

Neural Representations of the Target (Goal) of Visually Guided Arm Movements in Three Motor Areas of the Monkey

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SUMMARY AND CONCLUSIONS

1. This study was designed to determine whether the supplementary motor area (SMA), the primary motor cortex (MC), and the putamen, all of which are components of the basal ganglia-thalamocortical "motor circuit," contain neural representations of the target or goal of a movement, independent of specific features of the movement itself. Four rhesus monkeys were trained to perform two visuomotor delayed step-tracking tasks in which the subject used a cursor to track targets on a display screen by making flexion and extension movements of the elbow. Single-cell activity was recorded from the SMA, MC, and putamen while the monkeys performed the two tasks. In the Standard task, the cursor and the forearm moved in the same direction. The Cursor/Limb Inversion task was identical to the Standard task except that there was an inverse relationship between the directions of movement of the forearm and cursor. Together, these tasks dissociated the spatial features of the target or goal of the movement from those of the movement itself. Both tasks also included features that made it possible to distinguish neuronal activity related to the preparation for movement from that related to movement execution. A total of 554 directionally selective, task-related neurons were tested with both tasks (SMA, 207; MC, 198; putamen, 149).

2. Two types of directionally selective *preparatory* activity were seen in each motor area. Cells with *target-dependent* preparatory activity showed selective discharge prior to all preplanned movements of the cursor toward one of the side targets (right or left), irrespective of whether the limb movement involved extension or flexion of the elbow. Comparable proportions of target-dependent preparatory cells were seen in the SMA (36%), MC (40%), and putamen (38%). Cells with *limb-dependent* preparatory activity showed selective discharge prior to all preplanned elbow movements in a particular direction (extension or flexion), irrespective of whether the target to which the cursor was moved was located on the right or left side of the display. The SMA contained a higher proportion of limb-dependent preparatory cells (40%) than either MC (15%) or putamen (9%).

3. Two types of directionally selective *movement-related* activity were also seen in each motor area. For cells that showed limb-dependent activity, the movement-related discharge was associated with elbow movements in a particular direction (extension or flexion). In contrast, for the cells that showed target-dependent activity, the movement-related discharge was associated with all movements of the cursor toward one of the side targets (right or left) regardless of whether the elbow was being extended or flexed. Most movement-related neurons in all three motor areas were limb dependent (SMA, 65%; MC, 71%; putamen, 63%). However, some movement-related cells showed target dependence, with the percentages of such cells in the SMA (16%) and MC (14%) being twice as high as that in the putamen (6%).

4. These results indicate that the SMA, MC, and putamen each contain neurons that represent the *target or goal* of a limb movement as well as neurons that represent the direction of the limb

movement itself. Moreover, both aspects of motor control appear to be represented in all three areas during the *preparation* for movement as well as during movement *execution*. The fact that target-dependent representations were more common during the preparation for movement, whereas limb-dependent representations were predominant during movement execution, suggests that relatively "high" levels of motor processing are emphasized during the preparation for movement, with an incomplete shift toward "lower" levels during movement execution. Nevertheless, the observation that both target-dependent and limb-dependent variables were represented simultaneously in all three motor areas (SMA, MC, and putamen) indicates that multiple levels of motor processing progress largely *in parallel* during both the preparation and execution of visually guided limb movements.

5. Within the MC, many of the target-dependent cells, both preparatory and movement-related, showed 1) discrete sensorimotor fields restricted to the elbow or shoulder, 2) short-latency "proprioceptive" responses to torque application, and/or 3) "muscle-like" responses to loads that opposed or assisted the task-related limb movements. A small number of such cells were also seen in the SMA and putamen. These findings appear to be at variance with a strictly hierarchical, serial/analytic model of motor processing.

INTRODUCTION

Regardless of whether visually guided limb movements are controlled in a predominantly serial or parallel fashion, it seems clear that the brain must contain neural representations of the target or goal of the movement, as well as of the movement itself (Bernstein 1984). The question that motivated this study is whether such representations occur within the motor system. It has been suggested that for limb movements that involve direct reaching to targets, the primary variable controlled by the brain might be the endpoint of the hand within a spatial (Cartesian) frame of reference that also includes the target (Morasso 1981; Soechting and Lacquaniti 1981). This is an attractive hypothesis, as it would readily explain the observation that target-directed movements tend to have straight trajectories, which are difficult to achieve by controlling joint dynamics (Abend et al. 1982; Morasso 1981). Moreover, as suggested long ago by Bernstein (Bernstein 1984), the well-known phenomenon of "motor equivalence" [the fact that hand trajectories are easily scaled both in time and space, despite disproportionately complex changes in the associated joint dynamics (Soechting and Lacquaniti 1981; Viviani and Terzuolo 1982)] suggests that the organization of movements in terms of targets or goals might be a general principle of motor control, and not limited to movements directed toward visual targets.

Nevertheless, it is conceivable that the motor system is concerned only with *translating* the goal or target of a movement into the appropriate muscle activation patterns, and not with the goal or target itself. So the question remains: do representations of the target or goal of a movement, reflecting the coordinate system of external space, occur within the motor system, and if so, in which structures do they occur and how widespread is their distribution? The preceding papers have shown that neurons may be found in the supplementary motor area (SMA), primary motor cortex (MC), and putamen that discharge selectively during the planning (Alexander and Crutcher 1990) and/or execution (Crutcher and Alexander 1990) of directionally specific arm movements, irrespective of the joint dynamics (i.e., regardless of the loading conditions) associated with the movements. Although it may be natural to assume that this type of activity (especially when recorded in motor structures) is specifically related to the *direction of arm movement*, there is no assurance of this unless the direction of arm movement has been clearly dissociated from the *target or goal* of the movement.

In direct reaching to targets, both the location of the target and the trajectory of the hand are readily defined within the same Cartesian coordinate system, even though the hand's trajectory is fundamentally associated with a body-centered frame of reference (Hogan et al. 1987; Saltzman 1979). The optimal frame of reference for describing the hand's trajectory need not coincide with that of the target, however, as is demonstrated by situations in which reaching or tracking movements are guided by indirect visual feedback (from a mirror, for example, or a cursor). This principle can be exploited experimentally by varying the spatial features of indirect visual feedback, to dissociate the neural events subserving arm movement from those subserving the more abstract process of target capture. In the experiments described in this paper, monkeys performed a pair of arm movement tasks in which the spatial features of the target or goal of the movement were dissociated from those of the limb movement itself. The task-associated activity of preparatory and movement-related neurons was recorded in the arm regions of the SMA, MC, and putamen.

METHODS

The general methods used in this study, including surgical, recording, data acquisition, and data analysis procedures, were described in the preceding reports (Alexander and Crutcher 1990; Crutcher and Alexander 1990).

Behavioral paradigms

Four of the five rhesus monkeys used in the direction versus loading experiments reported in the preceding papers were also trained to perform a *second* visuomotor step-tracking task, which was identical to the basic or Standard task without loads (Alexander and Crutcher 1990) except that there was an inverse relationship between the directions of movement of the forearm and cursor (Fig. 1). Thus on the Standard trials the forearm and cursor moved in the same direction (so that targets were "captured" by moving the forearm in the same direction as the target appeared to move), whereas on the Cursor/Limb Inversion trials the forearm and cursor moved in opposite directions (so that targets were

captured by moving the forearm in the direction opposite to that of apparent target movement). The two tasks were administered in separate blocks of trials, making it unnecessary to provide an external cue as to which of the two tasks were being administered. In these experiments, the Inversion trials were invariably presented without torque loads. The Standard trials were usually presented both with and without such loads, however, to dissociate the direction of movement from the pattern of muscle activity (see Alexander and Crutcher 1990; Crutcher and Alexander 1990).

Both paradigms required the monkey to align the cursor with a series of targets, by making flexion and extension movements of the elbow. Each trial required two successive lateral movements of the forearm to capture one of the two side targets. The first lateral movement was preceded by a *preinstruction* interval in which the monkey was unaware of which side target he would be required to capture and thus was unable to preplan the direction of the forthcoming movement. Both side targets were presented to trigger the second lateral movement, but the monkey was always required to recapture the same target that had triggered the first lateral movement. Thus, during the *postinstruction* interval that preceded the second lateral movement, the monkey was not only able to preplan the direction of the impending movement but was required to do so, as he was required to remember the directional instruction to make the movement in the correct direction.

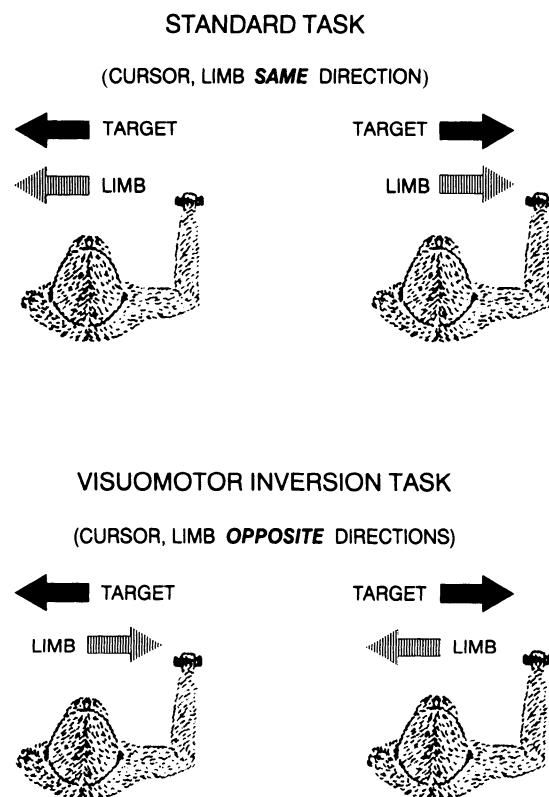


FIG. 1. Schematic illustration of the 2 tasks used to dissociate expected target location and direction of intended limb movement. In the standard task, the cursor that the monkey used to "capture" the targets moved in the same horizontal direction as the monkey's forelimb. Thus, when the target shifted from the center position to the right, the monkey would move his right forearm to the right (elbow extension) to position the cursor over the target. In contrast, for the visuomotor inversion task, the cursor and forearm moved in opposite directions. Thus, when the target shifted from the center position to the right side position, the monkey would move his forearm toward the left (elbow flexion) to move the cursor to the right and capture the target.

Data analysis

Neural and analog data collected in this study were analyzed in the same manner described in the preceding papers. For all raster displays illustrated in the RESULTS section, it is assumed for clarity of exposition that the monkey was performing the task with his right arm, in accordance with the schematic shown in Fig. 1.

RESULTS

Task performance

For the Cursor/Limb Inversion trials, all subjects showed $\geq 95\%$ accuracy in capturing the correct target at the end of the postinstruction interval (i.e., there were $\leq 5\%$ directional errors). Performance accuracy for the Standard trials was $\geq 98\%$.

The patterns of muscular activity associated with task performance were similar for both the Standard and the Inversion trials. This is illustrated in Fig. 2 by the activity recorded from a prime extensor of the elbow (m. triceps lateralis). As indicated in this example, EMG activity was similar for the first and second movements, as well as for the pre- and postinstruction intervals. Of the 39 different muscle groups sampled, only one, the cervical rhomboid, showed directional activation during the postinstruction interval, but its maximal activation was during movement execution. This was true for both of the subjects in whom this particular muscle was sampled. All directionally selective muscles showed activity patterns for the two types of tasks that followed the direction of limb movement, rather than that of the cursor.

Emphasis was placed on each monkey's performance accuracy: there were no constraints on the subject's eye movements, and only minimal constraints on reaction time (RT) and movement time (MT) (combined RT + MT ≤ 900 ms). Scleral search coil recordings from each monkey showed no differences in the patterns or frequency of eye movements during the two types of trials. On both Standard and Inversion trials there were frequent, randomly timed saccades (2–5 per trial) between the center target and *both* lateral target locations throughout the pre- and postinstruction intervals. The frequency of saccades was slightly higher in the postinstruction interval, but there was no directional preponderance associated with the location of the correct visual target. Despite the frequent saccades, gaze was fixed on the center target throughout most of the durations of the pre- and postinstruction intervals, and there were no consistent differences between the proportions of time in which the gaze was fixed on the correct versus the incorrect target. After presentation of the lateral target(s) at the end of the pre- and postinstruction intervals, there was invariably a saccade to the correct visual target. This saccade immediately preceded the limb movement that was associated with the attempt to capture the target with the cursor.

Database

Of the total sample of 554 directionally selective, task-related neurons tested with both the Standard and the Inversion tasks, 207 were located within the SMA, 198 within

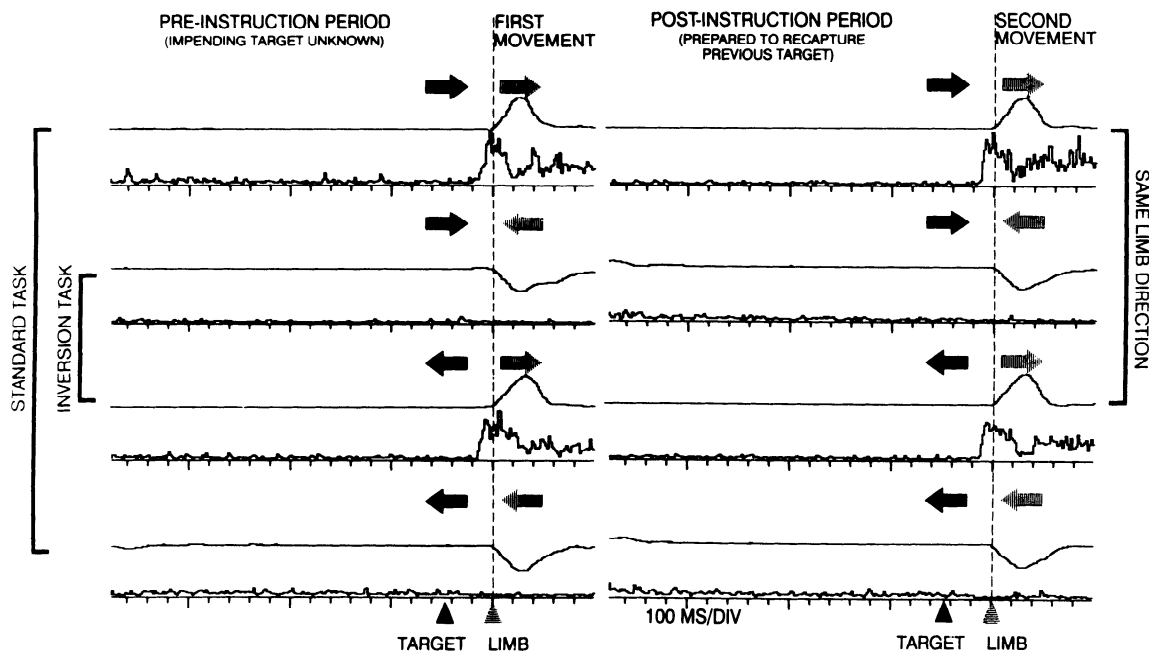


FIG. 2. EMG activity recorded from the lateral triceps, a prime extensor of the elbow, is shown for the 4 different trial types. For each trial type, the average velocity record is presented above the corresponding EMG activity averaged across 10 trials. Extension is represented by an upward deflection of the velocity trace. The solid black arrows indicate the direction of target displacement from center to side position, and the shaded arrows indicate the direction of forearm movement that was used to move the cursor from the center to the side target. In this and subsequent figures, the arrows are oriented as if the monkey were using his right arm to perform the task (regardless of the arm that was actually used). Thus a shaded arrow pointing to the right indicates an extension movement of the elbow. In this and other prime movers (e.g., brachialis), there were no significant differences between the pre- and postinstruction period for either the standard or the inversion trials. For the extensor muscle whose activity is illustrated here, there was consistent activation prior to the onset of extension movements of the elbow, both on the standard and the inversion trials.

TABLE 1. Database: directional neurons* tested with both (standard and inversion) tasks, by region/hemisphere

Subject/hemis.	B/L	B/R	C/L	D/L	E/L	Total
SMA	45	56			106	207
MC	25	39	107		27	198
Putamen		53	70	9	17	149

* Includes some neurons (42 in SMA, 44 in MC, 8 in putamen) with both directional preparatory activity and directional movement-related activity. B-E, subjects used in study; L and R, left and right hemisphere; SMA, supplementary motor area; MC, primary motor cortex.

MC, and 149 within the putamen. Their distributions across the different monkeys and hemispheres are indicated in Table 1. All neurons included within the database were located within a region of arm representation, as determined by the sensorimotor features of local neurons and/or the movements induced by local microstimulation (see Alexander and Crutcher 1990; Crutcher and Alexander 1990).

Neurons were classified as showing *preparatory* activity if their discharge rates during the postinstruction interval differed significantly from their preinstruction rates. As in the preceding reports (Alexander and Crutcher 1990; Crutcher and Alexander 1990), all functional classifications were based on analyses of variance (ANOVAs) carried out on the extracted epoch- and trial-specific discharge rates of each cell, with the use of a predefined significance level of $P < 0.001$. These were two-way ANOVAs (with orthogonal comparisons between means) that compared four epochs [2 movement conditions (*move 1* vs. *move 2*)

and 2 hold conditions (pre- vs. postinstruction)] \times 2 direction conditions (extension vs. flexion). This type of analysis is described in detail in the second paper of this series (Crutcher and Alexander 1990). Neurons whose discharge rates during the first and/or second movement interval differed significantly from their preinstruction rates were classified as showing *movement-related* activity. Only neurons that showed directionally selective preparatory and/or movement-related activity when tested with the Standard task were included in the database. For each cell tested, the directionality of its preparatory and/or movement-related activity was compared across the two types of trials, to determine whether it reflected the direction of limb movement or the direction of apparent target movement (i.e., the direction in which the cursor was moved).

Directionality of preparatory activity: limb versus target dependence

Directionally selective preparatory activity of both types (limb-dependent and target-dependent) was seen in all three motor areas. An example of *limb-dependent* directional preparatory activity is illustrated in Fig. 3, which shows the activity of an SMA neuron tested with both the Standard and the Inversion tasks. With the spatial frames of reference for the limb versus target/cursor dissociated between the two tasks, the postinstruction preparatory activity preceded all preplanned extension movements, irrespective of whether the target to which the cursor was moved was located on the right (Standard trials) or left (Inversion trials) side of the display.

An example of *target-dependent* directional preparatory

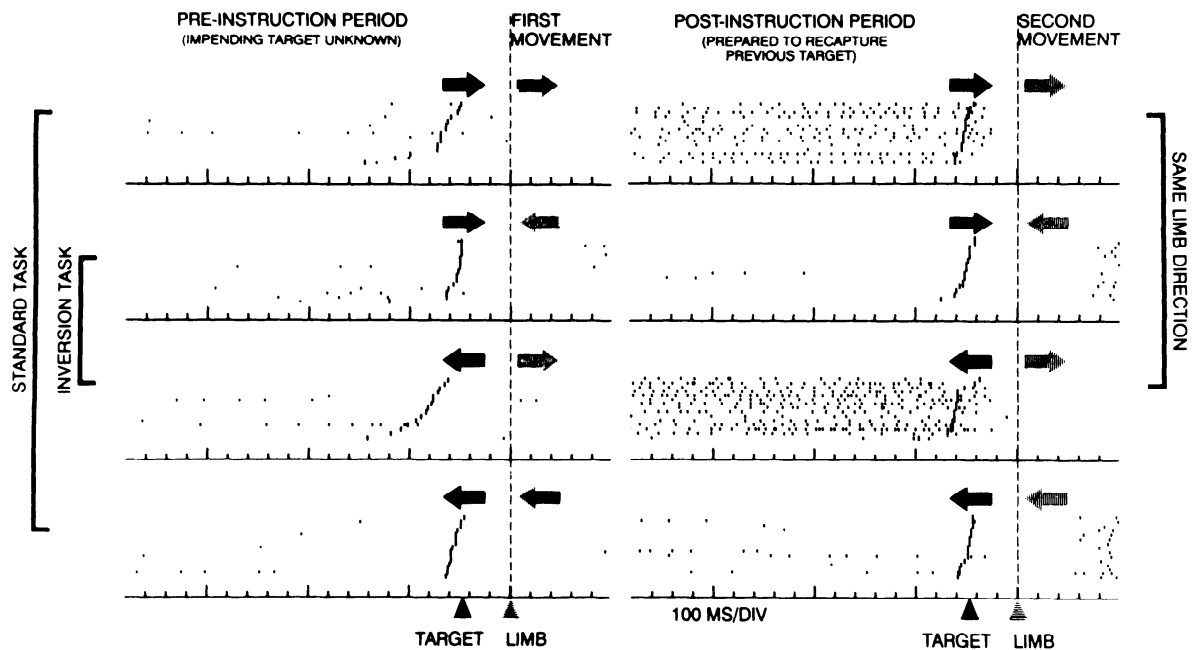


FIG. 3. Limb-dependent preparatory activity in the supplementary motor area. Each small tick indicates the occurrence of a single action potential and each row represents the neuronal activity recorded during one trial. Large ticks indicate the times of occurrence of the target shifts that triggered the first and second lateral movements of each trial. The trials from both the Standard and Cursor/Limb Inversion tasks are sorted by trial type and reaction time, and the split-plot rasters are aligned on the onsets of the first and second lateral movements. This cell showed sustained activation during the postinstruction period preceding elbow extensions that moved the forearm to the right, irrespective of the direction of cursor movement or target displacement. Limb direction is indicated by the shaded arrows and cursor direction by the solid arrows as in Fig. 2.

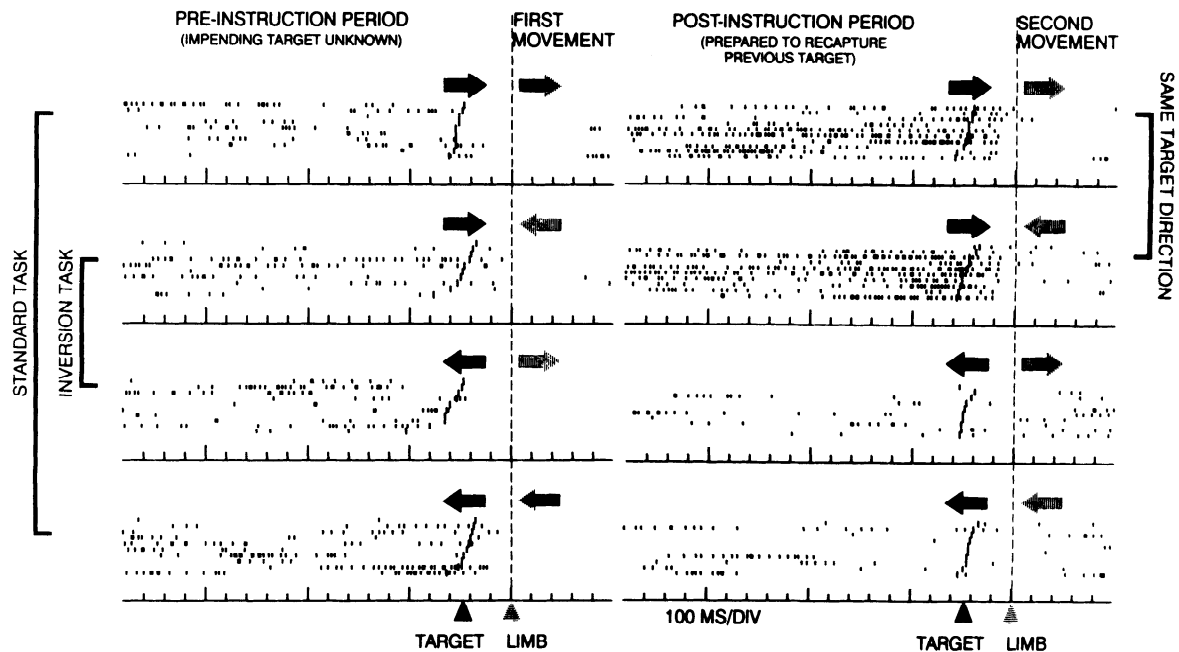


FIG. 4. Preparatory activity in the supplementary motor area that depended on the expected direction of displacement of the target. This neuron showed sustained activation throughout the postinstruction period prior to all preplanned movements of the cursor directed toward the right lateral target, regardless of whether the limb movement that was used to position the cursor involved elbow extension (as on standard trials, in which the forearm moved to the right) or elbow flexion (as on inversion trials, in which the forearm moved to the left). There was also a reciprocal reduction in activity during the postinstruction period that preceded preplanned movements to capture the left target.

activity recorded in the SMA is illustrated in Fig. 4. In this case, the preparatory discharge can be seen to precede all preplanned movements of the cursor directed toward the right lateral target, irrespective of whether the limb movement involved extension (Standard trials) or flexion (Inversion trials) of the elbow. An example of target-depen-

dent preparatory activity in MC is shown in Fig. 5. The directional preparatory discharge of this cell preceded movements of the cursor toward the left target, irrespective of the direction of the upcoming limb movement. Target-dependent preparatory activity within the putamen is illustrated in Fig. 6.

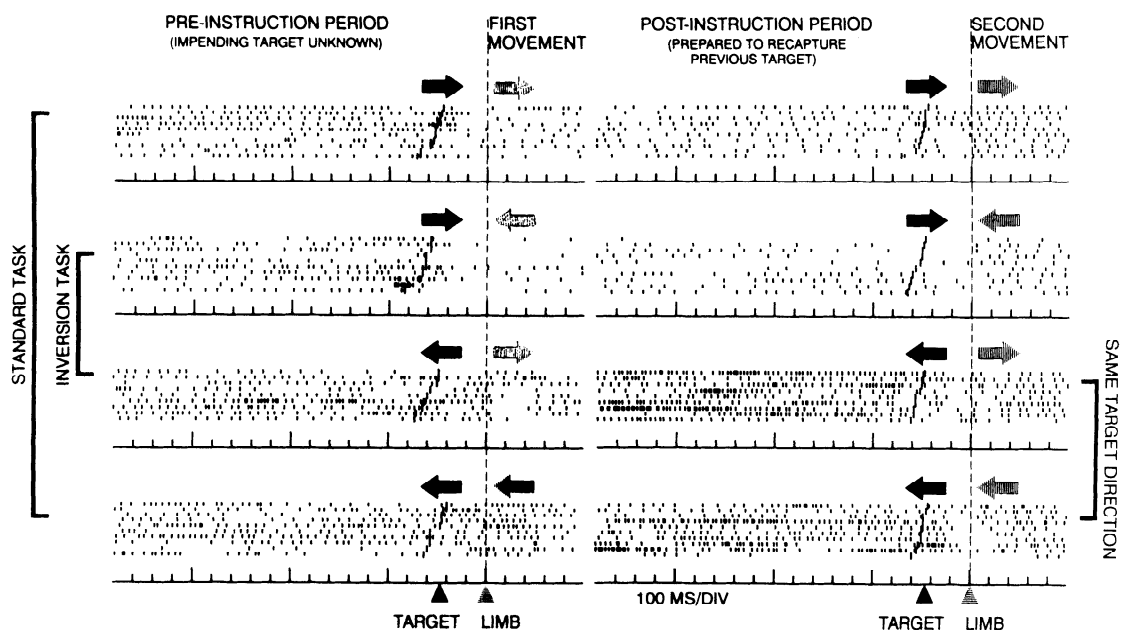


FIG. 5. Preparatory activity in motor cortex that depended on the expected direction of displacement of the target. This cell showed the same pattern of activity as the cell in Fig. 4, except that in this case the cell increased its rate of discharge during the postinstruction period that preceded preplanned movements to capture the left target. This activity was independent of the direction of arm movement required to capture the target. This cell also showed a reciprocal reduction in activity during the postinstruction period that preceded preplanned movements to capture the right target.

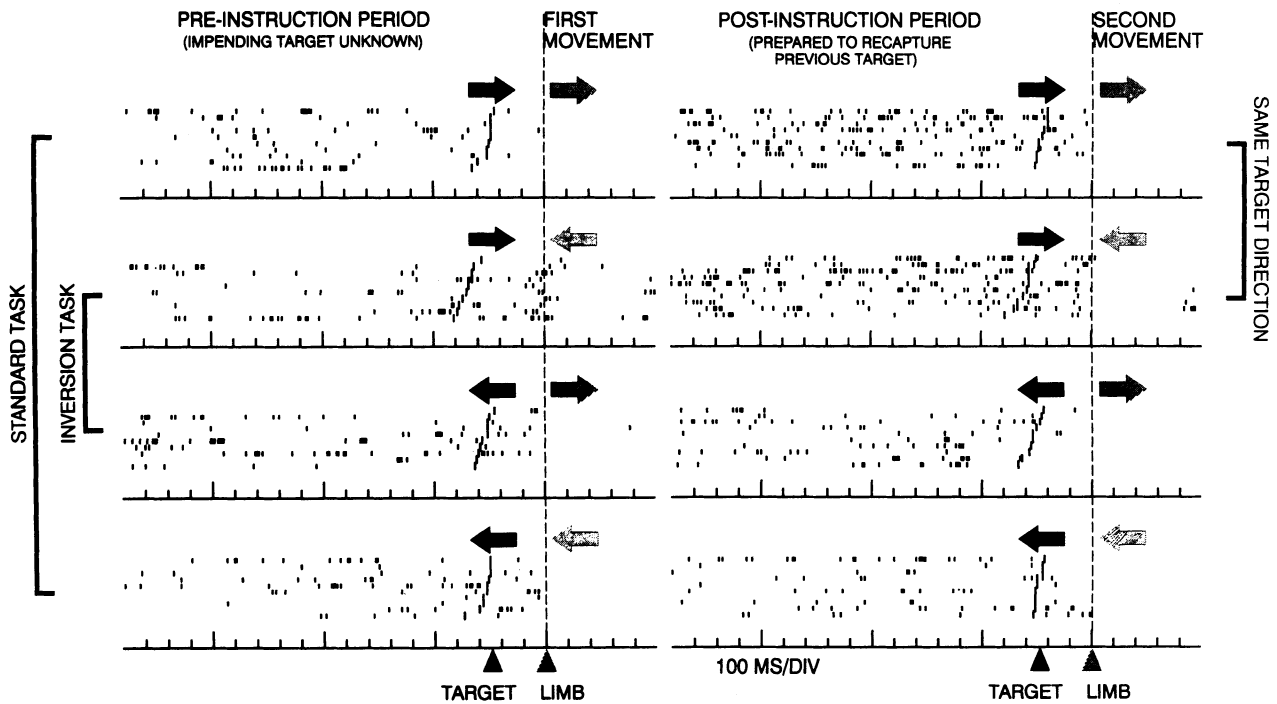


FIG. 6. Preparatory activity in the putamen that depended on the expected direction of displacement of the target. This cell showed a significant increase in discharge rate throughout the postinstruction period that preceded preplanned movements of the cursor to capture the right target. As in the cells shown in Figs. 4 and 5, the preparatory discharge was independent of the direction of limb movement required to capture the target.

The proportions of preparatory cells with each type of directionality are indicated in Table 2 for the three motor areas sampled. Some cells with directional preparatory activity in the standard task were not directionally selective in the inversion task ($P > 0.001$). These cells were classified as directionally indeterminate. χ^2 tests comparing the three areas with respect to the proportions of limb-dependent versus target-dependent versus indeterminate directionality showed significant differences between SMA and MC and between SMA and putamen. As indicated in Table 2, the proportions of target-dependent preparatory cells were similar for the three areas (SMA, 36%; MC, 40%; putamen, 38%). On the other hand, the SMA had a much higher

proportion of limb-dependent preparatory cells (40%) than either MC (15%) or putamen (9%). In addition, both the MC and putamen had much larger proportions of "indeterminate" cells (45%, 53%, respectively) than the SMA (24%).

Directionality of movement-related activity: limb versus target dependence

Directionally selective movement-related activity of both types was seen in all three motor areas. The proportions of movement-related neurons with each type of directionality are indicated in Table 3 for the three motor areas sampled. In each area, most of the movement-related activ-

TABLE 2. *Directionality of cells with preparatory activity: correlation with target vs. limb direction*

	SMA	MC	Putamen
Directionality with both tasks			
Same as target	37 (36)	26 (40)	12 (38)
Same as limb	42 (40)	10 (15)	3 (9)
Directionality indeterminate with inversion task	25 (24)	29 (45)	17 (53)
Total cells tested*	104 (100)	65 (100)	32 (100)
	[$P < 0.01$]	[NS]	
	[$P < 0.001$]		

* Includes neurons with both directional preparatory activity and directional movement-related activity. NS, not significant; other abbreviations, see Table 1.

TABLE 3. *Directionality of cells with movement-related activity: correlation with target vs. limb direction*

	SMA	MC	Putamen
Directionality with both tasks			
Same as target	23 (16)	25 (14)	8 (6)
Same as limb	95 (65)	126 (71)	78 (63)
Directionality indeterminate with inversion task	27 (19)	26 (15)	39 (31)
Total cells tested*	145 (100)	177 (100)	125 (100)
	[NS]	[$P < 0.001$]	
	[$P < 0.01$]		

* Includes neurons with both directional movement-related activity and directional preparatory activity. Abbreviations, see Tables 1 and 2.

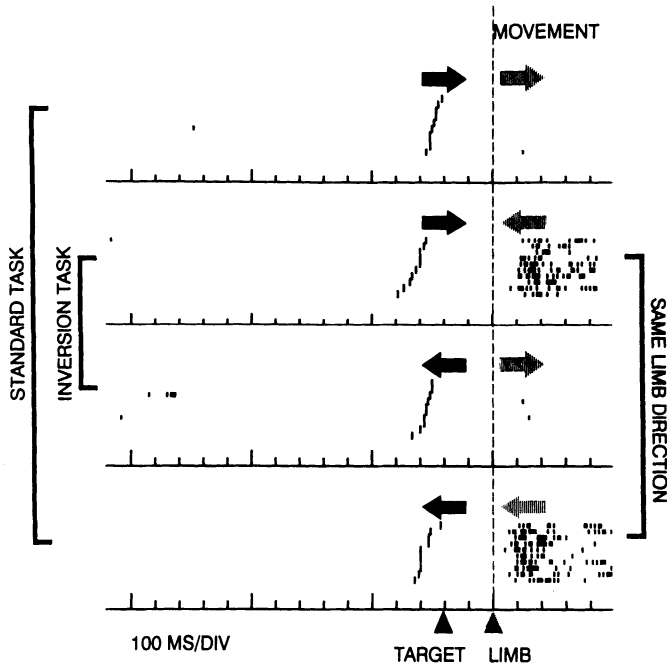


FIG. 7. Movement-related activity in the putamen that depended on direction of limb movement. This cell discharged during elbow flexions, in which the forearm moved to the left, irrespective of the direction of target displacement.

ity was related to the direction of the limb movement, irrespective of target displacement. Nevertheless, in all three structures there was a small but significant proportion of neurons whose movement-related activity was dependent on the direction of target displacement, rather than the direction of limb movement.

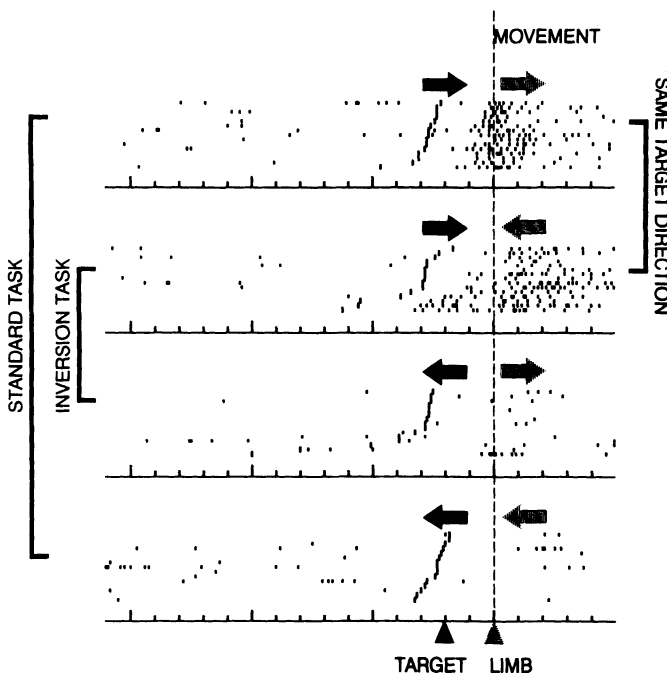


FIG. 8. Movement-related activity in the supplementary motor area that depended on the direction of target displacement. This cell discharged during movements of the cursor toward the right target, irrespective of the direction of forearm movement.

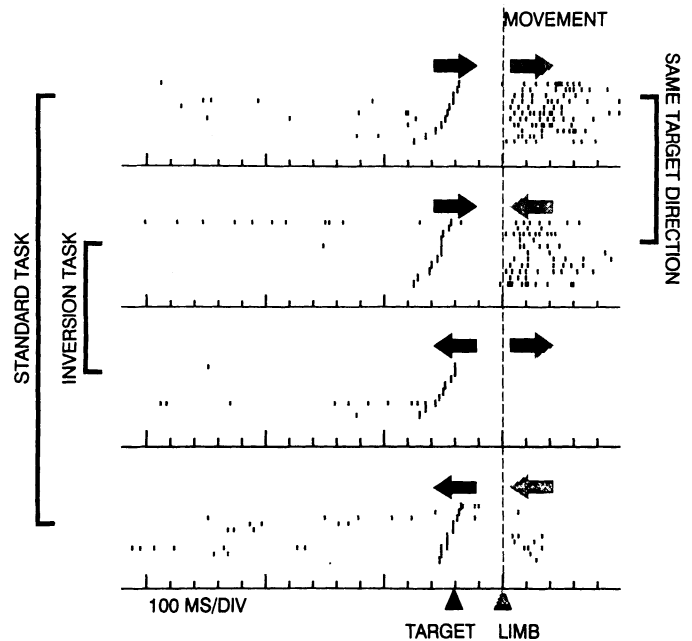


FIG. 9. Movement-related activity in motor cortex that depended on the direction of target displacement. This cell discharged during movements of the cursor to capture the right target, irrespective of whether the forearm was moving to the right (standard task) or to the left (inversion task).

An example of limb-dependent activity is illustrated in Fig. 7. The movement-related discharge of this putamen neuron was associated with elbow flexion, regardless of whether the cursor was being moved toward the left (Standard trials) or right (Inversion) side of the display.

In contrast, the directionality of the movement-related activity shown in Fig. 8 was target dependent. This SMA neuron discharged when the monkey moved the cursor toward the right target, regardless of whether the elbow was being extended (Standard trials) or flexed (Inversion trials). The activity of the target-dependent MC neuron illustrated in Fig. 9 was also related to movements to capture the right target. The directionality of the movement-related activity in Fig. 10 was also target dependent, but for this putamen neuron the discharge was associated with movements of the cursor toward the left target.

χ^2 tests comparing the movement-related activity in SMA, MC, and putamen with respect to the proportions of target-dependent versus limb-dependent directionality showed significant differences between the putamen and the two cortical areas, as indicated in Table 3. Although the proportions of movement-related cells that were limb-dependent were similar for all three structures (SMA, 65%; MC, 71%; putamen, 63%), the percentage of target-dependent cells in the putamen (6%) was less than one-half of the percentage in the SMA (16%) or MC (14%).

Cells with combined preparatory and movement-related activity

For the cells in each motor area that showed both preparatory and movement-related discharge, the target versus limb dependence of each type of activity was compared. Of

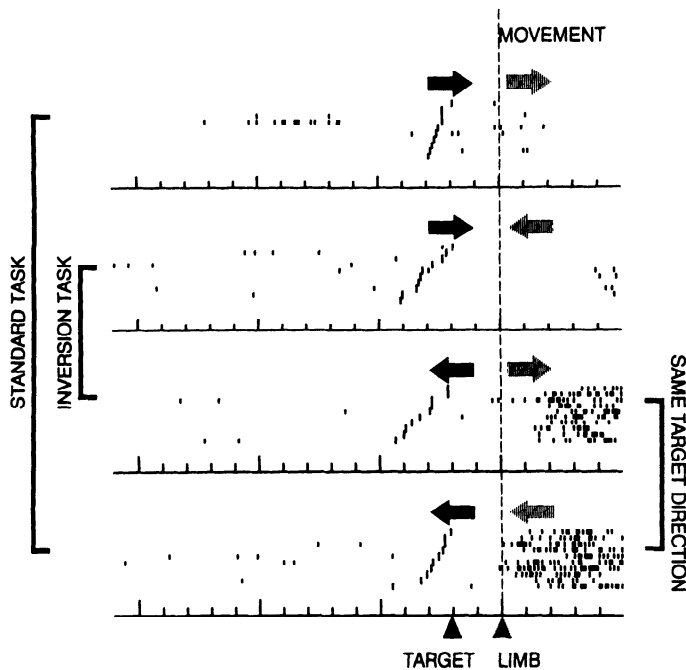


FIG. 10. Movement-related activity in the putamen that depended on direction of the displacement of the target. This cell discharged during forearm movements to capture the left target, irrespective of the direction of the limb movement itself.

the cells in which directionality could be determined for both the Standard and the Inversion tasks, most showed the *same* directionality (either limb- or target-dependent) for both the preparatory and movement-related responses (SMA, 19/22; MC, 11/15; putamen, 2/3). Three SMA neurons, four MC neurons, and one cell in the putamen

showed preparatory activity that was target dependent in combination with movement-related activity that was limb dependent. The activity of one of the SMA neurons showing this combination is illustrated in Fig. 11. This particular cell showed preparatory discharge prior to preplanned movements of the cursor toward the right target, irrespective of the direction of limb movement, and movement-related discharge during extension movements, regardless of which lateral target was being captured. No cells in any of the areas sampled showed the opposite pattern of response, i.e., limb-dependent preparatory discharge combined with movement-related discharge that was target dependent.

Locations of task-related neurons

Within each of the three areas studied, both target- and limb-dependent preparatory and movement-related neurons were intermingled along individual microelectrode penetrations. For each area, statistical comparisons of the relative rostrocaudal locations of target- versus limb-dependent cells were made by the use of *t* tests, as was described for the preparatory versus movement-related cells in the first paper (Alexander and Crutcher 1990). In the SMA, for both the preparatory ($t = 2.23$, $df = 77$, $P < 0.05$) and the movement-related cells ($t = 5.28$, $df = 116$, $P < 0.001$), there was a significant tendency for the target-dependent cells to be located more rostrally than the limb-dependent cells. This is illustrated in Figs. 12 and 13, respectively. In MC the target-dependent cells that were movement related were also distributed significantly more rostrally than their limb-dependent counterparts ($t = 3.41$, $df = 149$, $P < 0.001$). This is illustrated in Fig. 14. The corresponding distributions for the preparatory cells in MC were not significantly different. In the putamen, there were no significant differences between the spatial distributions

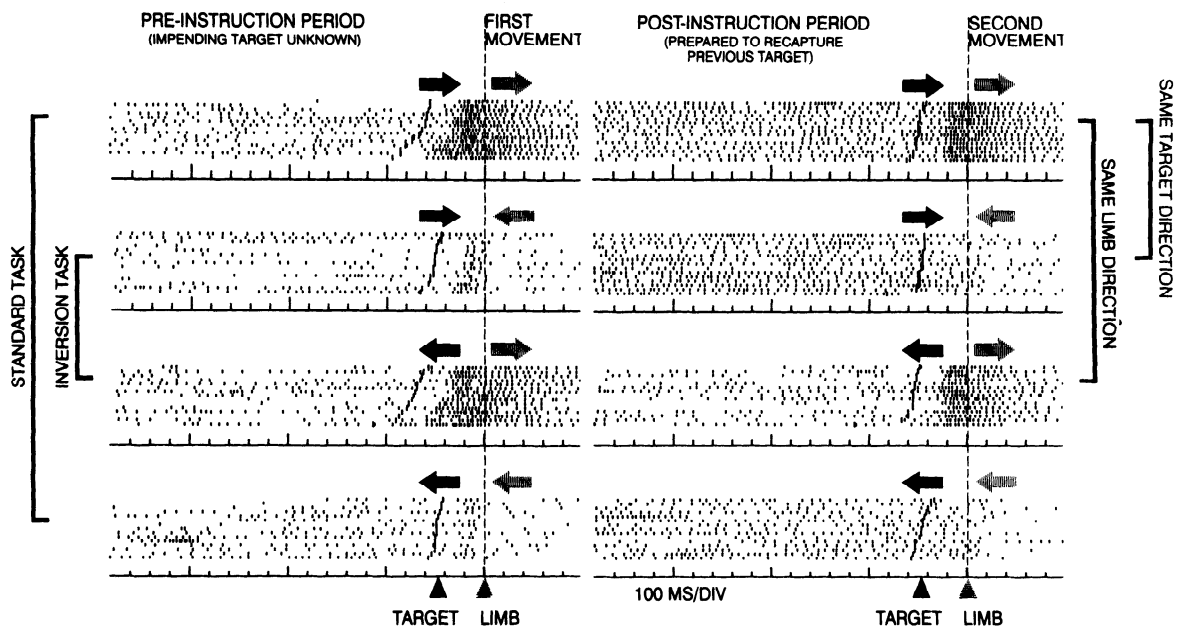


FIG. 11. SMA neuron with combined preparatory and movement-related activity. This cell showed target-dependent preparatory discharge during the postinstruction period prior to preplanned movements of the cursor to capture the right target, regardless of the direction of the required limb movement. The cell also showed limb-dependent, movement-related discharge during extension movement, irrespective of whether they were used to capture the right or the left target.

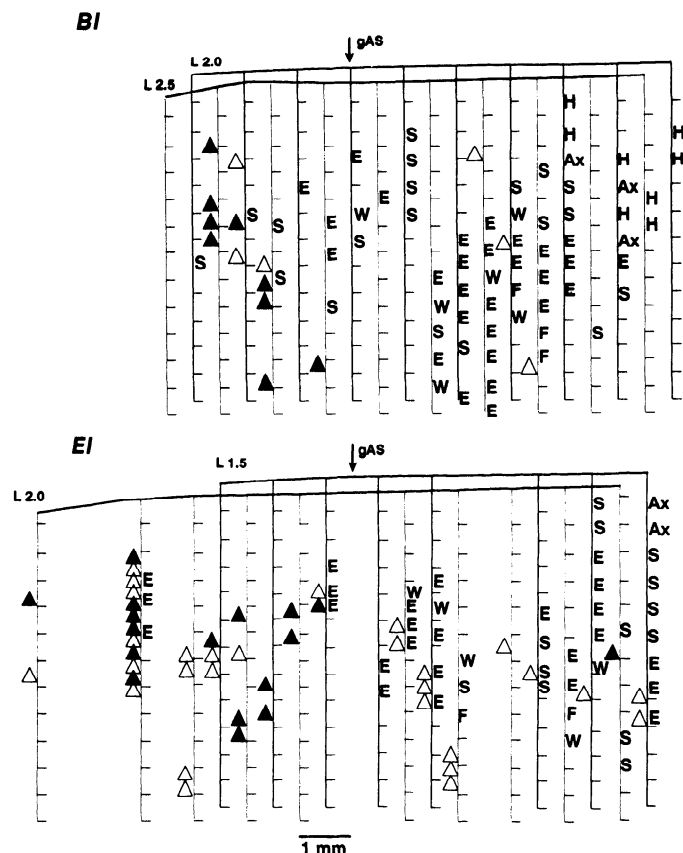


FIG. 12. Locations of SMA neurons with preparatory activity that was dependent on the direction of either target (▲) or limb (▲) displacement. The top and bottom panels show the data from 2 of the 3 hemispheres explored in this study. In each case, data from 2 adjacent parasagittal planes are presented. The more lateral plane is displaced slightly downward. The location of each set of tracks relative to surface landmarks is shown in Fig. 5 of the first paper in this series (Alexander and Crutcher 1990). In the present figure, rostral is to the left, and the coronal plane through the genu of the arcuate sulcus is indicated (gAS). Horizontal dashes indicate negative microstimulation sites. Letters denote the movements evoked at threshold where microstimulation was effective: E, elbow; S, shoulder; W, wrist; F, fingers; H, hip; Ax, axial.

of the target- and limb-dependent cells for either the preparatory or the movement-related categories.

Sensorimotor features of target-dependent neurons

As they would appear to participate at or near the "highest" level of motor processing, cells with target-dependent activity might not be expected to have many of the features associated with "lower" processing levels, including 1) discrete sensorimotor fields restricted to a specific limb joint, 2) "muscle-like" responses to loads that opposed or assisted the task-related movements, and 3) short-latency "proprioceptive" responses to externally applied torques. It might also be predicted, according to a strict notion of functional segregation within the motor system, that target-dependent cells would not be located in regions from which movements could be evoked by microstimulation. Because most of the neurons that were assessed for target versus limb dependence had also been studied with the methods outlined in the preceding two papers (Alexander

and Crutcher 1990; Crutcher and Alexander 1990), we had the opportunity to examine each of these issues.

The sensorimotor features of the cells with target-dependent preparatory activity are summarized in Table 4. In this analysis we excluded cells that showed combinations of target-dependent preparatory and limb-dependent movement-related activity, as the latter is by definition associated with lower levels of motor processing. As the table indicates, sensorimotor features usually associated with lower levels of motor processing were generally absent among the target-dependent preparatory cells within the SMA and putamen. In the MC, however, such cells frequently showed sensorimotor fields confined either to the elbow or the shoulder, and a few showed short-latency proprioceptive responses to torque application. Moreover, most of the MC neurons with target-dependent preparatory activity were located at sites from which elbow or shoulder movements were evoked by local microstimulation.

The sensorimotor features of the cells with target-dependent movement-related activity are summarized in Table 5. As there were no cells with combined limb-dependent preparatory activity and target-dependent movement-related activity, all of the cells with movement-related activity that was target dependent were included in this analysis. Among the cells with such activity in the SMA and puta-

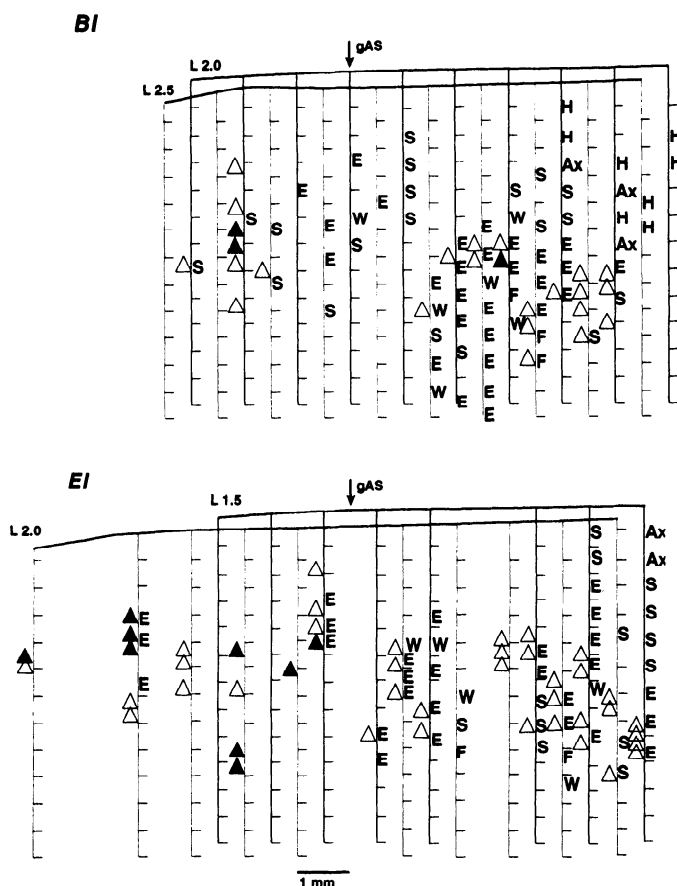


FIG. 13. Locations of SMA neurons with movement-related activity that was dependent on the direction of either target or limb displacement. Conventions are the same as in Fig. 12.

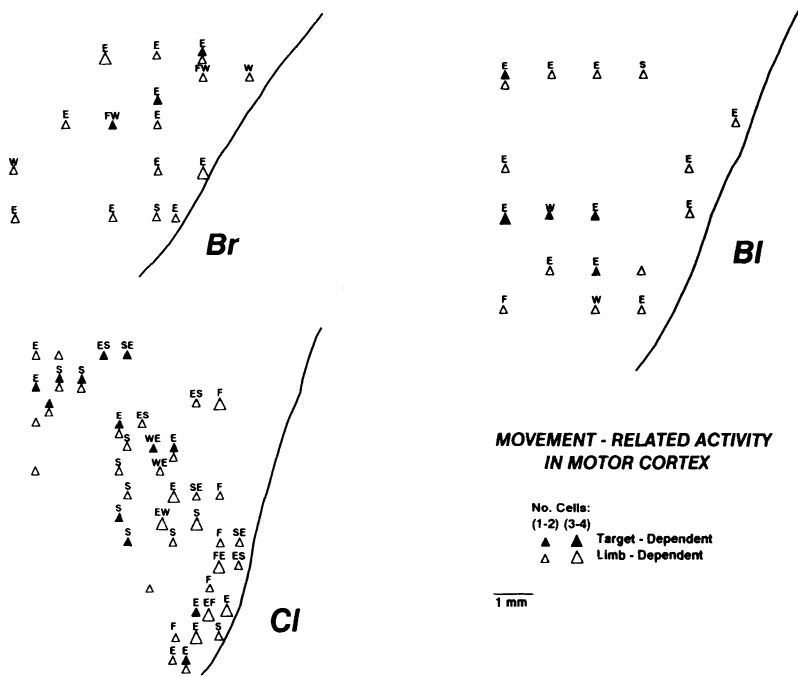


FIG. 14. Locations of MC neurons with movement-related activity that was dependent on the direction of either target or limb displacement. The locations are indicated in terms of the cortical entry points of the microelectrode penetrations. The separate panels show data from 3 of the hemispheres explored in this study. The central sulcus is indicated, and rostral is to the left (regardless of whether data are from the right or left hemisphere). Locations of the recording areas relative to other surface landmarks are indicated in Fig. 5 of the first paper in this series (Alexander and Crutcher 1990).

men, there was a relative paucity of sensorimotor features that are usually associated with lower levels of motor processing. In the MC, on the other hand, most of the cells with target-dependent movement-related activity showed discrete sensorimotor fields confined to either the elbow or shoulder, and substantial proportions showed muscle-like

TABLE 4. *Sensorimotor features of target-dependent cells with preparatory activity*

	SMA ^{a,b}	MC ^{a,c}	Putamen ^{a,d}
Sensorimotor field ^e			
Elbow	1	5	
Shoulder	1	5	
Distal			
Active arm	9	5	3
Negative	2	3	1
Not tested	21	3	7
Short-latency torque response ^f			
Yes		3	
No	13	16	7
Not tested	21	2	4
Local microstimulation ^g			
Elbow	3	10	
Shoulder	2	5	
Distal			
Negative	26	3	5
Not tested	3	3	6

Abbreviations, see Table 1. ^aIncludes cells with combined target-dependent preparatory and target-dependent movement-related activity. Excludes cells with combined target-dependent preparatory activity and limb-dependent movement-related activity. ^b $n = 34$; ^c $n = 21$; ^d $n = 11$. ^eFocus of active and/or passive movements that produced selective activation in sensorimotor exam. ^fCells activated by torque application and the associated passive displacement at latencies <60 ms. ^gFocus of movements evoked at threshold by microstimulation at recording site.

TABLE 5. *Sensorimotor features of target-dependent cells with movement-related activity*

	SMA ^{a,b}	MC ^{a,c}	Putamen ^{a,d}
Sensorimotor field ^e			
Elbow	2	9	
Shoulder	2	4	2
Distal	1	2	1
Active arm	5	3	2
Negative	4	3	1
Not tested	9	4	2
Load effects ^f			
Muscle-like	1	8	1
None			
(i.e., Directional)	5	14	4
Other	4	1	2
Not tested	13	2	1
Short-latency torque response ^g			
Yes		4	1
No	10	19	6
Not tested	13	2	1
Local microstimulation ^h			
Elbow	3	11	
Shoulder		7	
Distal		2	1
Negative	17	2	6
Not tested	3	3	1

Abbreviations, see Table 1. ^aIncludes cells with combined target-dependent preparatory and target-dependent movement-related activity. ^b $n = 23$; ^c $n = 25$; ^d $n = 8$. ^eFocus of active and/or passive movements that produced selective activation in sensorimotor exam. ^fClassification of movement-related cells according to whether or not they had load effects that were muscle-like or other than muscle-like; see Crutcher and Alexander (1990) for details of this analysis. ^gCells activated by torque application (and the associated passive elbow displacement) at latencies <60 ms. ^hFocus of movements evoked at threshold by microstimulation at recording site.

TABLE 6. *Timing of preparatory activity*

	SMA	MC	Putamen
Onset latencies, ms*			
Target-dependent	-54 ± 68 (37)	39 ± 99 (26)	108 ± 162 (12)
Limb-dependent	-55 ± 55 (42)	90 ± 136 (10)	230 ± 388 (3)
Offset latencies, ms†			
Target-dependent	178 ± 18 (23)	179 ± 15 (19)	173 ± 34 (8)
Limb-dependent	196 ± 14 (35)	147 ± 23 (5)	177 (1)

Values are means ± SE; number of cells are in parentheses. Abbreviations, see Table 1. *Measured from end of the preceding centering movement; †excludes cells for which the detection algorithm failed to find offsets for a minimum of 5 trials.

load effects and/or short-latency proprioceptive responses to torque application. As with the target-dependent preparatory activity, most of the MC cells with target-dependent movement-related activity were located at sites from which elbow or shoulder movements were evoked by local microstimulation.

Timing of preparatory activity

The times of onset and offset of preparatory activity were computed for each cell on a trial-by-trial basis, with the use of the algorithms described in the preceding papers (Alexander and Crutcher 1990; Crutcher and Alexander 1990). The results are summarized in Table 6. When the target-dependent and limb-dependent preparatory activity was considered separately, there were no significant differences among the SMA, MC, and putamen in terms of either the onset or offset latencies. Moreover, no differences were

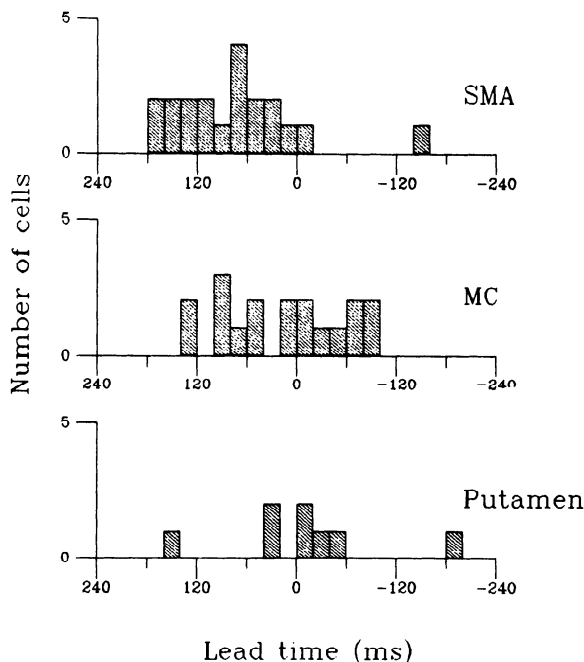


FIG. 15. Lead times for the onsets of movement-related activity that was dependent on the direction of target displacement. The distribution of lead times in the SMA was significantly earlier than those in MC or putamen.

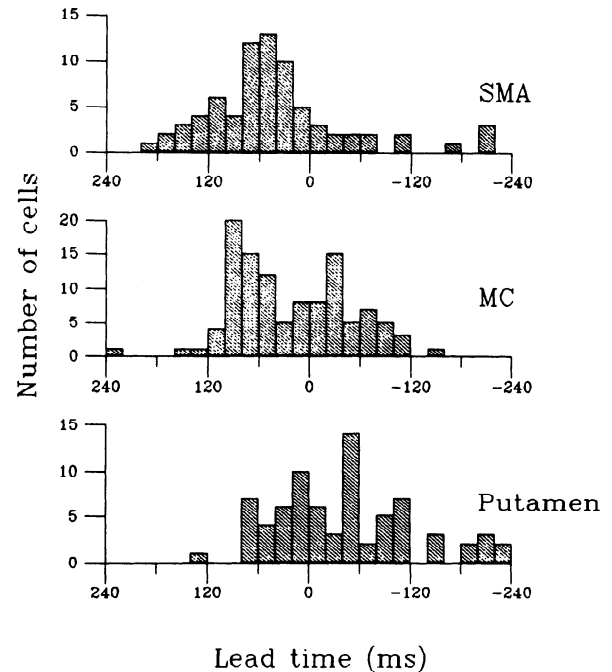


FIG. 16. Lead times for the onsets of movement-related activity that was dependent on the direction of limb movement. The distributions of onsets for SMA and MC were significantly earlier than those in the putamen.

found *within* each motor area between the latencies of either the onset or offset of target- versus limb-dependent preparatory responses.

Timing of movement-related activity

For cells with movement-related activity, the "lead time" (time of onset of neuronal activity relative to movement onset) was computed on a trial-by-trial basis, with the use of the algorithms described in the preceding paper. The median lead times of cells whose movement-related discharge was target dependent are shown in Fig. 15, and

TABLE 7. *Timing of movement-related activity*

	SMA	MC	Putamen
Target-dependent			
Median	76	13	-9
Mean ± SE	74 ± 17	16 ± 18	-9 ± 34
Number tested	20	18	8
	[P = 0.024]	[NS]	
	[P = 0.023]		
Limb-dependent			
Median	49	28	-41
Mean ± SE	38 ± 10	21 ± 7	-41 ± 9
Number tested	75	111	75
	[NS]	[P < 0.0001]	
	[P < 0.0001]		

Values exclude cells for which the detection algorithm failed to find onsets for a minimum of 5 trials. Abbreviations, see Tables 1 and 3.

those of the limb-dependent cells are shown in Fig. 16. Comparing *across* structures with *t* tests, the onsets of limb-dependent activity in both the SMA and MC were significantly earlier than those in the putamen, as indicated in Table 7. In contrast, for the target-dependent cells, the onsets of movement-related activity in the SMA were earlier than those in both MC and putamen. Comparing within structures, however, no significant differences between the onsets of target-dependent and limb-dependent activity were seen in the SMA, MC, or putamen.

DISCUSSION

All three motor areas examined in this study were found to contain neural representations of the target or goal of a visually guided limb movement that were independent of the kinematic features of the *movement itself*. Moreover, within each structure these representations appeared to be mediated by two largely separate populations of neurons: those active during the *preparation* for intended movements and those active during *movement execution*. The existence of such "spatial" representations within central motor structures was predicted by Bernstein (1984) over half a century ago, but this is the first demonstration of such representations within the motor system of primates.

Preparatory activity

The limb-dependent preparatory activity observed in this study appeared to represent a neural correlate of the process that is traditionally referred to as "motor set" (Evarts et al. 1984; Gibson 1941; Ryan 1970). That is, this type of activity represented an unambiguous signal of the intended direction of limb movement, independent of the target or goal of the movement. In contrast, the target-dependent preparatory activity could not be readily accommodated within traditional concepts of motor set, as it was shown to be independent of the subject's intended direction of arm movement. Rather, this type of activity appeared to be more consistent with the concepts of "perceptual set" (the expectation that a specific sensory stimulus is about to be presented) (Evarts et al. 1984; Gibson 1941) or selective spatial attention (Johnston and Dark 1986). Considering the fact that this activity was recorded from "motor" structures, however, it would seem even more likely that the target-dependent preparatory activity may have been related to a "high-level" form of motor set involving the target or goal of the intended movement, independent of specific kinematic or dynamic features of the movement itself.

One of the salient features of human motor behavior is the ease with which learned movements, even those with complicated trajectories such as drawing or writing, can be readily scaled in time and space, transferred between extremities, and adjusted for the use of hand-held tools (pointers, for example), all with little or no practice. This uniquely biological phenomenon of "motor equivalence" is well known (Bernstein 1984; Lacquaniti and Soechting 1982; Soechting and Lacquaniti 1981; Viviani and Terzuolo 1982), but its neural basis is poorly understood. Such

a capacity for ready adaptability to changing task demands is, by comparison, virtually absent in conventional robots (An et al. 1988; Benati et al. 1980; Paul 1981). One explanation for the ease with which subjects can modify previously learned movements is that motor control in humans and other primates may be organized primarily in terms of the spatial aspects of the task, rather than the kinematics and dynamics of the jointed limb (Bernstein 1984; Hogan et al. 1987; Hollerbach and Flash 1982; Morasso 1981).

In natural reaching to objects, the hand's trajectory tends to be straight and its velocity profile smooth and bell-shaped, as would be expected if such movements were planned and controlled in terms of the coordinate system of external space (Abend et al. 1982; Morasso 1981). Because of the complex relations between multijoint (wrist, elbow, shoulder) kinematics and hand trajectory, however, if target-directed movements were controlled primarily in terms of joint kinematics, even small degrees of incoordination among the joints involved could produce irregular and more curvilinear hand trajectories (Hogan et al. 1987). Observations such as these have prompted several motor theorists to propose that goal-directed limb movements may be *planned* in terms of the target or goal of the movement, rather than the kinematic or dynamic features of the movement itself (Bernstein 1984; Hollerbach 1982).

Movement-related activity

The target-dependent movement-related activity appeared to be related to the high-level process of capturing the target with the cursor, independent of specific features of the required limb movement. Whether such activity represented the literal *target* of the movement, or the more abstract *goal* of moving the cursor into alignment with the target, could not be determined as the two were not dissociated in this study. (The former, of course, would represent a type of visual response.) Alternatively, some of these responses might have been related to saccadic eye movements, as the monkeys invariably made a saccade to the target prior to capturing it with the cursor. We find this implausible, however, as the movement-related cells that showed target-dependent responses were *never* seen to discharge in relation to the numerous spontaneous saccades (to and from all 3 target locations) made during the pre- and postinstruction intervals.

There have been a number of single-cell recording studies in primates in which directional, movement-related neuronal activity in the SMA (Tanji and Kurata 1982), the MC (Georgopoulos et al. 1982, 1985; Kalaska et al. 1983; Kubota and Funahashi 1982; Murphy et al. 1982; Schwartz et al. 1988), and the putamen (Alexander 1987; Crutcher and DeLong 1984; DeLong 1973; Kimura 1986; Liles 1983, 1985) appeared to be correlated with the direction of visually guided limb movements. In each of these studies, it was assumed that directionally selective neurons were related to the direction of limb movement (whether or not their activity was thought to be independent of muscle activity patterns). In none, however, was this assumption tested by dissociating the direction of limb movement from

the direction of target displacement. There is only one published study in which this dissociation was carried out, and it was performed in cats rather than primates. Recording in the MC of cats trained to perform a step-tracking task that dissociated the direction of target displacement from that of a required forelimb movement, Martin and Ghez (1985) found that 32% of the neurons that became active immediately prior to movement initiation were related to the direction of target displacement, whereas 56% were related to the direction of limb movement. These authors were inclined to attribute the activity of target-dependent cells to a potential role in controlling neck musculature, rather than a role in representing the target (although they did not feel that the latter possibility had been excluded). In their paradigm, the visual display moved from side to side in close proximity to the cat's face, producing a combination of visual and somesthetic stimulation as the display brushed past the subject's vibrissae. This resulted in coordinated saccades and isometric head turning as the cat attempted to track the target. Thus the activity of the cervical musculature was strongly correlated with the direction of target shift and dissociated from that of the forelimb movement. In the present study, however, there was no basis for inferring that the target-dependent, movement-related neuronal activity was associated with the activation of cervical muscles. Electromyographic (EMG) recordings showed that each monkey's cervical musculature either was unrelated to task performance or was correlated with the direction of limb movement, rather than the direction of target displacement.

The limb-dependent movement-related activity observed in this study may have been related to any of several neurobehavioral processes implicated in movement execution. These include 1) directional motor commands, 2) efference copies of directional motor commands, and 3) proprioceptive feedback associated with the active limb movement. In the preceding paper (Crutcher and Alexander 1990), we showed that most SMA, MC, and putamen neurons with directional, movement-related activity did not appear to receive proprioceptive feedback that could account for their directional responses. Thus most of the limb-dependent movement-related activity in the present study was likely to represent either a directional motor command or an efference copy thereof. Of course, only activity that began well before the onset of movement could be suspected of involvement in movement initiation.

Combinations of preparatory and movement-related activity

Both in the SMA and MC the majority of cells with combined preparatory and movement-related activity showed the same directionality for both components of their task-related activity patterns (for the putamen, the sample of such cells was too small to merit discussion). According to traditional concepts of sequential processing in the brain, these cells might represent an important bridge between preparation to capture the target and initiation of the goal-directed movement. Of course, it is also possible that such cells may simply represent the results of

chance combinations of preparatory and movement-related inputs.

All cells with combined preparatory and movement-related activity of opposite directionality showed target-dependent preparatory activity and limb-dependent movement-related activity. This may reflect the fact that only a small fraction of the movement-related activity was target dependent, but such cells could also represent a neural correlate of the process of transforming the preparation to capture the target into specification of the direction of limb movement.

Serial versus parallel processing

The results of this study are relevant to several aspects of the question of whether motor processing is organized in a serial or parallel fashion. For example, the present results, in combination with those presented in the two preceding reports (Alexander and Crutcher 1990; Crutcher and Alexander 1990), indicate that *multiple levels of motor processing* are represented within the motor system. These studies have shown that within the arm regions of the SMA, MC, and putamen there are neural representations of the target (or goal), limb direction (or trajectory), and muscle pattern (or joint torques) associated with an overlearned, visually guided elbow movement. By demonstrating the representation of at least one intermediate level of processing, namely limb direction (kinematics), these results argue against the collapse of intervening levels into a direct (parallel) mapping of target coordinates onto muscle activation patterns. In other words, these findings suggest that at least three of the five analytically defined levels of motor processing (see Fig. 1 in Alexander and Crutcher 1990) are actually represented within the motor system. In addition, the fact all three levels are represented within each of the motor structures examined in this study provides strong support for the concept of parallel processing within the basal ganglia-thalamocortical motor circuit (Alexander et al. 1986).

The present results suggest that the functional levels of processing that are emphasized during the preparation for movement may be different from those emphasized during movement execution. Thus, within the three motor areas studied, target-dependent representations were more common than limb-dependent representations during the preparation for movement (except in the SMA, where there were comparable proportions of both types of preparatory responses). Conversely, during movement execution these same three areas (SMA, MC, and putamen) showed a marked predominance of limb-dependent representations. Moreover, the results presented in the preceding reports indicated that in these same three motor areas the overwhelming majority of preparatory representations reflected the *direction* of intended movement independent of force or muscle pattern (Alexander and Crutcher 1990), whereas substantial proportions of muscle-like representations were seen in each structure during movement execution (Crutcher and Alexander 1990). Together, these results suggest that, at least within the SMA, MC, and putamen, relatively high levels of motor processing are emphasized during the preparation for movement, with an incomplete shift toward the lower levels during movement execution.

Our comparisons of neuronal activity in the SMA, MC, and putamen support the view that motor processing is *spatially distributed*, rather than being strictly localized or hierarchically segregated. Thus, for example, roughly the same proportion of target-dependent preparatory cells was seen in each of the three motor areas (SMA, 36%; MC, 40%; putamen, 38%), and the same was true for the limb-dependent movement-related cells (SMA, 65%; MC, 71%; putamen, 63%). This is not to suggest that these three motor areas should be considered functionally equivalent, of course, as there was also abundant evidence in the present series of studies that certain types of motor processing (e.g., processing related to the preparation vs. execution of movements) were more strongly represented in one or the other of these structures (Alexander and Crutcher 1990; Crutcher and Alexander 1990). In addition, it should be emphasized that these experiments involved relatively simple, stimulus-triggered movements. It is possible that the functional differences between SMA, MC, and putamen would have been more striking if neuronal relations to more complex movements had been examined.

Within each of the three motor areas, there were no significant differences between target-dependent and limb-dependent preparatory activity in terms of either onset or offset latencies, suggesting that neural processes concerned with the expected direction of target displacement proceed in parallel and concurrently with those concerned with the intended direction of limb movement. Comparing across motor areas there were no significant differences in onset or offset latencies of directional preparatory activity, either for the target-dependent or the limb-dependent variety. Thus there was no evidence in this study for sequentially ordered processing of either target-dependent or limb-dependent preparatory influences among SMA, MC, and putamen. On the other hand, the results of the first set of experiments (Alexander and Crutcher 1990), which did not differentiate between target-dependent and limb-dependent responses and in which the total sample size was larger, indicated that the average onsets and offsets of directional preparatory activity in SMA and MC did precede those in the putamen by significant margins. It is possible, therefore, that significant differences between areas might have been seen in the present study with larger samples.

For the movement-related cells, the lead times of the target-dependent cells in the SMA were earlier than those in the MC and putamen, whereas the lead times of the limb-dependent cells in both the SMA and MC were significantly earlier than those in the putamen. Together, these results suggest a sequence of influences leading from the SMA to MC and putamen. It is important to note, however, that *within* each of these structures the processing of target-dependent and limb-dependent activity appeared to proceed concurrently. Moreover, although the overall timing of both preparatory activity (Alexander and Crutcher 1990) and movement-related activity (Crutcher and Alexander 1990) in the three motor areas suggested a sequential flow of information from SMA and MC to putamen, there was considerable temporal overlap in the distributions of neural activity changes among the three areas. Thus the primary impression that emerged from this set of studies

was that multiple levels of motor processing progress largely *in parallel* during both the preparation and execution of visually guided limb movements.

Finally, it should be noted that many of the target-dependent cells within the MC, and a few within the SMA and putamen, were found to have sensorimotor features that are not generally associated with motor processing levels as high as that of the target or goal of the movement. Thus, for example, some of the target-dependent cells were found to have sensorimotor fields restricted to the elbow or shoulder, and some had muscle-like responses to external loads. These findings would appear to be at variance with a strictly hierarchical, serial/analytic model of motor processing, where target-level processing is construed as being logically antecedent to (and therefore separate from) processing related to joint- and/or muscle-level specifications.

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