Changes in the Temporal Pattern of Primary Motor Cortex Activity in a Directional Isometric Force Versus Limb Movement Task

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Sergio, Lauren E. and John F. Kalaska. Changes in the temporal pattern of primary motor cortex activity in a directional isometric force versus limb movement task. *J. Neurophysiol.* 80: 1577–1583, 1998. We recorded the activity of 75 proximal-arm-related cells in caudal primary motor cortex (MI) while a monkey generated either isometric forces or limb movements against an inertial load. The forces and movements were in eight directions in a horizontal plane. The isometric force generated at the hand increased monotonically in the direction of the target force level. The force exerted against the load in the movement task was more complex, including a transient decelerative phase during the movement as the hand approached the target. Electromyographic (EMG) activity of proximal-arm muscles reflected the task-dependent changes in dynamics, showing a ramp increase in activity during the isometric task and a reciprocal triphasic burst pattern in the movement task. A sliding 50-ms window analysis showed that the directionality of the EMG, when expressed in hand-centered spatial coordinates, remained stable throughout the isometric ramp but often showed a significant transient shift during the limb movements. Many cells in M1 showed corresponding significant changes in activity pattern and instantaneous directionality between the two tasks. This momentary dissociation of discharge from the directional kinematics of hand displacement is evidence that the activity of many single proximal-arm related M1 cells is not coupled only to the direction and velocity of hand motion.

INTRODUCTION

Many studies showed that primary motor cortex (MI) cell activity is often correlated to parameters of task dynamics or kinetics under isometric conditions in single-joint tasks (Ashe 1997; Cheney and Fetz 1980; Evarts 1969; Humphrey and Tanji 1991) and in whole arm tasks (Ashe 1997; Georgopoulos et al. 1992; Sergio and Kalaska 1997; Taira et al. 1996). Similarly, the covariation of discharge of many MI cells with the direction of external loads acting on the arm during reaching movements (Kalaska et al. 1989) suggests that kinetic parameters of motor output are also represented in MI during reaching. If so, the laws of motion predict that movement-related cell activity should show a good relation to the time course of hand acceleration. However, the only study to test this prediction during reaching found only modest correlations with acceleration (Ashe and Georgopoulos 1994). In contrast, MI single-cell activity was frequently correlated with other spatial kinematic parameters of handpaths, including the direction and velocity of hand movement and target distance (Ashe and Georgopoulos 1994; Fu et al. 1995; Georgopoulos et al. 1982; Kalaska et al. 1989; Schwartz 1992; Schwartz et al. 1988). Therefore published studies to date would appear to suggest that the representation of motor actions in MI is better correlated with task kinetics under isometric conditions and with task kinematics under movement conditions. However, the validity of this apparent task dependence has not been confirmed experimentally. No study has compared the activity of the same MI cells during both whole-limb isometric and reaching tasks with similar spatial (i.e., directional) behavioral constraints and with direct measures of the output forces at the hand. The present study attempts to fill this void.

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METHODS

A juvenile male rhesus monkey (*Macaca mulatta*, 5 kg) was trained to perform both an isometric force task and a limb-movement task against an inertial load. The isometric force task is described elsewhere (Sergio and Kalaska 1997). Briefly, the animal exerted a force with its right arm against a handle attached to a 6-df force/torque transducer (Assurance Technologies, F3/T10 system) placed in front of him. In the movement task, an identical handle/force transducer assembly was housed in the base of a 1.6-m long weighted pendulum. The weight of the transducer assembly was 1,300 g, and that of the pendulum plus transducer was 2,600 g. An emitter attached to the pendulum base allowed a sonic digitizer (Science Accessories, model GP-9) to measure the *x*-*y* position of the base at 55 Hz with 0.1-mm resolution. The monkey's starting hand location in the movement task was identical to that in the isometric task.

A computer monitor was positioned at eye level 60 cm in front of the monkey. In the isometric task, a cursor displayed on the monitor gave continuous feedback corresponding to the current force level applied to the force transducer in the *x*-*y* (horizontal) plane. At the start of each trial, a circle appeared at the center of the monitor, and the monkey generated a small static force (0.3 N) away from its body to position the cursor within the central force target for a variable period of time (1–3 s). The central target then disappeared, and one of eight peripheral force targets (0.28 N diam) arrayed in a circle around the central target appeared. The separation of the centers of the central and peripheral targets corresponded to a 1.5 N change of force. The monkey generated a force ramp in the indicated direction to displace the cursor into the peripheral target and hold it there for 2 s. Target directions were spaced at 45° intervals, starting from 0° (directly to the right) and rotating counterclockwise. The eight targets were repeated five

times in a randomized-block design. These 40 trials comprised one data file.

An identical sequence was followed in the movement task, but the cursor position now indicated the *x-y* location of the pendulum base. The monkey had to push the pendulum slightly away from its body to position the cursor in the central target. Movements of 8 cm were required to displace the cursor from the central to the peripheral targets. The force exerted by the monkey as it held the weighted pendulum at the peripheral targets ranged from 0.75 to 1.2 N.

For both tasks, a deviation of force in the vertical (z) direction of more than ± 0.26 N throughout the trial resulted in an error, and the trial would restart. In this way the animal produced force trajectories confined to a horizontal plane ($\pm 10°$).

Conventional single-unit recording techniques were used to record the activity of single cells in MI during the tasks (Kalaska et al. 1989). Data were collected from cells related to shoulder girdle, shoulder, and elbow movement, identified on the basis of their response to passive limb manipulation and by microstimulation at the recording site. The order in which the monkey performed the two tasks varied from cell to cell.

Four sequential behavioral epochs were defined in both tasks. Center hold time (CHT) ended when the peripheral target appeared. Reaction time (RT) was the interval between presentation of the peripheral target and the first significant change in force applied to the transducer. Movement time (MT) ended when the cursor first stabilized at a constant force level or spatial position within the peripheral target circle. Target hold time (THT) was the remaining period of static hold in the target window.

Data comprising mean single-trial firing rates from two epochs, RT and MT, were analyzed with the use of a repeated-measures analysis of variance (ANOVA) to test for a significant main effect of direction and task and for direction-task interactions ($P < 0.01$, 5V program, BMDP Statistical Software, Los Angeles, CA).

In addition, a temporal analysis of directional tuning was performed on a trial-by-trial basis. Spike data were aligned to the moment of force onset (i.e., end of RT epoch) for all trials in each task. Cell discharge rate, including partial spike intervals, was then calculated within a 50-ms sliding time window at a fixed time interval relative to force onset for each trial. The cell activity within the window for the 40 trials in each task was tested for a significant relation to direction (ANOVA, $P < 0.01$), and the instantaneous preferred direction (PD) of the windowed activity was calculated for the complete data set of 40 trials (Mardia 1972). A bootstrapping procedure was then used to estimate the 95% confidence interval (CI) for the instantaneous PD of the complete windowed data set. We generated an estimate of the directional tuning curve of the cell by random selection of the discharge rate in one of the five single-trial windows in each of the eight directions. Next, the PD of that randomly selected tuning curve was calculated. This was repeated 100 times to generate a distribution of 100 bootstrapped PDs. The absolute difference of each bootstrapped PD from the instantaneous PD of the complete windowed data set was calculated, and these 100 differences were rank ordered. The 95% CI was defined as the sixth largest PD difference. The evolution of the directional tuning of each cell's activity was studied by advancing the sliding window in 10-ms steps, beginning 200 ms before force onset and ending 1,200 ms after force onset, during the period of static hold of the cursor at the peripheral target.

To assess the effects of task dynamics on motor output, task-related activity was recorded from a total of 16 shoulder and elbow muscles. Muscles were implanted percutaneously with the use of Teflon-coated single-stranded stainless steel wires during separate recording sessions. The muscles studied were biceps brachii, brachialis, deltoid (anterior, medial, and posterior heads), dorsoepitrochlearis, infraspinatus, latissimus dorsi, pectoralis, subscapularis, supraspinatus, teres major, trapezius (rostral and caudal heads), and triceps brachii (long and medial heads). The methods used to process the electromyographic (EMG) activity are described elsewhere (Sergio and Kalaska 1997). A temporal analysis of the directional tuning of muscle activity between the two tasks was performed in the same manner as for cell data.

RESULTS

Task performance

The directionality of the *x-y* trajectories of hand movements and isometric forces in the two tasks was very similar (Fig. 1), without abrupt directional shifts or large inflections in velocity profiles. This similarity indicates that the animal produced comparably smooth changes of the experimentally controlled variable in each task (output force at the hand, or hand displacement) to displace the cursor between targets.

In contrast, the temporal profile of the forces measured at the hand differed between tasks. A temporal force profile was calculated as the component of the force resolved along the axis of target direction, averaged across all five trials in that direction. In the isometric task, the force profile consisted of a ramp increase in the direction of the target force level (Fig. 1*A*). The force profile in the movement task was considerably more complex, including first an accelerative pulse, then a decelerative phase, and finally a static force level required to hold the pendulum over the peripheral target (Fig. 1*B*).

Neural activity

Cell activity was recorded in the anterior bank of the central sulcus in the left MI. To be included in the data sample, a cell had to be related to movements of the proximal arm (see METHODS) and directionally tuned in at least one of the tasks. Complete data sets in both tasks were collected from 75 cells. All cells tested were active to one degree or another in both tasks. There was no evidence of significant populations of cells that were preferentially related to only the isometric or movement tasks.

In the isometric task, many cells showed a simple step or ramp increase in their tonic discharge at their PD (''tonic'' cells, 27/75, 36%) or a tonic increase with an initial dynamic overshoot (Fig. 1*A*, ''phasic-tonic'' cells, 21/75, 28%). Of the remaining cells, 22 of 75 (29.3%) emitted a single phasic burst in their PD or were unclassifiable (5/75, 6.7%). Cell activity typically showed a simple reciprocal phasic or tonic decrease in activity in the opposite force direction.

The activity pattern often changed between the isometric and movement tasks. Many of the 48 cells that were tonic or phasic-tonic in the isometric task changed to a more complex and fragmented response profile, characterized by a burst-pause-tonic increase pattern in their PD (Fig. 1*B*; 42/48, 87.5%; 42/75, 56% for the total sample). In addition, many of those same cells displayed a reciprocal pattern in opposing directions, including a delayed burst during the movement itself (Fig. 1*B*; 31/42, 73.8%). Moreover, 10 of 22 cells (45.4%) that were monophasic in the isometric task displayed multiple phasic bursts in their PD in the movement task. The latter cells also often emitted delayed bursts in

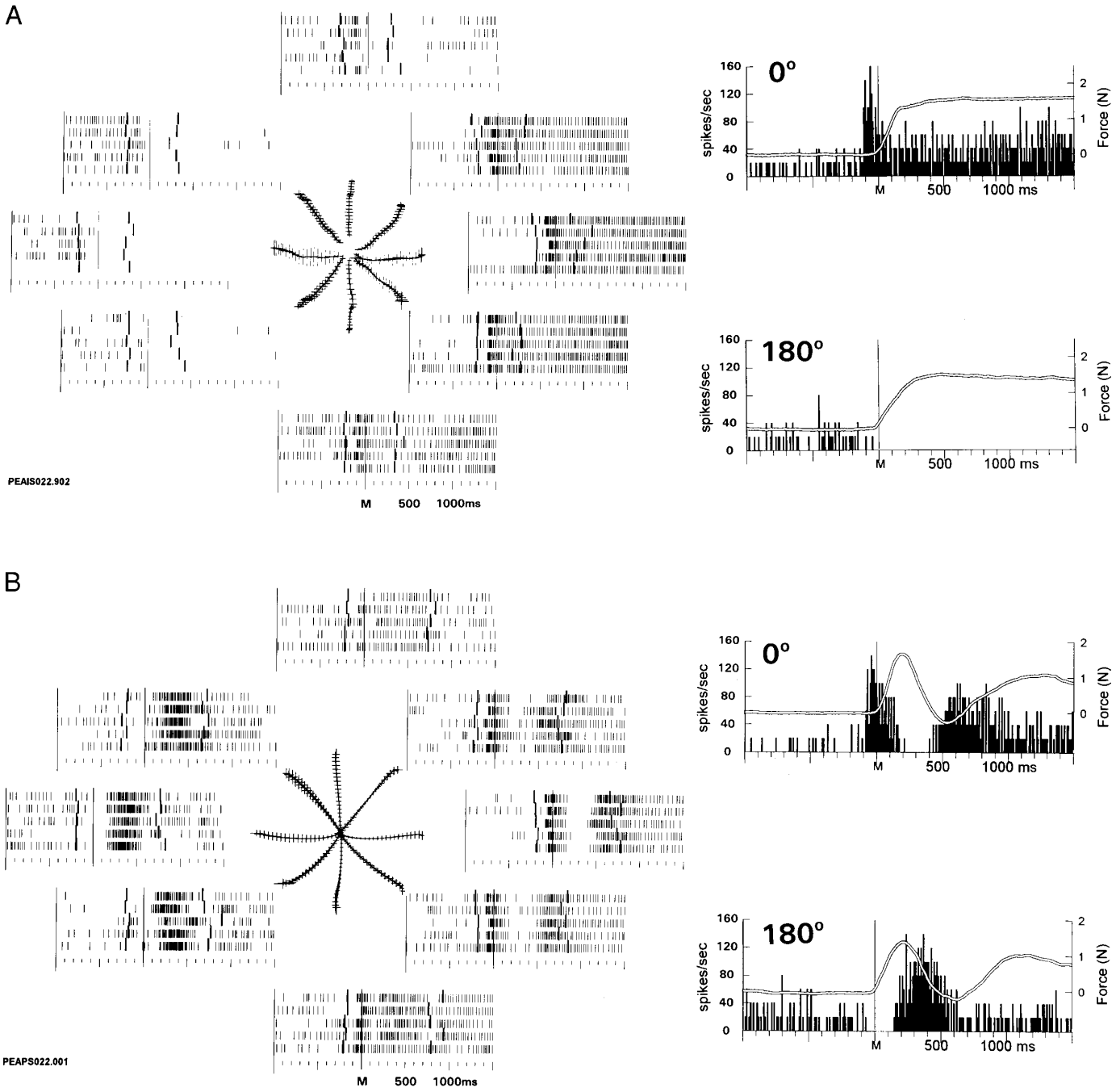

FIG. 1. Discharge pattern of a shoulder-related M1 cell during the isometric force task (*A*, *left*) and the movement task (*B*, *left*). Each raster illustrates cell activity during 5 trials, and raster location corresponds to the direction of force or movement away from the starting central target. Data are aligned on the 1st significant force change, denoted by a solid vertical line (M). For each trial, the heavy tick mark to the left of the cursor movement onset line shows the time of target onset and the heavy tick mark to the right shows the time at which the final static level of force or position within the peripheral target was attained. The mean force/movement trajectories (crosses denote SDs at 20 equidistant points) are shown at the center of the raster displays. *Panels to the right* display cell discharge in histogram format (10-ms bins) during force/movement to the right (0°) and the left (180°) with the average temporal force profile for those directions overlaid.

directions opposing their PD, which were not seen in the isometric task.

The change in the pattern of activity of the shoulder-related cell in Fig. 1 appeared to parallel the differences in force profile in both tasks. However, like all other cells, it was not simply signaling the temporal profile of force output in each task, which is uniform in all directions. Instead, the response profile of the cells varied systematically with direction (Fig. 1).

An ANOVA assessed the effect of task and direction on cell discharge (for technical reasons, one cell could not be tested). The discharge rate of most cells was significantly

affected by direction across tasks (main effect of direction) during both RT (65/74 cells, 88%) and MT (67/74, 91%). In addition, most cells showed a significant modulation of their overall discharge rate between the two tasks (main effect of task) during RT (39/74, 53%) and MT (47/74, 64%). Most notably, the number of cells whose directional properties were significantly different between tasks (task-direction interaction) increased from the RT (31/74, 42%) to the MT (65/74, 88%) epoch. The cell in Fig. 1 showed a significant main effect of direction during both RT and MT epochs but a significant effect of task and task-direction interaction only during MT. This change from RT to MT was one consequence of the increased complexity of response profiles for many cells in the movement task.

One approach that better captures the details of the temporal response pattern of activity in each task is to describe the time-varying profile of the instantaneous directionality with the use of a sliding-window analysis (see METHODS). When applied to the cell in Fig. 1, the instantaneous PD remained relatively constant throughout the trial in the isometric task (Fig. 2*A*; mean CI 31.4° from −100 to +1,000 ms relative to force onset). In contrast, the pattern of directionality was considerably more complex in the movement task, including a transient deviation of almost 180° during the movement itself (Fig. 2*B*; mean CI 31.9°).

Figure 2*C* illustrates the results of a comparison of instantaneous directionality at different times within each task and at corresponding times between the tasks for the entire cell sample. The instantaneous PD of most cells (88.7 ± 3.2%, mean ± SD of directionally related cells for each 10-ms

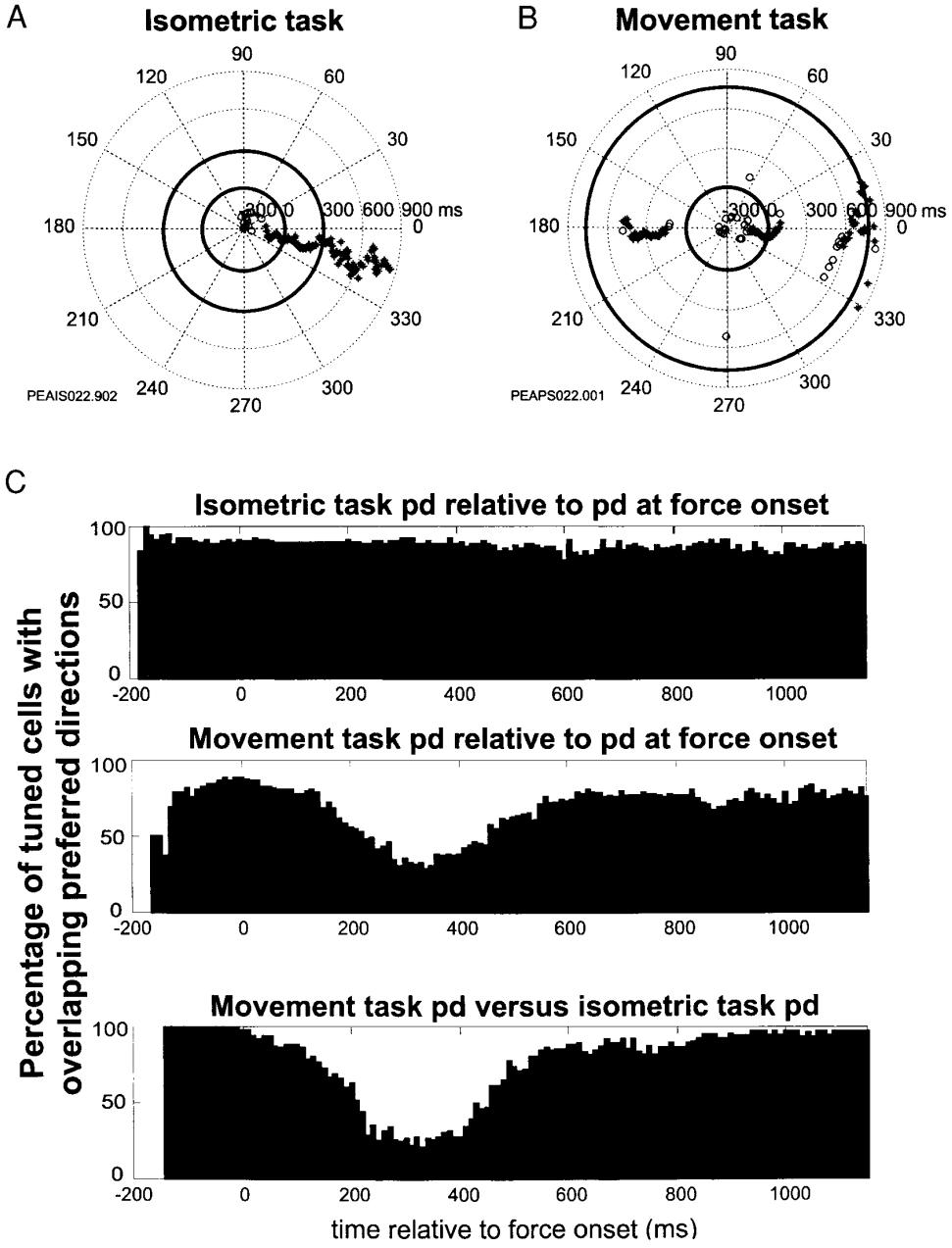

FIG. 2. Temporal trajectory of the instantaneous preferred direction (PD) of the cell shown in Fig. 1, in the isometric (*A*) and movement (*B*) tasks, determined by a 50-ms sliding-window analysis (see METHODS). Time windows within which the cell was significantly related to direction [analysis of variance (ANOVA), $P < 0.01$] are shown by an asterisk. Time windows within which the cell was not directionally related are shown by ○. Large thick circles denote movement/force ramp onset and offset. *C*, *top panel*: percentage of cells in which there was an overlap in the 95% confidence interval of the instantaneous PD in a particular window and the PD during a 100-ms reference time window centered at isometric force onset. The time (*x*-axis) denotes the start of the 50-ms time window used in the comparison. Only cells that were significantly directional (ANOVA, $P < 0.01$) in a given time window were included. *C*, *middle panel*: equivalent comparison for all cells in the movement task, using as reference a 100-ms time window centered on force onset in the movement task. *C*, *bottom panel*: percent of cells whose instantaneous PD at a given time in the isometric task does not differ significantly from the PD in the same relative time window in the movement task.

increment in the sliding window) did not differ significantly at a given time throughout the trial from their PD at force onset in the isometric task (Fig. 2*C*, *top panel*; mean CI sample 33.8°). In contrast, an increasing number of cells had an instantaneous PD during the MT epoch of the movement task that deviated significantly from their PD at force onset in the movement task, reaching a maximum of 71% of directionally tuned cells at 340 ms after force onset (Fig. 2*C*, *middle panel*; mean CI during MT 39.3°).

When the instantaneous PD was compared at the same relative time between the two tasks, the initial directionality was the same (Fig. 2*C*, *bottom panel*). During RT, 98–100% of cells had PDs that did not differ significantly (mean angular difference, 17°). However, starting at force onset, the instantaneous PD of an increasing number of directionally tuned cells differed significantly between the two tasks. The maximum mean difference of 117° occurred 330 ms after force onset, approximately halfway through MT in the movement task, when 78% of the cells that were directionally tuned in that time window had instantaneous PDs that were significantly different between the two tasks (Fig. 2*C*, *bottom panel*). Later in the trial, the PDs again overlapped between the two tasks for >80% of the cells (mean angular difference, 600–1,200 ms post-onset, 24°).

Muscle activity

Twenty-eight sets of EMG activity were collected from 16 proximal arm-related muscles (see METHODS). All muscles

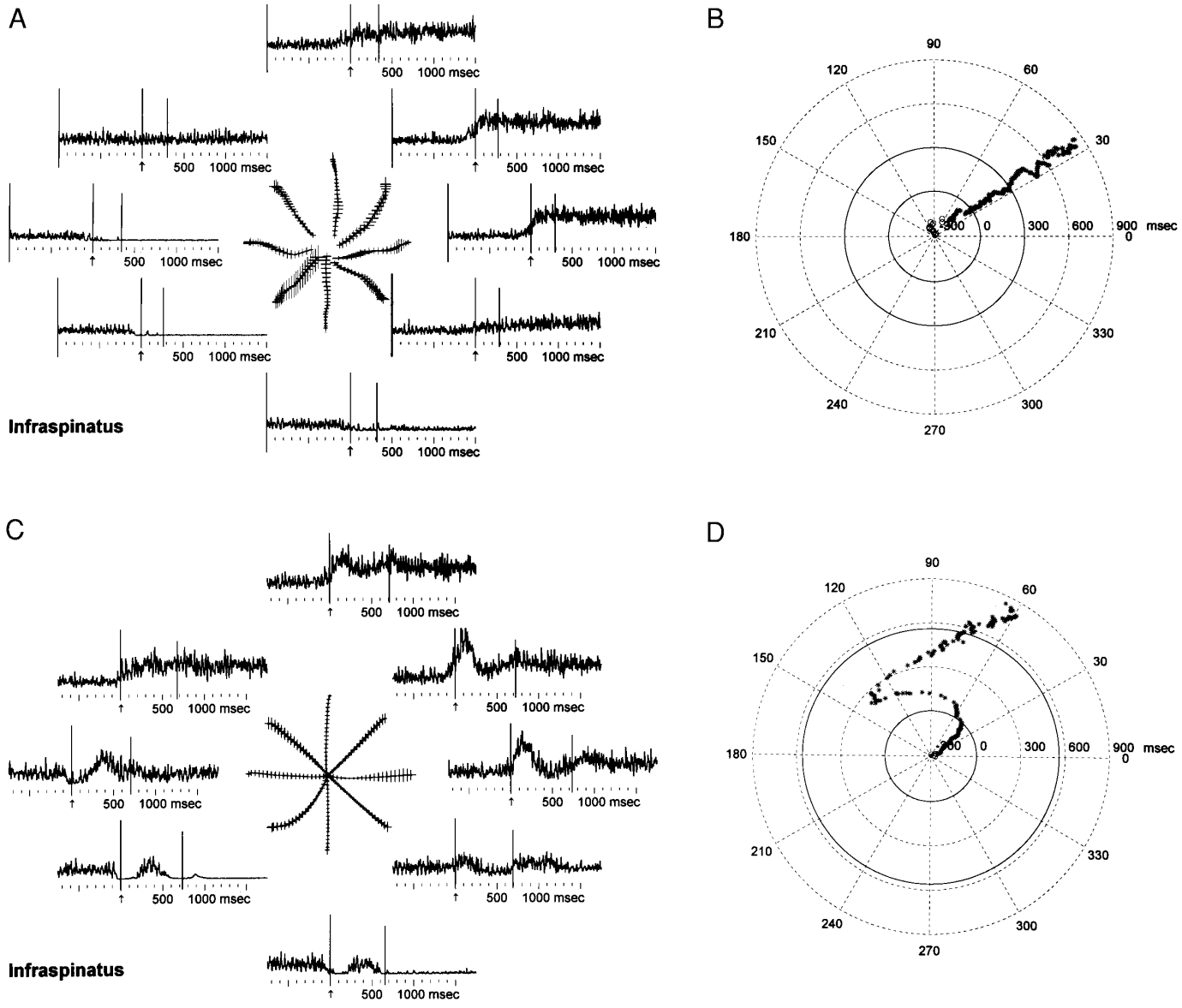

FIG. 3. Electromyographic (EMG) activity of the infraspinatus muscle in the 2 tasks. *A* and *C*: histograms of rectified, integrated, and summed EMG activity in each direction surround the mean force/movement trajectories. Same format as in Fig. 1. In each panel, the vertical line to the right of the movement onset line is the average end of force/movement for the five trials in that direction. All EMG traces have the same gain. *B* and *D*: temporal trajectories of the muscle PD in the 2 tasks. Same format as in Fig. 2, *A* and *B*.

studied showed task-related activity in both tasks. The change in muscle activity observed between the isometric and limb movement tasks was qualitatively comparable to the change in MI cell activity. Muscles acting at the shoulder typically showed ramplike tonic activity changes as a function of force direction during the isometric task (Fig. 3*A*) and a reciprocal triphasic burst pattern in the movement task (Fig. 3*C*). Consequently, the apparent instantaneous directional tuning of muscle activity also varied between the two tasks (Fig. 3, *B* and *D*). For all of the muscles examined, the instantaneous PD of 95–100% of muscle data sets did not differ significantly at a given time during isometric trials (mean 95.7 ± 1.1%) with respect to their PD in a time window centered on force onset. When the instantaneous directionality of the muscles was compared between the isometric and movement tasks, the PD of only 4% of muscle data sets differed significantly during RT. Very rapidly after force onset, however, the directionality of muscle activity began to deviate between the two tasks, reaching a maximum of 67% of data sets at 380-ms post-onset (mean angular difference, 86°).

DISCUSSION

The key finding in this study is that many cells in the caudal part of MI, located within the central sulcus, show marked changes in the temporal profile of their activity between isometric force production and reaching movements. A sliding window analysis showed that the instantaneous directionality of cell activity is generally similar before force onset in both tasks, followed by an apparent deviation in the instantaneous directionality of cell discharge after force onset in the movement task compared with that in the isometric task. In contrast, the directional attributes of the behaviorally controlled hand-centered variables in the two tasks, i.e., monotonic ramp changes in the isometric force output and hand position, were comparable. The changes in cell response profile and directionality would not be expected if they were related only to those global attributes of the motor output. In particular, the discharge of many caudal MI cells did not appear to covary only with hand kinematics (direction and velocity) during reaching against inertial loads (Fu et al. 1995; Schwartz 1992). The current findings also suggest that motor signals in caudal M1 during reaching are not simple ramps (Bullock and Grossberg 1992; Feldman and Levin 1995).

The systematic variation in EMG response profile and timing with movement direction resembles that described in previous multidirectional tasks (Flanders 1991; Hoffman and Strick 1990; Wadman et al. 1980). The instantaneous directionality of the muscles also showed an apparent deviation during the movement phase of the movement task.

The apparent transient deviation in instantaneous directionality does not imply that cell or muscle activity shows labile coupling to the directionality of motor output parameters during reaching. It is likely an artifact of representing that activity in a hand-centered kinematic parameter space. We used those coordinates here only as a convenient way to capture the difference in response profiles of activity between tasks. At that level of descriptive analysis, the important finding is that many proximal arm muscles and many MI cells express qualitatively similar transient directional shifts during reaching. The true significance of this observation will only become clearer when cell activity is analyzed in other parameter spaces.

Likewise, it is premature to draw strong conclusions based on the superficial similarity of the activity patterns of many M1 cells across task conditions to the force output profiles and prime-mover muscle activity beyond what we have already done. A rigorous quantitative regression analysis of the temporal profile of cell activity against the dynamic time course of many different motor output parameters is still required.

We also emphasize that the movement task used here should not be considered free-arm reaching. The monkey was required to displace an instrumented pendulum with a total mass of ~2,600 g toward targets. Therefore a prominent feature of the current movement task was that the monkey generated accelerative and decelerative forces at the hand to overcome the inertia of the pendulum to displace it in the desired direction.

Nevertheless, the prominent burst-pause-tonic pattern in M1 cell activity seen in this task was not solely a product of the extra behavioral constraints imposed by the mechanical properties of the task apparatus. In two previous reaching studies, nearly 30% of caudal MI cells also displayed that pattern (so-called ''phasic-tonic'' cells in Crammond and Kalaska 1996; Kalaska et al. 1989). The increase in the frequency of such cells (to 42/75, 56%) in this study may be because the manipulandum was substantially more massive than in the previous studies and therefore had a greater effect on the inertial characteristics of the load (arm and manipulandum) against which the monkey was exerting muscular forces. Cells with the burst-pause-tonic pattern become much less common in the more anterior part of MI on the exposed surface of the cortex (Crammond and Kalaska 1996), where much of the data in previous studies of reaching movements was collected (Fu et al. 1995; Georgopoulos et al. 1982; Schwartz 1992). This difference in sampling may account for the failure to find many cells with strong correlations to acceleration (Ashe and Georgopoulos 1994), which is the hand-centered kinematic parameter that would most closely resemble the temporal profile of forces during the movement.

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