic factors. The first possibility we considered was that the larger proximal muscles required greater effort and/or energy expenditure to use. Since the scaling factor converting muscle activity to cursor movement was arbitrarily based on the subject’s “comfortable contraction” (see METHODS), there may have been systematic differences in how this instruction was interpreted across muscle groups. We found no significant difference between the level of “comfortable contraction” expressed as a percentage of maximum voluntary contraction for each group (hand: 10 ± 2% of MVC; arm: 14 ± 2%, P = 0.14, unpaired t-test). However, the larger arm muscles require greater energy to achieve this level, which could have led to a general preference for their avoidance if the task were achievable using hand muscles instead. However, during each nonintuitive set of trials, two of the eight recorded muscles had no effect on the cursor and an equally strong distal versus proximal preference should also be expected in these muscles. The average tuning curves for hand and arm muscles that were not involved in cursor control are compared in Fig. 6E. Since these muscles have no defined DoA these curves are aligned to the target that produced the greatest activation for each muscle. There was no significant difference between the mean level of activation of hand (29 ± 7%) and arm (27 ± 5%) muscles that were not involved in the task (Fig. 6F; P = 0.8, unpaired t-test). Therefore rather than displaying a general predisposition against activating arm muscles, subjects avoided only those specific arm muscles that acted on the cursor.

Accuracy. A plausible explanation for this pattern of muscle use would be if high levels of motor noise in proximal muscles meant subjects preferentially chose distal muscles to minimize position variability (similar to the high-/low-variability effect seen in Fig. 6A). Hamilton et al. (2004) found that motor noise, quantified as the CV of force production, was in fact higher for distal muscles than for proximal muscles; however, it is not clear whether a similar result should be expected for control signals derived from muscle EMG recordings. Therefore we calculated CVs for the control signals from each muscle assuming a linear relationship between mean and SD. For each muscle, the SD of control signal during each 1-s hold period was plotted against mean level on a trial-by-trial basis (Fig. 7A), and the gradient of the best-fit line through the origin was used to estimate that muscle’s CV. This analysis failed to reveal any significant difference between coefficients for hand and arm muscle groups (Fig. 7B; hand: 0.102 ± 0.004, arm: 0.096 ± 0.003, P = 0.3, unpaired t-test). To validate the sensitivity of this analysis, we calculated CVs for muscles in the added variability condition. In this case there was a clear difference in CV between low- and high-variability control signals (Fig. 7C; low variability: 0.087 ± 0.005, high variability: 0.120 ± 0.007, P = 0.0004, unpaired t-test).

Independent muscle activation. Although cocontraction of muscles that are not involved in cursor control does not influence performance of the task, cocontraction of muscles that move the cursor in opposing directions is detrimental. For instance, all three arm muscles in Fig. 4 exhibited similar tuning functions despite having different DoAs, which suggests the subject had difficulty activating these muscles individually. Note also that for targets in directions opposed to the DoA, arm muscles were slightly more active than hand muscles (Fig. 6C). We therefore hypothesized that the preference for distal muscles may reflect their greater flexibility for forming appropriate (and decoupling inappropriate) muscle synergies, thus avoiding inappropriate cocontraction. To test this we examined changes in coupling between pairs of muscles as subjects learned the MCI task. For each muscle, the average control signal during 12 consecutive hold periods (consisting of one target in each direction) was regressed against corresponding mean levels for other muscles. Pairs of muscles were defined as “similar” if their DoAs were separated by 60° or “opposing” if the separation was 120 or
ports the hypothesis that the distal motor system has greater flexibility for forming and dissociating task-specific muscle synergies.

Finally, to ensure this difference could not be explained by cross talk between muscle recordings we analyzed 200-s sections of unsmoothed, unrectified EMG recorded during the task. Cross-correlation functions were compiled using the third derivative of the unrectified EMG since this renders physiological correlations negligible (Kilner and Baker 2000). Cross talk was quantified as the maximum $R^2$ value corresponding to cross-correlation peaks or troughs. Across subjects, average cross talk between pairs of arm muscles was in fact significantly lower than that between pairs of hand muscles (arm: $0.0015 \pm 0.0005$, hand: $0.014 \pm 0.004$, $P = 0.002$, unpaired $t$-test).

**Experiment B**

ROLE OF NONVISUAL FEEDBACK IN LEARNING THE MCI. The preceding results suggest that there is considerable flexibility within the motor system for learning novel control algorithms, especially within the motor networks controlling distal musculature. However, in experiment A subjects received tactile and proprioceptive feedback during learning, which would be unavailable in many neural prosthetics applications. To investigate the role of nonvisual feedback we applied noise-modulated vibration to the hand during experiment B while subjects learned nonintuitive algorithms controlled by hand muscles (see METHODS). If sensory feedback from the limb is required for learning, then introducing noise into this signal would be expected to slow the rate at which subjects’ performance improved.

Figure 9A shows the improvement in movement time during sets of 96 trials with and without hand vibration. Although it is clear that learning occurred during both sets, performance was consistently poorer in the presence of vibration, with movement times increased on average by $3.9 \pm 2.0$ s ($P = 0.04$, paired $t$-test). This difference could reflect either a slower rate of learning or an increase in task difficulty. To dissociate these possibilities, we analyzed the third set of trials in which hand vibration was introduced only during the second half of the set. If accurate proprioceptive feedback is necessary to learn the task, then it is the vibration during early trials that causes the poor performance in later trials. Therefore introducing vibration midway through the set should not degrade performance to the same extent. On the other hand, if sensory noise makes the task harder to perform but does not interfere with learning, then movement times during the latter half of the set should be equivalent to those when vibration was applied throughout.

As can be seen from Fig. 9B, vibration introduced halfway through the set did degrade performance relative to the no vibration condition. After a large transient increase when vibration began at trial 48, movement times approached those equivalent to those when vibration was applied throughout. Combining data across three blocks of trials (Fig. 9C) revealed that during trials 13–48 movement times were not significantly different from the set without vibration, but from trials 51–96 movement times increased by $5.5 \pm 1.4$ s relative to the no vibration condition ($P = 0.0003$, paired $t$-test). This increase was comparable to that when vibration was applied throughout. These results are consistent with a model in which perturbing sensory feedback makes the MCI task more difficult.
but does not affect the rate at which subjects’ performance improved with practice.

**DISCUSSION**

**Rapid learning of a nonintuitive myoelectric interface**

A clear finding of this study was that subjects were able to learn myoelectric control of a 2-D cursor to a high standard even when the action of individual muscles was unrelated to their normal effect on the hand. Although initial performance was substantially poorer than an intuitive interface in which cursor movement matched natural muscle actions, this difference progressively diminished with training. After several hundred trials, the cursor moved quickly and directly to the target, suggesting subjects were using feedforward control. This is in general agreement with previous studies demonstrating the ability of the motor system to acquire inverse models of novel visuomotor transformations. For example, Mosier et al. (2005) showed that subjects were able to learn an arbitrary mapping between hand movements and cursor position to produce straight and accurate trajectories. Our experiments extend these findings to a task in which overt movements of the limb were restrained, with control signals instead obtained from EMG recording.

**Predictions from optimal control models**

In the MCI task, like most natural movements, different patterns of muscle activation can produce equivalent movements to each target (i.e., the task is ill-posed). It has been suggested that, faced with this redundancy, the motor system uses the strategy that minimizes the influence of neuromotor noise on the variance of task-relevant movement parameters (Harris and Wolpert 1998). In some respects our results are consistent with this framework. Individual muscles exhibited broad tuning functions with significant activity over a range of targets on either side of the DoA such that multiple muscles were typically activated for each target. In the presence of signal-dependent motor noise in which the SD of force production increases linearly with mean force, shared effort between multiple effectors leads to a lower variability than use of a single effector alone. Applying these constraints to a model of multiple effectors acting in different directions predicts the cosine-tuning functions seen for motor cortical neurons (Todorov 2002) and for wrist muscles during step-tracking movements (Haruno and Wolpert 2005). Similarly, tuning curves for muscles in this experiment also approximated cosine functions. Furthermore, when we artificially increased the variability of specific muscles by reducing the length of the smoothing window used to derive a subset of control signals, subjects responded by reducing the contribution of these muscles to cursor control.

However, proximal and distal muscles did not contribute equally to cursor control despite their comparable coefficients of variance. Preferential activation of distal muscles therefore appears to be a suboptimal strategy for minimizing cursor variability, which could not be explained by a general bias against activating proximal muscles (e.g., due to metabolic considerations) since proximal muscles not involved in controlling the cursor were considerably active during the task. This discrepancy, however, may be explained by subjects’
apparent difficulty in learning to dissociate pairs of proximal muscles, even when their actions on the cursor were in opposite directions. A greater degree of cocontraction may normally be required for stabilizing arm movements than for fine finger control. Furthermore, the dimensionality of digit movements is greater than that of arm movements, so controlling the full repertoire of hand function requires considerable neuromuscular flexibility. Lang and Schieber (2004) found that the principal limitation on independent finger movement arises from interdigit mechanical coupling rather than neuromuscular constraints. The ability of humans to make individuated finger movements is thought to rely on the corticospinal pathway and, in particular, monosynaptic corticomo-motoneuronal connections that preferentially target distal motoneurons (McKierman et al. 1998; Porter and Lemon 1993). Our results suggest that neuromuscular constraints are more significant for proximal muscles and limit the extent to which neuromotor patterns during unnatural tasks such as myoelectric control can be optimized for cost functions such as movement variability.

**Role of nonvisual sensation for learning myoelectric control**

*Experiment B* examined the role of proprioceptive and tactile feedback for learning the MCI task. We speculated that a lack of nonvisual sensory feedback in conventional BCI implementations might prevent acquisition of an internal model for feedforward control leading to poor performance relative to MCIs. Specifically, the motor system must acquire an inverse model (Fig. 10A), transforming the location of the target on the screen (i.e., visual coordinates) into the required motor output (i.e., muscle coordinates). One possibility (Fig. 10B) is that proprioceptive information from muscle or tendon receptors could be used to learn the mapping between visual and muscle coordinate frames (Welch 1978). However, we found that task performance improved even when unpredictable sensory noise was introduced by hand vibration. Although the ultimate performance level at the end of a set of trials was slightly impaired by vibration, the degree of impairment was not influenced by whether vibration had been applied during the first half of the set and therefore did not reflect a different rate of learning during these trials. We conclude that proprioceptive feedback is not required to learn nonintuitive MCI arrangements. Although we did not test the effect of vibration with intuitive arrangements, it seems likely that the same is also true for the smaller improvements in performance that occurred during intuitive sets in experiment A.

One possibility is that efference copy rather than proprioceptive feedback provided the necessary information for learning the mapping to muscle-based coordinates (Fig. 10C). Due to the delays and ambiguities involved in peripheral feedback, the efference copy may play an important role in state estimation (Kawato 1999; Proske 2006; Todorov and Jordan 2002) and it is interesting to note that prism adaptation has long been known to require active rather than passive movement (Held and Hein 1958). In the MCI task, where movements are controlled by signals derived directly from the motor command to muscles, the efference copy may be particularly useful for state estimation since sensory feedback will be subject to peripheral sources of noise that do not reflect cursor position.

Rather than making the task more difficult to learn, sensory noise did make the task more difficult to perform, perhaps by modulating motoneuron excitability via peripheral reflex pathways. Notably, vibration was most detrimental when introduced halfway through the set, perhaps because in this case subjects were already using feedforward control, which would be most susceptible to unpredictable spinal transmission. However, this impairment was transient, suggesting that subjects could learn to suppress spinal reflexes to some degree, perhaps by increasing presynaptic inhibition of afferent input (Rudomin and Schmidt 1999).

**Implications for neural prosthetics**

The apparent ease with which subjects could learn abstract, nonintuitive MCI operation in the absence of overt movements or accurate proprioceptive feedback suggests that similar learning mechanisms may also apply in BCI paradigms. If so, then exploiting these mechanisms may ultimately be more important than accurate biomimetic decoding. One example of how this might be achieved is in the choice of control signals. Since the BCI paradigm owes much to scientific studies of the neural control of reaching, it is natural that early BCI implementations used signals derived from electrodes implanted in arm areas of motor cortex. However, our results suggest that the distal motor system is more flexible for learning novel neuromotor associations. Although the differences between arm and hand muscles found in our study may in part be explained by the anatomy of the descending motor pathways, it is likely that the cortical architecture mediating control of hand movements also reflects this greater flexibility. Therefore neurons in the hand areas of motor cortex may be a better source of control signals than the traditional arm area recordings, even when the task is cursor or robotic arm control.
Our results also offer a new interpretation for the success of targeted reinnervation approaches following amputation. Kuiken et al. (2007) speculate that the improved performance of myoelectric prostheses controlled by proximal muscles that have been reinnervated with distal motor nerves is due to the “intuitive” nature of control. We suggest that an additional factor may be a greater ability of the distal motor system to adapt to residual differences between natural and prosthetic control.

Several groups are currently working on methods to supply artificial sensation to the brain in an effort to improve BCI performance (Fitzsimmons et al. 2007; London et al. 2008; Romo et al. 1998). Certainly loss of proprioception results in a profound impairment of natural movement (Rothwell et al. 1982; Sanes et al. 1985) and the discrepancy between predicted and actual sensory consequences of actions provides valuable information about an uncertain environment (Wolpert and Flanagan 2001). However, such signals may be less important in simple BCI implementations (such as control of a computer cursor) when motor output is an entirely predictable consequence of efference copy. Further work will be needed to determine whether efferent signals being available to the motor system in the form of efference copy. Further work will be needed to determine which particular movement parameters (e.g., limb position, velocity, joint angles, or muscle activity) should be optimally used to facilitate this process.

GRANTS

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