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RESEARCH ARTICLE

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# Differential relation of discharge in primary motor cortex and premotor cortex to movements versus actively maintained postures during a reaching task

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**Abstract** The activity of cells in primary motor cortex (MI) and dorsal premotor cortex (PMd) were compared during reaching movements in a reaction-time (RT) task, without prior instructions, which required precise control of limb posture before and after movement. MI neurons typically showed strong, directionally tuned activity prior to and during movement as well as large gradations of tonic activity while holding the limb over different targets. The directionality of their movement- and posture-related activity was generally similar. Proximal-arm muscles behaved similarly. This is consistent with a role for MI in the moment-to-moment control of motor output, including both movement and actively maintained postures, and suggests a common functional relation for MI cells to both aspects of motor behavior. In contrast, PMd cells were generally more phasic, frequently emitting only strong bursts of activity confined mainly to the behavioral reaction time before movement onset. PMd tonic activity during different postures was generally weaker than in MI, and showed a much more variable relation with their movement-related directional tuning. These results imply that the major contribution of PMd to this RT task occurred prior to the onset of movement itself, consistent with a role for PMd in the selection and planning of visually guided movements. Furthermore, the nature of the relative contribution of PMd to movement versus actively maintained postures appears to be fundamentally different from that in MI. Finally, there was a continuous gradient of changes in responses across the rostrocaudal extent of the precentral gyrus, with no abrupt transition in response properties between PMd and MI.

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## Introduction

The primary motor cortex (MI) and adjacent premotor cortex (PM) have been subdivided into a number of smaller cortical fields. Lateral PM has been divided into dorsal (PMd) and ventral (PMv) divisions (Barbas and Pandya 1987; Tanji et al. 1988; Dum and Strick 1991; Kurata 1991, 1993; Stepniewska et al. 1993), and even into three divisions (F2, F3, F4; Matelli et al. 1985). MI likewise has been divided into rostral (MIr) and caudal (MIc) fields on the basis of connectivity patterns (Holsapple et al. 1991; Kurata 1991; He et al. 1993; Johnson et al. 1993; Stepniewska et al. 1993, 1994), cytoarchitectonic features (Weinrich and Wise 1982; Stepniewska et al. 1993), and electrophysiological responses (Tanji and Wise 1981; Strick and Preston 1982). A major question remains as to whether these multiple precentral fields are functionally distinct motor representations or continuous gradients of somatotopic and functional properties within a larger cortical zone.

The contribution of these cortical areas to motor control is still under study. There is a general consensus that PM is more involved in the selection and preparation of motor responses, whereas MI is more closely associated with the implementation of the selected response (Weinrich and Wise 1982; Weinrich et al. 1984; Halsband and Passingham 1985; Wise and Mauritz 1985; Petrides 1986; Wise et al. 1986, 1992; Okano and Tanji 1987; Kurata and Wise 1988; Tanji et al. 1988; Georgopoulos et al. 1989, 1993; Passingham 1989; Riehle and Requin 1989; Halsband and Freund 1990; Georgopoulos 1991; Lurito et al. 1991; Mitz et al. 1991; Mushiake et al. 1991; di Pellegrino and Wise 1991, 1993; Halsband et al. 1993; Kurata 1993; Crammond and Kalaska 1994). Rather than being strictly segregated, however, those same studies have shown that these roles are unequally distributed but shared between MI and PM, with neuro-

nal correlates of both movement planning and execution in both cortical areas with different degrees of prominence. For instance, during the delay period of an instructed-delay task, cells in both PMd and MI show changes in activity that covary with the nature of the instructed movement, but that activity is more prominent in PMd than in MI (Weinrich and Wise 1982; Weinrich et al. 1984; Riehle and Requin 1989; Crammond and Kalaska 1994). Furthermore, the increasing prominence of neuronal correlates of movement planning is gradual, not abrupt, when progressing anteriorly from MI into PMd (Weinrich and Wise 1982; Weinrich et al. 1984).

A gradient also appears to exist in the properties of movement execution-related discharge in MI and PM. MI cells generally show a stronger correlation with the parameters of movement kinematics and kinetics than do PMd cells (Kubota and Hamada 1978; Weinrich et al. 1984; Wise et al. 1986; Bauswein et al. 1991; Werner et al. 1991). In contrast, PM cells more often show a stronger dependence than MI cells on the behavioral context in which movements are made, such as stimulus-triggered versus self-paced movements (Kurata and Tanji 1986; Okano and Tanji 1987; Kurata and Wise 1988; Tanji et al. 1988; Mushiake et al. 1991).

Studies have identified many similarities in the movement-related activity of these two areas during multijoint reaching movements, including broad directional tuning of single cells and the covariation of the summed population signal with such attributes of reaching movements as its direction and even its spatiotemporal trajectory (Georgopoulos et al. 1988; Schwartz et al. 1988; Caminiti et al. 1991; Hocherman and Wise 1991; Fu et al. 1993, 1995; Schwartz 1993). These results demonstrate that, whatever their respective roles in motor control, the movement-related representations in both areas have many features in common.

There is some discrepancy, however, about the degree to which MI and PM are related to actively maintained postures. If a neuronal population is implicated in the moment-to-moment control of motor output, it should show strong correlations with both active movements and postures. If, in contrast, it is more concerned with the planning of impending motor acts, it may show stronger discharge covariation with the attributes of different movements than of different postures, which require only maintenance of the current motor status quo. Strong posture-related gradations of cell activity can be seen in MI (Georgopoulos et al. 1984; Kalaska et al. 1989). However, studies of discharge covariations with different arm postures in PM have reported that they were as common as in MI (Caminiti et al. 1991), were less frequent in PM (Bauswein et al. 1991; Werner et al. 1991), or were absent in PM (Weinrich et al. 1984; Wise et al. 1986). The latter findings are not consistent with a postulated role for PMd in the control of posture, body orientation, and axial stabilization during reaching movements (Freund and Hummelsheim 1985).

Therefore, we compared the activity of cell populations in MI and PMd during reaching movements in a reaction-time (RT) task without prior instructions, which required precise control of both arm movements and stable limb postures. In multiple-choice RT paradigms, all neuronal processes essential for the selection and initiation of movement are presumably effected during the short behavioral reaction time between the appearance of the triggering stimulus and the onset of the overt motor response. Significant differences in the response properties of cells in MI and PMd were found, in particular in their relation to movement versus actively maintained postures.

## Materials and methods

### Task

The task apparatus consisted of a horizontal target panel, over which was suspended a pendulum-like handle (Kalaska et al. 1989). The target panel contained nine triplets of red, green and yellow miniature light-emitting diodes (LEDs), one triplet at the center of the panel and eight distributed evenly around it in a circle of 8 cm radius (Fig. 1). The yellow LEDs were not used in the tasks described here. The monkeys were trained to grasp the lower end of the handle and to hold it over whichever of the red LEDs was illuminated. This required precise control of different arm postures. The position of the handle over the target panel was measured every 10 ms by an ultrasonic digitizer (Graf/Pen 3; Science Accessories; Kalaska et al. 1989).

Two types of trials where used in this task, standard RT trials, and instructed-delay trials called direct-delay (DD) trials (Fig. 1). All trials began when the central red LED was illuminated. The monkey positioned the handle over it for a variable period (2–6 s) until it was extinguished and one of the peripheral red target LEDs was illuminated as the go signal. The monkey then displaced the handle from the center to the red target LED and held it there for a fixed period of 2 s. In RT trials, no further signals appeared, so that the monkey did not know the direction of movement until the go signal appeared (Fig. 1). In DD trials, a green LED (the cue signal) was illuminated during the center-hold (CHT) period at one of the eight peripheral target locations (Fig. 1) and indicated which of the red target LEDs would be illuminated at the go signal. The green cue remained illuminated for the remaining duration of the CHT period and was extinguished at the go signal. The two types of trials and eight directions of movement were presented in a pseudorandom sequence, using a randomized-block design with ten replications of each trial type in each direction.

### Trial epochs

Each RT trial could be divided into three major parts (Fig. 1), the 2- to 6-s-long CHT period before the appearance of the go signal, the reach period from the appearance of the go signal to the end of movement, and the 2-s-long target-hold (THT) period. The reach period was subdivided into RT and movement-time (MT) epochs, using the motion of the handle to detect the onset and the end of movement, when the handle became stationary over the target (Kalaska et al. 1989).

The CHT period of DD trials could be further divided into a precue epoch before the appearance of the cue signal, and a cue epoch during which the cue signal remained illuminated until the go signal. Each was of 1–3 s duration. The CHT period of RT trials comprised corresponding early and late CHT epochs of 1–3 s, with a time marker inserted into the trial record when the cue would have been presented had it been a DD trial.

### Data collection

After training was completed, the monkeys were surgically prepared for data collection, using barbiturate anesthesia and stan-

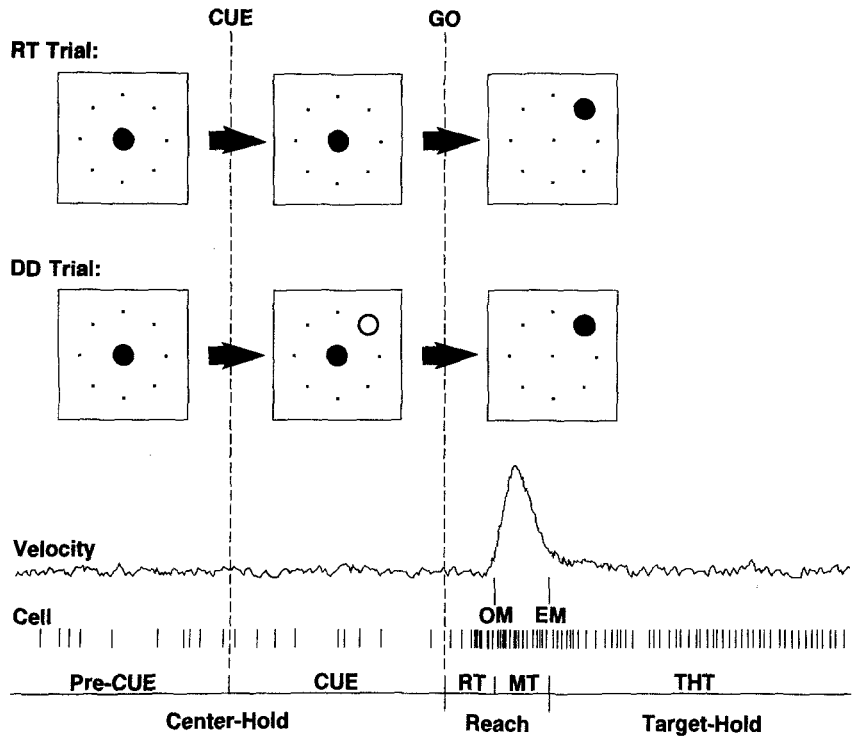



**Fig. 1** Replicas of the target panel, illustrating the sequence of stimulus events in reaction-time (*RT*) and direct-delay (*DD*) tasks. The *large solid circles* indicate red LEDs and the *open circle* indicates a green LED. *Right vertical dotted line* and *left vertical dotted line*, the time at which an instructional cue (green LED) appeared in DD trials, and the go signal appeared in both RT and DD trials, respectively. *Below the target panels* is an example of the velocity trace from a single trial, calculated by differentiation of the *x-y* position of the manipulandum over the target panel, to indicate the different behavioral epochs and periods in each trial (*OM* onset of movement, *EM* end of movement)

dard aseptic techniques. A Plexiglas recording chamber was positioned to span the precentral gyrus between the central and arcuate sulci.

After a postoperative recovery period, the monkeys began daily recording sessions. Using standard recording procedures (Kalaska et al. 1989), cells were isolated, tested in the task, and examined for their response properties outside of the task. All the cells collected for analysis met two criteria. First, their discharge was related to the proximal arm or shoulder girdle, on the basis of responses to passive inputs and during active movements of different limb segments. Cells that were related to the distal arm or trunk were not collected, even if active in the task. Second, the cells had to show significant changes in activity in one or more epochs of the trial in either of the two trial types, whether or not that response appeared to be directional. At many recording locations, intracortical microstimulation (ICMS; 11 pulses, 0.2 ms duration, 330 Hz) was used to identify output target muscles and the threshold currents required for muscle activation. At the end of certain penetrations, microlesions (10 μA, 10–20 s) were made in the cortex at specific locations along the electrode track.

Data collection lasted 8–10 weeks in each chamber. When the experiments were completed, the monkeys were deeply anesthetized and perfused with saline and then 10% formalin solutions. The cortex was blocked and 30-μm frozen sections were cut. The sections were stained with cresyl violet and used to reconstruct the locations of the penetrations.

Throughout all stages of the experiment, the guidelines and principles respecting the use of animals in research, approved by the Americal Physiological Society and the Canadian Council on Animal Care, were followed.

## Data analysis

The mean spike activity of single cells during the various trial epochs was subjected to three different statistical tests for directional responses. A two-way ANOVA (directions vs replications) detected statistically different responses with the direction of movement ($P<0.01$), whether or not there was any consistent directional pattern. In contrast, the Rayleigh test (Mardia 1972) detected cell responses with significant unimodal directional tuning ($P<0.01$). A third, nonparametric "bootstrapping" test was also used (Georgopoulos et al. 1988). In this test, the degree of directional bias in a cell's task-related activity was determined by calculating the mean length $R_m$ of the distribution of its discharge across all eight movement directions (Mardia 1972). The mean length is calculated from the sums of the sine and cosine of movement direction $\phi_i$, weighted by the mean discharge of the cell, $f_i$, for that movement, for each of the trials ($n$=1,$i$) in the data set for that cell:

$$C = \Sigma(f_i \cdot \cos\phi_i) \quad (1)$$

$$S = \Sigma(f_i \cdot \sin\phi_i) \quad (2)$$

$$R_m = \sqrt{[(C/\Sigma f_i)^2 + (S/\Sigma f_i)^2]} \quad (3)$$

A cell that discharged uniquely for one movement direction would have a mean length of 1.0, whereas the mean length of a cell with uniform activity across all eight directions would be zero. To determine whether the cell's directional tuning in the task arose by chance, the single-trial data were randomly reassigned to different "movement directions," and the mean length of the distribution of shuffled trials was calculated. The shuffling procedure was repeated up to a maximum of 4000 times, and the mean lengths of the shuffled data were compared with that calculated for the task-related response distribution. If fewer than 40 shuffled mean lengths exceeded the task-related mean length of the cell, the cell was considered directionally tuned ($P<0.01$).

Generally, there was a good correspondence between the results of the three tests on each cell. However, each test was preferentially sensitive to different features of cell activity. Therefore, the decision to label a response as directional in a particular epoch was based on a consensus – at least two of the three tests had to be significant. This consensus approach proved quite successful, with a very good agreement to a subjective judgement as to the presence of a directional response based on visual inspection of rasters and histograms.

Even at the 0.01 level, the ANOVA and bootstrap tests were very sensitive, sometimes indicating as significant responses that were difficult to see subjectively by eye. As a result, comparison of the frequency of significant statistical results between two populations can give only a partial indication of the relative sensitivity of the two populations to an experimental parameter and can even be misleading. Therefore, as a quantitative measure of the strength of the directional changes, we calculated a directional dynamic

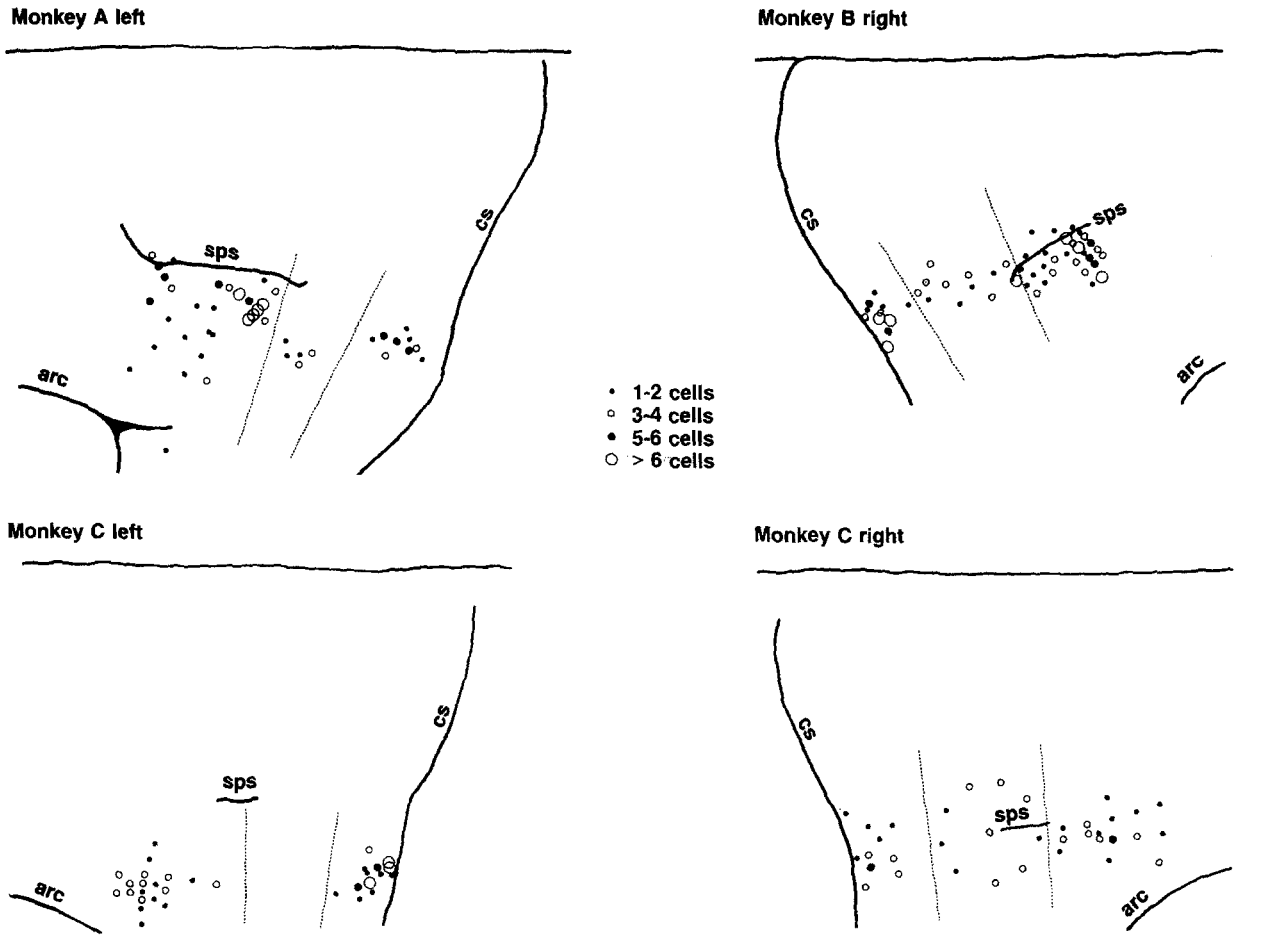



**Fig. 2** Distribution of the recording sites of the cells in the precentral gyrus of each monkey. The *dotted lines* indicate the arbitrary division of the recording region into dorsal premotor cortex, and rostral and caudal primary motor cortex, based primarily on the threshold of peripheral muscular responses to intracortical microstimulation (*cs* central sulcus, *sps* superior precentral sulcus, *arc* arcuate sulcus)

range, the difference between the strongest and weakest responses recorded in different directions during each epoch.

### Electromyographic recordings

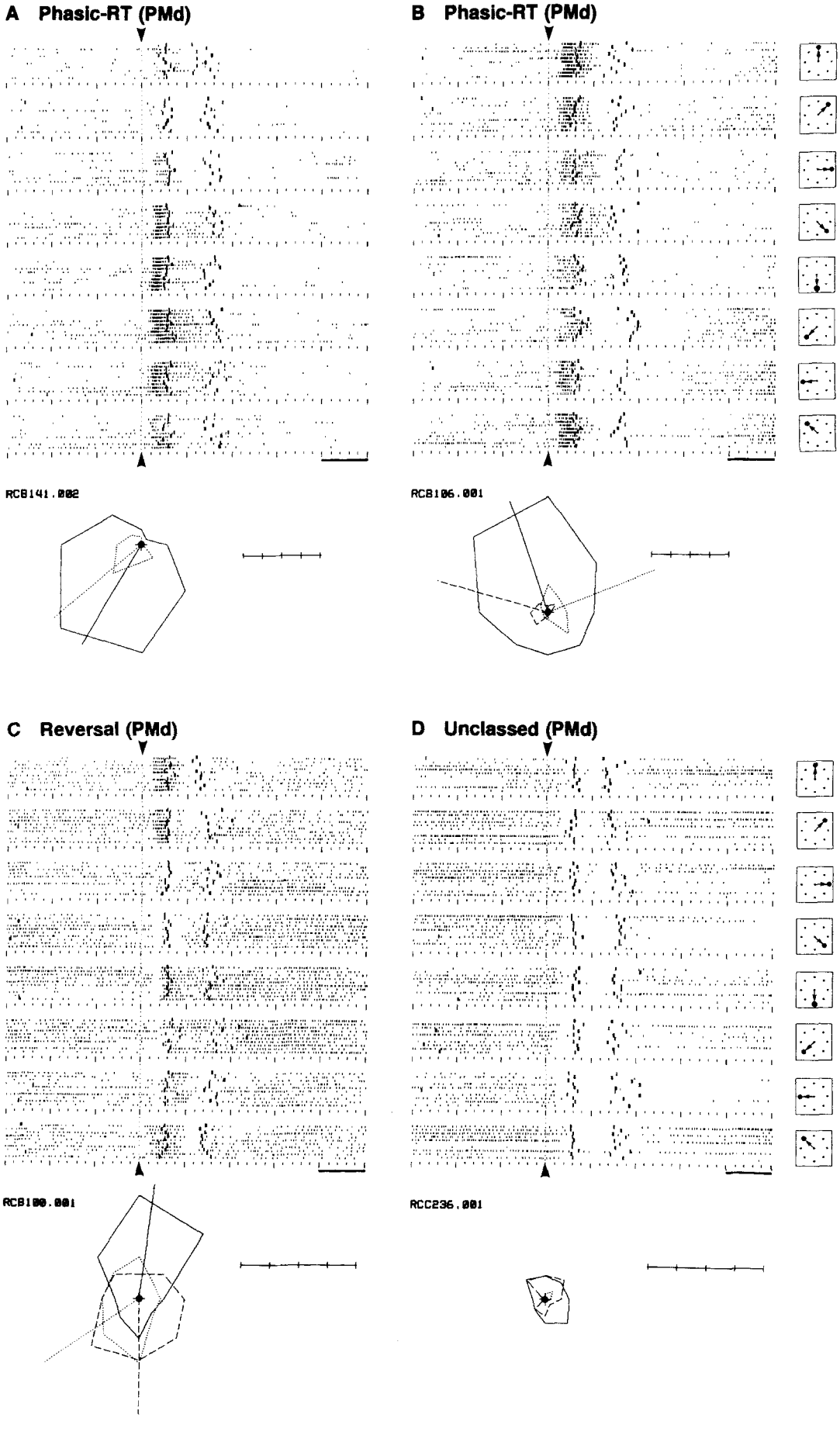
The task-related electromyographic (EMG) activity of all the major muscles of the shoulder joint and shoulder girdle, as well as several axial, paraspinal, and neck muscles were recorded at various times prior to, during, and after the several months of data collection in each monkey. Pairs of fine, Teflon-insulated stainless steel wires were inserted percutaneously into the bellies of selected muscles, using 30-gauge hypodermic needles. The identity of the implanted muscles was verified by observation of EMG activity outside of the task and by microstimulation of the implanted muscles via the recording electrodes. If microstimulation failed to evoke a crisp palpable local contraction of the desired muscle belly and the expected joint motions, the electrodes were removed and reinserted until a satisfactory implantation was achieved.

## Results

### Data set

Usable data were collected from 503 cells in the precentral gyrus of three juvenile, male rhesus monkeys (*Macaca mulatta*), including 279 in PMd and 224 in MI (Fig. 2). The border between PMd and MI was placed at

**Fig. 3A–D** Raster and polar-plot representations of the task-related responses of four dorsal premotor cortex (*PMd*) cells in reaction-time (*RT*) trials. **A** A phasic-RT cell that was strongly directional during RT and less active during movement time (MT), but was not directionally tuned during THT (i.e., ++-; see Table 2). **B** A phasic-RT cell that was directionally tuned in all three post-go epochs (i.e., +++) and whose tuning during RT and THT was similar. **C** A "reversal" cell, directional in all three epochs (i.e., +++), but whose directional tuning was opposite in the RT and THT epochs. **D** A PMd cell that was not directionally tuned in any post-go epoch in RT trials (i.e.,---), but which was strongly activated and directional during the instructed-delay period of DD trials (not shown). Direction of movement is indicated by the replicas of the target panel to the *right* of the rasters. Each raster is aligned on the appearance of the go signal (*arrows and vertical dotted lines*). The two *thick markers* in each raster line to the *left* of go indicate the time of onset and end of movement, respectively, and so delimit the RT, MT, and THT epochs. Horizontal calibration *bars* 500 ms. In the polar plots, *solid lines* are the mean response of the cell for each movement direction during the RT epoch, *dotted lines* for the MT epoch, and *dashed lines* for THT. The apparent preferred direction of the cell in each epoch is indicated by the vector in the corresponding line type. *Scale bar* for polar plots, 10 spikes/s per division


A Phasic-RT (PMd)
B Phasic-RT (PMd)
RCB141.002
RCB106.001
C Reversal (PMd)
D Unclassed (PMd)
RCB100.001
RCC236.001

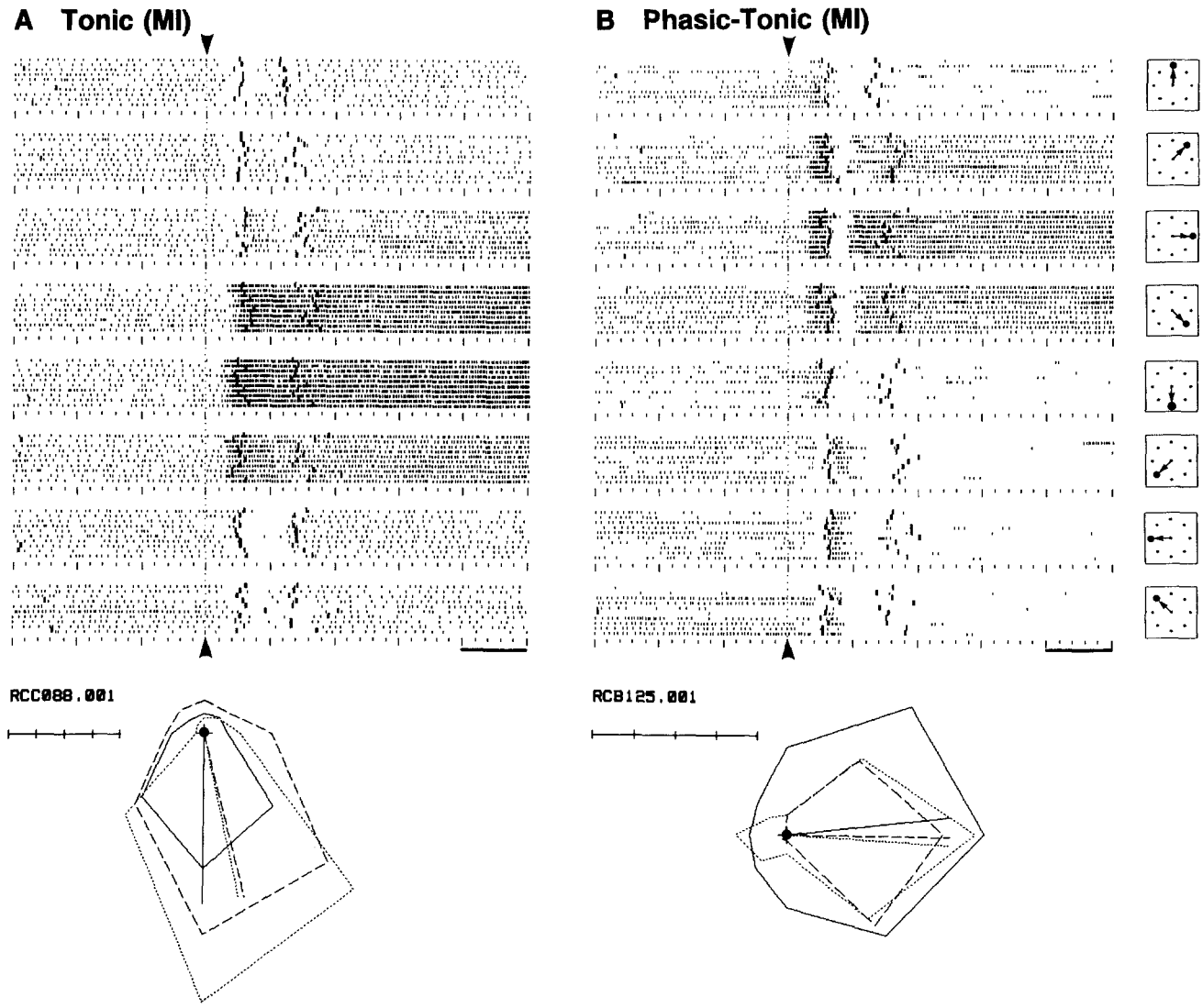



**Fig. 4A,B** Raster and polar-plot representations of the task-related responses of two caudal primary motor cortex (*MIc*) cells in reaction-time trials. **A** A tonic cell. **B** A phasic-tonic cell (note the apparent transient reversal of the directionality of discharge during the early part of the MT epoch, a property of many but not all phasic-tonic cells). Same format as Fig. 3

that point in front of which standard ICMS (11 pulses, 0.2 ms duration, 330 Hz) failed to evoke visible movements or muscle contractions at stimulus strengths up to 50 μA (Fig. 2). The medial extension of this border passed through the caudal end of the precentral sulcus in two of the three monkeys (Fig. 2; Kurata and Tanji 1986; Kurata 1989, 1993). MI was further subdivided into rostral and caudal parts (MIr and MIc). MIr and MIc contained 72 cells and 152 cells, respectively. MIc comprised the anterior bank and crown of the central sulcus, in which ICMS could often evoke brisk contractions of muscles in the proximal arm and shoulder girdle, with currents as low as 3–5 μA. In MIr, ICMS thresholds were typically higher, rarely less than 10 μA, and stimuli as high as 50 μA often failed to evoke a visible response. This division into three zones does not reflect abrupt transitions in the responses to ICMS. Instead, there was a continuum of sensitivity to ICMS across the precentral gyrus, which we divided into three parts.

Only data collected in RT trials will be described here; the results from DD trials will be reported elsewhere. The directional tuning properties of MI and PMd cells in RT trials have already been described in detail (Georgopoulos et al. 1988; Kalaska et al. 1989; Caminiti et al. 1991). The fundamental observation of those studies, that the discharge of many cells in both regions covaried in a broad and continuously tuned manner with movement direction (Figs. 3, 4) was confirmed here. However, some striking differences were observed in the activity of PMd and MI cells that have not been reported before.

## Temporal response patterns of post-go activity in RT trials

As in previous studies (Kalaska et al. 1989, 1990), the discharge of most MI and PMd cells at their preferred movement direction showed one of five arbitrary temporal response profiles. Phasic-RT cells emitted a phasic

**Table 1** Frequency distribution of the different temporal response patterns (*P-RT* phasic reaction time, *P-MT* phasic movement time, *T* tonic, *P-T* phase tonic, *R* reversal, *Un.* unclassed, *PMd* dorsal premotor cortex, *MIr* rostral primary motor cortex, *MIc* caudal motor cortex)

| | P-RT | P-MT | T | P-T | R | Un. |
|---|---|---|---|---|---|---|
| PMd | | | | | | |
| *n* | 122 | 32 | 34 | 4 | 32 | 55 |
| % | 43.7 | 11.5 | 12.1 | 1.4 | 11.5 | 19.7 |
| MIr | | | | | | |
| *n* | 26 | 9 | 12 | 8 | 8 | 9 |
| % | 36.1 | 12.5 | 16.7 | 11.1 | 11.1 | 12.5 |
| MIc | | | | | | |
| *n* | 17 | 19 | 61 | 42 | 6 | 7 |
| % | 11.2 | 12.5 | 40.1 | 27.6 | 3.9 | 4.6 |
| EMG | | | | | | |
| *n* | 4 | 6 | 27 | 36 | 0 | 3 |
| % | 5.3 | 7.9 | 35.5 | 47.4 | 0.0 | 3.9 |

burst confined to the RT epoch or peaking before movement onset and declining during MT, with little difference in tonic activity during the THT epoch over the peripheral targets (Fig. 3A,B). Phasic-MT cells were similar but their peak occurred later, during the MT epoch. Tonic cells showed mainly tonic activity increases that began prior to or during movement and were sustained during the THT (Fig. 4A). Phasic-tonic cells showed a brisk early phasic burst during the RT epoch in their preferred direction, followed by a momentary decline or pause in activity, and then a second tonic increase that was sustained throughout THT (Fig. 4B). MIc cells with these four response profiles often, but not necessarily, showed reciprocal decreases in activity for movements in the opposite direction. Note, for instance, the reciprocal triphasic responses of the phasic-tonic cell for movements to the right and left (Fig. 4B). A fifth response profile, called "reversal" (Fig. 3C), was different in that, for one direction, there was a brisk phasic burst during RT often followed by a sustained suppression of activity, while in the opposite direction, the reverse pattern was recorded – a momentary pause followed by a sustained tonic increase (Kalaska et al. 1990).

Most cells in MIc had tonic and phasic-tonic profiles (Table 1; 103/152; 67.8%). Fewer cells had phasic RT or phasic MT (36/152; 23.7%) and reversal patterns (6/152; 3.9%), and 7 cells (4.6%) could not be classed. Therefore, a prominent characteristic of cell activity in MIc is sustained tonic discharge covarying with different, actively maintained arm postures.

In contrast, the most prominent response pattern in PMd was a brisk phasic burst during the RT epoch (Fig. 3). Overall, 154/279 PMd cells (55.2%) were phasic-RT or phasic-MT, and only 38 cells (13.6%) had tonic or phasic-tonic profiles (Table 1). Another 32 cells (11.5%) showed the reversal profile, and 55 neurons (19.7%) could not be classed, both higher proportions than in MIc. Many of the unclassed cells showed a modest or complete nondirectional suppression of activity during the RT epoch, which was either sustained for the rest of the trial (Fig. 3D) or was replaced by weakly directional tonic activity later in THT.

The distribution of temporal response profiles recorded in MIr was intermediate between PMd and MIc, but more similar to that in PMd than in MIc (Table 1). These differences among the three areas were highly significant ($\chi^2$=154.54; $P$<0.001).

This classification by temporal response profiles is qualitative and subjective. However, the impression that PMd was more phasically related to movement and less tonically related to different active arm postures than cells in MIc was supported by rigorous statistical analysis (Table 2). For instance, most MIc cells (109/152; 71.7%), but only 90/279 PMd cells (32.3%), were directional in all three post-go epochs (+++, Table 2). Far more cells in PMd (88/279; 31.5%) than in MIc (13/152; 8.6%) were directional during the reach period only, but not during the THT period (++-, +--, -+-). Moreover, 27 PMd cells (9.7%) were not directionally tuned in any post-go epoch in RT trials (Fig. 3D; they are in the data set because of activity changes during the delay period of DD trials). No similar cells were seen in MIc. Consequently, far more cells in PMd (115/279; 41.2%) than in MIc (13/152; 8.6%) were *not* directionally tuned during the THT epoch (++-, +--, -+-, ---). Finally, PMd cells showed a much greater range of combinations of directional tuning in different behavioral epochs, suggesting a more complex and variable relation to movement and posture than was the case for MIc cells. The cells in MIr were intermediate in their properties (Table 2). The differences in the frequency distribution of directional tuning in the post-go epochs of RT trials among the three cortical zones were statistically significant (Table 2; $\chi^2$=85.25; $P$<0.001).

These differences in temporal response profiles are also evident in mean population response histograms (Fig. 5A–C). In each area, there was a brisk burst of activity during the RT epoch at the preferred movement direction. The MIc population showed strong, reciprocally tuned tonic activity during THT, while holding the limb

**Table 2** Frequency distribution of statistically significant directional tuning during the three post-go trial epochs (reaction time/movement time/target hold) in reaction-time trials (+: significant directional tuning for the corresponding behavioral epoch ($P<0.01$); -: not directionally tuned in that epoch; i.e.: +++ significant directional tuning for all three post-go epochs)

| | +++ | ++- | +-+ | -++ | +-- | -+- | --+ | --- |
|---|---|---|---|---|---|---|---|---|
| PMd | | | | | | | | |
| *n* | 90 | 42 | 21 | 30 | 32 | 14 | 23 | 27 |
| % | 32.3 | 15.1 | 7.5 | 10.8 | 11.5 | 5.0 | 8.2 | 9.7 |
| MIr | | | | | | | | |
| *n* | 34 | 11 | 4 | 9 | 5 | 3 | 0 | 6 |
| % | 47.2 | 15.3 | 5.6 | 12.5 | 6.9 | 4.2 | 0.0 | 8.3 |
| MIc | | | | | | | | |
| *n* | 109 | 9 | 6 | 20 | 1 | 3 | 4 | 0 |
| % | 71.7 | 5.9 | 3.9 | 13.2 | 0.7 | 2.0 | 2.6 | 0.0 |
| EMG | | | | | | | | |
| *n* | 70 | 0 | 0 | 4 | 0 | 0 | 2 | 0 |
| % | 92.1 | 0.0 | 0.0 | 5.3 | 0.0 | 0.0 | 2.6 | 0.0 |

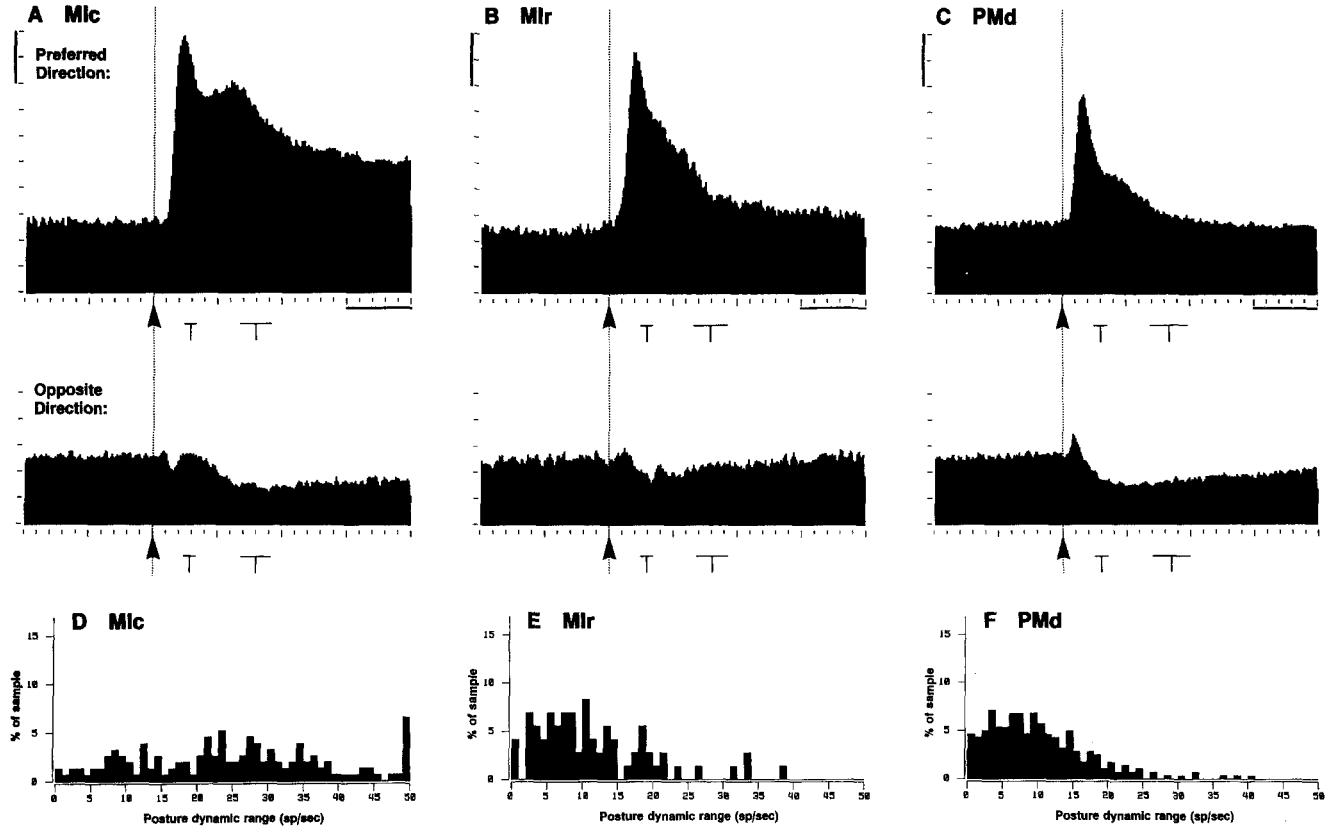



**Fig. 5** **A–C** Mean population response histograms of cell samples at their preferred movement direction during the RT+MT epoch (*upper row*) and the opposite direction (*lower row*), oriented to the appearance of the go signal (*vertical dotted lines and arrowheads*). The *T-bars* below each histogram indicate the mean±SD of the behavioral reaction times (i.e., movement onset) and the mean time of movement offset, for all trials in each histogram. They were statistically similar in all cases. Note the strong late tonic postural discharges in caudal MI (*MIc*) (**A**), compared with the much weaker mean population responses after movement offset in rostral MI (*MIr*) (**B**) and PMd (**C**). *Horizontal calibration bar* 500 ms, *vertical calibration bar* 10 spikes/s. **D–F** Frequency distribution of the postural dynamic range of activity (spikes/s) recorded during the target-hold period in cells in MIc (**D**), MIr (**E**), and PMd (**F**)

over targets in opposite locations relative to the start position (Fig. 5A). In contrast, there was much less difference in tonic activity over the different targets in MIr (Fig. 5B) and PMd (Fig. 5C), when the single-cell responses were oriented for averaging to their preferred direction during the RT+MT epoch.

To assure that the differences between the population histograms in Fig. 5 were not due to a few MIc cells with very strong tonic discharges, we compared the distribution of single-cell postural dynamic ranges in each area, that is, the difference between the strongest and weakest tonic response for each cell during THT over different targets. Cells in MIc showed a broad range of posture-re-

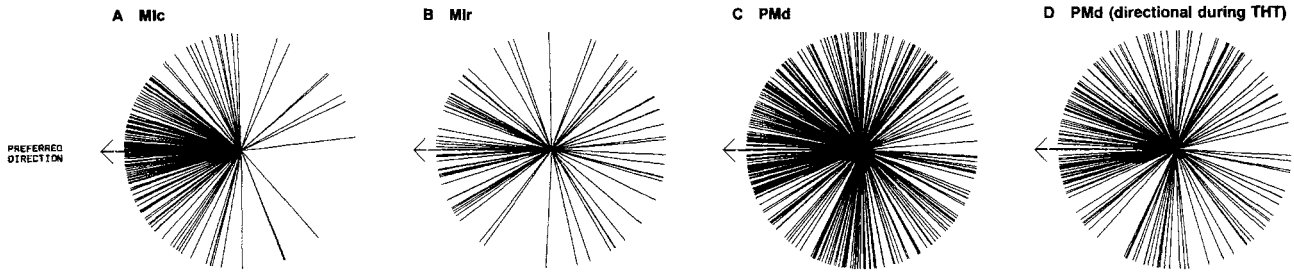



**Fig. 6A–D** Comparison of the directional tuning of cells during movement versus posture. The preferred direction of each cell during the RT+MT epoch was arbitrarily rotated to the left (*broken arrow*). The *lines* represent the preferred direction of the cell activity during the target-hold period relative to its preferred direction during RT+MT. **A** MIc; **B** MIr; **C** PMd, total sample; **D** PMd, only the cells that were significantly directionally tuned during the target-hold period

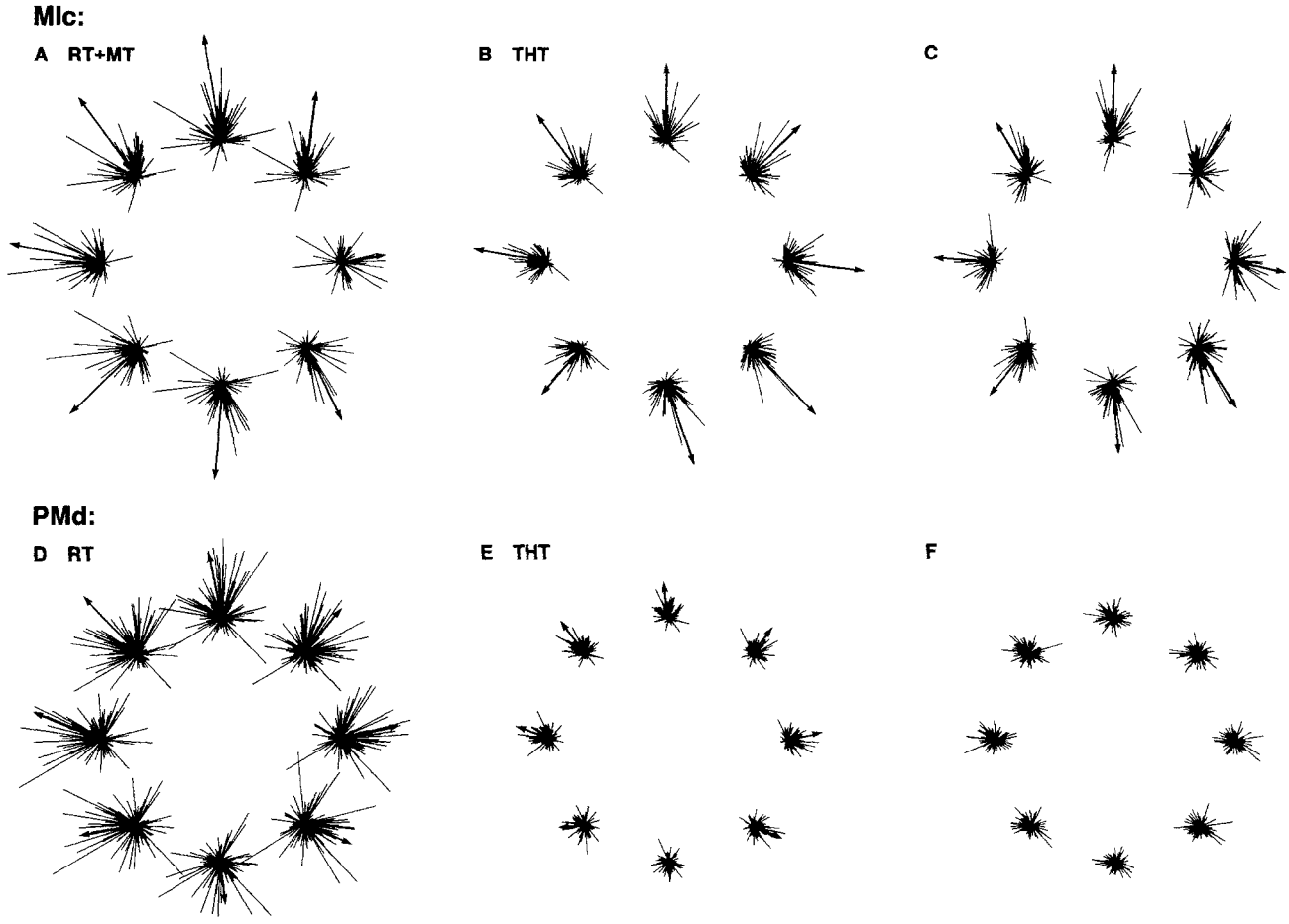



**Fig. 7** Vectorial representation of the population activity of cells in MIc (**A–C**) and in PMd (**D–F**). Each *line* is the activity of a single cell for each of the directions of movement, oriented along the axis of its preferred direction. The *large arrows* are the population vectorial sums. **A** The activity of the MIc sample during the RT+MT epoch, using the mean direction of each cell during that epoch. **B** The activity of the cells during THT, using the mean direction of each cell in that epoch. **C** The MIc population activity pattern during THT, but using the preferred direction of the cell during the RT+MT epoch. Note the strong positional signal in **B** and the relatively minor change in **C**, compared with **B**. **D–F** show the corresponding results for PMd. Note the weak covariation with arm posture in **E** and the nearly complete loss of a directional population signal in **F**. For **D** and **F**, we used the preferred direction recorded during RT, rather than RT+MT, since most PMd cells were most active prior to movement onset (see Figs. 3A–C, 5C)

lated activity, with a mean value of 25.5 sp/s (Fig. 5D). In contrast, the postural dynamic ranges were skewed toward lower values in PMd (mean 10.1 sp/s) and in MIr (mean 11.5 sp/s; Fig. 5E,F). This confirmed that the mean histograms of Fig. 5A–C were a fair representation of population behavior.

## Spatial coupling of directional tuning during movement versus posture

A second major difference between MI and PMd was in the constancy of directional tuning between the reach and

**Table 3** Frequency distribution of the different temporal response patterns in instruction-related and movement-only PMd cells

| | P-RT | P-MT | T | P-T | R | Un. |
|---|---|---|---|---|---|---|
| instruct | | | | | | |
| *n* | 113 | 22 | 30 | 3 | 30 | 52 |
| % | 45.2 | 8.8 | 12.0 | 1.2 | 12.0 | 20.8 |
| move | | | | | | |
| *n* | 9 | 10 | 4 | 1 | 2 | 3 |
| % | 31.0 | 34.5 | 13.8 | 3.4 | 6.7 | 10.3 |

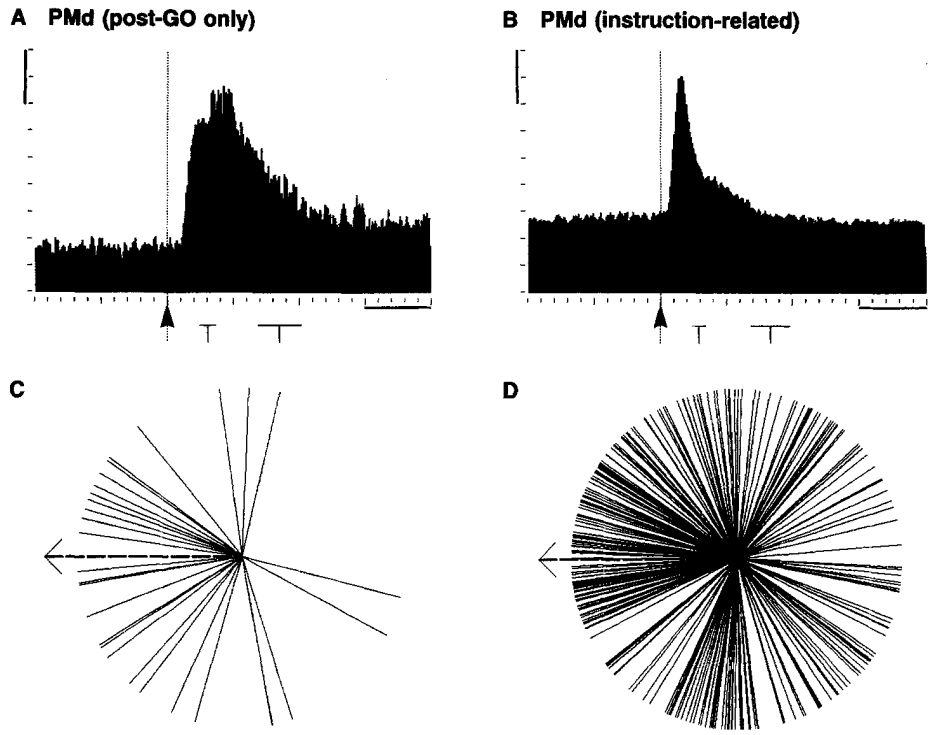



**Fig. 8** **A,B** Mean response histograms of 29 movement-only PMd cells (**A**) and 250 instruction-related PMd cells (**B**) at their preferred movement direction. Same format as Fig. 5. **C,D** Comparison of the directional tuning of the movement-only (**C**) and instruction-related (**D**) PMd cells during the target-hold period, relative to their preferred direction during reach. Same format as Fig. 6

target-hold periods of the trial. In MIc, there was a strong tendency for the tuning during RT+MT and THT to be very similar (Fig. 4). When the movement-related preferred direction of all MIc cells during RT+MT was rotated to the left (180°) and the preferred direction of their THT activity was plotted relative to that (Fig. 6A), there was a strong tendency for them to cluster about 180° (mean direction 176.1°; mean absolute angular difference 33.4°; mean length of distribution 0.73). In contrast, there was considerable variability in the directional tuning of PMd cells between the reach and THT periods (Fig. 6C; mean direction 177.0°; mean absolute angular difference 70.4°; mean length 0.26). Part of this variability could have resulted from the greater proportion of PMd cells without significant directional tuning during THT – their weak fluctuations in discharge during THT would be randomly related to the directional tuning for movement. Nevertheless, when the analysis was repeated after excluding the 115 PMd cells that were not directionally tuned during THT, there was only a modest improvement (Fig. 6D; mean direction 164.9°; mean absolute angular difference 66.7°; mean length 0.32). Therefore, the directional tuning of PMd cells was far more variable at different times between the posture and movement phases of the task than were MIc cells. MIr cells were more similar to PMd cells than to MIc neurons in this respect (Fig. 6B; mean direction 169.5°; mean absolute angular difference 71.3°; mean length 0.24).

A consequence of these differences is shown by a vectorial representation of population activity in MIc and PMd (Fig. 7). Cells in both areas showed a strong directional signal prior to and during movement (Fig. 7A,D). Both areas also showed a covariation with active arm postures, but the signal in MIc (Fig. 7B) was substantially stronger than in PMd (Fig. 7E). However, Fig. 7B,E was constructed using the preferred direction of the cells during THT. When population activity was redrawn using the preferred direction during movement but the activity levels recorded during posture, the MIc data still showed a strong signal covarying with arm position (Fig. 7C), but not the PMd data (Fig. 7F). Similar results were obtained for the MIc and PMd samples when we did the opposite, generating vectorial representations of

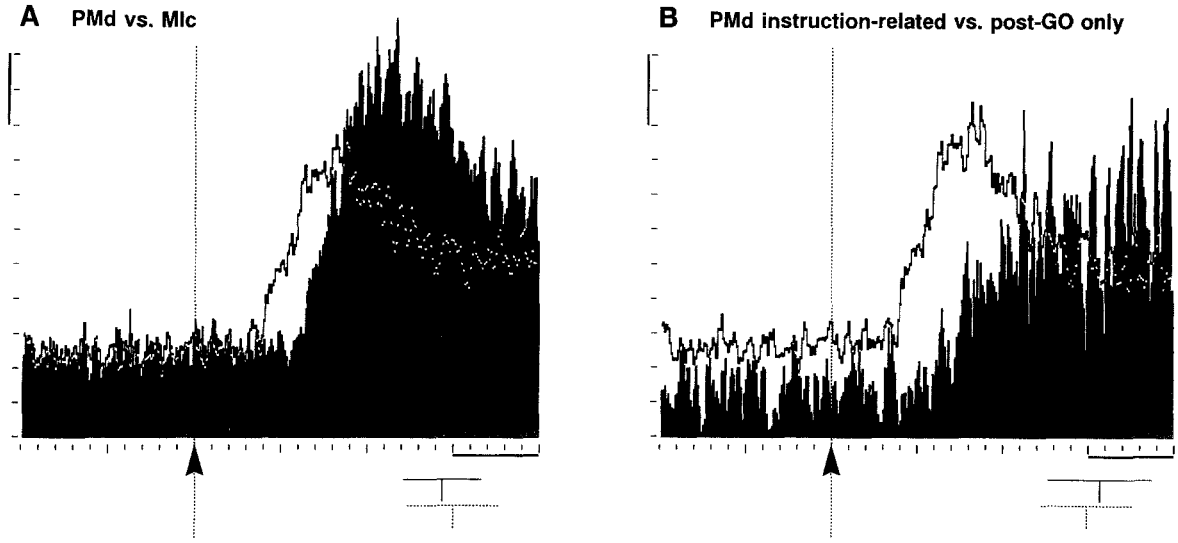



**Fig. 9** **A** Mean population histograms of MIc (*solid*) and PMd (*outline*) cell activity at the preferred direction of each cell. Same data as in Fig. 5A,C, but with a fivefold expansion of the timebase. The *solid T-bars* and *dotted T-bars* below the histograms indicate the mean (±SD) of the behavioral reaction times of the MIc and PMd populations, respectively. **B** Mean population histograms of PMd movement-only (*solid*) and instruction-related (*outline*) cell activity. Same format as in **A**. *Horizontal calibration bar* 100 ms, *vertical calibration bar* 10 spikes/s

movement-related activity, but using the directional tuning during posture (data not shown). This indicates that the posture-related tuning of cells was a good predictor of the movement-related signals generated by those cells for the different movement directions in MIc, but not in PMd.

## Comparison of PMd cells with and without activity during instructed-delay period

Comparison of two subpopulations of PMd cells suggest that the differences between PMd and MIc cells just described were related to differences in their roles in the control of movement, and not just to their cortical location. The majority of PMd cells (250/279; 89.6%) showed significant changes in activity after the presentation of instructional cues during the cue epoch of DD trials (instruction-related cells; D.J. Crammond and J.K. Kalaska, unpublished work). The remaining 29 cells showed only post-go movement-related activity in the task. Movement-only cell response properties were significantly different from those of instruction-related cells.

First, 10 of 29 (34.5%) of the movement-only cells were phasic-MT neurons and 9 of 29 (31.0%) were phasic RT, whereas only 22 of 250 (8.5%) of the instruction-related cells were phasic MT and 113 of 250 (45.2%) were phasic RT (Table 3). The difference in the frequency of the temporal response properties was highly significant (Table 3; $\chi^2$=19.15, 5 *df*; $P$<0.005). This is also seen in the mean population response histograms, in which the movement-only cells showed activity coextensive with the movement (Fig. 8A), whereas the discharge of the instruction-related cells was confined predominantly to the RT epoch (Fig. 8B).

Second, although there was no significant difference in the size of the postural dynamic range of the two groups of PMd cells during THT (mean value of 10.6 spikes/s for the movement-only cells and 10.0 spikes/s for instruction-related cells; $P$<0.1, $t$-test), there was a clear difference in the movement-posture coupling. The directional tuning of the activity between RT+MT and THT tended to be much more similar for movement-only PMd cells (Fig. 8C; mean direction 188.8°; mean absolute angular difference 53.3°; mean length 0.51) than for instruction-related cells (Fig. 8D; mean direction 174.0°; mean absolute angular difference 72.4°; mean length 0.23). In that sense, the movement-only PMd cells more closely resembled MIc cells than the instruction-related PMd cells.

## Timing of movement-related activity

Examination of the population histograms at greater temporal resolution than in Fig. 5 revealed that the activity of the PMd population began less than 100 ms after the appearance of the go signal, much earlier than in MIc, and was approaching its peak at about the same time as the MIc population was beginning to respond (Fig. 9A). MIr cell activity was also substantially later than than in PMd and had an onset with similar timing to that in MIc (data not shown). Again, the difference in response latency was related more to the functional properties of cells than to their cytoarchitectonic location. When the responses of the instruction-related and movement-only PMd cells were compared, the former clearly preceded the latter (Fig. 9B), and the latter had a response latency similar to that of the MIc population.

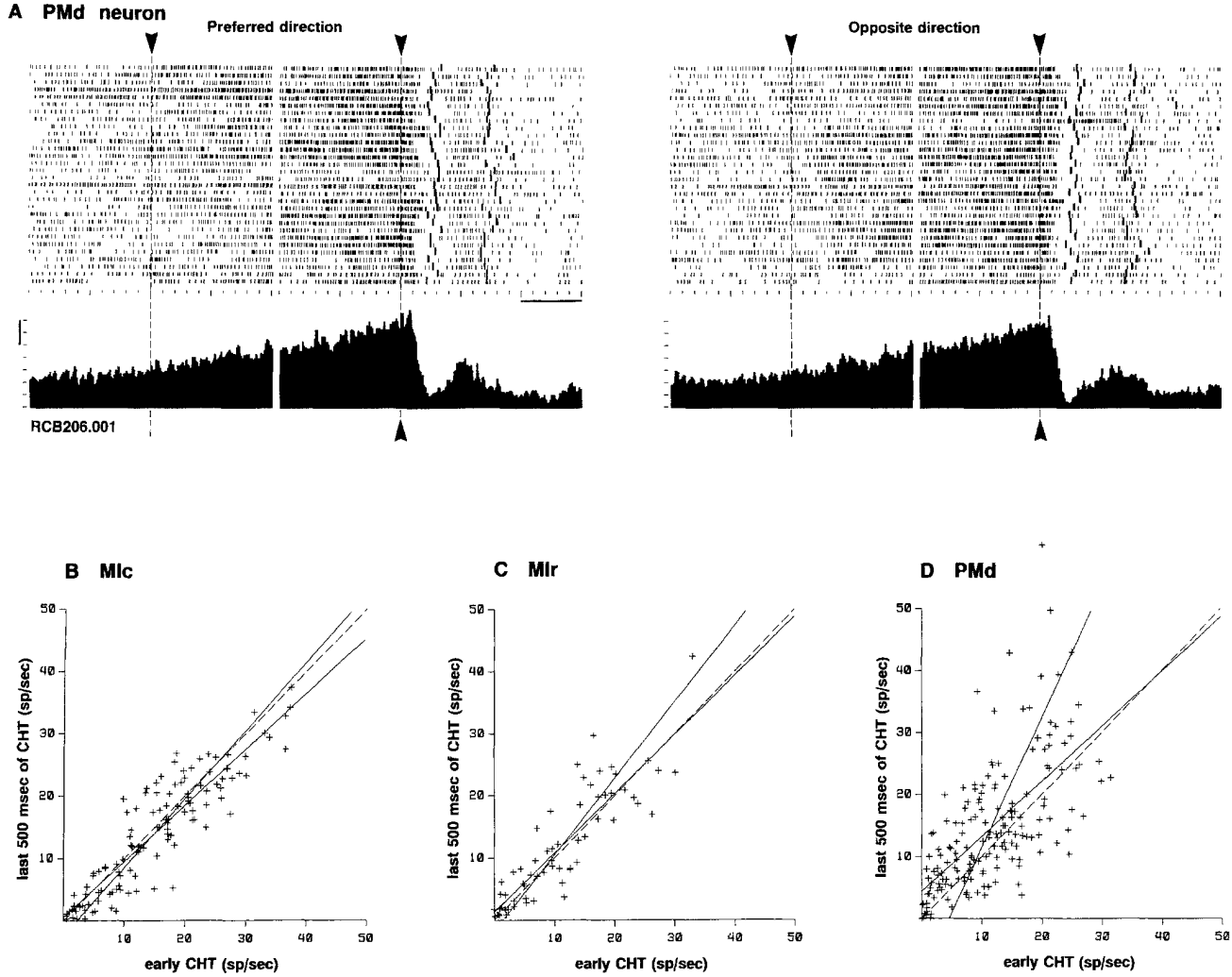



**Fig. 10** **A** Rasters and histograms of the responses of a PMd cell in RT trials at its preferred direction (*left*) and the direction opposite to it (*right*). The cell was weakly directional after the appearance of the go signal in the two opposite directions (*right vertical dotted line* in each raster; the cell was much more directional in the delay period of DD trials) and showed a gradual nondirectional increase in tonic activity prior to the appearance of the go signal. The *left vertical dotted lines* in each raster; indicate the arbitrary division between the early and late parts of the center-hold period (*CHT*), that is, the time at which a cue would have been presented had these been DD trials. **B–D** Scatter plots of the mean tonic rate of cells in the first part of the CHT in RT trials (*abscissa*) versus that in the last 500 ms of the CHT epoch before the appearance of the go signal (*ordinate*). There is a strong correlation in MIc (**B**) and in MIr (**C**), indicating that the tonic activity of the cells tended to remain fairly stable throughout the CHT period. In contrast, PMd cells (**D**) showed a much greater scatter, indicating a prominent trend for large changes in tonic rate during the CHT period. The *two intersecting solid lines* are the regression lines for ordinate on abscissa and abscissa on ordinate. The *diagonal dashed line* is the identity line

## Activity during the CHT period

A further difference between MIc and PMd concerned the degree of stability of the tonic activity of cells during the CHT period. In PMd, it was common to see nondirectional progressive increases or decreases in tonic activity throughout the CHT period of RT trials (Fig. 10A), whereas the tonic activity of cells in MIc tended to be more constant. In some PMd cells, this variation in tonic rate was more or less continuous throughout the entire CHT period, but in others it began later in the CHT period.

Figure 10B–D shows scatter plots of the tonic rate during the early part of the CHT period in RT trials, versus that in the last 500 ms before the go signal appeared. The data distribute close to the identity line in MIc (Fig. 10B; $r$=0.905), indicating considerable stability of the tonic rate in MIc between the beginning and end of the CHT period. In contrast, cells in PMd showed much greater tonic variability during the CHT period (Fig. 10D; $r$=0.65) and a trend for higher tonic rate at its end. Area MIr was again intermediate in its behavior (Fig. 10C; $r$=0.88), but resembled MIc more than PMd.

Cells that showed a large variation in tonic rate during the CHT period were arbitrarily defined as those cells that underwent at least a twofold increase or decrease in activity between the early CHT epoch and the last 500 ms before the go signal. More than a quarter of the PMd sample exceeded this criterion (73/279; 26.2%), whereas only 10 of 72 MIr cells (13.9%) and 17 of 152

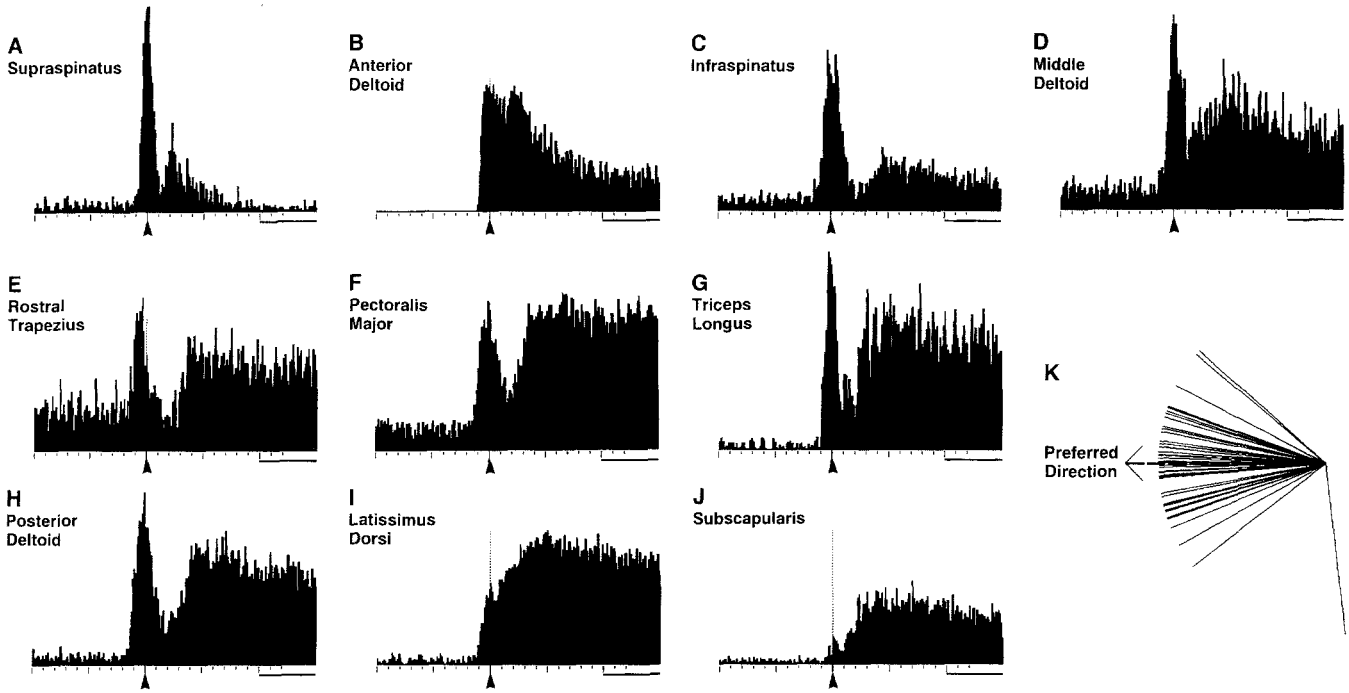



**Fig. 11 A–J** Histograms of the responses of different muscles at their preferred movement direction. The histograms were generated by rectifying and summing the EMG activity recorded from percutaneously implanted pairs of wire electrodes during ten reaching movements. All histograms are oriented to the onset of movement. **K** The directional tuning of the muscles during the target-hold epoch, relative to that during the reach period (*broken arrow*). Same format as Fig. 6

MIc cells (11.2%) did so. Moreover, nearly all MIc cells (16/17) with a large change in tonic rate showed a decrease in activity during the CHT period, whereas the majority of cells in MIr (7/10) and PMd (54/73) showed an increase. In MIc, the mean absolute change in activity of these cells with large changes in tonic rate was 5.0 s/s and the largest change seen was a decrease of 12.8 s/s. In contrast, the mean absolute change was nearly twice as large in PMd (9.6 spikes/s), and the largest change seen was an increase of 40.2 spikes/s.

### EMG activity

The contractile activity of proximal arm and shoulder girdle muscles could be analyzed in the same way as the neuronal responses. These analyses showed that the gradient of response properties seen between PMd and MIc continued from MIc to the peripheral musculature.

For instance, similar temporal response profiles could be recognized in the activity of muscles as of cells (Fig. 11), except that no muscle exhibited the reversal pattern (Table 1). Even more muscle recordings (63/76; 82.9%) showed strong tonic response components that varied with different actively maintained arm positions than was seen in MIc and the most common EMG response profile was phasic-tonic (Table 1). Predominantly phasic response profiles were less common in muscle activity than in any cell population (Fig. 11, Table 1). The statistical analysis of EMG activity also showed the same trend (Table 2). The large majority of EMG records (70/76; 92.1%) were directionally tuned in all three behavioral epochs, a larger pecentage than even in MIc, and every EMG record was directionally tuned during the THT epoch (Table 2). Finally, the similarity of directional tuning of muscles between the RT+MT and THT epochs was even closer than for cells in MIc (Fig. 11 K; mean direction 181.4°; mean absolute difference 14.9°; mean length 0.93).

## Discussion

The activity of cells in MI and PMd in a RT task has a number of similarities (Georgopoulos et al. 1988; Schwartz et al. 1988; Caminiti et al. 1991; Kalaska and Crammond 1992; Fu et al. 1993, 1995). However, this study indicated that the two areas also demonstrate striking differences in temporal response profiles in RT trials. Most PMd cells emit their strongest task-related response prior to and during movement and show relatively weaker tonic covariations with limb postures. This is shown by the lower proportion of PMd than MIc cells that are directionally tuned during the THT period, the smaller, mean posture-related dynamic discharge range of PMd cells, and the weak spatial coupling of the postural and movement-related activity. In contrast, many cells in MIc show strong directionally tuned responses both prior to and during movement and also during active maintenance of arm postures over the different target locations. Moreover, the movement- and posture-related response components typically show tight spatial cou-

pling, in that they tend to be oriented in the same direction. This suggests a fundamental difference in the relationship of these two cortical arm-related areas to arm movement versus actively maintained postures. Overall, the data suggest a continuous gradient of increasingly prominent tonic signals covarying with different arm postures and increasingly tighter spatial coupling of the directionality of activity during movement and posture progressing from PMd through MIr to MIc and finally to the peripheral musculature itself.

These differences between MIc and PMd have been largely overlooked to this point, for several likely reasons. The first is a bias toward conceptual issues concerning the planning and execution of movements, per se, that leads to the design of tasks in which movement is paramount and postural control is often secondary or nonexistent and usually ignored during analysis. Such tasks typically require an animal only to press a button or to attain briefly a certain target joint angle or hand position before returning rapidly to the start position in anticipation of the next trial. Many studies have also used a restricted range of movement directions and target endpoints. In contrast, our task placed a premium on precise postural performance. The monkey had to maintain its arm and a freely moving manipulandum accurately against gravity within a small target area at several different spatial locations for extended periods of time to perform the trials successfully.

## Posture versus movement

The terms "posture" and "movement" can apply to several different levels of representation of arm motor behavior. In the most general sense, they distinguish the functional state of static equilibrium from the dynamic state of the arm in motion, independent of specific metrics. Alternatively, they refer to the kinematic description of stationary arm configuration and the metrics of the changes in its configuration. Finally, they can relate to the kinetic parameters (forces, muscle activity) causal to either functional state (note that the terms "kinematics" and "kinetics" are being used here only as convenient descriptors of different classes of movement parameters, and do not imply that the motor system explicitly encodes parameters of newtonian mechanics). For instance, to actively maintain a particular posture, the motor system must generate the muscular forces that overcome the passive viscoelastic restorative forces inherent in the peripheral skeletomuscular system, and any external loads, such as those imposed by gravity acting on the arm's mass and the mass of the manipulandum used in this task. Since muscle activity clearly has a common causal link to both posture and movement via the forces they generate during both motor states, it is highly relevant that the activity of nearly all muscles acting on the shoulder and scapula covaried with different directions of movement and with different postures, and that their directional tuning was very similar between movement and posture.

Since the task-related discharge of MI and PMd cells covaried with different movement directions and also often with different arm postures, it is likely that their activity was related to the latter two levels of representation and was not merely signaling the states of posture or movement. Although the degree to which activity in MI and PMd relate to the spatiotemporal kinematics of motor acts versus the causal forces and muscle activity underlying them remains controversial, the consensus of many experiments is that neuronal correlates of forces and muscle activity during both movement and posture are more prevalent in MI than in PMd (Kalaska et al. 1989; Bauswein et al. 1991; Werner et al. 1991).

This is supported by the gradient of response properties observed across the precentral gyrus in this study. Movement and postural covariations are almost as strongly linked in the discharge of MIc neurons as they are in the activity of muscles. This spatial coupling is also evident in the PMd cells that are only movement-related under the conditions of our task and do not show activity changes during an instructed-delay task. Therefore, this spatial coupling of movement- and posture-related activity is a property of cells that, like muscles, appear to be predominantly related to movement execution, independent of their location in the precentral gyrus. The similar directional tuning during movement and posture is circumstantial evidence of a common functional link between the activity of those cells and instantaneous motor output during both static and dynamic conditions.

In contrast to MIc, the task-related activity of many instruction-related cells in PMd covaried mainly with attributes of an impending limb movement and less with the stable limb postures between movements, even though the latter are also behaviorally relevant active motor events in this task, requiring considerable precision. Moreover, their activity did not demonstrate the spatial coupling between posture- and movement-related activity to the same degree. Instruction-related PMd cells are implicated in response selection and the specification of movement parameters (Weinrich et al. 1984; Wise and Mauritz 1985; Kurata and Tanji 1986; Kurata and Wise 1988; Riehle and Requin 1989; Hocherman and Wise 1991; Mitz et al. 1991; Mushiake et al. 1991; di Pellegrino and Wise 1991, 1993; Wise et al. 1992; Fu et al. 1993, 1995; Kurata 1993; Crammond and Kalaska 1994). Their responses in this study suggest that presumed "higher-order" motor planning processes in PMd either involve representations of motor behavior in terms of attributes that do not reflect a common link between posture and movement like that seen in muscle activity, or represent that causal link in a manner that is fundamentally different from that in more caudal parts of the precentral gyrus. This in turn suggests that the neuronal representation of movement and posture is not uniformly distributed throughout the motor control system and, furthermore, that a functionally significant distinction between movement and posture may exist at certain levels in the motor control system.

These observations have implications for the conceptual background of equilibrium-point models of motor

control (Hogan 1984; Latash and Gottlieb 1992; Feldman and Levin 1995). These models argue that the central control of movement and posture are causally linked through the viscoelastic properties of antagonist muscle sets, so that the command for movement is a time-varying tonic signal specifying, in one form or another, a sequence of postural equilibria between the initial and final position of the limb (Hogan 1984; Latash and Gottlieb 1992; Feldman and Levin 1995). Proponents of equilibrium-point models might even find some resemblance between the population response histogram in MIc and the complex time course of the equilibrium trajectories for rapid movements predicted in some formulations of the model (Hogan 1984; Latash and Gottlieb 1992). If the assumption of those models is correct in that there is a causal link between postural signals and movement, our data suggest that this linkage could only be expressed primarily in the discharge of cells that are most strongly related to movement execution, whether in MIc or PMd. We do not suggest, however, that the response patterns during movement and posture in MIc are the neuronal correlates of shifting equilibria. Those same signals have been related elsewhere to many other parameters of movement, including limb trajectories, forces, torques, and muscle activity (Georgopoulos 1991; Fetz 1992; Kalaska and Crammond 1992; Kalaska and Drew 1993).

The predominantly phasic responses of PMd cells are not in themselves incompatible with equilibrium-point models. For instance, the lambda model (Feldman and Levin 1995) includes a phasic "cocontraction" (C) command during movement. However, the C command only signals the degree of coactivation of antagonist muscles – it cannot cause a shift in the equilibrium point on its own and so cannot specify the nature of the movement (Latash and Gottlieb 1992; Feldman and Levin 1995). The latter is accomplished in the lambda model by ramp-like shifts in the level of tonic "reciprocal" commands, but we found that tonic signals in PMd are weaker than in MIc and are a poor predictor of movement direction (Fig. 7F). It is therefore not obvious how to reconcile the predictions of the lambda model about the control signals for movement and our observations on PMd activity, especially in light of the evidence supporting its role in response selection and movement parameter specification. In the VITE model (Bullock et al. 1993), in contrast, a phasic "difference vector" is critical to initiation and termination of movement, as it signals the difference between current and intended endpoint postures. Unlike the other equilibrium-point models, therefore, the VITE model distinguishes movement from posture by a separate phasic signal that indirectly determines the metrics of movement.

## Function of MI versus PM

The RT trials of the task used in this study were not designed to test specific hypotheses about the functional role of the post-go activity in MI and PMd. However, the neuronal responses reported here during visually guided reaching movements provide circumstantial evidence supporting the concensus that PMd is more implicated in higher-order aspects of motor control, including the selection of the appropriate motor response to instructional signals, whereas more caudal parts of the precentral gyrus are more closely related to the moment-to-moment specification of motor output during both static and dynamic states.

For instance, PMd cells showed a preferential relation to movement over posture compared with cells in MI. Furthermore, PMd cells began to respond well before the MIc cells, and their activity had declined substantially by the onset of movement (Figs. 5, 9; Weinrich et al. 1984; Kalaska and Crammond 1992; Okano 1992). This implies that the major contribution of many PMd cells to the control of visually guided reaching movements in RT paradigms is made during the behavioral reaction time prior to movement onset. Further circumstantial evidence was the prevalence in PMd of cells that showed nondirectional, ramp-like changes in tonic rate during the CHT period of RT trials. This is reminiscent of the anticipatory activity described in PMd, which was related to the expectation of the animals for the presentation of instructional signals or other task events, rather than to the preparation of any specific movement (Mauritz and Wise 1986; Vaadia et al. 1988). The prevalence of this activity in PMd is consistent with the presumed involvement of this area in more cognitive aspects of the task, even without overt instructional signals. The presence of similar activity in MIc supports a possible contribution for this area to such cognitive functions (Georgopoulos et al. 1989, 1993; Georgopoulos 1991; Lurito et al. 1991). However, its relative rarity and weakness in MIc indicates that it is more closely coupled to motor aspects of the task, in this case maintenance of the limb over the central target until the presentation of the go signal.

That MIc is more closely coupled to movement execution is also supported by the continual gradient of response properties seen in our data from PMd to MIc and then to the muscles themselves. This is not to say that MIc cells generate muscle-specific signals or precisely define muscle contractile activity levels. These are probably specified only at the spinal level. However, the gradient of response properties is consistent with the proposal that the posterior part of MI is more tightly coupled than PMd to the mechanical details of the implementation of movement and contributes to the transformation of movement-related cortical activity from a representational level that is more abstract to one that is more closely related to the causal kinetic parameters of movement and actively maintained postures (Kalaska et al. 1989; Kalaska and Crammond 1992; Kalaska and Drew 1993).

The data indicate a significant rostrocaudal gradient of properties even within MI proper. According to all the criteria examined, MIr cell properties were intermediate between those in MIc and in PMd. A number of other studies demonstrate gradients of anatomical connectivity

(Holsapple et al. 1991; Johnson et al. 1993; Stepniewska et al. 1993, 1994) and functional properties (Tanji and Wise 1981; Strick and Preston 1982; Kalaska et al. 1989; Bauswein et al. 1991; Werner et al. 1991) within MI. Wise and colleagues (Weinrich and Wise 1982; Weinrich et al. 1984; Mitz et al. 1991) even identified a transition zone between PMd and MI proper on the basis of a number of criteria, including a rapidly declining rostrocaudal gradient of cells that showed significant activity changes during the delay period of DD trials.

These several lines of evidence suggest that even within the proximal-arm representation of MI there are regional differences in response properties. MI may not be a functionally homogeneous structure, but part of a larger rostrocaudal gradient of cell populations in which representations of arm movement at different levels of abstraction are distributed in partially segregated but overlapping manner across the precentral gyrus from the central to the arcuate sulcus.

Some controversy exists over whether the anterior part of the precentral sulcus should be considered part of the PM (Dum and Strick 1991; He et al. 1993), or MI (Kwan et al. 1978; Sessle and Wiesendanger 1982; Galea and Darian-Smith 1994). The latter conclusion would serve to increase the slope of the rostrocaudal gradient of properties within MI and strengthen the conclusion that MI plays a major role in presumed higher-order aspects of motor control. However, since the properties of the cells in the anterior precentral sulcus described here and elsewhere are sufficiently different from those in MIc and more like those found in more rostral cortex (Weinrich et al. 1984; Kurata and Tanji 1986; Kurata and Wise 1988; di Pellegrino and Wise 1991, 1993; Mitz et al. 1991; Mushiake et al. 1991; Wise et al. 1992; Kurata 1993; Crammond and Kalaska 1994), to include it in MI would seem misleading and counterproductive to an understanding of the relative functional roles of the MI and PM. Neuronal correlates of different levels of movement representation can be found in both areas, but they are not uniformly distributed across the precentral gyrus, and the transition between these two regions is gradual, not abrupt. As a result, where one choses to draw the arbitrary "border" between them on the precentral gyrus will have a large impact on the apparent degree of overlap in the function of MI and PM.

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