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Covariation of Primate Dorsal Premotor Cell Activity With Direction and Amplitude During a Memorized-Delay Reaching Task

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Messier, Julie and John F. Kalaska. Covariation of primate dorsal premotor cell activity with direction and amplitude during a memorized-delay reaching task. J Neurophysiol 84: 152–165, 2000. Extensive behavioral evidence suggests that the direction and amplitude of reaching movements are planned as two independent parameters by the motor system. However, whereas direction-related activity has been well documented by neurophysiological studies in many motor structures including the dorsal premotor cortex (PMd), there is much less consensus about the prominence and timing of amplitude-related premotor activity. We studied this issue using an instructed-delay task in which prior information about target location (direction and distance) must be memorized before movement initiation. The results show that prior information about distance is reflected in PMd activity during the delay period well before movement initiation, and begins to be expressed as early as 150 ms after presentation of target location. The prominence of neural correlates with direction is relatively constant throughout the trial, but distance correlates become gradually more prominent with time, both during and after the delay period. A small majority of cells were modulated only by direction during the delay period, but very few were modulated only by distance, and most of the rest were modulated by both. Therefore PMd neurons usually process information about distance only in conjunction with directional information. These results do not support a separate neuronal substrate for distance in PMd, but do not preclude its existence elsewhere. The results also support a progressive change in the nature of the movement-related representation in PMd with time in an instructed-delay paradigm.

INTRODUCTION

Visually guided reaching is presumed to involve a series of neuronal events that transform visual information about target location into the metrics of an arm movement, culminating in the force vectors generated by arm muscles. These events are often described as a sequence of sensorimotor transformations between representations of movement in different parameter spaces (Flanders et al. 1992; Kalaska et al. 1997), or as a set of processes that each specify a different movement parameter (Rosenbaum 1980). Direction and amplitude are widely considered to be two parameters that are specified during these processing stages. Understanding how they are planned will provide insight into the computational structure of the motor system.

The representation of movement distance in PMd activity is more controversial. In one instructed-delay task, very few PMd cells showed any influence of prior information about amplitude, suggesting either strict serial processing of direction before amplitude in PMd, or separate processing of amplitude outside of PMd (Riehle and Requin 1989). Neurocorrelates of movement direction are well established in delay-period and movement-related activity at both the single-cell and population levels in dorsal premotor cortex (PMd) (Caminiti et al. 1991; Crammond and Kalaska 1996; Fu et al. 1993, 1995; Wise et al. 1986, 1996; Wise and Mauritz 1985).

One prominent issue is the degree of independence in the planning of direction and amplitude. Many behavioral studies suggest that the two parameters are initially processed independently by two separate “channels” (Berkinblit et al. 1995; Bock and Arnold 1993; Boucher et al. 1992; Gordon et al. 1994a,b; Messier and Kalaska 1997, 1999; Soechting and Flanders 1989a,b). Nevertheless, other results suggest at least some sharing of neuronal resources implicated in their planning (Bhat and Sanes 1998; Favilla et al. 1989, 1990; Ghez et al. 1997). A second prominent issue concerns the temporal relationship between direction and distance processing and has yielded even more conflicting results. Many studies support serial hierarchical planning of direction before amplitude (Bhat and Sanes 1998; Larish and Frekany 1985; Megaw 1972). Other studies suggest that the planning of amplitude could occur simultaneously with or even before direction (Favilla et al. 1989, 1990; Favilla and De Cecco 1996; Ghez et al. 1997; Rosenbaum 1980).

There have been relatively few neurophysiological studies of the planning of direction and amplitude in the primary motor and premotor cortex (Fu et al. 1993, 1995; Kurata 1993; Riehle and Requin 1989; Schwartz and Georgopoulos 1987). Neuronal correlates of movement direction are well established in delay-period and movement-related activity at both the single-cell and population levels in dorsal premotor cortex (PMd) (Caminiti et al. 1991; Crammond and Kalaska 1996; Fu et al. 1993, 1995; Wise et al. 1986, 1996; Wise and Mauritz 1985).

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processing, with direction predominant before movement onset, and amplitude mainly after movement onset. Given the diversity of task design and results in those studies, we re-examined how the two putative psychophysical channels for direction and amplitude are reflected in PMd cell discharge. We used a task that combined features of all three previous studies, with the additional requirement that target location be memorized during a delay period and recalled during the movement phase of the trials. This demanded maximum use of the direction- and amplitude-related information provided by the instructional cues to perform the task. A major focus of interest in this paper is the temporal evolution of cell activity during the first 500 ms after the appearance of the instructional cues.

METHODS

Comparison of previous paradigms

Differences in the tasks used in previous studies of direction and distance in PMd may have had a significant impact on results. In one (Fu et al. 1993, 1995), monkeys made whole-arm reaching movements in a horizontal plane, in a reaction-time paradigm without prior information. The "go" signal in each trial was a visual stimulus presented at the target location (complete information about direction and distance), which remained visible for the rest of the trial. There were 48 target locations arrayed in 6 concentric circles (1.4–5.4 cm radius) of 8 targets spaced at 45° intervals. In contrast, Riehle and Requin (1989) and Kurata (1993) both used only two opposing directions of movement (flexion, extension) of the wrist and two movement amplitudes (15 or 30°, and 3 or 15°, respectively). Both also used instructed-delay paradigms that provided different degrees of prior information, but in different ways. In Riehle and Requin (1989), the location of visual stimuli explicitly signaled both direction and distance, thereby requiring a sensorimotor transformation with high stimulus-response compatibility. Different combinations of visual stimuli at the beginning of the delay period signaled either complete information about target location, partial information (direction or distance only) or no information. The go signal at the end of the delay period always provided complete information about target location and remained visible for the rest of the trial. Kurata (1993) used two sequential delay periods. In the first, the monkey received only partial information (direction or distance), and in the second delay, it always received complete information. The location of visual stimuli signaled direction, but two auditory tones signaled distance. The gain between movement distance and visual feedback about wrist displacement was also scaled so that the monkey received no visual input about distance. As a result, the stimulus-response compatibility for direction was high, but the arbitrary cross-modal association for distance had low compatibility. Finally, whereas directional information was present after the go signal, amplitude information was not.

Apparatus and task

The memorized-delay task used here required whole-arm reaching movements in multiple directions and amplitudes (Fu et al. 1993, 1995) in an instructed-delay paradigm (Kurata 1993; Riehle and Requin 1989). Unlike those studies, however, the instructional cues always provided complete information about direction and distance at the start of the delay period and were presented for only a brief period of time, and the go signal provided no target information.

The X-Y position of a manipulandum in the horizontal plane was measured to 0.1-mm resolution at 55 Hz (Science Accessories, model G/P-9) and displayed continuously as a cursor on a monitor screen placed at eye level 60 cm in front of a monkey (Fig. 1). There was a 1:1 scaling between displacements of the manipulandum and of the cursor. A young male rhesus monkey (Macaca mulatta; 4.5 kg) learned to make reaching movements with the manipulandum to displace the cursor from a central start position to 24 target locations in 8 different directions at 45° intervals (starting at 0° to the right), arrayed in 3 concentric circles of 2.5, 5.0, and 7.5 cm radius.

At the start of each trial, a green circle (1.5 cm diam) appeared at the center of the monitor screen (Fig. 1, screen 1). The monkey positioned the cursor within this circle for a variable period of time (1–3 s; Fig. 1, screen 2). After this center hold time, a visuospatial instructional cue (a red circle) appeared for 500 ms at one of the 24 target locations (Fig. 1, screen 3). The cue then disappeared, and the monkey had to remember its location for the remainder of the delay period (1,000–2,500 ms; Fig. 1, screen 4). At the end of the memorized delay period, the disappearance of the central circle served as a nonspatial go signal to move to the remembered target location (Fig. 1, screen 5). If the monkey held the cursor within the target window for 1 s, it received a liquid reward. At the end of all trials, whether successes or errors, the monkey was given knowledge of results. This took the form of the last measured position of the cursor and a white circle indicating the acceptable limits of the target window (Fig. 1, screen 6). This information was displayed for 500 ms, before the screen was blanked in preparation for the next trial.

The targets were presented in a randomized block pattern. A single replication of the task involved one successful movement to each of the 24 targets in a pseudo-random sequence. Data files comprised 3–10 complete replications (72–240 successful trials).

Behavioral control for direction and amplitude

The task requires subjects to use visual information to scale the dimensions of a delayed movement to a memorized target location. Ideally, one would like to assume that each response is a valid observation of the subjects’ conscientious effort to perform the task, without judgment as to success or failure. This strategy can produce stable performance in motivated human subjects (Gordon et al. 1994a,b; Messier and Kalaska 1997, 1999), but not in behaving monkeys. Reward criteria had to be used to ensure continued motivated involvement of the monkey throughout each session. This took the form of large circular target windows within which the monkey had to end each movement to receive a reward. However, if the size of the target window is kept constant, the degree of accuracy required for reward will increase sharply with distance but not with direction. This confound of accuracy with amplitude could manifest itself as a false-positive main effect of amplitude or as an amplitude-direction interaction in cell discharge even if a cell was only influenced by directional information.
One solution would be to scale window diameter as a function of target distance. This would be adequate if variable errors of reaching direction and distance both scaled equally with amplitude, but human studies have shown that they do not (Gordon et al. 1994a,b; Messier and Kalaska 1997, 1999). Furthermore, if the window size was large and increased as a fixed percentage of amplitude, windows for different target distances along a given direction would rapidly overlap. As a result, subjects could be rewarded for moving in the “correct” direction but the “wrong” distance, which could have unpredictable effects on results. As a compromise between these confounds, we used window diameters of 2.25, 2.75, and 3.25 cm for target distances of 2.5, 5.0, and 7.5 cm, respectively. This permitted the largest possible windows, thereby reducing the number of unrewarded trials, while minimizing their overlap, to compel the monkey to make maximum use of cue information to perform the task.

Data recording

Aseptic surgical methods were used to implant a recording cylinder over the PMd contralateral to the trained arm. Standard single-unit recording techniques were used to study the activity of single cells in PMd during the task. Isolated cells that were active in the task were studied further if they were preferentially related to active or passive motions of the proximal arm. Cells responsive to distal arm and trunk movements were excluded. After several weeks of recordings in one cylinder, the monkey was trained to perform the task with the other arm, and a second cylinder was implanted over the contralateral PMd. Isolated cells that were active in the task were recorded techniques were used to study the activity of single cells in PMd during the task. Isolated cells that were active in the task were excluded. After several weeks of recordings in one cylinder, the monkey was trained to perform the task with the other arm, and a second cylinder was implanted over the contralateral PMd. At the end of recordings in each cylinder, electrolytic lesions (25 μA, 10 s) were made at several cortical locations to confirm the sites of penetrations in PMd.

Activity of all major shoulder and axial muscles was recorded at the end of cell data collection in each cylinder. The muscles studied included the supraspinatus, infraspinatus, rostral and caudal trapezius, subscapularis, pectoralis, deltoit (medial, anterior, and posterior), biceps, triceps (medial, long, and lateral), teres major, latissimus dorsi, and brachialis. Pairs of fine Teflon-coated stainless steel wire electrodes were implanted percutaneously into the selected muscles. EMG activity was amplified, rectified, and integrated (10-ms interval) to generate summed histograms of activity over 10 trials for each of the 24 target locations.

Data analysis

This paper describes the effects of direction and amplitude on the mean discharge rate of single cells for only those trials whose movements ended within the intended target window.

Each trial was divided into six behavioral epochs: 1) center hold time, while holding the pendulum at the central target before cue presentation; 2) Cue, the 500 ms during which a red circle was presented at 1 of the 24 target locations; 3) Pre-go, the last 500 ms of the memorized delay period immediately preceding the go signal; 4) reaction time (RT), from the go signal (disappearance of the central green circle) to movement onset, defined as the first time the instantaneous velocity of movement exceeded 10% of the peak velocity for that trial; 5) movement time (MT), from movement onset to movement end, the time at which the instantaneous velocity fell below 10% of the peak velocity; and 6) target hold time (THT), from the end of the movement to the end of the trial. The basic datum for analysis was the mean discharge rate, including partial spike intervals, of a cell during each epoch of a trial. For electromyographic (EMG) records, the equivalent datum was the area under the rectified and integrated single-trial activity trace during each epoch.

Variation in activity with direction and amplitude was evaluated by several tests. First, a two-way ANOVA (8 directions × 3 amplitudes) with repeated measures (program 5V, BMDP Statistical Software) determined whether direction and distance had a significant main effect on the discharge in each behavioral epoch. The ANOVA also identifies significant interaction effects, in which the response to one factor is significantly dependent on specific levels of the other factor. Interaction effects can imply that directional tuning was significantly altered as a function of distance, or that the effect of distance varied as a function of target direction, or both. Alternatively, it can imply that specific target locations (specific combinations of direction and distance) had a significant effect on discharge.

The two-way ANOVA provides limited information about the details of the main effects on activity, because it tests only for significant differences in the grand mean of activity for each level of treatment of one factor across all levels of treatment of the other. It cannot answer more specific questions such as whether and how much directionality changed with distance, whether the effect of distance was uniform across all directions or was limited to only a few directions, and whether there was linear scaling of activity with distance.

To examine directional effects in more detail, we calculated the preferred direction of cell activity for the data subset at each target distance in each epoch, using standard trigonometric procedures (Georgopoulos et al. 1982). Next, significant directional tuning was determined for each data subset by bootstrapping (Georgopoulos et al. 1988; Sergio and Kalaska 1998). This method estimates the probability that the experimental data set was directionally tuned on the basis of the inter-trial variability of the data. The strength of the directional bias of the experimental data set was determined by calculating its mean length (Batschelet 1981), which can vary from 0.0 (perfect uniformity) to 1.0 (active uniquely for only 1 direction). If the data are strongly directionally tuned with relatively low inter-trial variability, random shuffling of the single-trial data across directions should generate a data distribution whose mean length will be less than that of the experimental data set. In contrast, if the data are weakly tuned or if there is high intertrial variability, random shuffling could by chance generate a distribution whose directional bias is stronger than the experimental distribution. Therefore repeated reshuffling of the data provides an estimate of the probability that the directional bias of the experimental data could have arisen by chance. We reshuffled the data for a given trial epoch 1,000 times and calculated the mean length of the new data distribution after each shuffle. If fewer than 10 shuffles produced a distribution with stronger directional bias than the experimental data set, it was considered significantly directionally with a probability of approximately 0.01. For each case of significant directional tuning, a 99% confidence interval was next determined about the preferred direction, again by bootstrapping (Georgopoulos et al. 1988; Sergio and Kalaska 1998). Finally, a comparison of directional tuning was made across different distances within the same epoch, and across different epochs for the same distance. The difference in preferred direction was calculated for only those pairs of data sets that were both significantly tuned. The difference was considered significant if the confidence intervals about the preferred directions of the two data sets did not overlap.

To examine in more detail the nature of amplitude effects, two different analyses were undertaken. A one-way ANOVA (1 direction × 3 distances) with repeated measures (program 5V, BMDP Statistical Software) was used to evaluate the influence of intended movement amplitude along each individual direction. To further characterize the form of significant amplitude effects found with the one-way ANOVA, linear regressions were performed between discharge rates and movement amplitudes for each direction. Amplitude values used for regression analysis were the actual movement amplitudes reached by the monkey, not the intended target distances that were used for the ANOVAs. This change was necessary because grouping of observations about the three intended target distances in the repeated-measures task reduced the degrees of freedom in the regression analysis to one (Sokal and Rohlf 1981), which imposed a severe penalty on the identification of linearity.

Two further analyses examined the earliest responses of PMd cells after the presentation of the cues. First, the Cue epoch was divided...
into five successive 100-ms intervals, and the mean spike rate was calculated within each interval. A two-way ANOVA was performed on the cell activity for each 100-ms interval. Second, single-cell spike rates were computed in bins of 10 ms to generate population histograms.

RESULTS

Data base

The activity of 162 task-related PMd neurons was recorded from two hemispheres of one monkey (Fig. 2) performing reaching movements from a central start position to memorized target locations at three distances along eight different directions. The size of the data set varied from cell to cell, ranging from 3 to 10 movement replications to each target (72–240 trials). EMG activity was recorded from 16 proximal arm muscles. All EMG data sets comprised 10 complete replications. The four main trial epochs of interest were Cue, Pre-go, RT, and MT.

Response correlates of direction and distance

A two-way ANOVA assessed the overall effect of direction and distance and their degree of convergence on the activity of PMd cells and arm muscles.

Figure 3A shows the EMG activity of one muscle (medial deltoid) that is typical of the behavior of most muscles in the task. There was broad directional tuning during the MT epoch centered on a preferred direction of 118° for the activity pooled across all 24 targets, and a systematic increase of the area of the histogram after the go signal as a function of target distance. A two-way ANOVA for the MT found a significant interaction (Dir/Amp/I, main effect of both direction (Dir) and amplitude (Amp) and a significant interaction (I) between them (i.e., Dir/Amp/I, main effect of both direction and amplitude without an interaction (Dir/Amp) during MT. In contrast, the profile of the cell in Fig. 4C changed from Dir/I in the Cue epoch to Dir/Amp/I during the Pre-go and RT epochs, and to Dir only during the MT epoch. On the other hand, the cell in Fig. 4D showed a Dir/Amp/I profile for all epochs. However, the activity underlying this profile differed across epochs. During the Cue period the amplitude effect took the form of a decrease in mean firing frequency with target distance, whereas it increased during all other epochs (Fig. 4D).

Figure 5A shows the total rate of occurrence of main effects of direction and amplitude for each epoch. The majority of PMd cells (88.9 –92.0%) showed a main effect of direction in each epoch, while a smaller proportion of cells (34.0 –55.6%) showed an amplitude effect (Fig. 5A). Figure 5B illustrates the rate of segregation versus convergence of effects on single cells. A sizeable fraction of cells (35.2 –58.7%) showed a main effect of direction only (Dir) during the Cue epoch, but a main effect of direction and an interaction (Dir/I) during the Pre-go and RT epochs, and a main effect of both direction and amplitude without an interaction (Dir/Amp) during MT. In contrast, the profile of the cell in Fig. 5C changed from Dir/I in the Cue epoch to Dir/Amp/I during the Pre-go and RT epochs, and to Dir only during the MT epoch. On the other hand, the cell in Fig. 4D showed a Dir/Amp/I profile for all epochs. However, the activity underlying this profile differed across epochs. During the Cue period the amplitude effect took the form of a decrease in mean firing frequency with target distance, whereas it increased during all other epochs (Fig. 4D).

Looking across epochs, most PMd cells were influenced by both parameters at one time or another. First, 99.4% of cells showed a main effect of direction during at least one epoch of the task, 80.2% showed a main effect of amplitude, and 80.2% showed a significant interaction at one time or another. Furthermore, 79.0% of the cells showed a main effect of both direction and distance in the same behavioral epoch for at least one epoch in the trial.

These results revealed that direction and distance correlates were expressed by PMd cells at all times during the trial and indicated an extensive convergence of direction and amplitude information on PMd single-cell activity. In particular, a main effect of amplitude in a given epoch was usually accompanied by a main effect of direction or a significant interaction. Cells with significant Dir, Amp, Dir/Amp, and I effects were distributed uniformly across recording sites in all epochs, with no evidence for a gradient of responses across the cortical region sampled (data not shown).

Description of amplitude effects

The amplitude modulation was highly variable across directions and epochs in PMd. For example, the cell in Fig. 4A showed decreases in activity with distance during the Cue, Pre-go, and RT epochs that were stronger at 45° and 135° than at its preferred direction (90°). In contrast, the cell in Fig. 4C showed a distance-related increase in activity during the Pre-go and RT epochs around its preferred di-
rection (180°) for these two epochs, but decreases in activity near the opposite direction (0°). For the cell in Fig. 4D, discharge increased with distance during MT for movements near its preferred direction (90°) but decreased with distance along the opposite (225° and 270°) directions. This was preceded by a suppression of activity during the Cue epoch for all directions, which scaled with distance at 225° and 270°.

A one-way ANOVA (1 direction × 3 distances; \( P < 0.01 \)) quantified how PMd discharge was influenced by intended movement amplitude along each movement direction separately. Most cells showed significant amplitude effects along a restricted number of directions (Table 1). Because each cell was tested eight times in a given epoch for this analysis, the effective probability of at least one false positive result increased to \( P < 0.08 \) for a given cell. As a result, the number of cells that could be expected to show a false positive effect by chance in a given epoch should be 13/162 for 1 direction, 1/162 for 2 directions, and vanishingly small for 3 or more directions. The incidence of significant results far exceeded that expected by chance (Table 1). We repeated the analysis using the Bonferroni correction for eight repeated tests (i.e., \( P < 0.00125 \)). This reduced the incidence of significant amplitude effects by about 30% in all epochs, but the trends seen in Table 1 were retained (data not shown). Significant amplitude effects were found for all...
movement directions, with some tendency for the frequency of effects to be greatest near the preferred direction in all trial epochs (Fig. 6).

A high proportion of PMd cells in each epoch (75.9 – 87.0%) showed a significant amplitude effect along at least one direction (Fig. 7A). However, when the total number of significant results in each epoch (Table 1) were expressed as a percentage of the total number of tests performed (162 cells × 8 directions), the incidence of significant amplitude effects was low at all times (20.4% during Cue, 37.8% during MT).

Linear regressions were next performed between discharge rates and movement amplitudes for each direction (Fig. 7B). In each trial epoch, a large proportion (46.7 – 80.7%) of PMd cells that showed a significant amplitude effect (1-way ANOVA; Fig. 7A) for at least one direction of movement also showed significant linear scaling ($P < 0.05$) with amplitude along at least one direction (Fig. 7B). Each of those cells could show a significant amplitude effect for more than one movement direction (Table 1).

The large majority of all those cases of a significant effect of amplitude in the one-way ANOVA also showed significant linear scaling with amplitude for PMd cells (77.2 – 89.2% for different epochs, data not shown in Fig. 7). A greater number of significant linear regressions were observed along the preferred direction of

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**FIG. 4.** Discharge pattern of 4 more PMd cells, illustrating the range of response patterns seen in the data sample. Same format as Fig. 3B.
cells than along the opposite direction (Table 2; cf. Fig. 6). The majority of significant linear regressions showed positive slopes, which were also more frequent at the preferred direction, especially during MT (Table 2).

Variation in directional tuning of cells with movement amplitude

The directionality of PMd activity was evaluated in more detail by bootstrapping (see METHODS). Pooling across all 24 targets, 80.9% of the cells were significantly directionally tuned during the Cue epoch, 88.3% during Pre-go, 86.2% during RT, and 78.4% during MT. These values agree well with the incidence of main effects of direction in the two-way ANOVA (Fig. 5A). The percentages cannot be expected to be identical, however, because the bootstrapping test is based on the degree of unimodal directional bias in the data, whereas the ANOVA tests for differences in activity across directions without respect to their directional distribution.
Bootstrapping was then used to test the directional tuning of the data subsets at each distance separately, in each epoch. The vectors at the bottom of Figs. 3 and 4 show the preferred directions for only those cases of significant tuning. The incidence of significant directional tuning decreased for the data subsets at each distance separately, compared with the data pooled across distances (Table 3). Furthermore, the probability of significant tuning increased with increasing movement amplitude. The directionality of the cells tended to remain fairly constant across different reaching amplitudes in a given epoch. For instance, the preferred direction of the cell in Fig. 4A during the Cue epoch was 79.7, 87.1, and 95.2° for movements of 2.5, 5.0, and 7.5 cm, respectively. Bootstrapping determined that the cell was significantly tuned at each distance and that the 99% confidence intervals about the preferred direction at each distance were 39.1, 29.5, and 34.0°. As a result, there were no significant amplitude-dependent directional differences during the Cue epoch for that cell. Of 1,069 total tests across all 3 distances and all epochs, only 3 cases of significant directional changes were found.

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Directional tuning tended to be somewhat more variable across epochs at a given distance, than across distances within a given epoch (Fig. 4). Comparing against the directionality of a cell during the Cue epoch, the incidence of significant changes in preferred direction was always low (0.0–16.5%), but increased systematically from the Pre-go to the MT epochs, at each distance, and was more pronounced for the larger distances (Table 4).

**Time course of directional and amplitude modulation**

Target distance showed a progressively increasing influence on PMd activity as time progressed in the trial. First, the majority (58.7%) of task-related cells showed only a main effect of direction during the Cue period, but this gradually decreased in frequency in subsequent epochs. In contrast, cells showing main effects of both direction and amplitude increased systematically throughout the trial, as did the proportion of cells showing a significant interaction between direction and amplitude (Fig. 5B). These time trends also suggested that the degree of convergence of direction and amplitude correlates in PMd single-cell discharge increased progressively with time during the task.

The one-way ANOVA (Figs. 6 and 7A) and regression (Fig. 7B) analyses also indicated an increase in amplitude correlations with time. Finally, linear amplitude effects at the single-cell level spread out over a progressively wider range of movement directions with time (Table 2). For instance, there was a gradual decrease in the proportion of cells showing linear amplitude scaling along only one or two directions from the Cue to the MT epochs, and a reciprocal gradual increase in the proportion of cells with linear scaling along three directions or more (Fig. 8).

**Activity during the Cue epoch**

The analyses presented so far suggest that neuronal correlates with direction predominate in PMd during the Cue epoch, and that distance correlates become relatively more prominent in subsequent epochs. An important question is whether there is a latency difference in the appearance of direction and distance correlates within the Cue epoch itself, or do both appear simultaneously but amplitude effects increase more slowly? To examine this issue, spike rates were computed for each successive 100-ms interval of the Cue epoch and subjected to a two-way ANOVA (Fig. 9). Direction effects increased abruptly during the 100- to 200-ms interval after cue appearance and attained their maximum frequency during the 200- to 300-ms interval (Fig. 9A). In contrast, the frequency of the amplitude and interaction effects increased more gradually and with very similar time courses from the 100- to 200-ms to the 300- to 400-ms intervals.

The incidence of cells that showed only a main effect of direction was highest in the 100- to 200-ms interval (Fig. 9B), and then declined slightly. At all times, most of the cells that

### Table 1. Distribution of the numbers of PMd cells that showed a significant amplitude effect for one to eight movement directions in each epoch*

<table>
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<td>8</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>RT</td>
<td>39</td>
<td>27</td>
<td>21</td>
<td>16</td>
<td>13</td>
<td>8</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>MT</td>
<td>26</td>
<td>19</td>
<td>23</td>
<td>23</td>
<td>16</td>
<td>16</td>
<td>6</td>
<td>4</td>
</tr>
</tbody>
</table>

PMd, dorsal premotor cortex; RT, reaction time; MT, movement time.

* One-way ANOVA, $P < 0.01$. 

---

**FIG. 5.** 

A: frequency of significant main effects for direction (Dir) and amplitude (Amp), as well as no significant task relation (N) for each epoch for PMd cells. 

B: frequency of occurrence of different combinations of main effects (Dir only, Amp only, Dir/Amp) and interaction effects (I).
showed a main effect of amplitude also showed a main effect of direction (Fig. 9B). This analysis within the Cue epoch suggested that the expression of target distance correlates is slightly delayed relative to that for direction at least in terms of the number of cells showing a main effect of each factor. It also confirmed that at no time during the Cue epoch did a large population of PMd cells covary only with distance, at least at a temporal resolution of 100 ms.

To examine at still higher resolution the temporal evolution of activity during the Cue epoch, single-cell spike rates were calculated in 10-ms bins (Fig. 10). A striking feature of the resulting population histograms at the preferred direction of each cell (Fig. 10A) is that distance had a relatively modest effect on the mean discharge rate of the total population. This arises in part from the fact that significant amplitude effects were least common during the Cue epoch (Figs. 5–7), and in part because they could have either a positive or negative slope (Table 2). Therefore we generated separate histograms for only those cells that showed a positive (Fig. 10C) or a negative (Fig. 10D) regression slope at their preferred direction. These histograms show that cell activity began to increase about 100 ms after cue appearance. Differential scaling of activity with distance became evident at about 150 ms and was maximal by about 200 ms after Cue onset. This appeared to contradict the ANOVA results (Fig. 9), which indicated that the incidence of main effects of amplitude increased twofold between the 100- to 200-ms and 200- to 300-ms intervals. This apparent discrepancy likely resulted from the different temporal resolution of the two analyses. Because the differential discharge rates related to distance are only evident during the last half of the 100- to 200-ms interval (Fig. 10), this effect is diluted when averaged over the entire 100- to 200-ms interval for the ANOVA, thereby reducing the probability of finding a significant effect (Fig. 9). In contrast, the differences are fairly constant throughout the 200- to 300-ms interval (Fig. 10) and so are faithfully captured by the mean rate within that interval (Fig. 9).

The rising phase of the histograms for different distances tended to have fairly similar slopes, and there was a progressive increase in the time-to-peak discharge for the different distances (Fig. 10, C and D). This suggests that the earliest task-related population activity may increase at a relatively fixed rate independent of distance, and plateaus once it reaches a level appropriate for the intended distance.

**DISCUSSION**

This study showed that activity covarying with the direction and amplitude of intended arm movements arises rapidly in dorsal premotor cortex 100–300 ms after the presentation of prior information about target location in a memorized instructed-delay task, and continues to evolve more slowly throughout the rest of the trial. These results also indicate that direction and amplitude, which often appear to be processed independently by the motor system at the behavioral level, show extensive convergence at the single-cell level in PMd.

**Comparison with previous studies**

Neurophysiological studies of direction- and distance-related activity in PMd have yielded widely varying results. The

<table>
<thead>
<tr>
<th>Task Epochs</th>
<th>Significant Positive Slopes</th>
<th>Significant Negative Slopes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Preferred direction</td>
<td>Opposite direction</td>
</tr>
<tr>
<td>Cue</td>
<td>32 (19.8)</td>
<td>17 (10.5)</td>
</tr>
<tr>
<td>Pre-go</td>
<td>50 (30.9)</td>
<td>17 (10.5)</td>
</tr>
<tr>
<td>RT</td>
<td>47 (29)</td>
<td>22 (13.6)</td>
</tr>
<tr>
<td>MT</td>
<td>64 (39.5)</td>
<td>5 (3)</td>
</tr>
</tbody>
</table>

For abbreviations, see Table 1. * Linear regressions, $P < 0.05$; number of cells is 162.
discrepancies may be largely due to differences in task design and data analysis, as well as in how direction and amplitude information are processed in PMd in different behavioral contexts.

In the present study, the brief cue signal always completely specified direction and distance. The delayed go signal was uninformative, compelling the monkey to remember the cue location for the duration of the trial. Under these conditions, PMd activity covaried with target direction and distance in all task epochs.

In contrast, Riehle and Requin (1989) found very little distance-related activity, especially during the delay period. However, their task studied the independence of processing of direction and distance by specifying these parameters in two sequential steps. Cues provided only partial or no target location information during the delay period of 75% of the trials, and the go signal always completely specified target location. This may have reduced the ability or need to process information about direction and distance until the go signal. Similarly, the task used by Kurata (1993) provided complete target information in two steps, but in the form of two successive delay periods, so that the movement parameters were completely specified during the second delay before the go signal. Far more PMd cells were active in the second delay period (complete information) than in the first (partial information), again suggesting that PMd may not have become fully engaged in response preparation until complete information was provided.

Kurata (1993) also observed that far more cells were modulated by amplitude only, especially during the movement phase, compared with the present study and Riehle and Requin (1989). In the latter studies, the monkeys’ behavior was guided by simple sensorimotor transformations with high stimulus-response compatibility (see METHODS). In contrast, Kurata (1993) signaled distance using an arbitrary stimulus-response association, which has strong and complex effects on PMd discharge (Mitz et al. 1991; Shen and Alexander 1997a,b; Wise et al. 1996). The extra amplitude-related activity observed by Kurata (1993) may have reflected extra neuronal processing to associate different auditory tones with different movement amplitudes. In summary, many of the differences in results may be due to differences in task design.

Analytic procedures also had an impact. There are many similarities between our results and those of Fu et al. (1993), who used similar ANOVA and regression methods. When Fu et al. (1995) reanalyzed their data using multiple linear regression on a time series of successive 20-ms bins, they reported far fewer amplitude correlations before movement onset than in their earlier analysis. However, their regression model partitioned distance information between two terms: target location and movement distance. The first term accounted for any planar covariation of cell activity with both direction and distance and began to be expressed before movement onset. The second term captured only systematic nondirectional changes in activity with distance and was expressed mainly after movement onset. Therefore all three reaching studies found neuronal correlates of distance before movement onset.

### Table 3

Number (and percent) of total sample of PMd cells that are significantly directionally tuned at each movement amplitude, in each epoch

<table>
<thead>
<tr>
<th></th>
<th>Distance 1</th>
<th>Distance 2</th>
<th>Distance 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cue</td>
<td>92 (56.8)</td>
<td>101 (62.3)</td>
<td>107 (66.0)</td>
</tr>
<tr>
<td>Pre-go</td>
<td>107 (66.0)</td>
<td>113 (69.8)</td>
<td>116 (71.6)</td>
</tr>
<tr>
<td>RT</td>
<td>113 (69.8)</td>
<td>115 (71.0)</td>
<td>121 (74.7)</td>
</tr>
<tr>
<td>MT</td>
<td>91 (56.2)</td>
<td>99 (61.1)</td>
<td>109 (67.3)</td>
</tr>
</tbody>
</table>

Number of cells is 162. For abbreviations, see Table 1.

### Table 4

Number (and percent) of PMd cells that show significant changes in directional tuning between different epochs, at each movement amplitude

<table>
<thead>
<tr>
<th></th>
<th>Distance 1</th>
<th>Distance 2</th>
<th>Distance 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cue vs. Pre-go</td>
<td>0/72 (0.0)</td>
<td>2/83 (2.4)</td>
<td>3/91 (3.3)</td>
</tr>
<tr>
<td>Cue vs. RT</td>
<td>3/75 (4.0)</td>
<td>4/78 (5.1)</td>
<td>9/92 (9.8)</td>
</tr>
<tr>
<td>Cue vs. MT</td>
<td>3/55 (5.5)</td>
<td>8/67 (11.9)</td>
<td>13/79 (16.5)</td>
</tr>
</tbody>
</table>

For abbreviations, see Table 1.
either as a main effect of amplitude in an ANOVA, or as a target location term in a multiple linear regression model.

In this study and in Fu et al. (1993), cell directional tuning remained fairly stable across target distances and trial epochs. In contrast, Johnson et al. (1999) reported large variations of directional tuning with time when analyzed at 20-ms intervals. The difference may be partly due to averaging of cell data over epochs of several hundred milliseconds, which would mask some of the temporal variability in tuning. It may also reflect differences in the sensorimotor processes required to perform movements to stationary targets (present study; Fu et al. 1993) versus interception and pursuit of targets moving at different speeds (Johnson et al. 1999).

Independent channels for direction and amplitude: spatial segregation

Two separate cell populations would be the simplest substrate for the putative independent channels for direction and distance. Consistent with this hypothesis, all studies found significant numbers of cells that covaried only with direction at a given moment in time (Fu et al. 1993, 1995; Kurata 1993; Riehle and Requin 1989; present study). However, most of the studies found very few amplitude-only cells (Fu et al. 1993; Riehle and Requin 1989; present study), implying that if an independent channel for amplitude exists, it must be located outside of PMd. At the temporal resolution used in the present study, amplitude is almost always expressed in conjunction with direction at the single-cell level, in the form of significant main effects for both parameters or as a significant response interaction between them. This single-cell convergence is consistent with behavioral evidence of some sharing of neuronal resources in the processing of direction and amplitude (Bhat and Sanes 1998; Favilla et al. 1989, 1990; Ghez et al. 1997).

Independent channels for direction and amplitude: temporal segregation

Temporal differences in the evolution of direction and distance in motor output are another line of evidence supporting independent planning channels (Favilla et al. 1990; Favilla and De Cecco 1996; Ghez et al. 1997; Gordon et al. 1994b; Messier and Kalaska 1997, 1999). The present study revealed some differences in the time course of expression of direction and distance correlates in PMd. Paradoxically, our results suggest that this differential time trend actually reflects an increasing convergence of both parameters in the discharge of single cells. This suggests that while the temporal dynamics of processing of both parameters may be independent, it is implemented on overlapping populations of PMd cells.

There was also evidence of a latency difference between direction and amplitude correlations. Directional correlates predominated in PMd during the brief time interval 100–200 ms after cue appearance, whereas amplitude correlates increased more gradually (Figs. 9 and 10). This is consistent with some degree of serial processing of direction before amplitude, but the overall trend is for extensive temporal overlap (Fu et al. 1993). Indeed, the representation of both parameters evolved rapidly between 100–300 ms after cue presentation. This agrees well with the time course of specification of direction and amplitude in behavioral studies using a timed-response paradigm (Favilla et al. 1989, 1990; Ghez et al. 1997).

Temporal independence has also been assessed by the degree to which one parameter can be processed without knowledge of the other. Some studies suggest that distance information cannot be processed until direction is specified (Riehle et al. 1994; Riehle and Requin 1989), while others suggest more flexibility or overlap in their specification (Fu et al. 1993; Kurata 1993). This issue is best addressed by signaling direc-
tion and distance separately in different temporal orders (Kurata 1993; Riehle and Requin 1989). Since both parameters were specified simultaneously by the cue in the present study, it is not a sensitive test of this question.

Simultaneous covariation of single-cell activity with multiple parameters could introduce uncertainty about its information content. Fu et al. (1995) argued that this ambiguity would be eliminated and independent planning preserved by temporal segregation of the processing of different parameters over short time intervals. However, when we divided the Cue epoch into five 100-ms intervals, we still found that most cells with an amplitude effect also had a directional effect, indicating that this was not an artifact of averaging together temporally segregated representations of two parameters across a long time interval.

Because distance information in our task is evident in PMd during the delay period prior to movement onset, it would appear to be centrally generated and implicated in movement planning. It could not be generated principally by peripheral sensory reafference arising during the movement itself, or used only for movement error correction or for signaling the new position of the arm in anticipation of future movements (Fu et al. 1993, 1995).

**Psychophysical channels and sensorimotor transformations**

The separate-channel hypothesis for direction and distance is representative of a parametric model of motor planning whereby each parameter is specified by separate neuronal processes, whose outputs are then combined to specify the intended movement. Because amplitude correlates are only seen in conjunction with directional correlates in PMd in this task, the parametric model predicts that PMd must function at a level subsequent to the putative distance-only channel, and contributes to the process that links together the different parameters.

However, the covariation of discharge with the direction and distance of hand displacement does not prove that PMd cells are explicitly processing those particular parameters. Cells in PMd and primary motor cortex (MI) do not show invariant relations to either parameter. Movement-related cell activity is often modulated by hand spatial location and arm geometry, implicating those cells in the sensorimotor transformations between representations of movement in extrinsic and intrinsic parameter spaces (Caminiti et al. 1990, 1991; Scott and Kalaska 1997; Scott et al. 1997; Sergio and Kalaska 1997).

The prominence of statistical interactions between direction and distance may be relevant in this context. The direction and amplitude of reaching movements are independent when considered in terms of the hand’s extrinsic spatial coordinates. For this reason, behavioral evidence of their independence is often interpreted as indicating that reaching movements are initially planned in hand-centered coordinates. However, direction and distance are coupled by the arm’s anatomy when transformed into intrinsic parameters such as joint rotations or muscular forces. For instance, an inappropriate amplitude of rotation about the shoulder or elbow joint during a reach usually produces an error in both direction and amplitude of hand displacement. As a result, any putative planning stage involved in the transformation from extrinsic to intrinsic parameters (Flanders et al. 1992; Gordon et al. 1994a,b; Soechting and Flanders 1989a,b) should theoretically take that interdependence into account. The finding that response interactions between direction and distance were as frequent as the incidence of convergent main effects on both single-cell and muscle activity is consistent with a contribution by PMd to the transformation from extrinsic to intrinsic parameters of motor output (Kalaska et al. 1997; Scott et al. 1997; Shen and Alexander 1997a,b; Zhang et al. 1997).

This transformation appears to occur over an extended period of time. The earliest task-related activity was mainly related to direction. This was replaced by an increasing frequency of convergent direction and distance correlates and of statistical interactions. This trend is consistent with other evidence that the movement representation in PMd and MI changes with time, progressing from more global spatial attributes of the task to more specific details of the motor output (Riehle et al. 1994; Shen and Alexander 1997a,b; Zhang et al. 1997).

**Limitations to interpretation of results**

Several studies have found that the neuronal correlates of direction are more prominent than for amplitude in both PMd and MI (Fu et al. 1993, 1995; Kurata 1993; Riehle and Requin 1989; Schwartz and Georgopoulos 1987; Taira et al. 1996; present study). Such comparisons are valid, however, only if both factors were tested over an equivalent range of values in each parameter space. It could be argued that whereas direction was tested uniformly over the entire 360° continuum in this study, the range of amplitudes was more restricted. Nevertheless, the maximum amplitude used in the present study (7.5 cm) was nearly 50% larger than that used by Fu et al. (1993), but did not result in a marked increase in amplitude correlations, and Schwartz and Georgopoulos (1987) reported comparable results for reaching movements as large as 12 cm. Kurata (1993) found far stronger amplitude correlations during the delay period than did Riehle and Requin (1989), even though the latter study used much larger movements. Therefore the actual size of the movements did not have any consistent effect across studies. Furthermore, the movements were confined to a plane in all of those studies and so tested the cells over only a very restricted part of their full three-dimensional directional tuning function (Caminiti et al. 1990, 1991; Georgopoulos et al. 1988). This issue will only be resolved by using a task that involves more of the full range of motion of the arm.

Nevertheless, the evidence that direction has a stronger influence than amplitude on PMd and MI discharge may have at least one behavioral parallel. Studies typically report greater constant and variable errors in the amplitude than the direction of movements (Bock and Arnold 1993; Ghez et al. 1997; Gordon et al. 1994a,b; Messier and Kalaska 1997, 1999; Soechting and Flanders 1989a,b). This suggests that at some planning stage, more information is transmitted about direction that distance (Soechting and Flanders 1989a,b). The greater modulation of discharge by direction than amplitude could be one of the neuronal origins of the differential patterns of motor output variability. Of course, factors related to the precision of control of each parameter during movement execution could also contribute.

As already noted, PMd activity may not represent intended direction or distance of hand displacement, per se. Many other
movement parameters covaried systematically with direction and distance. For instance, peak velocity typically scales with distance (Gordon et al. 1994a,b; Messier and Kalaska 1997, 1999). The monkey’s behavior showed the same effect (data not shown). Kinetic parameters (forces, torques, and EMG activity) in turn scale with velocity. Many parameters also covary with direction of hand movement, including patterns of joint rotations, kinetics, and EMG activity. We did not attempt to dissociate these various interdependent parameters. The purpose of this study was to investigate the general question of neuronal correlates of the putative separate channels for direction and distance in PMd. Our task was not designed to clarify the more specific question of the precise nature of the coupling of PMd discharge to motor output parameters. Therefore part or all of the observed neuronal correlations with target direction and distance may be related to other movement parameters.

Two more potential confounding factors are the direction of gaze (Boussaoud 1995; Boussaoud et al. 1998) and of attention (Di Pellegrino and Wise 1991, 1993a,b; Wise et al. 1996), which can modulate arm movement-related activity in PMd. Although the direction of gaze and attention are often aligned, they can be covertly dissociated. This suggests several alternative interpretations for the results in this study. One is that all PMd cells process information about arm movement direction, but some of them receive a convergent signal about target location (direction and distance) in gaze coordinates. Alternatively, two separate populations of PMd cells process information about arm movement direction and distance, but the latter also receive convergent gaze-related input about target location. We did not measure or control eye movements. However, repeated observation of the monkey’s eyes during the task revealed that it did not systematically fixate its gaze on the target location from the moment the cue appeared to the end of the trial. Instead, it continually scanned all parts of the monitor and task apparatus throughout the trial. As a result, the direction of gaze varied frequently within a trial and across trials, which might tend to reduce a systematic gaze-related effect on the results in this study. Independent of its oculomotor behavior, the monkey may have shifted its attention covertly toward the target location at different times in the trial, which may have also contributed to varying degrees to the correlations of different PMd cells with target direction and distance.

These distinctions are important for understanding the causal origin of the response correlates in this task. They would also be important functionally if for instance an external observer, including other parts of the motor system, could distinguish the components of PMd activity related to arm movement and to the direction of gaze or attention, and processed them separately to extract different types of information. Alternatively, the gaze and attentional inputs into PMd may simply serve as complementary sources of the target location information needed to perform the sensorimotor transformations between visual input and motor output (Boussaoud et al. 1998; Flanders et al. 1992; Kalaska et al. 1997). This study was designed only to describe the presence and degree of independence of direction and distance correlates in PMd in a memorized delay task. Their causal physiological origin, such as the degree to which they might arise from centrally generated signals about arm movement parameters, direction of gaze, direction of attention, retinal error signals or other sources, and the functional role of these different inputs, are separate questions that must be addressed in further studies that manipulate and dissociate these potential causal factors.

Finally, these data were collected from two hemispheres of one monkey. A convergence of circumstances made it impractical to verify them in a second monkey. It is therefore possible that they are a unique result of an idiosyncratic feature of the monkey’s behavior. However, our results largely confirm those of Fu et al. (1993) during the RT and MT epochs, when task conditions and data analysis were most similar, while also demonstrating directional and distance correlates during the delay period. They are also in basic agreement with those of Kurata (1993) during the second delay period of that task. We would argue that our results are not so skewed by an uncontrolled or aberrant quirk of the monkey’s behavior as to render them invalid.

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REFERENCES

PREMOTOR CORRELATES OF DIRECTION AND DISTANCE


