Comparison of neural responses in primary motor cortex to transient and continuous loads during posture

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Abstract

The present study examined whether neurons in primary motor cortex (M1) exhibited similar responses to transient and continuous loads applied during posture. Rapid responses to whole-limb perturbations were examined by transiently applying (300 ms) flexor and extensor torques to the shoulder and/or elbow during postural maintenance. Over half of M1 neurons responded to these transient loads within 80 ms and many responded within 20 to 40 ms. These rapid responses exhibited a broad continuum of modulation patterns across load directions. At one extreme, neurons exhibited reciprocal increases and decreases in activity for opposing loads. At the other extreme, neurons (particularly those with onset times of 20 to 40 ms) displayed relatively uniform increases in activity for all loads. Activity of proximal arm muscles displayed a narrower distribution of modulation patterns characterized by broadly tuned excitation combined with little or no reciprocal inhibition. Both neurons and muscles showed a directional preference for whole-limb flexor and whole-limb extensor torques (flexor at one joint and extensor at the other). Most neurons with rapid responses also showed steady-state responses to continuous loads although these responses generally displayed reciprocal increases and decreases in activity for opposing loads. Importantly, the preferred-torque directions were quantitatively similar across tasks. For example, a neuron with a maximal rapid response to a transient elbow flexor torque tended to exhibit a maximal steady-state response to a continuous elbow flexor torque. Activity of proximal arm muscles also showed this preservation of directional tuning. These results illustrate that M1 neurons respond rapidly to transient multi-joint loads and their patterns of activity share some, but not all, features related to continuous multi-joint loads applied during posture.
Introduction

It is well established that primary motor cortex (M1) plays an important role in generating volitional motor behaviors (reviewed in Porter and Lemon 1993). However, early electrophysiological studies in anesthetized animals also showed that M1 receives an abundance of sensory feedback from the motor periphery (reviewed in Marchiafava 1968; Brooks and Stoney 1971; Asanuma 1975). Based on this and other observations, Phillips (1969) proposed that M1 may lie within a transcortical feedback loop that provides the neural substrate for the long-latency motor reflex generated by rapid stretch of a muscle. With the advent of physiological studies in awake behaving animals, Evarts (1973) confirmed that individual M1 neurons of non-human primates respond to proprioceptive feedback from the arm within 20 ms, short enough to influence muscle activity within ~40 ms of stimulus onset.

Numerous studies during the late-1970s and early-1980s continued to examine the richness of proprioceptive and cutaneous feedback to M1 neurons. Notably, feedback responses were found to be modulated by behavioral goals, including the direction of an impending (Evarts and Tanji 1974, 1976) or ongoing movement (Conrad et al. 1974, 1975), and the direction of forces applied while maintaining a static posture (Wolpaw 1980b; Fromm et al. 1984). The notion that M1 neurons participate in a transcortical feedback loop was also strengthened when rapid responses (onset < 40 ms) were observed in identified corticomotoneurons, which have a direct synaptic connection with spinal motor neurons (Cheney and Fetz 1984).

With the exception of a few studies (Bauswein et al. 1991; Picard and Smith 1992, Boudreau and Smith 2001), interest in examining sensory feedback to M1 has largely been abandoned since the 1980s due to two key factors (reviewed in Scott 2008). First, the dominant conceptual framework used to guide experiments on neural processing in M1 shifted from servo-control to...
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sensorimotor transformations. Rather than focusing on the influence of afferent feedback on neural processing, this latter framework emphasizes the importance of the initial feedforward component of motor behavior. Second, there was an increased prevalence of studies on neural activity during whole-limb motor behaviors. Compared to previous studies that mostly examined single-joint behaviors, the mechanical complexity of whole-limb tasks made it technically difficult to perturb the limb mechanically and quantify afferent feedback.

Recently however, the importance of afferent feedback for voluntary control has been re-illuminated by the hypothesis that the volitional motor system may behave like an optimal feedback controller (Todorov and Jordan 2002; Todorov 2004). If volitional motor behaviors are produced via feedback control principles, such as those of optimal feedback control (OFC), ‘reflexive’ and ‘voluntary’ control processes should be intimately linked (Scott, 2004). In fact, we have recently shown that rapid motor responses following multi-joint perturbations (50 to 100ms) consider limb dynamics (Kurtzer et al., 2008) and are modified to initiate appropriate motor actions for various spatial targets (Pruszynski et al., 2008). Thus, sophisticated sensorimotor processing previously observed for the voluntary motor system is also present for reflexive behaviors.

Our interest is to understand the link between rapid and steady-state responses to loads in primary motor cortex during postural control. Studies have shown that M1 neurons related to volitional movements (Evarts and Fromm 1977; Fetz et al. 1980; Lemon 1981; Flament and Hore 1988; Scott 1997; Scott and Kalaska 1997) or maintaining posture while countering loads (Thach 1978; Wolpaw 1980a) commonly exhibit relevant ‘sensory’ responses. The latter two studies highlight similarities between rapid and steady-state responses to loads imposed during
posture, although they were limited to identifying only the direction of neural modulation for wrist flexion and extension.

This present study uses a multi-joint paradigm to investigate the relationship between neural responses to transient and continuous loads in M1 during posture. In accordance with the aforementioned single-joint studies, we hypothesized that neural responses to transient loads would be similar to those observed for continuous loads during posture. First, we characterized rapid responses of M1 neurons by quantifying their response to multi-joint perturbations (transient mechanical torques at elbow and/or shoulder joints) applied while monkeys maintained a constant arm posture. Second, we compared each neuron’s rapid response to transient loads with its steady-state response when the monkeys maintained the same arm posture while countering continuous loads. Here we show that some but not all aspects of each neuron’s activity pattern were maintained across the two contexts. Notably, preferred-torque directions and response magnitudes were correlated, but the relative contributions of excitation and inhibition varied considerably across transient and continuous load conditions.

Methods

Subjects and apparatus

Four male rhesus monkeys (*Macaca mulatta*, 6 to 12 kg) were trained to perform whole-limb visuomotor tasks while wearing KINARM (BKin Technologies, Kingston, ON), a robotic exoskeleton that supports the arm, permits planar shoulder and elbow motion, and can apply mechanical torques at the shoulder and/or elbow (Scott 1999). A virtual reality system presented visual targets within the limb’s movement plane while permitting the monkeys to view their entire limb. All procedures were approved by the Queen’s University Animal Care Committee.
Behavioral tasks

PERTURBATION TASK The monkeys’ goal was to maintain their hand at a visual target (6 mm radius) displayed near the center of the arm’s workspace (angles of approximately 30° at the shoulder and 90° at the elbow) where passive viscoelastic forces of the limbs are relatively small (Graham et al. 2003). The monkeys initiated each trial by moving their hand to the visual target and maintaining it within the target’s acceptance window (8 mm radius) for 1000 to 1500 ms. One of nine mechanical loads was then transiently applied to the monkeys’ arm for 300 ms. The nine load conditions included four single-joint torques (shoulder flexion, ShoFlx; shoulder extension, ShoExt; elbow flexion, ElbFlx; and elbow extension, ElbExt), four multi-joint torques (ShoFlx+ElbFlx; ShoFlx+ElbExt, ShoExt+ElbFlx, ShoExt+ElbExt), and an unloaded ‘catch’ condition (Fig. 1A). Each load (except for the unloaded condition) perturbed the hand from the target’s acceptance window (Fig. 1B). The monkeys were required to return their hand to the visual target within 1500 ms and maintain it there for another 1000 to 1500 ms to receive a liquid reward. The nine load conditions were presented in a pseudo-random block design with each block repeated five times for a total of 45 trials.

In order to treat shoulder and elbow torques as independent factors, a fixed magnitude of torque was applied at each joint. Thus, the load conditions were uniformly distributed in joint-torque space but the total torque magnitude for multi-joint conditions was $\sqrt{2}$ greater than single-joint conditions. Torques of ±0.12 Nm were applied to each joint in Monkeys A–C and torques of ±0.32 Nm were used in Monkey D due to his larger size. Note that the loads illustrated in Figure 1A are based on the torques applied by the robot, but all subsequent diagrams and analyses plot these loads based on the joint torques required to counter the loads (i.e., equal in magnitude but opposite in direction).
**POSTURE TASK**  The monkeys’ goal was to maintain their hand at a visual target (same position, size, and acceptance window as the perturbation task) by countering continuous mechanical loads (Kurtzer et al. 2006a; Herter et al. 2007). Prior to the onset of each trial, one of the nine loads (same load conditions as the perturbation task) was applied to the limb. The visual target was then displayed and each trial began when the hand was moved to the target. The monkeys had to maintain their hand within the target’s acceptance window for 3000 to 4000 ms to complete each trial. Steady-state posture was maintained from about 1000 ms after the hand was moved to the target until the end of each trial (see Fig. 1B in Kurtzer et al. 2006a).

**Data collection**

Neural data was collected from the shoulder/elbow region of M1 using standard extracellular recording techniques (Herter et al. 2007). Microelectodes were advanced through M1 until neural activity was observed in response to active or passive arm movements. Single neurons were then isolated and neural activity was recorded from all neurons that were related to active or passive movements of the shoulder and/or elbow, but not the wrist and/or fingers.

Electromyographic (EMG) activity was collected from proximal arm muscles with considerable flexion or extension pulling action at the shoulder and/or elbow (Graham and Scott 2003) using standard techniques for acute and chronic recording (Loeb and Gans 1986; Kurtzer et al. 2006a). Acute recordings were obtained from pairs of single-strand wires that were percutaneously inserted within the muscle belly approximately 5 mm apart. Chronic recordings were attained from bipolar multi-strand electrodes that were subcutaneously implanted within the superficial muscle belly. All recording locations were verified with micro-stimulation. All data were recorded at 1 kHz (Monkeys A) or 4 kHz (Monkeys B–D), full-wave rectified, and integrated into 5 ms bins. Muscles were only included in the analyses if they were recorded in
both tasks and obtained a score of $\geq 3$ (1 = poor and 5 = excellent) from a subjective rating of signal quality in both tasks (Kurtzer et al. 2006a). A total of 28 samples from the four monkeys were included in our analyses (Table 1). Each of these samples was recorded in a single session.

Joint angles, velocities, and applied torques were recorded at 1 kHz (Monkeys A–C) or 4 kHz (Monkey D). Cartesian hand positions and tangential hand speed were calculated from joint angles and velocities.

**Data analyses**

**M1 neurons: perturbation task** All analyses were restricted to *perturbation-related neurons*, defined as those neurons with rapid responses to transient loads. Although these rapid responses have been traditionally viewed as “reflexive”, the dichotomy between “reflexive” and “voluntary” responses is an oversimplification (Pruszynski et al. 2008). We nevertheless ensured that rapid responses did not include a significant “voluntary” contribution by requiring perturbation-related neurons to meet two criteria: 1) their activity was significantly modulated during a static *post-perturbation epoch* (25 to 100 ms after perturbation onset) and 2) their onset latency was between 20 and 80 ms.

A three-way ANOVA was used to identify neurons that were significantly modulated by perturbations. This analysis treated shoulder torque, elbow torque, and time (−100 to 0 ms versus 25 to 100 ms post-perturbation epochs) as independent factors. Neurons were flagged if they exhibited a main effect of time epoch ($P < 0.05$), a two-way interaction between shoulder torque and time epoch ($P < 0.05$), a two-way interaction between elbow torque and time epoch ($P < 0.05$), and/or a three-way interaction between shoulder torque, elbow torque, and time epoch ($P < 0.05$).
Onset latencies were obtained from spike frequencies that were calculated at 5 ms intervals with an asymmetric spike density filter (Thompson et al. 1996). This process convolves each neural spike with a double exponential kernel that mimics a post-synaptic potential (1 ms rise and 20 ms fall). Onset latency was taken as the first time in which spike frequency increased monotonically for at least three consecutive points (15 ms) and extended beyond 4 SD of the mean pre-perturbation baseline activity. Because spike frequencies of individual trials were generally very noisy, onset latencies were obtained from spike frequencies that were averaged across the three spatially adjacent load conditions with the highest mean activity during the post-perturbation epoch (n = 15 trials).

Similar to our examination of opposing single-joint activities during the posture task (Herter et al. 2007), a reciprocal-comodulation (R-C) score was used to assess the relationship between responses to opposing loads in our multi-joint perturbation task. This measure quantified the ratio between the mean torque-related activities (i.e., mean change between the –100 to 0 ms pre- and 25 to 100 ms post-perturbation activity) at the three spatially adjacent load conditions that evoked the largest change in activity (ΔMax) and their opposing load conditions (ΔOpp):

\[ R-C \text{ score} = \frac{\Delta \text{Opp}}{\Delta \text{Max}} \] (1)

Neurons that were reciprocally modulated (i.e., reciprocal increases and decreases for opposing load directions) obtained R-C scores near –1, neurons that were unidirectionally modulated (i.e., increases for preferred loads and little or no change for opposing loads) received R-C scores close to 0, and neurons that were comodulated (i.e., increases for preferred and opposing directions) were assessed R-C scores approaching 1.
Each neuron’s preferred combination of shoulder and elbow torques was quantified using planar regression fits that adjusted for the unequal torque magnitudes in the single- and multi-joint conditions (Kurtzer et al. 2005). For this analysis, changes in neural activity were related to the joint torques (equal and opposite of the mechanical torques applied by the robot) that the monkeys were required to produce at the shoulder and elbow joints. Using flexor torque as positive and extensor torque as negative yields ShoFlx = 0º, ElbFlx = 90º, ShoExt = 180º, and ElbExt = 270º. For each neuron with a significant planar fit ($F$-test, $P < 0.05$), coefficients related to the shoulder (Sho) and elbow (Elb) were used to calculate two important properties: 1) preferred-torque direction — $\text{atan2}(\text{Elb}, \text{Sho})$ — which describes the angle associated with the greatest increase in activity by calculating the orientation of the plane in joint-torque space and 2) torque-sensitivity — $(\text{Sho}^2 + \text{Elb}^2)^{\frac{1}{2}}$ — which expresses the sensitivity of neural activity to changes in torque along the preferred-torque direction by computing the norm of the plane’s slope in Hz/Nm. Note that torque-sensitivity is equivalent to gain (Kurtzer et al. 2005) and analogous to torque-slope (Herter et al. 2007). In addition to analyzing the static 25–100 ms post-perturbation epoch, we also performed planar regression fits on each 5 ms interval of the spike frequency data described above. This allowed us to examine temporal changes in preferred-torque directions and torque-sensitivities.

Unimodal and bimodal Rayleigh tests were used to determine whether distributions of preferred directions were statistically unimodal or bimodal relative to a uniform distribution (Baschelet 1981). This statistic is based on the mean vector length which describes similarity across a sample of angles (e.g., preferred-torque directions). For the unimodal test, a mean vector length of 0 is obtained if all angles are uniformly distributed and a value of 1 is obtained if all angles are identical. The value of a mean vector length along this continuum provides an index
of unimodality that is compared with a Rayleigh distribution. The average orientation of angles in circular coordinates provides the preferred direction of a unimodal distribution. The bimodal test is identical to the unimodal test except that all angles are multiplied by two, which creates a unimodal distribution if the underlying distribution is symmetrically bimodal. The preferred axis of the bimodal distribution is obtained by dividing the average orientation by two.

**M1 NEURONS: POSTURE TASK** To assess neural activity related to continuous loads in the posture task, the mean neural activity in each load condition was calculated from 1000 to 3000 ms after the hand entered the target’s acceptance window (see Kurtzer et al. 2006a; Herter et al. 2007). *Posture-related neurons* were flagged with a two-way ANOVA that identified neurons related to torques at the shoulder (main effect of shoulder torque, \( P < 0.05 \)) and/or elbow (main effect of elbow torque, \( P < 0.05 \)). Torque-related activity of all posture-related neurons was obtained by subtracting mean activity in the unloaded baseline condition from mean activity in the eight loaded conditions. Preferred-torque directions and torque-sensitivities were obtained for posture-related neurons with significant planar fits (\( F \)-test, \( P < 0.05 \)). Note that all M1 neurons recorded in the posture task come from the same sample of neurons described in our previous study that characterized steady-state responses to loads during postural control (Herter et al. 2007).

**M1 NEURONS: INTER-TASK COMPARISONS** A major goal of the current study was to compare torque-related activity between the perturbation and posture tasks. These analyses were restricted to those neurons recorded in both tasks.

**MUSCLE ANALYSES** To compare and contrast the patterns of activity of M1 neurons with proximal arm muscles, the preceding analyses used on M1 neurons were also carried out on the
EMG activity of our sample of proximal arm muscles. Perturbation- and posture-related muscles were flagged by ANOVAs ($P < 0.05$) and preferred-torque directions were obtained for muscles with significant planar fits ($P < 0.05$).

**Results**

*Kinematics of the perturbation task*

The monkeys’ hand normally returned within the target’s acceptance window well after perturbation offset (mean ± SD; Monkey 1: 497±23 ms, Monkey 2: 519±36 ms, Monkey 3: 565±50 ms, Monkey 4: 512±40 ms). This suggests that the monkeys generally permitted the loads to push their hand away from the target before returning their hand to the target following perturbation offset (e.g., Fig. 1B).

Although the mechanical loads applied to the shoulder and elbow were uniformly distributed in joint-torque space (Fig. 1A), the resultant hand (Fig. 1C) and joint (Fig. 1D) motions were highly nonuniform due to intersegmental dynamics. Notably, during the first 100 ms after perturbation onset, each single-joint torque produced multi-joint motion (Fig. 1D, black, blue, cyan, and green lines) and two of the multi-joint torques generated single-joint motion (Fig. 1D, brown and orange lines). During the same period, the magnitude of joint motion resulting from the other two multi-joint torques was much greater than the other load conditions (Fig. 1D, red and magenta lines).

*Responses of M1 neurons to single and multi-joint perturbations*

Previous perturbation studies have not examined rapid responses of M1 neurons to transient torques imposed at multiple joints. To address this issue, we examined the activity of 265 neurons recorded in the shoulder-elbow region of M1 (Monkeys A–D: n = 15, 7, 140, 103)
during perturbations applied to the shoulder and/or elbow. Over half of these neurons (n = 150, 57%) were perturbation-related; i.e., their activity was significantly modulated between the pre- and post-perturbation epochs (3-way ANOVA, \( P < 0.05 \), see Methods) at relatively short latencies (onset latency of 20 to 80 ms, see Methods). Only a small number of neurons flagged by the ANOVA has a response latency less than 20 ms (n = 2) or greater than 80 ms (n = 29).

For didactic purposes, we investigated whether perturbation-related activity of M1 neurons is generally related to torques at one or more joints. Perturbation-related neurons were divided into three categories: shoulder-only neurons (single interaction between shoulder torque and time epoch, \( P < 0.05 \)), elbow-only neurons (single interaction between elbow torque and time epoch, \( P < 0.05 \)), and multi-joint neurons (both preceding interactions and/or an interaction between shoulder torque, elbow torque and time epoch, \( P < 0.05 \)). Of the 150 perturbation-related neurons, we found 53 single-joint neurons (16 shoulder-only and 37 elbow-only) and 55 multi-joint neurons. The other 42 neurons were modulated by the perturbations but did not exhibit a specific relationship to torques at the shoulder and/or elbow (main effect of time epoch only, \( P < 0.05 \)). In general, these neurons were similarly modulated by all loads and could be considered multi-joint neurons.

*M1 neurons exhibit a broad range of modulation patterns during multi-joint perturbations*

Previous single-joint studies have observed that M1 neurons exhibit a variety of modulation patterns in response to opposing perturbations (Conrad et al. 1975; Evarts and Tanji 1976; Wolpaw 1980a; Cheney and Fetz 1984; Bauswein et al. 1991). These include reciprocal modulation (i.e., increases for one direction and decreases for the opposite), unidirectional modulation (i.e., increases for one direction and little or no change for the other), and comodulation (i.e., increases for both directions).
Our sample of neurons also exhibited a range of excitatory and inhibitory modulation patterns in response to the different load directions in our multi-joint perturbation task. Most perturbation-related neurons showed a continuum modulation patterns that was largely dominated by excitatory responses relative to their baseline activity. At one extreme, neurons showed a relatively uniform excitatory response to each perturbation (Fig. 2A, grey shading). At the other end, neural activity was excited by a few adjacent perturbation conditions while opposing perturbations evoked relatively weak inhibitory or excitatory responses (Fig. 2B, grey shading). In the middle of this continuum, neural activity increased in response to most or all perturbation conditions but in a graded manner across joint-torque space (Fig. 2C, grey shading). Surprisingly, relatively few neurons displayed reciprocal excitation and inhibition in response to opposing perturbations in joint-torque space.

Figure 3 examines changes of activity evoked by perturbations in our sample of 150 perturbation-related neurons. Neural responses to the three spatially adjacent perturbation conditions that evoked the largest mean change of post-perturbation activity ($\Delta$Max) are compared with the responses to the three opposing perturbation conditions ($\Delta$Opp). Individual perturbation-related neurons exhibited phasic bursts in their $\Delta$Max activity at delays of 20 to 80 ms from perturbation onset (Fig. 3A). The magnitude of their $\Delta$Max response varied with onset time (Fig. 3B) such that neurons with the earliest onset times (20–40 ms, n = 69, red line) displayed a greater $\Delta$Max response, on average, than neurons recruited at later time intervals (40–60 ms, n = 47, green line; 60–80 ms, n = 33, blue line). The average $\Delta$Opp response (Fig. 3C) of the early-recruited neurons also displayed a phasic burst, whereas the average $\Delta$Opp response of the neurons with later onsets showed little modulation. It is also evident that neural responses were not restricted to the static epoch of 25 to 100 ms used to define perturbation-
related neurons (Fig. 3A–C). Rather, perturbation-related neurons exhibited a range of temporal profiles, highlighting that “reflexive” and “voluntary” activities likely reflect overlapping temporal processes.

The relationship between ∆Max and ∆Opp activity is investigated in Figure 3D. Perturbation-related neurons exhibited a broad range of R-C scores (see Methods) consistent with reciprocal modulation (R-C scores ≈ −1), unidirectional modulation (R-C scores ≈ 0), and comodulation (R-C scores ≈ 1). Early-recruited neurons (red circles) tended to have the largest changes in ∆Max activity and R-C scores that were generally between 0 and 1 (median R-C score = 0.46, interquartile range of R-C scores = 0.18 to 0.68), whereas neurons with later onset times (green and blue circles) had smaller changes in ∆Max activity and R-C scores that were broadly distributed between −1 and 1 (median R-C score = 0.12, interquartile range of R-C scores = −0.14 to 0.41).

One possibility is that the bias towards excitation and its influence on RC-scores may have been related to relatively low baseline activity (median = 11 spikes/s, interquartile range = 6 to 17 spikes/s). In fact, ∆Max activity commonly showed excitatory changes in activity that were several fold greater than baseline (median ratio = 3.2 times). Surprisingly however, only 31 of 79 (39%) neurons with baseline activity greater than 10 spikes/s displayed inhibitory ∆Opp responses. Furthermore, differences in RC-scores observed between neurons with earlier (20 to 40 ms) and later (40 to 80 ms) onsets were not related to baseline activity since the onsets of both groups exhibited similar underlying distributions (Kolmogorov-Smirnov test, P = 0.52).

M1 neurons exhibit a bimodal distribution of preferred-torque directions

Perhaps the most robust finding in our studies of torque-related activity (Cabel et al. 2001; Gribble and Scott 2002; Kurtzer et al. 2005, 2006a, 2006b; Herter et al. 2007) is that both
M1 neurons and proximal arm muscles exhibit a bimodal distribution of preferred-torque directions that is biased towards whole-limb flexor (ElbFlx+ShoExt) and whole-limb extensor (ElbExt+ShoFlx) torques. Here we investigate whether a similar bimodal distribution is observed during multi-joint perturbations.

Figure 4 illustrates directional tuning properties of perturbation-related neurons. Neurons that were unimodally-tuned in joint-torque space (85 of 150, 57%) exhibited a significant bimodal distribution of preferred-torque directions that was biased towards whole-limb flexor and whole-limb extensor torques (Fig. 4A; bimodal Rayleigh test, bimodal axes = 120–300°, mean vector length = 0.58, $P < 10^{-12}$; unimodal Rayleigh test, mean vector length = 0.11, $P = 0.33$). These neurons also displayed a broad range of torque-sensitivities (Fig. 4B; range = 11 to 197 Hz/Nm, median = 54 Hz/Nm).

Due to intersegmental dynamics two of the load conditions produced considerably greater joint motion (Fig. 1D, red and magenta lines). To control for this, planar fits that included all load conditions were compared with planar fits that excluded these load conditions (see Supplemental Material). This analysis revealed the same pattern: a bimodal distribution of preferred-torque directions (axes = 121–301°, mean difference = –2°, median absolute difference = 5°) and highly correlated torque-sensitivities (range = 9 to 235 Hz/Nm, median = 66 Hz/Nm, $r = 0.94$, $t$-test for correlation, $P < 10^{-12}$).

We also examined whether the bimodal distribution of preferred-torque directions was related to differences in onset times, baseline activities, or the relative contribution of excitation and inhibition. Accordingly, we examined whether these parameters were different for neurons located in quadrants 1 and 3 compared with those in quadrants 2 and 4. Importantly, these two
groups of neurons exhibited similar distributions of onset times, baseline activities, and RC-scores (Kolmogorov-Smirnoff tests, $P = 0.99$, $P = 0.25$, and $P = 0.91$, respectively).

We have analyzed our experimental data based on the applied torques, but the data can also be examined based the joint or hand motions produced by the mechanical perturbations. For completeness, we also examined directional tuning in joint-motion and hand-motion space (see Supplemental Material). Notably, preferred directions in both of these coordinate frames also exhibited bimodal distributions.

Comparison of rapid and steady-state load responses in M1

A total of 196 neurons were recorded in the perturbation and posture tasks. Of these, 157 neurons were related to continuous loads and 93 of these neurons were also related to transient loads (117 of 196 were related to transient loads). Most neurons that were unimodally-tuned in the perturbation task (56 of 68, 82%) were also unimodally tuned in the posture task.

Figure 5 illustrates the patterns of activity observed in an exemplar neuron recorded in both the perturbation and posture tasks. Notably, the joint torques that evoked the largest rapid responses in the perturbation task (Fig. 5A) were also associated with the highest level of steady-state activity in the posture task (Fig. 5B). In other words, the portion of the motor periphery represented by this neuron was constant across both tasks. This is reflected by a high degree of similarity between this neuron’s preferred-torque directions in the perturbation and posture tasks (Fig. 5C, direction of the arrows).

Despite the similarity in the representation of joint torques between tasks, this exemplar neuron exhibited two key differences between its rapid and steady-state response to loads. First, this neuron’s pattern of modulation was more reciprocal in the posture task than the perturbation task (R-C scores = −0.70 and −0.26, respectively). Second, this neuron displayed different
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Reponse magnitudes in the two tasks (78 spikes/s compared to 27 spikes/s in the whole-limb flexor load condition; see Figs. 5A and B, respectively). This resulted in a greater torque-sensitivity in the perturbation task (Fig. 5C, length of the arrows), which could reflect either a random or systematic change in response magnitude at the level of the population.

Figure 6A examines the relationship between the patterns of modulation in the perturbation and posture tasks across all 93 neurons that were related to loads in both tasks. Notably, the distributions of R-C scores were significantly different from each other (Kolmogorov-Smirnov test, \( P < 10^{-5} \)). Most neurons were biased towards comodulation and unidirectional modulation in the perturbation task (median R-C score = 0.25, interquartile range of R-C scores = –0.07 to 0.58) whereas reciprocal and unidirectional modulations were favored in the posture task (median R-C score = –0.10, interquartile range of R-C scores = –0.53 to 0.11).

Figure 7 compares directional tuning features of rapid and steady-state responses to loads in our population of 56 neurons that were unimodally tuned in joint-torque space in both tasks. Notably, both preferred-torque directions and torque-sensitivities were well conserved across both tasks. During the static post-perturbation epoch, differences between preferred-torque directions were unimodally distributed (Fig. 7A) and the systematic bias was relatively small (mean difference = –13°, unimodal Rayleigh test, mean vector length = 0.53, \( P < 10^{-6} \)). Torque-sensitivities (Fig. 7D) were also well correlated (\( r = 0.59, t \)-test for correlation, \( P < 10^{-5} \)) though they were twice as high, on average, in the perturbation task (median ratio = 2.0, median values = 49 and 29 Hz/Nm, Wilcoxon signed rank test, \( P < 10^{-6} \)) indicating that rapid responses to loads were systemically greater than steady-state responses.

A number of interesting results were also revealed by analyses of temporal changes in directional tuning in the perturbation task compared with the posture task. Shortly after
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At perturbation onset (50 to 100 ms post-perturbation), there was a consistent correlation between preferred-torque directions, indicated by relatively high mean vector lengths ranging from 0.50 to 0.69 (Fig. 7B). Furthermore, the mean difference between preferred-torque directions remained near 0° (Fig. 7C) indicating that preferred-torque directions did not systematically shift across tasks. During this same period, torque-sensitivities were well correlated, ranging from 0.51 to 0.71 (Fig. 7E), and the median ratio of torque-sensitivities peaked at a value of 3.0 (Fig. 7F) indicating that changes in torque-sensitivity were systematic rather than random.

Many neurons were also modulated by unloading at perturbation offset (Fig. 2A–C, second vertical line). As a result, many trends seen at perturbation onset were also observed 50 to 100 ms after perturbation offset (i.e., time = 350 to 400 ms, Fig. 7 B, C, E, and F) except that preferred-torque directions pointed in the opposite direction (Fig. 7C, mean difference ≈ 180°). Note that the average response to perturbation onset (Fig. 3B, 0–300 ms) was greater than that evoked by perturbation offset (Fig. 3C, 300–600 ms). This may be related to differences in the behavioral context (Evarts and Tanji 1974, 1976); the monkeys were more likely to resist perturbations when the arm was pushed away from the target at perturbation onset and less likely to intervene at load offset when the arm was perturbed towards the target.

M1 neurons reflect many patterns of activity seen in muscles at the motor periphery

As expected, nearly all muscles (n = 27, 96%) in our sample of 28 proximal arm muscles (Table 1) exhibited perturbation-related EMG activity (3-way ANOVA, P < 0.05) at short latencies (onset latency ≤ 80 ms). All 27 of the perturbation-related muscles were also unimodally tuned in joint-torque space in both the perturbation task (F-test, P < 0.05) and posture task (2-way ANOVA, P < 0.05 and F-test, P < 0.05).
Figure 8 illustrates the patterns of EMG activity recorded from the posterior deltoid muscle of Monkey A in both the perturbation and posture tasks. Similar to the exemplar neuron seen previously (Fig. 5), the multi-joint loads that evoked the largest excitatory responses in the perturbation task (25 to 100 ms post-perturbation) were associated with the highest level of steady-state activity in the posture task (Fig. 8, A and B). As a result, similar preferred-torque directions were observed in both tasks (Fig. 8C). Unlike like the exemplar neuron however, this muscle’s EMG activity exhibited unidirectional modulation in both tasks (R-C scores = 0.03 and –0.02, respectively).

Figure 6B examines the relationship between the patterns of modulation across tasks in all 27 upper arm muscles related to loads in both the perturbation and posture tasks. Unlike the neurons, R-C scores of the muscles were similar in both tasks (Kolmogorov-Smirnov test, \( P = 0.26 \)). The muscles exhibited a narrow range of R-C scores reflecting reciprocal and unidirectional modulation in both tasks (perturbation task: median R-C score = –0.08, interquartile range of R-C scores = –0.27 to 0.01; posture task: median R-C score = –0.24, interquartile range of R-C scores = –0.39 to –0.06). These distributions were significantly different from those of the neurons in both the posture and perturbation tasks (Kolmogorov-Smirnov tests, \( P < 0.01 \) and \( P < 10^{-5} \), respectively).

Although their patterns of modulation were different from the neurons, other trends observed in our M1 neurons were evident in our sample of proximal arm muscles (Fig. 9). Preferred-torque directions of muscles in the perturbation task exhibited a bimodal distribution (Fig. 9A) that was similar to our M1 neurons (Fig. 4A). Our sample of proximal arm muscles (Table 1) included fewer elbow extensors and shoulder flexors (n = 6) than elbow flexors or shoulder extensors (n = 11) resulting in a greater number of preferred-torque directions within
the upper left versus the lower right quadrants of joint-torque space. This distribution was generally similar to that observed previously in the posture task (Fig. 7D in Kurtzer et al. 2006a). Importantly, preferred-torque directions were highly conserved across tasks resulting in differences between preferred-torque directions (Fig. 9B) that were unimodally distributed with an average near 0° (mean difference = –3°; unimodal Rayleigh test, mean vector length = 0.98, $P < 10^{-10}$) and a median absolute difference that was significantly less than expected from a random distribution ($10° < 90°$, Wilcoxon signed rank test, $P < 10^{-5}$).

Our temporal analyses of preferred-torque directions also revealed similarities and differences with our neurons (Fig. 9, C and D). Similar to the neurons, the mean difference between preferred-torque directions approached 0° within 50 ms and remained near 0° for the entire perturbation duration (Fig. 9D). Unlike the neurons however, the correlation between preferred-torque directions (Fig. 9C) approached 1 within 50 ms and then remained high for the entire perturbation time. Furthermore, perturbation offset did not generally evoke significant changes in EMG activity although a few individual muscles exhibited systematic changes in EMG activity following the perturbation offset (see e.g., Fig 8A). As a result, perturbation offset produced modest effects on preferred-torque directions across the population.

**Discussion**

It is well established that M1 plays an important role in initiating voluntary motor behaviors and also receives an abundance of sensory feedback from the motor periphery (reviewed in Porter and Lemon 1993). Nevertheless, interest in examining sensory feedback to M1 was largely cast aside in the 1980s due to the absence of a plausible theoretical framework linking sensory feedback to volitional motor control (reviewed in Scott 2008). The recent hypothesis that
Rapid and steady-state responses to loads in M1

Volitional motor behaviour is well described by an optimal feedback controller (Todorov and Jordan 2002; Todorov 2004) re-illuminates the importance of afferent feedback for interpreting neural processing in regions such as M1 (Scott 2004). The goals of the present study were to: 1) quantify how M1 neurons respond to transient loads applied to multiple joints during postural maintenance and 2) identify whether rapid responses to transient loads are correlated with steady-state responses to the continuous loads imposed during postural maintenance control.

The relationship between M1 neuron activity and the motor periphery

A key feature of M1 is the portion of the motor periphery that is reflected in the activity of its constituent neurons (Scott 2000). A neuron’s activity could be related to a relatively small portion of the motor periphery such as the activity of a single muscle or muscle group, or it could reflect a larger portion of the motor periphery such as an entire limb. Spike-triggered averaging studies have demonstrated that individual corticomotoneurons can innervate one or more muscles spanning multiple joints (Fetz and Cheney 1980; Buys et al. 1986; McKiernan et al. 1998). Neural activity in M1 is also correlated with the activity of individual or groups of muscles acting at a single joint or across multiple joints (Holdefer and Miller 2002; Bennett and Lemon 1996; Drew et al, 2008) and reflects details on the timing and magnitude of muscle activity (Smith et al. 1975; Drew 1993; Scott 1997). Furthermore, studies of individuated finger movements have found that M1 neurons are generally related to movements of more than one digit (Schieber and Hibbard 1993; Poliakov and Schieber 1999).

Here we used multi-joint perturbations to quantify the relative response of M1 neurons to rapid motor output at each joint. The distribution of preferred-torque directions was skewed towards one of two quadrants in joint-torque space, whole-limb flexor and whole-limb extensor torques (Fig. 4A). Evoked activity in shoulder and elbow muscles was also skewed towards these
two quadrants (Fig. 9.4) even though most of these muscles only spanned one of the two joints (i.e., monoarticular) and the anatomical action of the biarticular muscles are in the opposite quadrants (Graham and Scott 2003). A similar bias has been observed for load-related activity in M1 and proximal arm muscles when continuous loads were applied during postural control (Cabel et al. 2001; Kurtzer et al. 2006a; Herter et al. 2007) and both viscous and continuous loads applied during reaching (Gribble and Scott 2002; Kurtzer et al. 2006b).

This prominent bias in M1 neurons and proximal arm muscles could reflect two different processes. One possibility is that the greater representation of whole-limb flexor and extensor loads means that M1 represents these two prominent muscle synergies more than other combinations of muscles. Bernstein (1967) proposed that motor control could be simplified if motor behaviors were accomplished by generating patterns of muscle activation from appropriate combinations of muscle synergies, sets of muscles that are collectively activated to form functional units. Accordingly, muscle synergies have been identified across a broad range of tasks and species including postural control and locomotion in humans (Henry et al. 1998; Ivanenko et al. 2004) and cats (Macpherson et al. 1986; Buford and Smith 1990; Ting and MacPherson 2005; Krouchev et al. 2006), and a variety of natural behaviors in frogs (d’Avella et al. 2003). Synergistic patterns of muscle activity have also been observed during reflex responses to cutaneous stimulation in spinalized frogs (Tresch et al. 1999; Hart and Giszter 2004). Furthermore, patterns of M1 activity during multi-joint motor tasks tend to reflect various muscles synergies (Donoghue et al. 1992; Holdefer and Miller 2002; Park et al. 2004; Drew et al. 2008). Together, these studies suggest that muscle synergies may form the basis of a common language to create complex motor patterns.
Alternatively, our results are also consistent with motor patterns arising from the optimization of muscle activity. We have shown that computational models that minimized net muscle activation (i.e., summed muscle force, metabolic energy, and noise) exhibited similar biases in their representation of loads in joint-torque space (Kurtzer et al. 2006a, 2006b). Notably, this bias was only observed when biarticular muscles were included in these models, indicating how the anatomical organization of the musculoskeletal system can impact muscle recruitment patterns. These models suggest that patterns of activity of both proximal arm muscles and M1 neurons reflect optimal strategies given the behavioral goal and constraints imposed by the anatomical organization of the musculoskeletal system (Kurtzer and Scott 2007).

*Do M1 neurons exhibit similar rapid and steady-state responses to loads during posture?*

Correlations between rapid and steady-state responses in M1 were observed over 25 years ago in two studies examining single-joint motor tasks (Thach 1978, Wolpaw 1980a). Neurons commonly responded to both transient and continuous loads and their responses to these loads were qualitatively similar. The present study quantifies the directional tuning properties of neurons across multiple joints and provides a more detailed temporal analysis to compare changes in load-related activity both during and after transient loads.

The present results illustrate that the preferred-torque directions of individual neurons were highly conserved across rapid and steady-state responses to loads applied during posture. We also observed a similar conservation of preferred-torque directions in response to continuous loads imposed during posture and movement conditions (Kurtzer et al., 2005). These results suggest that the activity of individual M1 neurons is associated with a portion of the motor periphery that involves one or more joints and this territory remains relatively constant across different behaviors. Interestingly, the directional correlation flips 180 degrees after the transient
load is removed even though the muscle EMG showed no strong reciprocal response during this phase. This suggests that M1 neurons possess a large transient response to changes in environmental loads that is not necessarily conveyed to the musculature.

Other aspects of M1 activity are also correlated across rapid and steady-state responses to loads. The correlation between the magnitude of responses to transient and continuous loads was initially around 0.70, though it dropped somewhat during the 300 ms time period. Notably, this correlation is much higher than that observed for continuous loads applied during posture and movement tasks (Kurtzer et al., 2005), in which magnitude of load-related activity changed randomly across tasks. In the extreme, some neurons responded to loads only during posture and others only during movement. Thus, the ongoing motor behavior (posture versus movement) has a much more profound influence in neural processing in M1 than the nature of loads (transient versus continuous) applied to the limb within a given behavior.

Perhaps the largest difference between rapid and steady-state responses is the prevalence for reciprocal versus comodulation patterns of activity. Numerous single-joint studies have observed that some M1 neurons are comodulated by opposing continuous (Evarts et al. 1983; Werner et al. 1991) and transient loads (Conrad et al. 1975; Evarts and Tanji 1976; Wolpaw 1980a; Cheney and Fetz 1984; Bauswein et al. 1991). However, by using multi-joint loads during postural control, we illustrated that most neurons which were comodulated by continuous loads at the shoulder were reciprocally modulated at the elbow, and vice-versa (Herter et al. 2007). Nearly all of these neurons were unimodally tuned in joint-torque space with preferred-torque directions that were roughly aligned with the joint that produced reciprocal modulation. This indicates that comodulation observed at a single joint for continuous loads was usually a byproduct of broad tuning across multiple joints.
In the present study, we expected that most perturbation-related neurons would also show broad tuning across multiple joints. However, we found that transient perturbations generally evoked increases in activity and in many cases neurons were not directionally tuned in joint-torque space because relatively similar increases in activity were generated across all load conditions (e.g., Fig. 2A). This pattern of activity was particularly prevalent for neurons that responded in less than 40 ms following load onset. Figure 6A illustrates this important difference as a function of reciprocal modulation versus comodulation. Many neurons that exhibited comodulation (R-C Score >> 0) in response to transient loads were reciprocally modulated (R-C Score << 0) by continuous loads. However, those neurons that were comodulated by continuous loads were also comodulated by transient loads.

Perhaps those neurons that exhibited comodulation received rapidly adapting cutaneous information that produced similar responses to limb motion regardless of load direction. Although some M1 neurons respond to cutaneous stimuli applied to the arm, hand, leg, and/or foot (Lemon and Porter 1976; Strick and Preston 1978, 1982; Wong et al. 1978; Fetz et al. 1980; Lemon 1981; Tanji and Wise 1981; Wise and Tanji 1981), systematic examination of cutaneous responses was infeasible because the KINARM exoskeleton covers large sections of the arm. However, neurons related to the proximal arm tend to respond predominantly to passive joint motion (i.e. muscle afferents) rather than cutaneous stimulation (Lemon and Porter 1976; Wong et al. 1978; Fetz et al. 1980; Lemon 1981).

Another possibility is that comodulation responses could reflect a potential source for cocontraction commands to antagonist muscle pairs. However, proximal arm muscles did not share this prevalence for comodulation across opposing loads (Fig. 6B); proximal arm muscles that were significantly related to perturbations were unimodally tuned in joint-torque space and
exhibited either unidirectional or reciprocal modulation of their activity. These observations indicate that comodulation in M1 neurons was not transmitted to the motor periphery in this task. Admittedly however, our task was not specifically designed to explore the neural basis of co-contraction.

In conclusion, the present results illustrate that many M1 neurons respond rapidly to the application of transient loads at one or more joints during postural control. The rapid response of these neurons to the onset of applied loads illustrates the impact and importance of afferent feedback to this cortical region. Furthermore, these rapid responses to transient mechanical perturbations share some, but not all, features with steady-state responses to continuous loads applied during postural control. M1 may be viewed as a population of neurons in which each neuron possesses a relatively fixed association to a portion of the motor periphery (i.e. motor field), but its recruitment pattern (and role within the distributed network) is labile across motor behaviors.

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References


**Figure Legends**

Fig 1. Load conditions and perturbation-evoked kinematics. *A*: Arrangement of the nine load conditions applied to the monkeys’ limb in the perturbation and posture tasks. Joint torques imposed at the shoulder and elbow joints are represented along the x and y axes, respectively (flexor torque positive and extensor torque negative). Joint torques are plotted in Figure 1*A* based on the torques applied by the robot, but all subsequent diagrams plot torques based on the required muscle torques generated by the monkeys. *B–D*: Trial-by-trial kinematics evoked by perturbations in an exemplar set of data (Monkey D, Session 883). Colors of each line are associated with the corresponding load condition in *A*. *B*: Hand motion relative to the visual target (grey circle) in Cartesian space (x-axes, left and right; y-axes, towards and away from the body) during the first 600 ms after perturbation onset in the eight loaded conditions. Black dots indicate the time in which the perturbation ended (300 ms after the perturbation onset). *C, D*: Hand motion in Cartesian space (*C*) and joint motion in joint-angle space (*D*) during the first 100 ms after perturbation onset.

Fig. 2. Activity of three exemplar M1 neurons during the perturbation task. *A*: Activity of a neuron that exhibited similar increases in activity for each perturbation: R-C score = 0.73 (left side, rasters and histograms of the nine load conditions). This neuron was not unimodally tuned
in joint-torque space due to its relatively uniform modulation (right side, planar fit). PTD, preferred-torque direction. B: Activity of a unimodally-tuned neuron that displayed robust increases in activity when a shoulder extensor torque was required to counter the imposed load: R-C score = –0.06. C: Activity of a neuron that increased in activity following each perturbation but in a graded manner that produced unimodal tuning in joint-torque space: R-C score = 0.19. Vertical lines at 0 and 300 ms indicate perturbation onset and offset. Grey shaded areas under the histograms show the post-perturbation time (25–100 ms) used for ANOVAs and planar fits.

Fig. 3. Changes of activity in perturbation-related neurons. A: Mean changes in the normalized activity of each perturbation-related neuron (n = 150) in response to the three adjacent loads that produced a maximal increase in activity (i.e., ∆Max). Neurons are sorted by their onset latencies indicated by the small circles. B: Median changes in ∆Max activity of those neurons with onsets between 20 and 40 ms (red lines, n = 80), 40 and 60 ms (green lines, n = 54), and 60 and 80 ms (blue lines, n = 16). C: Median changes in ∆Opp activity (response to the three perturbation conditions opposite those that produced a maximal increase in activity) of those neurons with onsets between 20 and 40 ms (red lines), 40 and 60 ms (green lines), and 60 and 80 ms (blue lines). D: R-C score versus ∆Max activity of those neurons with onsets between 20 and 40 ms (red circles), 40 and 60 ms (green circles), and 60 and 80 ms (blue circles).

Fig. 4. Tuning features of M1 neurons that were unimodally tuned in joint-torque space during the post-perturbation epoch (25–100 ms). A: Polar histogram indicating the number neurons with a preferred-torque direction in each 15° bin. Thick lines show the bimodal axes (PD). MVL, mean vector length. B: Relationship between preferred-torque directions and torque-sensitivities
Fig. 5. Activity of an exemplar M1 neuron that was unimodally tuned in joint-torque space in both tasks. A: Activity (rasters and histograms) during each load condition in the perturbation task. Vertical lines at 0 and 300 ms indicate perturbation onset and offset. Grey shaded areas show the post-perturbation epoch (25–100 ms) used for static analyses. B: Activity (rasters and histograms) during each load condition in the posture task. C: Planar fits for the perturbation (left) and posture (middle) tasks and their preferred-torque direction (PTD) comparison (right). Direction and length of each arrow indicate the preferred-torque direction and torque-sensitivity respectively.

Fig. 6. Relationship between R-C scores of M1 neurons (A) and upper arm muscles (B) that were related to loads in both the perturbation and posture tasks.

Fig. 7. Inter-task relationship between tuning features in joint-torque space of M1 neurons that were unimodally tuned in both tasks. A: Distribution of preferred-torque direction (PTD) differences. Arrow indicates the direction (PD) of the mean difference between preferred-torque directions. MVL, mean vector length. B: Temporal changes in the correlation (mean vector length) between preferred-torque directions. Significance of the distribution (unimodal Rayleigh test) at each point in time is indicated by closed ($P < 0.05$) and open (Rayleigh test, $P \geq 0.05$) symbols. Vertical lines at 0 and 300 ms indicate perturbation onset and offset. C: Temporal changes in the bias between preferred-torque directions. D: Relationship between torque-sensitivities (T-S) in the perturbation and posture tasks. R, correlation coefficient; Ratio, median ratio of torque-sensitivities (perturbation/posture). E: Temporal changes in the correlation between torque-sensitivities. Significance of the correlation ($t$-test for correlation) at each point in time is indicated by closed ($P < 0.05$) and open ($P \geq 0.05$) symbols. F: Temporal changes in the median ratio of torque-sensitivities (perturbation/posture).
Fig. 8. Activity of an exemplar proximal arm muscle (posterior deltoid) that was unimodally tuned in joint-torque space in both tasks. A: EMG activity during each load condition in the perturbation task. Vertical lines at 0 and 300 ms indicate perturbation onset and offset. Thin grey lines, individual trials; thick black lines, mean activity. B: EMG activity during each load condition in the posture task. C: Planar fits for the perturbation (left) and posture (middle) tasks and their preferred-torque direction (PTD) comparison (right). Direction and length of each arrow indicate the preferred-torque direction and torque-sensitivity respectively.

Fig. 9. Inter-task relationship between preferred-torque directions (PTD) of proximal arm muscles that were unimodally tuned in joint-torque space in both tasks. A: Distribution of preferred-torque directions in the perturbation task. White, black, and gray symbols indicate shoulder monoarticulars, elbow monoarticulars, and biarticulars; circles and squares indicate flexors and extensors. Thick line shows the bimodal axes (PD). MVL, mean vector length. B: Distribution of differences between preferred-torque directions. Arrow indicates the direction (PD) of the mean difference between preferred-torque directions. C: Temporal changes in the correlation (mean vector length) between preferred-torque directions. Significance of the distribution (unimodal Rayleigh test) at each point in time is indicated by closed ($P < 0.05$) and open (Rayleigh test, $P \geq 0.05$) symbols. Vertical lines at 0 and 300 ms indicate perturbation onset and offset. D: Temporal changes in the bias between preferred-torque directions.
Figure 1

A. Joint Torque (0-300 ms)

B. Hand Motion (0-600 ms)

C. Hand Motion (0-100 ms)

D. Joint Motion (0-100 ms)
Figure 2

A

Neuron 47443c
R–C Score = 0.73

Neuron 44261c
R–C Score = −0.06

Neuron 43451c
R–C Score = 0.19

B

C

PTD = NS

PTD = 142°

PTD = 314°
Figure 3
Figure 4

A

B

Preferred−Torque Direction (deg)

Torque Sensitivity (Hz/Nm)

PD = 120−300°
MVL = 0.58
**Figure 5**

**A**
Neuron 44131a – Perturbation Task

**B**
Neuron 44131a – Posture Task

**C**
Perturbation  Neuron 44131a Posture  PTD Comparison

- **Elbow Torque (Nm)**
- **Shoulder Torque (Nm)**
- **Activity (Hz)**

- **Perturbation**
- **Posture**
Figure 6

A  M1 Neurons

B  Upper Arm Muscles

Perturbation R–C Score  Posture R–C Score

-1  -0.5  0  0.5  1
-1  -0.5  0  0.5  1

-1  -0.5  0  0.5  1
-1  -0.5  0  0.5  1
A  Posterior Deltoid – Perturbation Task

Required Shoulder Torque

B  Posterior Deltoid – Posture Task

Required Shoulder Torque

C  Perturbation Posture PTD Comparison

Elbow Torque (Nm) Shoulder Torque (Nm)
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