Random change in cortical load representation suggests distinct control of posture and movement

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Accurately maintaining a fixed limb posture and quickly moving between postures underlies both everyday skills, including holding and lifting a cup of coffee, and expert skills, such as an Olympic wrestler's holding and throwing an opponent. A fundamental question in limb motor control is whether the brain manages these contrasting goals of posture and movement through a single, robust control process or whether each engages a specialized control process. We addressed this question by examining how individual neurons in the primary motor cortex of macaque monkeys represent mechanical loads during posture and movement tasks. Notably, approximately half of the neurons that expressed load-related activity did so exclusively during either posture only or movement only. Further, those neurons with load-related activity during both tasks randomly switched their magnitude of response between tasks. These random changes in load representation suggest specialized control processes, one for posture and one for movement.

A fundamental and unresolved question in motor control research is whether posture and movement involve similar[1–4] or specialized[5–7] neural control processes. The use of a similar control process has the advantage of generality and conserved neural circuitry. This is exemplified by equilibrium point control[1,4], in which movement results from shifts in postural references with the detailed force requirements delegated to peripheral reflex control and intrinsic muscle stiffness. In contrast, using specialized control processes for posture and movement tasks has the advantage of context dependency and flexibility, as exemplified by using multiple internal models[5,8] or an optimal feedback controller[9,10], but requires circuitries with greater functional dedication and expertise. Determining which strategy is used by an organism is basic to understanding both posture and movement control and to explaining how the limb motor system weighs the conflicting requirements of generality and flexibility.

Behavioral evidence bearing on this question has been equivocal, with researchers disagreeing whether the modulation of limb stiffness during movement[3,11,12], motor adaptation to new movement-dependent forces[4,6,13,14] and patterns of movement accuracy[7] reflect the operation of distinct control processes or of a more unified and robust control process that supports both posture and movement. Likewise, changes in reflex[15,16] and perceptual function[17] have been observed between posture and movement, but these data cannot indicate how descending motor commands treat these distinct tasks.

A more direct approach is to analyze the underlying neural commands during motor control such that as in primary motor cortex (M1), the principal cortical region for voluntary motor execution[18,19]. Researchers have observed changes in the activity of individual M1 neurons during different hand grips[20], between ramp and hold movements and ramp and hold isometric forces of the wrist[21], and between whole-limb isometric and movement tasks[22]. However, these alterations in neuron activity could have reflected many different factors, including changes in the musculature involved in the task or changes in movement kinematics.

Appropriately comparing neural processing during posture and movement is difficult because the two tasks involve inherently different kinematics—one is stationary and the other is moving. This difficulty can be resolved by instead comparing the neurons' representations of mechanical loads, a salient non-movement feature, during posture and movement tasks. Previous work has shown that load-related activity in M1 is highly predictable between single- and multijoint loads in both posture[23] and movement[24] tasks, suggesting that a neuron's role in motor control remains invariant within posture tasks and within movement tasks. If individual neurons also maintain a similar role across movement and posture tasks, then their responses to mechanical loads should be invariant across tasks. In contrast, substantial changes in load-related activity between tasks would indicate a shift in the neurons' role in each task. In two experiments, we observed significant changes in M1 neurons' load-related activity between posture and movement tasks, providing evidence for specialized control of posture and movement.

RESULTS

Experiment 1: Separate posture and reaching tasks

In this study, 94 M1 neurons associated with proximal forelimb control were recorded from four monkeys (monkeys A–D, $n = 26, 24, 31$ and 13, respectively) during separate posture and reaching tasks involving joint-based load compensation (Methods). Each task was performed

while the monkeys wore a robotic exoskeleton (KINARM) that allowed planar limb motion and could apply mechanical loads to the shoulder and elbow joints independently[25]. In the posture task, monkeys kept their hand at a central target while countering constant loads applied to the shoulder, elbow, both or neither joint[23]. In the reaching task, monkeys moved their hand from a central target to a peripheral target while countering resistive velocity-dependent loads applied to the shoulder, elbow, both or neither joint[24]. Because the monkeys were trained to achieve similar limb kinematics under various load conditions, any changes in neural activity between conditions
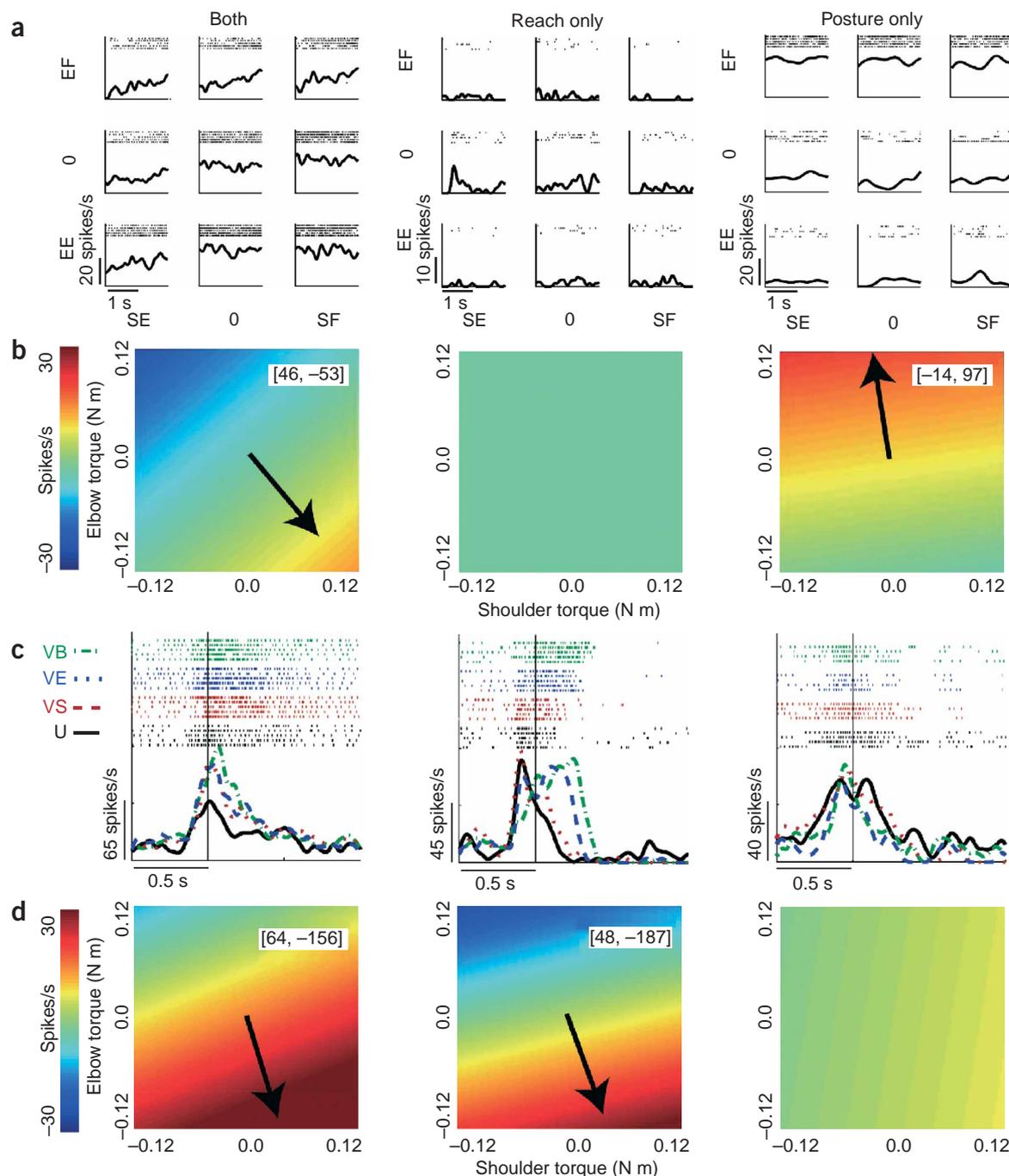
Figure 1 Neural activity of three cells during posture and reaching tasks. (**a–d**) Vertical columns show sample neurons expressing load-related activity during both tasks, reaching only and posture only: left, B59; middle, B34; right, A21. (**a**) Spike rasters and mean instantaneous firing rate under the nine load conditions of the posture task in a muscle-torque coordinate frame, shoulder extensor (SE) and flexor (SF) torques vs. elbow extensor (EE) and flexor (EF) torques. 0, no muscular torque. (**b**) Plane fits of ratio of change in neural activity to change in muscle torque during the posture task. Neuron's response gain and direction are indicated by strength and direction of the plane's color gradient; arrows and plane coefficients clarify and denote significant plane fit ($P < 0.01$). (**c**) Spike rasters and mean instantaneous firing rate under four viscous load conditions during reaching to a single target: VB, both; VE, elbow; VS, shoulder; U, unloaded. Data are for target direction closest to the cell's preferred direction in hand space during unloaded condition. Vertical line, start of movement. (**d**) Plane fits of ratio of change in neural activity to change in muscle torque during reaching task (format as in **b**).

reflect influences of the mechanical load (**Supplementary Note** and **Supplementary Fig. 1** online).

As observed previously[21,26–29], M1 neurons expressed a wide range of responses to the loads. In both tasks, roughly half the cells showed significant load-related responses (posture task: 50/94; reaching task: 53/94); this was determined by analyzing their change in activity during the loaded conditions relative to the unloaded condition with a planar regression model, $P < 0.01$ (Methods). The absolute magnitude of these responses, or response gain, ranged from very low to high firing rates (posture task, $1-152$ Hz·N^{-1}·m^{-1}; reaching task, $16-194$ Hz·N^{-1}·m^{-1}). Likewise, the neurons varied in what load direction evoked the largest response, termed the response direction, as a neuron could express changes in discharge preferentially related to elbow loads, shoulder loads or both. In both tasks we observed a nonuniform representation of response directions biased toward whole-limb flexion and extension muscle torques (Rayleigh bimodal test: $P < 0.01$ and $P < 0.001$, respectively)[23].

If these load-related neurons formed a single cortical controller for both posture and movement, they should have similar load-related activity in both tasks. Instead, we observed a broad breakdown among each possible category: load-related activity during posture only (21/94), reaching only (24/94), both tasks (29/94) and neither task (20/94), (**Figs. 1 and 2a**). Notably, most neurons that were load-related only during the posture task were also tuned to the direction of hand motion during reaching (16/21, 76%); that is, these neurons were systematically modulated during reaching, but were insensitive to the task's mechanical requirements (**Fig. 1**, right column). Additionally, the observed categorical breakdown among neurons did not mirror that of the proximal forelimb muscles. Virtually all shoulder and elbow muscles (97%) expressed some load-related activity and a larger percentage of these (64%) were load-related in both tasks than for M1 neurons (34%) ($\chi^2 = 16.9$, $P < 0.001$; **Fig. 2a**).

We examined the response gain and response direction of neurons with load-related activity in both tasks to assess several putative relationships between neural activity and behavior. Similarity in response gain and response direction would suggest an underlying tight association in the control of the two tasks. In contrast, random changes in both response gain and response direction tuning would suggest a more labile, and consequently complex, link between cortical processing and the motor periphery. Lastly, random changes in response gain paired with invariance in response direction would suggest that neurons maintain a constant relative association to a portion of the motor periphery (that is, shoulder, elbow or some combination of the two), but with an absolute contribution that varies with the behavioral context.

Similarity in response gain was assessed by a linear correlation of the gains measured for each task; a high or low correlation indicates that the neurons make a similar or random contribution across tasks, respectively. We found negligible intertask gain correlations when we examined neurons tuned in either task or those tuned in both tasks ($r_{either} = 0.02$, $P > 0.05$; $r_{both} = 0.13$, $P > 0.05$; **Fig. 2b**). Therefore, the absolute contribution of individual neurons varied greatly across posture and movement tasks; alternative measures of neural gain also produced very low correlations across tasks (**Supplementary Note** and **Supplementary Fig. 2** online).

Response direction was assessed by subtracting each cell's response direction in the posture task from its response direction in the reaching task. If response directions were maintained between tasks, then their absolute angular difference would be smaller than that of random pairings. Notably, and in contrast to what was observed for response gain, we found a neuron's response direction is generally conserved across tasks (mean absolute difference = 52° versus random $\sim 90°$, bootstrap $P < 10^{-4}$; **Fig. 2c**).

The observed difference in the neurons' intertask gain and direction correlations did not reflect a difference in the reliability of the measures, as both showed high intratask reliability (**Supplementary Note** and **Supplementary Fig. 3** online). Also, the neural responses did not entirely parallel the muscular responses. Unlike the neurons, both response gain and direction were conserved between posture and movement in muscles (response gain: $r_{both} = 0.81$, $P < 0.001$; response direction: mean absolute difference = 28° versus random $\sim 90°$, bootstrap $P < 10^{-4}$). Muscular response gains were also higher during the reaching task, presumably to compensate for the force-velocity relationship of muscle[30,31] (slope = 3.45, $P < 0.001$). Therefore, neurons retained a constant relative association with the motor periphery, although their absolute contribution was highly variable between tasks.

Experiment 2: Integrated posture and reaching task

In the experiment described above, we perturbed the monkey's limb with constant and viscous loads during the posture and reaching tasks, respectively. Consequently, our observation of a substantial change in load representation could have arisen from either a difference between the two tasks *per se* or a difference in the two types of loads
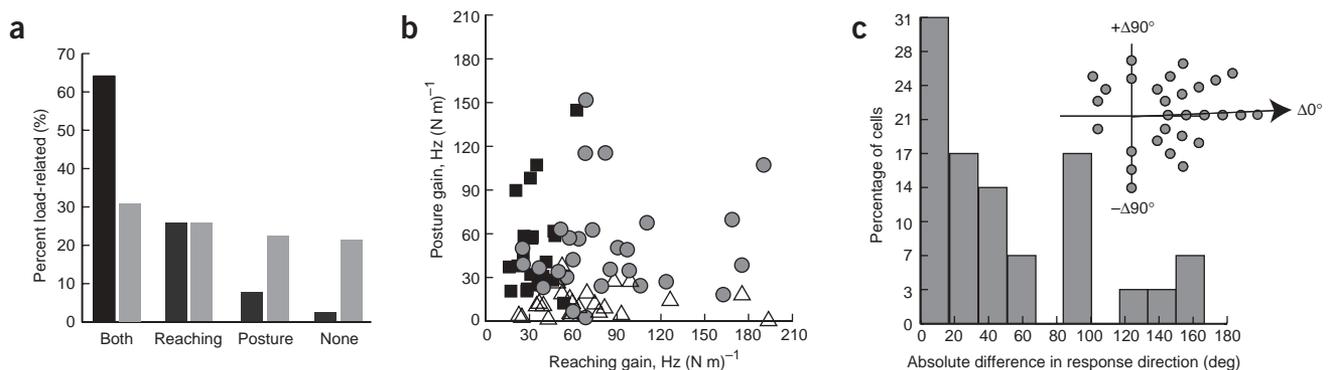

Figure 2 Load sensitivity of proximal forelimb muscles and M1 neurons during posture and reaching tasks. (**a**) Percentage of muscles and neurons with load-related activity. Gray bars, neurons; black bars, muscles. (**b**) Correlation of response gain of neurons between the reaching and posture tasks: gray circles, open triangles and black squares denote neurons with load-related responses during both tasks, reaching only and posture only, respectively. (**c**) Histogram of absolute difference in response direction between posture and reaching tasks. Inset, polar histogram of signed difference in response direction between posture and reaching tasks; arrow indicates mean change in direction.

used. Possibly one neural population was primarily sensitive to constant loads whereas another was primarily sensitive to viscous loads. Separate representations for different types of mechanical loads would allow a flexible control strategy and is consistent with some human behavioral studies[8,32–34].

We addressed this possibility with an experiment involving a single type of mechanical load applied during both posture and movement (monkey D, $n = 95$). In each trial the monkey countered a constant load applied to the shoulder, elbow, both or neither joint during a prereach postural period and continued to counter this constant load while reaching from the central target to one of two peripheral targets (see Methods). By comparing each neuron's load-related activity during a 1-s premovement postural period (epoch 1) with a 200-ms sliding window (epoch 2), we could observe how load-related activity evolved between behavioral contexts.

As before, we found exemplar neurons with load-related activity only during posture, only during reaching, during both periods and during neither period (**Fig. 3**). These across-epoch categorizations were summarized with a similarity score between 1 and –1. Akin to a categorical correlation, a similarity score of 1 signified that all neurons

were load-related in both epochs or not load-related in both epochs. In contrast, a score of 1 signified that all neurons 'flipped' their contribution between epochs, being load-related during one epoch and not load-related in the other (**Fig. 4a**).

Not surprisingly, the similarity score, response gain correlation and response direction correlation remained high before target onset because the two epochs overlapped in time. Then, during the reaction time period, the similarity score rapidly decreased to a value similar to random chance throughout the movement time period (bootstrap $P > 0.01$). The correlation in response gain between the two epochs also showed a corresponding drop during the reaction time period (**Fig. 4b**, solid line). In contrast, response direction was highly conserved across the reaction and movement time periods (**Fig. 4b**, dashed line). Near the end of the movement, the similarity score gradually returned close to its initial value, although the correlation in response gain did not reach premovement levels. That is, cells which expressed load-related activity at the central posture also tended to have load-related activity at the peripheral postures but with an altered response gain, probably owing to the influence of arm position[28,35]. The response direction at the peripheral
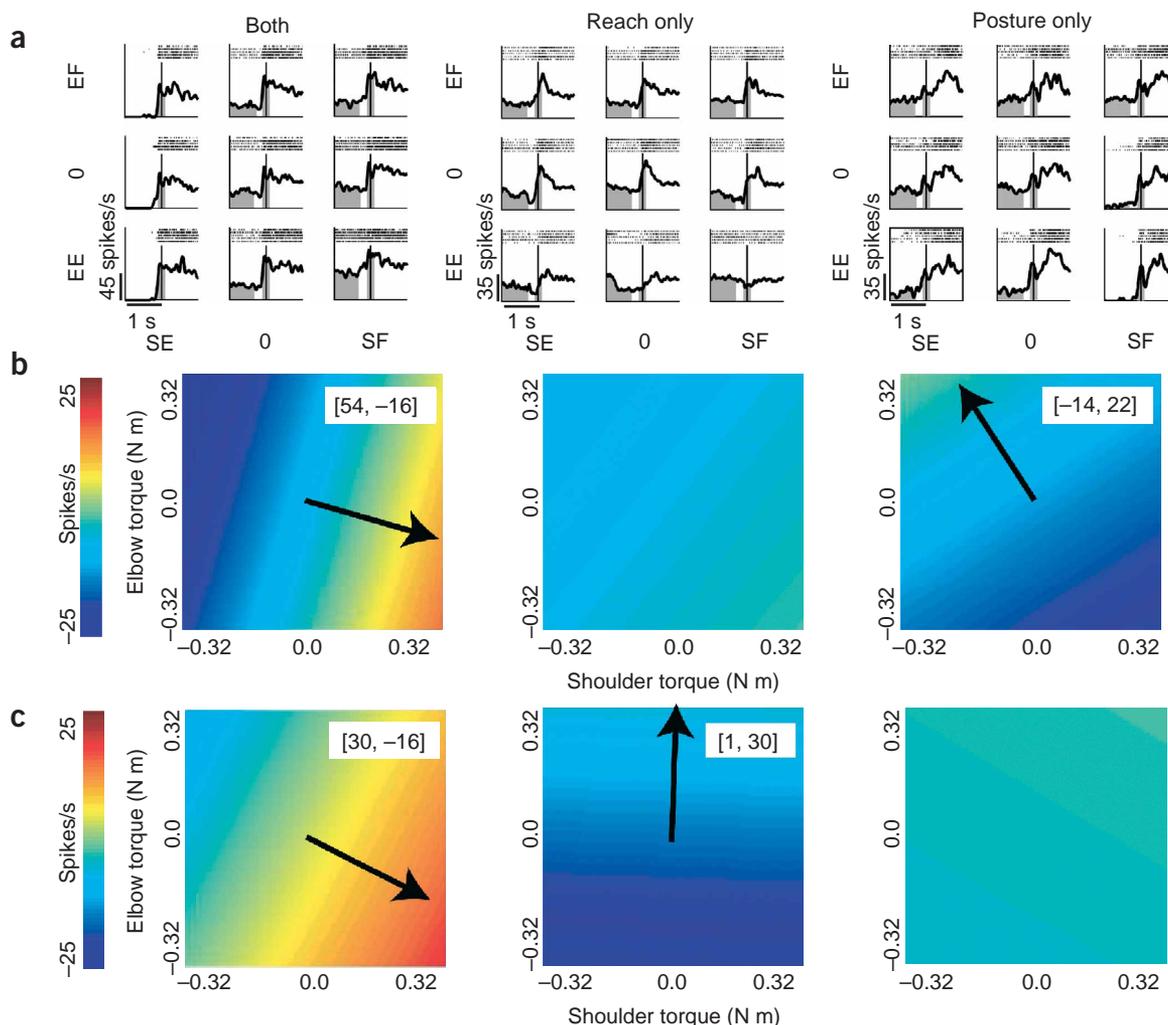

Figure 3 Load-related activity across posture and reaching periods with constant-magnitude load. (**a–c**) Vertical columns indicate exemplar neurons expressing load-related activity during both task periods (left: neuron D729_3e), only during the reaching period (middle: neuron D756_4e), and only during the posture period (right: neuron D724_4b). (**a**) Same format as **Figure 1a**. Vertical lines indicate movement onset; shaded regions denote posture and movement epochs used for plane fits displayed in subsequent panels. (**b,c**) Indicated plane fits during the posture and reaching epochs, respectively. Same format as in **Figure 1b**.

Figure 4 Running analysis of load-related activity during posture and movement. (**a,b**) Relationship between a fixed 1,000-ms premovement posture epoch and a sliding 200-ms epoch during Experiment 2. Left vertical line, gray window and central vertical line indicate average target onset, average movement time and average time of peak hand velocity, respectively. Horizontal error bars indicate standard deviations. (**a**) Thick vertical solid line denotes the measured similarity score. Thin solid and dashed horizontal lines denote the predicted mean similarity score and its confidence intervals ($P < 0.01$) for a random distribution between the two epochs. (**b**) Correlation of response gain (thick vertical solid line) and response direction (dashed line) across time for a cell tuned in both epochs. Mean vector length was used as a measure of angular correlation[45].
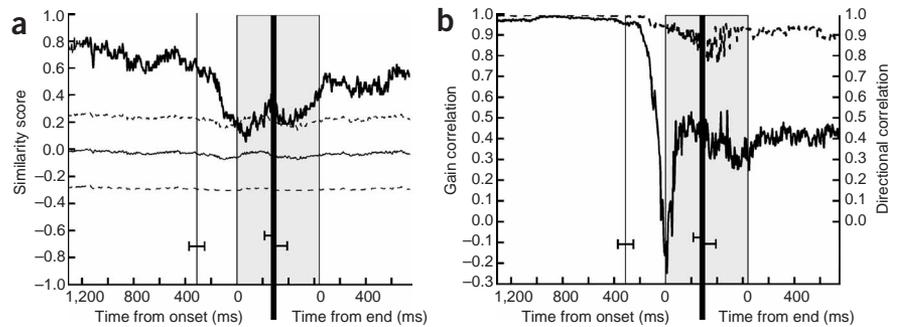
postures was highly correlated with the response direction at the central posture.

Notably, the one study[28] that had used a constant (hand-based) load during a posture and movement task reported high correlations in both direction and gain when the entire movement time (gain, $r_{MT} = 0.51$–0.86 across monkeys) or the combined reaction and movement time (gain, $r_{RT+MT} = 0.65$–0.90) were analyzed. However, early reaction-time and late movement-time activity can relate to postural control before and after movement, respectively[36], and when we used similar time windows, we also observed elevated gain correlations ($r_{MT} = 0.4$ and $r_{RT+MT} = 0.58$).

In summary, M1 neurons maintain a constant relative association with the motor periphery during both posture and movement, but their absolute contribution varies randomly across these behavioral contexts.

DISCUSSION

In this study we found a profound shift in load-related cortical processing during posture and movement, providing direct evidence for distinct control processes underlying the two behaviors. In the extreme, individual neurons can provide exquisite information on mechanical loads during posture and only reflect kinematic features during movement. These data are inconsistent with the notion that the control of movement is generated by shifts in positional control. Rather, there is an abrupt switch in neural processing in M1 starting just before the transition from a stationary posture to movement, consistent with task-dependent control strategies such as multiple internal models[5,8] and optimal feedback control[9,10]. It is likely that this change in neural processing is linked to previous observations that cortical field potentials are phase-locked to muscle field potentials during posture and diminish markedly upon movement[37].

It was possible that a task-dependent change in neural processing in M1 would invoke distinct and dedicated populations of neurons. For example, the observation that neurons can be qualitatively categorized as 'phasic' or 'tonic' in nature[21] could be assumed to reflect the fact that those in the former class are involved in dynamic control and those in the latter class in postural control. If posture and movement were supported by only two unique sets of neurons, the similarity score we obtained (**Fig. 4a**) should have become strongly negative during movement, reflecting a flip between these unique neural populations. Instead, the similarity score hovered within random levels during movement, reflecting the comparable presence of neurons expressing load-related activity exclusively to one task and those with load-related activity in both or neither task.

Most notably, those neurons with load-related activity in both tasks expressed random changes in their response gain, and hence their absolute contribution, between tasks. This random gain change strongly supports the notion of distinct control processes for posture and movement. Although it has been demonstrated that postural gain can change depending on the expected range of forces, this effect is modest and appears to be a systematic rather than a random change across conditions[29].

In contrast to the random change in response gain across posture and movement, the present work also illustrates that the response direction—that is, the preferred direction in muscle-torque space—was highly conserved across conditions. For example, if a neuron increases its activity for elbow flexor loads but is unresponsive to shoulder loads during posture, then this relative pattern of load-related activity is retained during movement. This invariance in response direction tuning would be expected if neurons maintained a fixed relative association with a group of limb muscles[38,39].

The present load-compensation protocol exposed a task-dependent change in the motor network for posture and for movement control. Future studies could use analogous load-compensation paradigms to determine whether M1 or other brain regions express additional task-dependent networks—possibly underlying rhythmic[40] or tracking limb motions.

With regard to clinical relevance, specialized control of posture and movement may explain why some neurological disorders result in difficulties associated with only one of the two states, or with transitions between these states, as with different types of tremors[41] and Parkinson disease[42], respectively. Practically, this work illustrates a potential challenge for developing neuroprosthetics to guide artificial motor actions. Whereas cortex-driven prostheses traditionally assume a fixed correlation between neural activity and motor output[43,44], shifts in load representation across behavioral tasks suggest that using a single algorithm would be suboptimal. Separate algorithms may be necessary to associate neural activity related to posture and to movement as well as a decisional process to identify transitions between behavioral contexts.

METHODS

Experiments. Four male rhesus monkeys (*Macaca mulatta*, 6–12 kg) were treated according to approved guidelines of the Queen's University Animal Care Committee. The monkeys were trained to counter flexion and extension loads applied at the shoulder and elbow joints by a robotic exoskeleton (KINARM, BKIN Technologies, Kingston, Canada) that allowed horizontal planar movement[25]. The entire limb remained visible, and the start and target

positions were presented as small circles in the movement plane through a virtual reality system.

Experiment 1 involved separate posture and reaching tasks as described in previous studies[23,24]. Posture task: monkeys maintained their right hand within the central target window (0.8-cm radius) for ~3 s while countering a constant flexion or extension torque at the shoulder, elbow, both or neither joint (monkeys A–C, ±0.12 N·m; monkey D, ±0.32 N·m). A total of 9 load conditions were presented in a pseudorandom block design, with each block repeated 5 times, for 45 trials total. Reaching task: monkeys moved their right hand from a central start window to eight (or, for monkey C only, two) peripheral targets (1-cm radius) distributed radially, with equal amplitude (6 cm) within 220–350 ms. Targets were presented in a pseudorandom block design, with each block repeated 6 (or 10) times, for 48 (or 20) trials total, respectively. In each reach set, the monkeys countered a velocity-dependent torque that impeded joint motion at the shoulder, elbow, both or neither joint (0.2 N·rad·m·s^{-1}). Load conditions were presented in a blocked design with a pseudorandom order between targets, which allowed the monkeys to adapt to each load after the first block; the initial trial was dropped from analysis. Monkeys A–C reached under all load conditions, whereas Monkey D reached in the 'no load' and 'both joints loaded' conditions only.

Experiment 2 (monkey D only) involved a combined task with both postural and reaching periods. Constant torques identical to those used in the earlier posture task in Experiment 1 were used (±0.32 N·m) while the monkey maintained his right hand at the start position for ~2 s, then reached to one of two targets (at 90° and 270°), and finally maintained his position at the target for another ~1.5 s. The 18 load conditions (9 loads for each target) were presented in a pseudorandom block design with each block repeated 5 times for a total of 90 trials per set.

Cell and muscle recording. Standard neurophysiological techniques were used for extracellular recordings in the shoulder-elbow region of M1 (refs. 24,28).

Electromyographic activity of proximal forelimb muscles was recorded in all four monkeys during Experiment 1. These included percutaneous and chronic recordings, for a total of 39 samples (see **Supplementary Note**).

Data analysis. Neuron and muscle activity were quantified by the mean change in spike rate and mean change in rectified voltage between the loaded and unloaded conditions for each task. In Experiment 1, the posture task used activity from final 2 s of hold; the reaching task used activity from movement onset to peak hand velocity. In experiment 2, epoch 1/premovement postural period used activity from 1,000 ms prior to target onset; epoch 2/sliding window used activity from the 200-ms window that was successively shifted in 5-ms steps across the pre-, peri- and postmovement time periods.

Muscle torque was estimated using the equations of motion for a two-joint system including the influence of mechanical properties of the limb and robotic device[25]. In all tasks, changes in muscle torque were calculated as the difference in mean elbow and shoulder muscle torque relative to the unloaded condition. For Experiment 2, we examined the load-related activity for the target that elicited the highest activity during unloaded reaching owing to the coupling of a neuron's preferred hand direction and load sensitivity[24].

Load-related responses were assessed by a plane-fit of the change in neuron and muscle activity versus the change in shoulder and elbow muscle torque; acceptance level was $P < 0.01$. The shoulder (S) and elbow (E) slope coefficients yielded two measures used throughout the experiments: response direction ($\mathrm{atan}(E/S)$) and response gain ($(E^2 + S^2)^{1/2}$). We performed a number of tests to ensure that both measures were highly reliable (see **Supplementary Note**). Further, several alternative measures of response gain and response direction provided similar results (see **Supplementary Note**). The similarity score obtained in Experiment 2 (**Fig. 4a**) was defined as the number of cells that retained the same load-related activity as flagged by the plane-fit (both and neither sensitive) minus the number of cells sensitive to loads in only one of the epochs (epoch 1 only and epoch 2 only) divided by the total number of cells. Mean and confidence interval for a random similarity score were derived from the χ^2 statistic, $P < 0.01$.

When comparing neural processing across tasks we used standard linear correlations for the response gain measure and bootstrapped circular analyses for the response direction measure. The bootstrap analysis randomly compared the measured mean absolute angular difference from that obtained by 10,000 random repeat reassignments[45], and also calculated the circular correlation as the mean vector length of the response directions[45] (**Fig. 4b**).

Note: Supplementary information is available on the Nature Neuroscience website.

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