Characterization of Torque-Related Activity in Primary Motor Cortex during a Multi-joint Postural Task


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Running Head: Torque-related activity during posture

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Abstract

The present study examined neural activity in the shoulder/elbow region of primary motor cortex (M1) during a whole-limb postural task. By selectively imposing torques at the shoulder, elbow, or both joints we addressed how neurons represent changes in torque at a single joint, multiple joints, and their inter-relation. We observed that similar proportions of neurons reflected changes in torque at the shoulder, elbow, and both joints and these neurons were highly intermingled across the cortical surface. Most torque-related neurons were reciprocally excited and inhibited (relative to their unloaded baseline activity) by opposing flexor and extensor torques at a single joint. While co-excitation/co-inhibition was occasionally observed at a single joint, it was rarely observed at both joints. A second analysis assessed the relationship between single-joint and multi-joint activity. In contrast to our previous observations, we found that neither linear nor vector summation of single-joint activities could capture the breadth of neural responses to multi-joint torques. Finally, we studied the neurons’ directional tuning across all the torque conditions, i.e., in joint-torque space. Our population of M1 neurons exhibited a strong bimodal distribution of preferred-torque directions (PTDs) that was biased towards shoulder-extensor/elbow-flexor (whole-limb flexor) and shoulder-flexor/elbow-extensor (whole-limb extensor) torques. Notably, we recently observed a similar bimodal distribution of PTDs in a sample of proximal arm muscles. This observation illustrates the intimate relationship between M1 and the motor periphery.
Introduction

It is known that primary motor cortex (M1) is an important region for executing volitional motor tasks (Hepp-Reymond 1988; Porter and Lemon 1993), though its specific role remains an area of active investigation. One key issue that remains unresolved is what portion of the motor periphery is reflected in the activity of individual neurons (Scott 2000). Specifically, is neural activity related to relatively localized motor patterns at a single joint, or distributed motor patterns across multiple joints?

A number of complementary approaches have provided insight into this issue. One set of approaches has examined relationships between the neural and muscle activity. Spike-triggered averaging techniques have demonstrated that some M1 neurons (corticomotoneurons) synapse directly onto pools of motoneurons that innervate one or more muscles acting at multiple joints of the limb (Fetz and Cheney 1980; Buys et al. 1986; McKiernan et al. 1998). However, corticomotoneurons are relatively rare and spike-triggered averaging examines patterns of connectivity with muscles but does not inherently address whether the activity of individual neurons reflects a similar, more focal, or broader representation of the motor periphery. Another approach relates the pattern of neural activity to the pattern of muscle activity during behavior. Several studies have shown that neural activity correlates 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) and reflect details on the timing and magnitude of muscle activity (Smith et al. 1975; Drew 1993; Scott 1997).

A second set of approaches has related neural activity to kinesiological parameters such as joint motion, joint torque, or forces applied to the limb. Since the motor system contains many more muscles than mechanical degrees of freedom, such kinesiological parameters provide a
simpler parameter space to examine the relationship between M1 activity and the motor periphery. By design, single-joint studies describe how neural activity correlates with motor patterns at a single joint (Evarts 1968, 1969; Thach 1978; Cheney and Fetz 1980; Evarts et al. 1983; Fromm 1983; Crutcher and Alexander 1990; Kakei et al. 1999), but cannot address how neural activity reflects motor patterns at multiple joints. Furthermore, most studies of volitional whole-arm control have correlated neural activity to hand-based parameters (e.g., Georgopoulos et al. 1982, 1992; Kalaska et al. 1989; Caminiti et al. 1990; Scott and Kalaska 1997; Moran and Schwartz 1999; Sergio and Kalaska 2003), thus they were not designed to identify whether neural activity is related to the shoulder, elbow, or both joints.

Perhaps the most extensive analysis of neural activity related to motor patterns at different joints was conducted by Schieber and colleagues, who studied neural activity related to individual finger movements (Schieber and Hibbard 1993; Poliakov and Schieber 1999). They found that individual neurons were generally related to independent movements of more than one digit suggesting that neurons may reflect a substantive portion of the motor periphery, at least for the hand. However, the activity of intrinsic and extrinsic finger muscles was often modulated by movements of unspanned digits (Schieber 1995), thus neural processing could reflect motion of many digits/joints or motor patterns of a small, select group of muscles.

We have introduced a planar, whole-limb paradigm that uses robotic technology to both monitor and perturb the mechanics of the shoulder and elbow joints independently (Scott 1999). Compared to the complex musculoskeletal organization of the hand, this whole-limb paradigm is relatively simple since most proximal arm muscles are monoarticular (spanning only the shoulder or elbow) with only four biarticular muscles representing about 19% of the total physiological cross-sectional area of all shoulder and elbow muscles (Cheng and Scott 2000).
The objective of this whole-limb paradigm is to facilitate exploring linkages between behavior, limb mechanics, muscle activity and neural processing.

The present study examined how neural activity in M1 reflects torques applied to the shoulder, elbow, or both joints during a whole-limb postural task. This behavioral task permitted us to examine torque-related activity, commonly recorded in previous single-joint studies, at two mechanical degrees-of-freedom spanning two joints. We directly compared neural responses to single-joint torques applied to each joint separately and show that most M1 neurons respond reciprocally to opposing torques at one or both joints. Furthermore, nearly all neurons that are co-activated or co-inhibited by opposing torques at one joint nevertheless exhibit unimodal directional tuning.

A second value of this paradigm was revealed in our parallel study of EMG activity recorded from proximal arm muscles during this postural task (Kurtzer et al. 2006a). The behavioral goal of this task was to maintain the hand at a spatial target while counteracting mechanical torques applied to the shoulder and/or elbow. Across all torque conditions, this task sampled a uniform distribution of torques at the shoulder and elbow (i.e., in joint-torque space). However, the maximal activity of proximal arm muscles was biased towards either shoulder-extensor/elbow-flexor (whole-limb flexor) or shoulder-flexor/elbow-extensor (whole-limb extensor) torques, thereby creating a bimodal distribution of preferred-torque directions (PTDs) in joint-torque space. If neural processing mirrors the behavioral requirements inherent in a task, then an equal proportion of M1 neurons should have represented each joint torque in this postural task. Alternatively, if neural activity is reflects the output patterns of muscles, then a greater proportion of neurons should have represented whole-arm flexor and whole-arm extensor torques in this postural task. Here we demonstrate that the maximal activity of M1 neurons
exhibits the same bias towards whole-arm flexor and whole-arm extensor torques that was observed in proximal arm muscles. The current study extends and elaborates on observations that we previously reported (Cabel et al. 2001).

Methods

Apparatus and task

Four male rhesus monkeys (Macaca mulatta, 6 to 12 kg) were used in this study following procedures approved by the Queen’s University Animal Care Committee. They were trained to perform motor tasks with their right arm 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.

The current task was designed to examine neural activity related to static joint torques at constant limb geometry. At the beginning of each trial a constant torque was applied at the shoulder, elbow, both, or neither joint. After a short delay a visual target (6 mm radius) was 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 are relatively small (Graham et al. 2003). The monkeys were required to maintain their hand within an acceptance window (8 mm radius) centered on the visual target for 3000 to 4000 ms. The task incorporated 9 torque conditions including 4 single-joint (shoulder flexion, SF; shoulder extension, SE; elbow flexion, EF; and elbow extension, EE), 4 multi-joint (SF+EF; SF+EE, SE+EF, SE+EE) and an unloaded baseline condition (Cabel et al. 2001; Kurtzer et al. 2005). 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. These torque conditions were presented in a pseudo-random block design with each block repeated 5 times for a total of 45 trials. A fixed magnitude of torque was always applied at each joint such that the total torque magnitude for multi-joint conditions was $\sqrt{2}$ greater than single-joint conditions. This design feature was important because it permitted us to treat shoulder and elbow torques as independent factors.

Data collection

Neural data was collected using standard extracellular recording techniques following surgical implantation of a cylindrical recording chamber over the shoulder/elbow representation of the left M1 (Scott and Kalaska 1997). Microelectrodes were advanced through M1 until neural activity was observed in response to active or passive movements of the shoulder and/or elbow. 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 movements of the wrist or fingers.

Joint angles, velocities, and torques applied by the robot were recorded at 1 kHz (Monkeys A–C) or 4 kHz (Monkey D). Cartesian hand positions and tangential hand velocity were calculated from joint angles and velocities. The equations of motion for a two joint, two degree-of-freedom system that included the influence of the mechanical properties of the arm and robotic device were used to calculate the instantaneous torques exerted by the monkey at the shoulder and elbow joints (Scott 1999; Cheng and Scott 2000). These were used to verify that the motors were properly functioning and the monkeys were adequately maintaining static posture. Data sets were excluded from analyses if the mean torque exerted at each joint was not within ±0.02 Nm (and opposite in sign) of the commanded torque.
Data analyses

All analyses examined neural activity with respect to the joint torques that counteracted the mechanical torques applied in each condition. Specifically, we studied torque-related activity, defined as changes in neural activity during loaded conditions relative to the unloaded baseline condition. For example, ΔSF refers to the change in neural activity relative to baseline when a shoulder flexor torque was generated by the monkey to compensate for an applied shoulder extensor torque.

Visual analysis of tangential hand velocity indicated that the hand decelerated for up to 1000 ms after entering the target’s acceptance window (Fig. 1A). These movements appeared to influence neural activity since the mean and standard deviation of neural activity also decreased during this period (Fig. 1B). All data was therefore analyzed by using their mean values obtained during the period from 1000 to 3000 ms after the hand entered the target’s acceptance window.

By treating shoulder and elbow torques as independent factors, we were able to use a two-way ANOVA (see Cabel et al. 2001) to coarsely identify neurons that were related to torques at the shoulder ($P < 0.01$ for main effect of shoulder) and elbow ($P < 0.01$ for main effect of elbow) in our task. All analyses were restricted to these torque-related neurons.

M1 topography. Three-dimensional reconstructions of M1 recording sites were created for Monkeys A–C. Post-mortem examination of the cortical surface was used to determine the angle of orientation of the central sulcus relative to recording chamber in each monkey. The stereotaxic coordinates of each neuron were then rotated in order to view the data relative to the orientation of the central sulcus. The center of mass of recorded neurons was then identified for each monkey and used to align the medial-lateral axes across monkeys. This permitted group analyses of the medial-lateral distribution of neurons related to the torques at the shoulder and/or elbow.
SINGLE-JOINT ANALYSES. These analyses uncovered important relationships between single-joint torques and torque-related activity. T-tests identified neurons that were significantly modulated by their respective flexor and extensor torques, relative to the unloaded baseline condition ($P < 0.05$). We also created three scores ranging continuously from $-1$ to $1$.

Reciprocal-comodulation (R-C) scores were calculated for the shoulder and elbow:

1) **Shoulder R-C Score** = $\text{sign}(\Delta SF \cdot \Delta SE) \cdot \min(|\Delta SF|, |\Delta SE|) \div \max(|\Delta SF|, |\Delta SE|)$

2) **Elbow R-C Score** = $\text{sign}(\Delta EF \cdot \Delta EE) \cdot \min(|\Delta EF|, |\Delta EE|) \div \max(|\Delta EF|, |\Delta EE|)$

These scores identified whether neurons that responded to flexor and extensor torques exhibited reciprocal modulation (i.e., equal in magnitude and opposite in direction, R-C Score = $-1$), unidirectional activity (i.e., related to flexor torque only or extensor torque only, R-C Score = $0$), or co-excitation/co-inhibition (equal in magnitude and direction, R-C Score = $1$).

Flexor-extensor (F-E) scores were also calculated for the shoulder and elbow:

3) **Shoulder F-E Score** = $(|\Delta SF| - |\Delta SE|) \div (|\Delta SF| + |\Delta SE|)$

4) **Elbow F-E Score** = $(|\Delta EF| - |\Delta EE|) \div (|\Delta EF| + |\Delta EE|)$

These scores established whether torque-related activity was related to extensor torque only (F-E Score = $-1$), extensor and flexor torques equally (F-E Score = $0$), or flexor torque only (F-E Score = $1$).

A shoulder-elbow (S-E) score was calculated across both joints:

5) **S-E Score** = $(|\Delta SF| + |\Delta SE| - (|\Delta EF| + |\Delta EE|)) \div (|\Delta SF| + |\Delta SE| + |\Delta EF| + |\Delta EE|)$

This score determined whether torque-related activity was related to the elbow only (S-E Score = $-1$), both joints equally (S-E Score = $0$), or the shoulder only (S-E Score = $1$).

PREDICTING MULTI-JOINT ACTIVITY. Our preliminary report based on two monkeys (Cabel et al. 2001) found that changes in neural activity related to multi-joint torques could be accurately predicted by vector summation of constituent single-joint activities. We re-examined this issue in
our sample of directionally-tuned neurons (bootstrap statistic, $P < 0.01$). Changes in activity at the shoulder ($\Delta S$) and elbow ($\Delta E$) were used to predict multi-joint activity using linear ($\Delta MJ_l$) and vector ($\Delta MJ_v$) summation models:

\begin{align*}
6) \quad \Delta MJ_l &= \Delta S + \Delta E \\
7) \quad \Delta MJ_v &= (\Delta S^2 + \Delta E^2)^{1/2}
\end{align*}

**Directional tuning in joint-torque space.** We examined issues related to multi-joint control by calculating directional tuning properties in joint-torque space. For this particular coordinate frame, neural activities related to the joint torques exerted across the shoulder and elbow joints are represented along the x and y axes respectively. This contrasts with the mechanical torques applied by the robot across the shoulder and elbow joints, which are equal and opposite the joint torques exerted by the monkey in our static postural task. Using flexor torque as positive and extensor torque as negative, trigonometric convention yields SF = 0º, EF = 90º, SE = 180º, and EE = 270º.

Directional tuning features were calculated with the plate method, which describes several features of directional tuning without assuming an underlying tuning function (Gribble and Scott 2002). This method characterized the “mass distribution” of torque-related activity by assuming that activity changes linearly between sampled torque directions and that torque magnitude is equal for each torque direction. By maintaining constant torques at the shoulder and elbow, the overall torque magnitude was greater in the multi-joint conditions (see Apparatus and Tasks). Multi-joint activity was consequently divided by $\sqrt{2}$ in order to normalize torque-related activity across all torque conditions; normalization was only carried in this specific analysis with the plate method. The lowest activity across all trials was then subtracted so that all values were greater or equal to zero.
The location of the center of mass, or centroid, in joint-torque space was used to calculate four directional tuning features. 1) Preferred-torque direction (PTD) describes the angle associated with the greatest increase in activity in joint-torque space. This was calculated as the direction of the centroid relative to the origin in joint-torque space. Importantly, PTDs were calculated as the average of two separate PTDs, one obtained from the four single-joint conditions and the other from the four multi-joint conditions (Cabel et al. 2001). Since the multi-joint PTD of each neuron was identical whether or not multi-joint activity was normalized, the overall PTD was unaffected by normalization. 2) Ratio of inertia (Ir) conveys information analogous to tuning widths calculated with model-based functions such as the Von Mises function. This was calculated as the ratio of torque-related activity perpendicular to the PTD axes versus torque-related activity along the PTD axes yielding values ranging from 0 to 1. A cosine obtains an Ir value of 0.44, while smaller values denote sharper tuning and larger values denote broader tuning. 3) Torque-slope expresses the change in torque-related activity per unit torque along the PTD. This was calculated by normalizing the magnitude of the centroid (Cr), defined as the radial distance between the centroid and origin, by the torque magnitude (0.12 or 0.32 Nm). 4) Excitation-inhibition score (E-I score) describes the relationship between increases in torque-related activity at the PTD and decreases in torque-related activity opposite the PTD. Torque-related activities at and opposite the PTD (ΔPTD and ΔOPP respectively) were obtained using linear interpolation and the E-I score was then calculated:

\[ E-I \text{ score} = \frac{ΔPTD + ΔOPP}{(ΔPTD−ΔOPP)} \]

E-I scores typically range from −1 to 1. Positive (negative) E-I scores occur when the magnitude of excitation at the PTD is greater (lesser) than the magnitude of inhibition opposite the PTD. Values near 0 occur arise when the magnitudes of excitation and inhibition are similar. E-I scores could go beyond 1 (−1) if both ΔPTD and ΔOPP exhibited excitation (inhibition).
The preceding measures were only examined for those neurons with statistically significant directional tuning as determined with a nonparametric “bootstrapping” test (Scott and Kalaska 1997). This statistic was calculated by comparing the actual value of Cr with bootstrap values of Cr obtained after the torque-related activity was randomly reassigned across all trials. A neuron was considered to have significant directional tuning if fewer than 100 of 10,000 bootstrap values of Cr were greater than the actual value of Cr \( (P < 0.01) \). This method produced results that were similar to those obtained from bootstrap methods using mean vector length (Scott and Kalaska 1997; Cabel et al. 2001) and \( F \)-tests from planar regression models [similar proportions (85, 89, and 90\%) of torque-related units exhibited significant directional tuning].

Reliability of the plate method was verified by comparing its results with those obtained from planar regression models that did not require normalization of data. In brief, the mean values of neural activity and actual torques exerted at the shoulder and elbow (obtained from the equations of motion) were used to calculate planar regression models for each neuron. The shoulder and elbow coefficients from these models were used to calculate PTDs and torque-slopes for each neuron (see Kurtzer et al. 2005). Directly comparing the two methods indicated that they produced similar PTDs (mean absolute difference = 4°) and torque-slopes \( (r = 0.96) \).

**Results**

*Categorization and topography*

A total of 359 M1 neurons were recorded in four monkeys (Monkeys A–D: 89, 61, 84, and 125, respectively). The activity of some neurons was modulated by torques at one joint only (Fig. 2A), whereas the activity of other neurons was modulated by torques at both joints (Fig. 2B).
For didactic purposes, we used a two-way ANOVA (see Cabel et al. 2001) to coarsely identify neurons related to torques at the shoulder ($P < 0.01$ for main effect of shoulder) and elbow ($P < 0.01$ for main effect of elbow). Within our population of 359 M1 neurons, 146 (41%) were significantly related to the shoulder (shoulder neurons) and 140 (39%) were significantly related to the elbow (elbow neurons). Many of these were classified as multi-joint neurons (n = 76, 36%) since they were related to both the shoulder and elbow. Other neurons were identified as shoulder-only neurons (n = 70, 33%) or elbow-only neurons (n = 64, 30%) since they were flagged by a main effect at only one of the two joints. In total, 210 of the 359 neurons recorded in this task (58%) were flagged as torque-related neurons.

The relationship between the different categories of torque-related neurons and their anatomical location within M1 was investigated using three-dimensional reconstructions of M1 in Monkeys A–C (Fig. 3A). Across the three monkeys, neurons related to torques at the shoulder only (red circles), elbow only (green circles), both joints (blue circles), or neither joint (black circles) were highly intermingled across the cortical surface (Fig. 3B–D). The only evidence of anatomical segregation was observed in Monkey B, where shoulder-only neurons were located medial to elbow-only (Kolmogorov-Smirnov test, $P < 0.001$) and multi-joint neurons (Kolmogorov-Smirnov test, $P = 0.02$). In Monkeys A and C, each category exhibited a similar distribution along the medial-lateral axes of M1 (Kolmogorov-Smirnov tests, $P > 0.1$). Furthermore, there was no evidence of anatomical segregation along the medial-lateral axes of M1 when data was grouped across all three monkeys (Fig. 3E) (Kolmogorov-Smirnov tests, $P > 0.1$).
Neural activity associated with single-joint torques

Of the 146 shoulder neurons, 44 (30%) were significantly modulated by flexor torque only, 30 (21%) by extensor torque only, and 26 (18%) by both flexor and extensor torques (t-tests comparing single-joint flexor and extensor torques with unloaded baseline, $P < 0.05$). Of the 140 elbow neurons, 25 (18%) were significantly modulated by flexor torque only, 35 (25%) by extensor torque only, and 22 (16%) by both flexor and extensor torques (t-tests, $P < 0.05$). The remaining 46 (32%) shoulder and 58 (41%) elbow neurons exhibited similar patterns of torque-related activity but failed to reach statistical criteria due to the weaker statistical power of the t-test (DF = 8) compared to the ANOVA (DF = 2, 36).

Relative to baseline activity in the unloaded condition, flexor and extensor torques at the shoulder (Fig. 4A) and elbow (Fig. 4B) were associated with increases and decreases in activity that ranged from –20 to 28 spikes/s at 0.12 Nm in Monkeys A–C and from –35 to 28 spikes/s at 0.32 Nm in Monkey D. Notably, the magnitude of changes in activity appears to be relatively independent of baseline activity, except that overall activity (with baseline) cannot drop below zero spikes/s (Fig. 4, A and B). As a result, changes in torque-related activity were broadly distributed with mean activities near zero (Fig. 4, C–F).

Figure 5 compares the changes in activity associated with flexor and extensor torques at the shoulder (A) and elbow (D). Most neurons exhibited reciprocal activity (quadrants 2 and 4) and few neurons exhibited co-excitation or co-inhibition (quadrants 1 and 3 respectively) ($\chi^2$ tests, $P < 0.001$). A number of neurons also exhibited unidirectional activity, as indicated by their presence near the 2 primary axes. Accordingly, R-C scores for shoulder and elbow neurons (Fig. 5, B and E respectively) exhibited a significant bias towards a reciprocal pattern of activity (median shoulder R-C score = –0.26; median elbow R-C score = –0.27; Wilcoxon signed rank
torques, \( P < 0.001 \). Comparison of changes in activity associated with flexor and extensor torques also illustrates that some neurons responded similarly to both flexor and extensor torques while other neurons responded stronger to flexor or extensor torques (Fig. 5, A and D). As a result, F-E scores for shoulder and elbow neurons were broadly distributed (Fig. 5, C and F respectively). Elbow neurons did not exhibit a preference for flexor or extensor torques (median elbow F-E score = −0.06; Wilcoxon signed rank test, \( P > 0.1 \)) while shoulder neurons were marginally more sensitive to flexor torques (median shoulder F-E score = 0.09; Wilcoxon signed rank test, \( P = 0.02 \)).

Figure 6A compares reciprocal changes in neural activity related to single-joint torques at the shoulder (\( \Delta SF-\Delta SE \)) and elbow (\( \Delta EF-\Delta EE \)). There was a significant bias in this relationship (\( \chi^2 \) test, \( P < 0.001 \)) such that disproportionately more neurons were sensitive to whole-arm flexor torque (quadrant 2; expected = 40, observed = 58) or whole-arm extensor torque (quadrant 4; expected = 67, observed = 85) as compared to flexor torques at both joints (quadrant 1; expected = 54, observed = 36) or extensor torques at both joints (quadrant 3; expected = 49, observed = 31). There was also considerable overlap between neurons that were categorized as shoulder-only (red), elbow-only (green) and multi-joint (blue).

S-E scores (Fig. 6B) examined whether changes in neural activity (reciprocal or co-excitation/co-inhibition) were related to the shoulder (1), elbow (−1), or both joints equally (0). Most neurons were influenced by torques at both joints, although elbow-only (green), multi-joint (blue), and shoulder-only (red) neurons were appropriately biased towards −1, 0, and 1 respectively. Surprisingly, a number of shoulder-only and elbow-only neurons exhibited S-E scores that were biased towards the elbow (< 0) or shoulder (> 0) respectively. This apparent switch reflects that a neuron can have a small but consistent change in activity related to torques.
at one joint and a large but highly variable response related to torques at the other joint resulting in only the former attaining statistical significance.

An interesting question is whether neurons that exhibited co-excitation/co-inhibition related to torques at one joint (Fig. 5, C and D) responded in a similar manner at both joints. Figure 6C compares shoulder and elbow R-C scores for the 76 multi-joint neurons. Notably, most (n = 48, 63%) multi-joint neurons exhibited reciprocal activity at both joints, another 22 (29%) displayed co-excitation/co-inhibition at one joint and reciprocal activity at the other, and only 6 (8%) showed co-excitation/co-inhibition at both joints. These values did not differ significantly from the expected values of a random distribution ($\chi^2$ test, $P > 0.1$).

**Predicting multi-joint activity**

Our initial report found the multi-joint activity could be predicted from vector summation of constituent single-joint activities (Cabel et al. 2001). Here we reinvestigated this issue and found that neither linear nor vector summation models accurately predicted multi-joint activity across our entire sample of directionally-tuned neurons (Fig. 7, A and B). On average, linear summation overestimated multi-joint activity (mean residual error = 2.6 spikes/s; t-test, $P < 0.001$) and vector summation underestimated multi-joint activity (mean residual error = –1.6 spikes/s; t-test, $P < 0.001$).

To verify that single-joint neurons did not create this conflicting result, we repeated our analysis on the subset of directionally-tuned neurons that were flagged as multi-joint neurons by the ANOVA (n = 74). Again, neither model accurately predicted multi-joint activity across the entire subset of multi-joint neurons (Fig. 7, C-D). Linear summation marginally overestimated multi-joint activity (mean residual error = 1.8 spikes/s; t-test, $P = 0.06$) and vector summation substantially underestimated multi-joint activity (mean residual error = –4.5 spikes/s; t-test, $P <$
T-tests were subsequently used to directly compare the predicted activity of linear and vector summation models with the actual multi-joint activity. Of the 74 neurons, 16 (22%) were categorized as “linear summation” neurons (linear, $P \geq 0.05$; vector, $P < 0.05$), 8 (11%) were classified as “vector summation” neurons (linear, $P < 0.05$; vector, $P \geq 0.05$), and 4 (5%) could not be labeled as either “linear summation” or “vector summation” neurons (linear, $P < 0.05$; vector, $P < 0.05$). Linear and vector summation models could not be differentiated from each other in the other 46 (62%) neurons (linear, $P \geq 0.05$; vector, $P \geq 0.05$).

**Tuning properties in joint-torque space**

Of the 210 torque-related neurons flagged by the ANOVA, 178 (85%) exhibited significant directional tuning in joint-torque space (plate method bootstrap statistic, $P < 0.01$). The various directional tuning properties in joint-torque space (see Methods) are illustrated with four exemplar neurons in Figure 8. Figure 8A illustrates neuron 11531b (see also Fig. 2A), which was maximally active during torque conditions that involved shoulder flexor torque and minimally active during torque conditions that engaged shoulder extensor torque. The pattern of torque-related activity across all joint-torque directions gave rise to a PTD of 6°, cosine-like sensitivity to changes in joint-torque direction ($I_r = 0.42$ compared to 0.44 for a cosine), and a torque-slope of 129 (spikes/s)/Nm ($C_r = 15.5$ spikes/s, torque = 0.12 Nm). Furthermore, the magnitude of excitation at the PTD was similar to the magnitude of inhibition opposite the PTD ($E-I$ score $= –0.02$).

The other exemplar neurons in Figure 8 illustrate divergent directional tuning properties. Relative to its baseline activity, Neuron 33171b ($B$) exhibited far greater inhibition opposite its PTD than excitation at its PTD ($E-I$ score $= –0.72$). Neuron 32441a ($C$) was sharply tuned ($I_r = 0.21$) relative to a cosine and showed strong excitation at its PTD and weak excitation relative to
baseline opposite its PTD (E-I score = 1.11). Neuron 12811a (D) was broadly tuned relative to a cosine (Ir = 0.82) and displayed greater inhibition opposite its PTD than excitation at its PTD (E-I score = –0.54). Furthermore, each of these neurons was associated with a different PTD and a lower torque-slope than neuron 11531b.

Figure 8 also illustrates the importance of removing baseline activity before calculating Ir. Neuron 11531a (A) exemplifies a case where the minimum overall activity including baseline was near 0 spikes/s (torque direction = 180º) resulting in similar values of Ir for the overall activity (center plot) and torque-related activity (right-side plot) in joint-torque space (Ir = 0.43 and 0.42 respectively). In contrast, neurons 33171b (B) and 12811a (D) had minimum overall activities that were well above 0 spikes/s (torque direction = 0 and 180º respectively) resulting in broader tuning for their overall activity (Ir = 0.72 and 0.94 respectively) compared to their torque-related activity (Ir = 0.50 and 0.82, respectively).

A number of interesting results were observed across the entire population of directionally tuned neurons. Most notably, PTDs exhibited a significant bimodal distribution (bimodal Rayleigh test, mean vector = 0.26, $P < 0.001$) oriented along the axes of 141–321º (Fig. 9A). Although PTDs also exhibited a significant, albeit weaker, unimodal distribution (unimodal Rayleigh test, mean vector = 0.17, $P < 0.01$), the mean vector for the bimodal distribution was consistently greater for each individual monkey. Furthermore, this bimodal distribution confirms the preference for whole-arm flexor and whole-arm extensor torques that we observed when single-joint torques were compared across the shoulder and elbow (Fig. 6A).

We found that torque-slopes, Ir values, and E-I scores were all broadly distributed (Fig. 9, B–D respectively). Torque-slopes were spread over a range of 4 to 129 (spikes/s)/Nm and a mean of 38 (spikes/s)/Nm (Fig. 9B). Notably, torque-slopes were higher at 0.12 Nm in Monkeys A–C
than at the 0.32 Nm in Monkey D [mean torque-slopes = 46 and 24 (spikes/s)/Nm respectively; t-test, \(P < 0.001\)]. This agrees with previous single-joint studies that observed smaller changes in torque-related activity at higher torque magnitudes (Evarts et al. 1983; Werner et al. 1990). Ir values were distributed over a range of 0.08 to 0.99 (Fig. 9C), but unlike torque-slopes, Monkeys A–D had a similar median Ir values of 0.37, 0.44, 0.41, and 0.42 respectively. E-I scores were spread over a range of –2.5 to 2.4 (Fig. 9D), and had a significantly positive mean of 0.25 (t-test, \(P < 0.001\)) indicating that increases in torque-related activity at the PTD were significantly greater than decreases opposite the PTD.

Since values of torque-slope and Ir were broadly distributed, we speculated that neurons with PTDs near 45 and 225° may exhibit higher torque-slopes or different tuning in order to compensate for their diminutive numbers. However, neither torque-slopes nor tuning widths (Ir) varied significantly between sparsely and densely populated regions of joint-torque space (Wilcoxon rank sum tests, \(P > 0.1\)). In fact, a negative correlation between Ir and E-I scores \((r = –0.49; \text{t-test for correlation, } P < 0.001)\) was the only significant relationship that we observed between the various properties of directional tuning (Fig. 9E). The presence of this relationship indicates that neurons with greater excitation than inhibition were sharply tuned at their PTD, whereas neurons with greater inhibition than excitation were sharply tuned opposite their PTD (sharp tuning opposite the PTD necessitates broad tuning at the PTD).

Since neural activity cannot decrease below zero spikes/s, we speculated that neurons with low baseline activity may account for the observation that increases in torque-related activity at the PTD were greater than decreases opposite the PTD (Fig. 9D). Accordingly, the mean E-I score of neurons with low baseline activity (<10 spikes/s) was significantly greater than zero (mean E-I score = 0.64; t-test, \(P < 0.001\)), whereas the mean E-I score of neurons with
higher baseline activities (> 10 spikes/s) was not different from zero (mean E-I score = 0.04; t-test, $P > 0.1$). Due to the relationship between Ir and E-I scores (Fig. 9E), the mean Ir of neurons with low baseline activities was significantly sharper than a cosine (median Ir = 0.28; Wilcoxon signed rank test, $P < 0.001$), whereas the mean Ir of neurons with higher baseline activities was not different from a cosine (median Ir = 0.45; Wilcoxon signed rank test, $P > 0.1$).

**Discussion**

A major goal of this study was to examine what portion of the motor periphery is reflected in the activity of individual M1 neurons by characterizing how neural activity is modulated by variations in torque exerted at two separate joints. Our approach provides a direct extension of studies that examine neural processing during single-joint motor tasks to consider multiple joints. Our methodology also shares certain similarities to previous studies that correlate load-related activity to hand-based parameters. We have therefore included complementary analyses reflective of previous single-joint and hand-based studies. Furthermore, the detailed descriptions of torque-related activity provide an important foundation for developing and assessing computational models of M1 processing.

In summary, we observed that many neurons in the shoulder/elbow region of M1 were quantitatively related to joint torques at the shoulder only (33%), elbow only (30%), or both joints (36%) and that these neurons were highly intermingled across the cortical surface. Relative to their unloaded baseline activity, most torque-related neurons were reciprocally modulated by opposing flexor and extensor torques at a single joint (Fig. 5, B and E). A small number of neurons were co-excited or co-inhibited by opposing torques at one joint, but these neurons generally exhibited reciprocal modulation at the other joint (Fig. 6C). Notably, our population of M1 neurons exhibited a bimodal distribution of PTDs that was biased towards whole-arm flexor
and whole-arm extensor torques (Fig. 9A). Other properties of directional tuning (torque-slope and tuning width) exhibited broad distributions (Fig. 9, B and C) that were unrelated to this bias. These observations have several implications regarding the neural basis of multi-joint control, which are discussed below.

M1 Topography

Classical studies of M1 in humans (Penfield and Rasmussen 1950) and monkeys (Woolsey et al. 1952) observed that movements of body parts evoked by stimulation were broadly segregated along the medial-lateral axes. Specifically, the legs, trunk, arms, face, and mouth were found to be represented within anatomically distinct sub-regions of M1. It is debated however, whether there is a functional organization within these major regions (reviewed in Sanes and Schieber 2001; Schieber 2001). In the arm representation for example, some studies have observed a random organization (Gould et al. 1986; Donoghue et al. 1992) whereas other studies have observed that the proximal arm (shoulder-elbow) is represented within a horse-shoe shaped region surrounding the distal arm (wrist-hand) (Kwan et al 1978; Park et al. 2001).

The current study addressed whether neurons within the shoulder-elbow region of M1 exhibit an orderly topography. Although our study was limited to neurons within the medial branch of the horse-shoe organization (hand/wrist related neurons were found laterally), we found that neurons related to the shoulder only, elbow only, or both joints were intermingled across the surface of M1 and did not exhibit distinct segregation along the medial-lateral axes of M1. Similar results have been reported for the hand representation, in which single neurons are generally related to movements of multiple digits and do not exhibit an obvious somatotopic organization (Schieber and Hibbard 1993; Poliakov and Schieber 1999). These observations support the notion that M1 possesses only a broad segregation of body parts. Substantive overlap
in the neural representations of the shoulder and elbow may reflect the behavioral requirements of many motor tasks in which these joints are coordinated together to move the hand in space (Schieber 2000; Sanes and Schieber 2001).

*Is co-contraction reflected in a small population of torque-related neurons?*

In everyday life, common motor behaviors may be affected by random mechanical perturbations. For example, our arms randomly experience clockwise and counter-clockwise perturbations while driving over rough terrain. Co-activation of antagonistic muscles (i.e., co-contraction) is one strategy to reduce the influence of limb perturbations that may occur while trying to maintain a static posture (e.g., McIntyre et al. 1996; Gomi and Osu 1998; Franklin and Milner 2003; Darainy et al. 2004).

Surprisingly little is known about the neural basis of co-contraction since few studies have examined neural activity during tasks that promote co-contraction. At the level of the cortex, Humphrey and Reed (1983) examined the responses of M1 neurons during slow and fast wrist perturbations that respectively produced reciprocal activation and co-contraction of opposing wrist muscles. They found two distinct populations of neurons, one that was only modulated during rapid perturbations and one that was only modulated during slow perturbations. This finding suggests that reciprocal activation and co-contraction of opposing wrist muscles might be represented by distinct neural processes in M1. However, muscles of the elbow and shoulder were also more active during rapid perturbations than slow perturbations, thus it is possible that one population was related to the wrist whereas the other was related to the shoulder and elbow.

Indirect evidence for distinct representations of reciprocal activation and co-contraction may also be interpreted from single-joint studies of torque-related activity in M1 (Evarts et al.
1983; Werner et al. 1991). These studies found that most torque-related M1 neurons exhibited a reciprocal pattern of activity in response to opposing torques; i.e., they were excited by torques applied in one direction and inhibited by torques applied in the opposing direction. However, they also found that a considerable number of torque-related neurons were excited or inhibited by both opposing torques. Since opposing torques primarily activate antagonistic muscle groups, these results suggest that this population of neurons may be related to co-contraction.

If neurons with similar responses to opposing single-joint torques are related to co-contraction, then neural correlates of co-contraction should also be observed in whole-limb studies. Specifically, one might expect to find neurons that exhibit bimodal or uniform changes in force- or torque-related activity relative to unloaded baseline. However, two comprehensive whole-limb studies, one postural and one isometric, did not report bimodal or uniform changes in force-related activity relative to baseline (Kalaska et al. 1989; Sergio and Kalaska 2003). The current study may explain why these whole-limb studies did not report such correlates of co-contraction. We found that a sizeable proportion of multi-joint neurons (28 of 76, 37%) showed co-excitation/co-inhibition at one of the two joints. If these neurons were related to co-contraction of antagonist muscles, one would expect that many would exhibit co-excitation/co-inhibition at both joints and few would exhibit unimodal tuning. Contrary to these expectations, few of these neurons (6 of 28, 21%) exhibited co-excitation/co-inhibition at both joints (Fig. 6C) and nearly all (26 of 28, 93%) were unimodally tuned (e.g., Fig. 8C).

While our results suggest that torque-related M1 neurons are not related to co-contraction, it is important to recognize that our task was not specifically designed to explore the neural basis of co-contraction. Several recent studies of human behavior have examined patterns of co-contraction during posture (Franklin and Milner 2003; Darainy et al. 2004) and reaching
(Burdet et al. 2001; Milner and Franklin 2005) and may provide a foundation for future studies designed to explore the neural basis of co-contraction.

Relationship between M1 and muscle activations

There are many different parameters or levels of information that can be used to describe the kinetics of forces applied to a limb: 1) contact forces between the limb/hand and load, 2) joint torques representing the combined action of all muscles spanning a given joint, 3) individual muscle forces and even 4) muscle activation patterns. The difference between these kinetic descriptions reflects how much the properties of the musculoskeletal system are incorporated into the kinetic measure. Contact forces do not consider any aspect of the limb except the site of contact. Joint torques include the influence of limb geometry and intersegmental dynamics. Muscle forces consider the mechanical action of individual muscles. Muscle activation patterns additionally include the mechanical properties of muscle including force-length and force-velocity relationships and excitation-contraction coupling.

Neural activity could be related to any of the above parameters, although it remains unclear which parameters are represented by supraspinal processes. Theoretical frameworks based on sensorimotor transformations (Hollerbach 1982; Soechting and Flanders 1992; Kalaska and Crammond 1992) indicate that all may be represented neurally, whereas other frameworks, such as optimal feedback control (Scott 2004), suggest that such a hierarchy of representations is not required.

In the present experiment, monkeys were trained to counteract a uniform distribution of torques. If neural processing reflected the range of behavioral requirements inherent in a task, one might expect that each torque direction would have been represented by an equal proportion of M1 neurons. In fact, a previous study observed that the activity of M1 neurons can reflect the
range of behavioral requirements (Hepp-Reymond et al. 1999). Specifically, force-related activity of individual was modulated by contextual cues indicating the upcoming range of forces and number of force steps in a grip force task. In the current study however, we observed a bimodal distribution of PTDs. Furthermore, we did not observe any systematic relationships between PTDs, torque-slopes, and tuning widths indicating that the relatively small proportion of neurons with PTDs near 45 and 225º did not possess higher torque-slopes or different tuning widths in order to compensate for the bimodal distribution of PTDs. Taken together, these findings indicate that M1 neurons as a population do not reflect the range of behavioral requirements inherent in our postural task.

Another possibility is that proprioceptive feedback during the task influenced M1 activity. Since many M1 neurons respond strongly to proprioceptive input (Lemon and Porter 1976; Wong et al. 1978; Evarts and Tanji 1976; Wolpaw 1980; Flament and Hore 1988; Scott and Kalaska 1997), one might expect that a greater proportion of neurons would have preferred joint torques that reflected the mechanical action of the shoulder and elbow muscles. While most shoulder and elbow muscles span only a single joint, the four biarticular muscles combine flexion or extension at both joints. However, these directions in joint-torque space were least represented across our population of M1 neurons.

Notably, our population of torque-related M1 neurons exhibited a bimodal distribution of PTDs that was biased towards whole-arm flexor and whole-arm extensor torques. This mirrored the pattern of torque-related EMG of a sample of proximal arm muscles in the same monkeys in this postural task (Kurtzer et al. 2006a). Other studies have also described close relationships between M1 and the motor periphery by comparing patterns of activity across populations of neurons and muscles. Notably, a greater proportion of neurons and muscles are maximally
activated when the hand moves towards or away from the body as compared to the left or right during planar reaching movements (Scott et al. 2001; Kurtzer et al. 2006b). Biases in their preferred directions of movement (Caminiti et al. 1990; Scott and Kalaska 1997; Kakei et al. 1999) and force (Sergio and Kalaska 2003) undergo similar rotations following changes in limb geometry. Both neurons and muscles exhibit similar temporal changes in their distributions of preferred movement direction (Todorov 2000; Sergio et al. 2005). Finally, both display a coupling between their onset time and magnitude of response (Scott 1997). Each of these findings highlights the intimate relationship between M1 and the motor periphery, but they do not imply a point-to-point mapping in which M1 neurons are merely upper motor neurons. Rather, they suggest that the activities of M1 neurons and peripheral muscles are shaped by similar constraints.

Biased representations of joint torque: muscle synergies or optimal strategies?

A fundamental issue in motor control is that the redundancy of the musculoskeletal system requires the CNS to select patterns of muscle activations from an infinite set of possible solutions in order to execute even the simplest multi-joint behaviors. Bernstein (1967) proposed that this problem could be simplified if a broad range of motor behaviors could be produced with a small number of distinct muscle synergies, sets of muscles that are collectively activated to form functional units. Accordingly, motor commands would be accomplished by activating appropriate combinations of muscle synergies.

A number of studies have subsequently provided empirical evidence suggesting that the CNS employs muscles synergies. Notably, patterns of muscle activity have been decomposed into a small number of muscle synergies 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.
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(Macpherson et al. 1986; Buford and Smith 1990; Ting and MacPherson 2005), 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 suggesting that such patterns are reflected in neural circuitry at the spinal level (Tresch et al. 1999; Hart and Giszter 2004).

The present data could be viewed as providing evidence that muscle synergies are expressed by neural processes at supraspinal levels. We found that in our planar task M1 neurons tended to represent torque-related activity in one of two multi-joint muscle synergies, whole-arm flexion and whole-arm extension. Since other studies have also observed that M1 activity reflects various muscles synergies (Donoghue et al. 1992; Holdefer and Miller 2002; Park et al. 2004), these observations could be viewed as evidence 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 optimal control strategies that are unrelated to the notion of muscle synergies (Scott 2004). Similar to earlier studies of the monkey wrist (Hoffman and Strick 1999), human forearm (van Zuylren et al. 1988; Buchanan et al. 1989), and human leg (Nozaki et al. 2004), we observed that the pattern of activations of monoarticular and biarticular shoulder and elbow muscles was systematically rotated away from their anatomical action towards whole-arm flexor or whole-arm extensor torques. Mathematical models illustrated that minimizing global measures of muscle activity could predict the observed PTD rotations of each group of upper arm muscles: shoulder flexors and extensors, elbow flexors and extensors, and biarticular flexors and extensors (Kurtzer et al. 2006a). These models suggest that M1 may control certain motor behaviors, such as postural maintenance, by producing patterns of neural activity that achieve the task goal by minimizing
muscle factors such as output noise. As a result, muscle synergies may not reflect an explicit
simplifying strategy for controlling movement. Rather, they may be the appropriate pattern of
muscle activities given the physical properties of the musculoskeletal system and the task goals.
This raises the problem of what evidence is required to demonstrate whether muscle synergies
are an explicit strategy for simplifying motor control or an emergent pattern of muscle activity
suitable for optimizing task goals.

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**Figure Legends**

Fig. 1. Temporal dynamics after the hand entered the target’s acceptance window (averaged across all torque conditions). *A*: tangential hand velocity (mean ± SD). *B*: mean (solid line) and standard deviation (dash-dotted line) of neural activity. Vertical lines in each panel indicate the
onset of the period that data were analyzed (1000 to 3000 ms after the hand entered the target’s acceptance window).

Fig. 2. Rasters and instantaneous firing rates illustrating exemplar patterns of neural activity during the analysis epoch (1000 to 3000 ms after the hand entered the target’s acceptance window). 

A: single-joint neuron with torque-related activity (i.e., changes in activity relative to baseline, middle sub-panel) that increased for shoulder-flexor torques, decreased for shoulder-extensor torques, and was largely uninfluenced by torques at the elbow. 

B: multi-joint neuron with torque-related activity that increased for shoulder-extensor/elbow-flexor torques and decreased for shoulder-flexor/elbow-extensor torques. SF, shoulder flexor; EF, elbow flexor; SE, shoulder extensor; EE, elbow extensor.

Fig. 3. Recording sites. 

A: Top-down view of the location of the shoulder-elbow region of M1 (left) and the coordinates of its three-dimensional reconstructions (right). 

B–D: Dorsal and sulcal views depicting the anatomical locations of recording sites (Monkeys A–C respectively) of M1 neurons related to the shoulder only (red circles), elbow only (green circles), both joints (blue circles), or neither joint (black circles). Penetration depths are displayed relative to the electrode’s initial electrical contact (assumed to be the top of the dura). Grid spacing = 1 mm. 

E: Illustration of the cumulative sum (percent) of neurons along the medial-lateral axes of M1 grouped across monkeys. Bin width = 0.25 mm.

Fig. 4. Changes in neural activity related to single-joint torques. 

A, B: torque-related activity of shoulder (A) and elbow (B) neurons relative to their baseline activity. Neural responses to flexor and extensor torques at the shoulder (ΔSF and ΔSE) and elbow (ΔEF and ΔEF) are shown separately for each shoulder and elbow neuron. Circles, significant responses to flexor torques (P < 0.05); diamonds, significant responses to extensor torques (P < 0.05); small dots,
nonsignificant responses to flexor and extensor torques \((P > 0.05)\); closed symbols, Monkeys A–C; open symbols, Monkey D. Diagonal lines indicate the largest negative change in activity that can occur for any given baseline activity. C–F: distributions of neural responses to flexor and extensor torques at the shoulder \((C \text{ and } E)\) and elbow \((D \text{ and } F)\).

Fig. 5. Comparison of responses to single-joint flexor and extensor torques. \(A, D\): responses to flexor versus extensor torques at the shoulder \((A)\) and elbow \((D)\). \(B, E\): distributions of R-C scores for shoulder \((B)\) and elbow \((E)\) neurons. Reciprocal = –1, unidirectional = 0, co-excitation/co-inhibition = 1. \(C, F\): distributions of F-E scores for shoulder \((C)\) and elbow \((F)\) neurons. Extensor torque only = –1, flexor and extensor torques equally = 0, flexor torque only = 1. Abbreviations same as Figure 4.

Fig. 6. Comparison of responses to single-joint torques at the shoulder and elbow. \(A\): responses of shoulder-only (red), elbow-only (green), and multi-joint (blue) neurons to single-joint torques at the shoulder \((\Delta SF–\Delta SE)\) versus the elbow \((\Delta EF–\Delta EE)\). Closed circles, Monkeys A–C; open circles, Monkey D. \(B\): distribution of S-E scores of shoulder-only (red), elbow-only (green), and multi-joint (blue) neurons. Elbow only = –1, shoulder and elbow equally = 0, shoulder only = 1. \(C\): comparison of shoulder versus elbow R-C scores of multi-joint neurons.

Fig. 7. Prediction of multi-joint activity from constituent single-joint activities. \(A, B\): relationships of predicted multi-joint activities from the linear \((A)\) and vector \((B)\) summation models versus actual multi-joint activity observed across all neurons with significant directional tuning. \(C, D\): relationships of predicted versus actual multi-joint activities in the sub-set of multi-joint neurons. Closed circles, neurons whose multi-joint activity does not differ significantly from linear \((A, C)\) and vector \((B, D)\) summation; open circles, neurons whose multi-joint activity differs significantly from the predicted activity.
Fig. 8. Exemplar patterns of directional tuning. A–D: four exemplar neurons with different patterns of directional tuning. Each panel consists of three different sub-panels. The left sub-panels illustrate linear plots of overall activity versus joint-torque angle. Unloaded baseline activity and cosine fits are shown as dotted and dashed lines respectively. The middle and right sub-panels respectively show polar plots of overall activity and torque-related activity (baseline removed) in joint-torque space. SF = 0°, EF = 90°, SE = 180°, EE = 270°.

Fig. 9. Properties of directional tuning in joint-torque space. A: circular histogram showing the distribution of PTDs in joint-torque space. Bin width = 15°. Solid line indicates the preferred-torque axes of the bimodal distribution (141-321°). B–D: linear histograms showing the distributions of torque-slopes (B), Ir values (C), and E-I scores (D). E: relationship between Ir and E-I scores. All panels include only those neurons with significant directional tuning in joint-torque space (bootstrap statistic, $P < 0.01$).
Figure 1
Figure 3
Figure 4
Figure 5

A

Shoulder Neurons

B

Elbow Neurons

Figure 5
Figure 6
Neuron 11531b: PD = 6°, Gain = 129 (spikes/s)/Nm, E-I score = -0.02

Neuron 33171b: PD = 176°, Gain = 45 (spikes/s)/Nm, E-I score = -0.73

Neuron 32441a: PD = 109°, Gain = 70 (spikes/s)/Nm, E-I score = 1.11

Neuron 12811a: PD = 218°, Gain = 52 (spikes/s)/Nm, E-I score = -0.54
Figure 9