Comparison of Onset Time and Magnitude of Activity for Proximal Arm Muscles and Motor Cortical Cells Before Reaching Movements

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Scott, Stephen H. Comparison of onset time and magnitude of activity for proximal arm muscles and motor cortical cells before reaching movements. *J. Neurophysiol.* 77: 1016–1022, 1997. The activity of motor cortical cells and proximal arm muscles during the initiation of planar reaching movements were analyzed to identify whether features of coordinated motor patterns of muscles spanning the elbow and shoulder were evident in the discharge patterns of motor cortical cells. Shoulder and elbow muscles were divided into four groups, flexors and extensors at each joint. Features of the initial agonist activity, onset time and magnitude, at the shoulder and elbow were compared for movements in different spatial directions. As observed for human movements, differences in the onset time and the relative magnitude of electromyographic activity (EMG) of muscles acting about the shoulder and elbow were dependent on the direction of movement. Motor cortical cells were categorized as elbow or shoulder related on the basis of their response to passive movement of the joints. Differences in the onset time and the relative magnitude of activity of cells related to the shoulder and elbow were both dependent on the direction of movement and were similar to those observed for muscles spanning these joints. There was a modest, but significant correlation between the onset time and magnitude of EMG for individual muscles. A similar magnitude-time coupling was observed for individual motor cortical cells. Variations in the discharge pattern of motor cortical cells before movement that mirror those observed for muscles spanning the shoulder and elbow support the potential role of primary motor cortex in the selection, timing, and magnitude of agonist motor patterns at the shoulder and elbow to initiate reaching movements.

INTRODUCTION

Reaching movements provide a useful model for understanding motor coordination because muscle activity acting at the shoulder must be controlled and sequenced with that at the elbow to move the hand in space. Several studies have shown that the activity of proximal arm muscles is broadly tuned to the direction of movement (Flanders et al. 1994; Turner et al. 1995; Wadman et al. 1980). Further, the onset time and magnitude of electromyographic activity (EMG) of muscles spanning the shoulder are coordinated with those of muscles spanning the elbow and are influenced not only by the initial start and final target positions, but also by limb geometry (Karst and Hasan 1991).

An important question remains as to how these coordinated motor patterns are generated by the CNS. Of particular interest is whether or not supraspinal structures such as the primary motor cortex are involved directly in developing these temporal and spatial patterns of motor output. Traditionally, this view was supported by observations that the magnitude of motor cortical cell discharge covaried with the magnitude of muscle force (Evarts 1968), and that the ensemble activity of cells could roughly predict the temporal pattern of EMG (Fetz et al. 1989; Humphrey 1972). Further, a study of motor cortical activity during reaching movements to grasp an object in space showed that cells related to the proximal arm were active earlier than cells related to the distal arm (Murphy et al. 1985). These shifts in cell onset time mirrored the associated shift in EMG onset between proximal and distal muscles related to the reach and grasp phases of movement, respectively, suggesting that motor cortex was involved in the selection and timing of muscle activity to generate volitional movements.

However, recent studies on motor cortical activity during reaching have focused not on its role in motor coordination, but on how spatial information related particularly to the direction of hand movement influenced neuronal activity (Fu et al. 1993; Georgopoulos et al. 1982; Schwartz 1992; Schwartz et al. 1988). While some studies continued to show the importance of variables related to muscle activity level or arm geometry (Caminiti et al. 1990; Kalaska et al. 1989; Scott and Kalaska 1995, 1997), it has become less clear how or whether motor cortex is specifically involved in coordinating the activity of the elbow and shoulder musculature during reaching. At the same time, studies on spinalized frogs have demonstrated that microstimulation in the spinal cord could coactivate groups of muscles resulting in a force at the end of the limb whose direction and magnitude varied with limb posture (Bizzi et al. 1991; Giszter et al. 1993). As in studies of motor cortical activity during reaching, these studies focused on the relation between spinal function and variables related to the entire limb as a whole rather than related to a portion of the peripheral motor apparatus. From these perspectives, descending commands provide global information related to movement direction, while circuitry in the spinal cord converts this information into the appropriate output commands to muscles (Bizzi et al. 1991; Georgopoulos 1996).

A recent study demonstrated that the activity of motor cortical cells was altered during reaching movements using similar hand trajectories but different arm orientations (Scott and Kalaska 1997). Those results indicated that the discharge of single motor cortical cells did not covary exclusively with global parameters of movement related to the motion of the hand in space. One of the arm orientations used in that study maintained the hand and the elbow at nearly shoulder level during reaching. These horizontal

movements involved predominantly flexion and extension movements at the shoulder and elbow joints, and thus, are comparable with previous planar reaching studies on the coordination of muscle activity in humans (Karst and Hasan 1991). The purpose of the present study was to examine whether the discharge of motor cortical cells during reaching could provide information required to coordinate motor output at different joints (Turner et al. 1995). The present study identifies differences in the onset time and relative magnitude of EMG activity of muscles spanning the shoulder and elbow of monkeys, as observed previously for human planar movements (Karst and Hasan 1991). More importantly, this study demonstrates similar changes in the onset time and magnitude of discharge of motor cortical cells related to the shoulder and elbow joints and thus supports the potential role of primary motor cortex in developing the temporal and spatial patterns of agonist activity to initiate reaching movements.

METHODS

The data base of cell and muscle activity patterns analyzed in this study derives from a previous study in which monkeys made reaching movements using similar hand trajectories, but different arm orientations (Scott and Kalaska 1997). Two juvenile monkeys were trained to move a pendulum-like handle located at shoulder level between light-emitting diode (LED) targets. In one condition, the monkey positioned a pointer at the bottom of the manipulandum at a central LED for 1–3 s and then moved the manipulandum to one of eight peripheral targets located on the circumference of an 8-cm radius circle (center-out). In another condition, the monkey held the pointer at one of the eight peripheral targets for 1–3 s and then moved to the central target (out-center) (data not presented in Scott and Kalaska 1997). Movement onset was defined by a recursive algorithm based on the manipulandum X-Y position data (Kalaska et al. 1989). The eight different movements in each condition were presented in a randomized-block design. The present study focuses on the movements performed when the monkey's arm was abducted nearly 90° (see Scott and Kalaska 1997). These nearly planar arm movements were generated predominantly by flexion and extension movements at the shoulder and elbow joints.

Standard neurophysiological techniques were used to record the activity of individual cells in primary motor cortex during reaching movements (for details see Scott and Kalaska 1997). A scale from 1 to 5 was used to grade the relative response of a cell to passive movement of the elbow and shoulder where 1 signified only elbow input and 5 only shoulder input (see Scott and Kalaska 1997). The present study focused on the activity patterns of cells during the reaction time (RT), between the onset of the target light and the onset of movement. The preferred direction of a cell was defined by vectorial summation of its discharge pattern during RT across all movement directions (Batschelet 1981; Kalaska et al. 1989). Cells identified as directionally tuned by the use of a bootstrap technique (Crammond and Kalaska 1996; Scott and Kalaska 1997) were analyzed further. Data collected when the monkey performed the task with the left arm were mirror-image transposed.

Motor cortical cells were divided into flexor and extensor groups at each joint based on two criteria. First, cells with passive scores of 1 or 2 (responded predominantly to passive elbow movements) were classified as elbow cells, whereas cells with passive scores of 4 or 5 (responded predominantly to shoulder movements) were classified as shoulder cells. Second, the preferred direction of elbow and shoulder cells were both found to be bimodally distributed with axes that were similar to those observed for elbow and shoulder muscles, respectively (see RESULTS). These bimodal distribu-

tions formed a natural division of the cells into flexor and extensor groups based on the two poles of the bimodal axis. A line was drawn perpendicular to the axis, and cells with preferred directions on one side of this line were grouped together. Therefore cells were categorized into four groups: shoulder flexors, shoulder extensors, elbow flexors, and elbow extensors.

Analysis of onset time and magnitude of motor cortical cell activity and its dependency on movement direction followed techniques described by Karst and Hasan (1991) for the analysis of EMG patterns of flexors and extensors at the shoulder and elbow. The onset time of cell activity was identified with the use of a sequential cumulative sum (CUSUM) technique, as described in Schwartz et al. (1988). Cell onset times were defined relative to the onset time of movement. The magnitude of the cell discharge was defined by its mean level of discharge from its onset time to the initiation of movement, minus its baseline activity before the illumination of the target light. The present study focused only on the onset time and magnitude when cell discharge increased before movement.

Several steps were required to compare the activity of shoulder and elbow cells for movements in different directions. First, for each cell group, the features of cell discharge (onset time and magnitude) were averaged to give a mean onset time and a mean discharge level for each movement direction. Second, for a given movement, the earliest mean onset time between flexor and extensor cell groups were defined as the ''agonist'' cell group at that joint. There were four possible combinations of agonists (agonist pairs): shoulder extensors and elbow extensors, shoulder flexors and elbow extensors, shoulder flexors and elbow flexors, and shoulder extensors and elbow flexors. Finally, the mean onset time and mean discharge level for the agonist cell group at the shoulder were compared with those for the agonist group at the elbow. As in the study by Karst and Hasan (1991), both the differences in the mean onset time and the ratio of the magnitude of shoulder and elbow cell activity were compared with the direction of movement relative to initial forearm orientation, Ψ. Zero degrees defined movements aligned with the long axis of the forearm and in front of (distal to) the hand. Positive and negative movement directions were counterclockwise and clockwise, respectively, from this neutral direction of movement (see Fig. 3C).

The activity of the proximal arm muscles spanning the shoulder and elbow were recorded during reaching movements (Scott and Kalaska 1997). EMG signals were band-pass filtered (100–3,000 Hz), integrated and sampled at 10-ms intervals. For a given arm, the onset time and magnitude of EMG for flexors and extensors at each joint were based on the following groups: elbow flexors included brachialis and brachioradialis, elbow extensors included lateral and medial triceps, shoulder flexors included anterior deltoids and pectoralis major, and shoulder extensors included middle and posterior deltoids, supraspinatus, and infraspinatus. Muscle activity patterns during RT were analyzed by the use of techniques similar to those used to analyze cell activity, described above. The amplitude of the EMG for a given muscle was normalized to its maximal value recorded during movement.

Flexor and extensor muscle EMG activity at the shoulder and elbow were recorded and analyzed in both the center-out and out-center tasks. However, the activity of cells representing each of the four groups (flexors and extensors at the shoulder and elbow) were not all recorded in the out-center paradigm. Therefore neuronal results are limited to the responses observed in both hemispheres in the first monkey and the left hemisphere of the second monkey in Scott and Kalaska (1997) based on the center-out task.

RESULTS

Muscle activity patterns

As demonstrated in previous studies on humans and monkeys (Flanders et al. 1994; Scott and Kalaska 1997; Turner

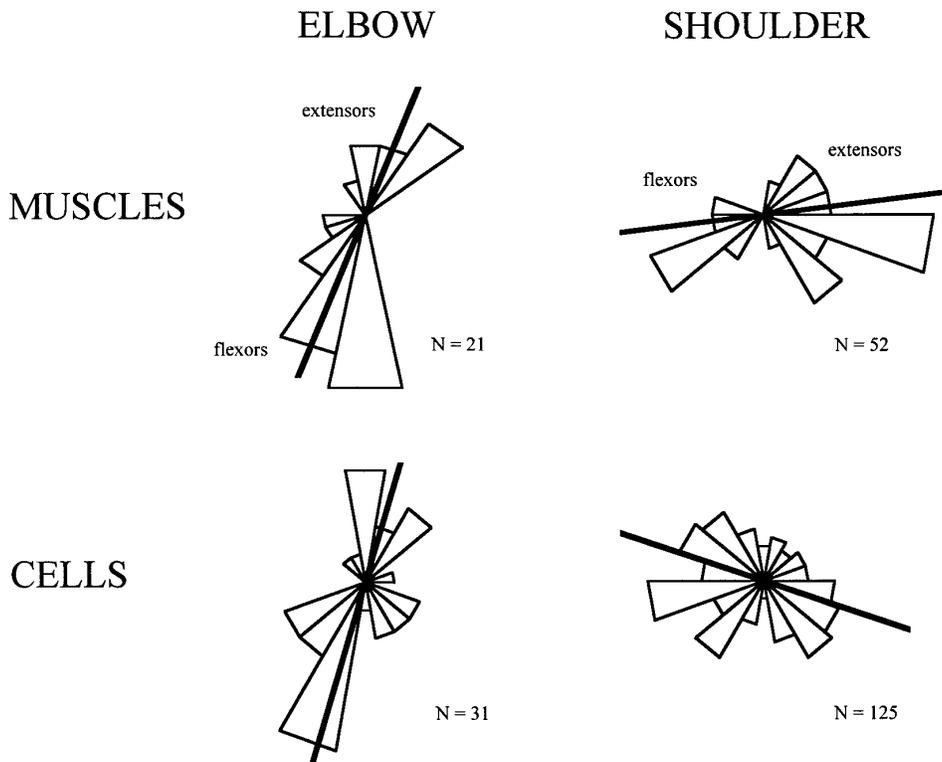ELBOW   SHOULDER

MUSCLES

CELLS

FIG. 1. Distribution of preferred directions of elbow and shoulder muscles and cells receiving passive input predominantly from either the elbow or shoulder. The size of each piece is proportional to the number of muscles or cells with preferred directions in that direction. Thick lines in each pie plot denote the major axis for each distribution. Angles for this diagram only are defined by trigonometric convention with 0° pointing to the right and angle increasing counterclockwise.

et al. 1995; Wadman et al. 1980), the EMG of shoulder and elbow muscles were broadly tuned to the direction of movement. The magnitude of EMG was maximal for movements in one direction and diminished for movements away from this preferred direction. The onset time of EMG before movement tended to parallel the variations in magnitude for movements in different directions, such that there was modest, but significant correlation between the magnitude and onset time of EMG ($r = 0.33$, $P < 0.05$, $n = 37$, muscles active for ≥ 4 movements).

The distributions of preferred directions for shoulder or elbow muscles were not uniform ($P < 0.001$; Rayleigh test) (Batschelet 1981). The distribution for elbow muscles was bimodal with a major axes oriented at 70–250° (Fig. 1; angles related to this diagram only are defined by trigonometric convention with 0° pointing to the right and angle increasing counterclockwise). Elbow flexors were maximally active for movements toward and to the left of the monkey, whereas elbow extensors were maximally active for movements in the opposite direction. The distribution for shoulder muscles was also not uniform ($P < 0.001$) but was bimodal with a major axis oriented at 7–187°. This bimodal distribution reflects the fact that shoulder flexors and extensors were maximally active for movements to the left and right, respectively, when the arm was in the abducted orientation.

The relative magnitude of shoulder and elbow EMG varied systematically with movement direction (Fig. 2A; angles defined relative to initial forearm orientation, see Fig. 3C), as observed previously for human movements (Karst and Hasan 1991). Each individual symbol represents the relative magnitude of agonist EMG at the shoulder and elbow for a single movement, and symbols of

a similar type (square, circle, etc.) represent a specific combination of agonists at the shoulder and elbow. For each agonist pair, there was a linear relationship between the ratio of the magnitude of shoulder and elbow EMG and Ψ. For example, the relative magnitude of agonist activity for the shoulder extensors and elbow extensors (squares in Fig. 2) was strongly influenced by the direction of movement. At $-150°$, the magnitude of EMG of the shoulder extensors was greater than that of the elbow extensors. At $-50°$, the reverse was true; the magnitude of EMG of the shoulder extensors was less than that of the elbow extensors. For each agonist pair, the correlation between movement direction and the relative magnitude of EMG at the shoulder and elbow were all significant (Table 1).

Differences in the onset time between agonist activity at the shoulder and elbow for each agonist pair also varied with movement direction. For each combination of agonists, the difference in the onset time of EMG between shoulder and elbow muscles followed a linear relationship with movement direction (Fig. 2B), and the correlation between the difference in onset time and Ψ was always significant (Table 1). Variations in the onset time of agonist activity at the shoulder and elbow mirrored variations in their relative magnitude. For each agonist pair, the sign of the correlation between movement direction and the shift in onset time was similar to that observed between movement direction and the ratio of the magnitude of shoulder and elbow EMG.

Cell activity patterns

The activity of 31 motor cortical cells related to the elbow and 125 related to the shoulder was analyzed in the present

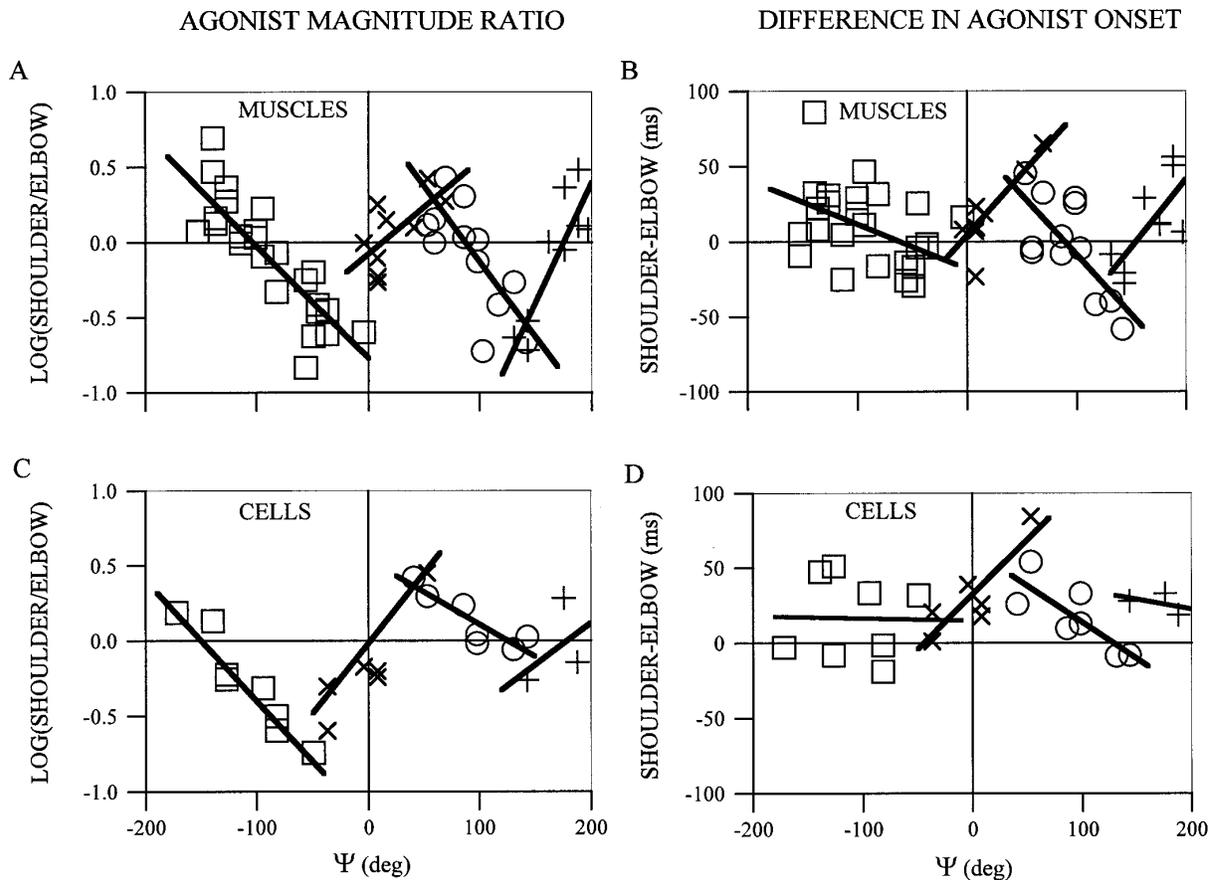## AGONIST MAGNITUDE RATIO

DIFFERENCE IN AGONIST ONSET

FIG. 2. Comparison of the agonist magnitude and onset time of muscles and cells with movement direction. Each icon denotes a different combination of agonist activity at the shoulder and elbow (agonist pair): squares denote shoulder and elbow extensors, crosses denote shoulder flexors and elbow extensors, circles denote shoulder and elbow flexors, and pluses denote shoulder extensors and elbow flexors. Thick lines denote the regression slope for each agonist pair. Values are plotted against Ψ, the direction of movement relative to initial forearm orientation (see Fig. 3C). Relationship between the relative magnitude of activity at the shoulder and elbow for muscle electromyogram (EMG; A) and cell discharge (C) compared with Ψ. Relationship between differences in the onset time of activity between shoulder and elbow muscle EMG (B) and cell discharge (D) with Ψ. See text for definition of cell types.

study. The activity of motor cortical cells before movement onset was similar to those observed for muscles acting about the shoulder and elbow joints. As observed previously, cells were broadly tuned to the direction of movement (Fig. 3). The magnitude of cell activity varied with movement direction, and this was often paralleled by variations in their onset time of discharge (Fig. 3B). As with proximal arm muscles, there was a modest, but significant correlation between the onset time of individual cells before movement and their magnitude of discharge ($r = 0.40$, $P < 0.01$, $n = 109$, cells active in ≥ 4 directions of movement). In other words, the modulation of onset time for a cell with movement direction tended to covary with its magnitude of discharge.

The distribution of preferred directions of elbow cells was not uniform ($P < 0.02$; Rayleigh test) but appeared bimodal with a major axis oriented at 75–255° (Fig. 1). The distribution of elbow cells was similar to that observed for elbow muscles ($P > 0.05$; Kuiper's test) (Batschelet 1981), and there was no difference in their major axes ($P > 0.05$; V test) (Batschelet 1981). The distribution of preferred directions of shoulder cells was also not uniform ($P < 0.05$) but appeared bimodal with a major axis oriented at 161–341°.

Although shoulder muscles and cells were both bimodally distributed with major axes oriented largely to the left and right, the two distributions were not identical ($P < 0.01$; Kuiper's test) partially due to the broader distribution for shoulder cells. Although the major axis for the shoulder cells was predominantly to the left and right as observed for the shoulder muscles, the exact orientation for shoulder cells was rotated clockwise ~25° relative to the axis for the shoulder muscles. The major axis of the distribution for elbow-related cells was roughly orthogonal to the axis for shoulder-related cells. It is interesting to note that cells that responded equally to passive movement of the shoulder and elbow (Score = 3) were uniformly distributed ($P > 0.10$; Rayleigh test; $n = 59$) and showed no bias in their distribution toward that observed for either the shoulder or the elbow musculature.

The relative magnitude of discharge of shoulder and elbow cells compared with Ψ mirrored the observed changes in the relative magnitude of EMG of shoulder and elbow muscles. For each agonist pair, there was a systematic relationship between the relative magnitude of cell discharge and Ψ (Fig. 2C) with statistically significant correlations for three of the four agonist pairs (Table 1). In each case, the sign of the
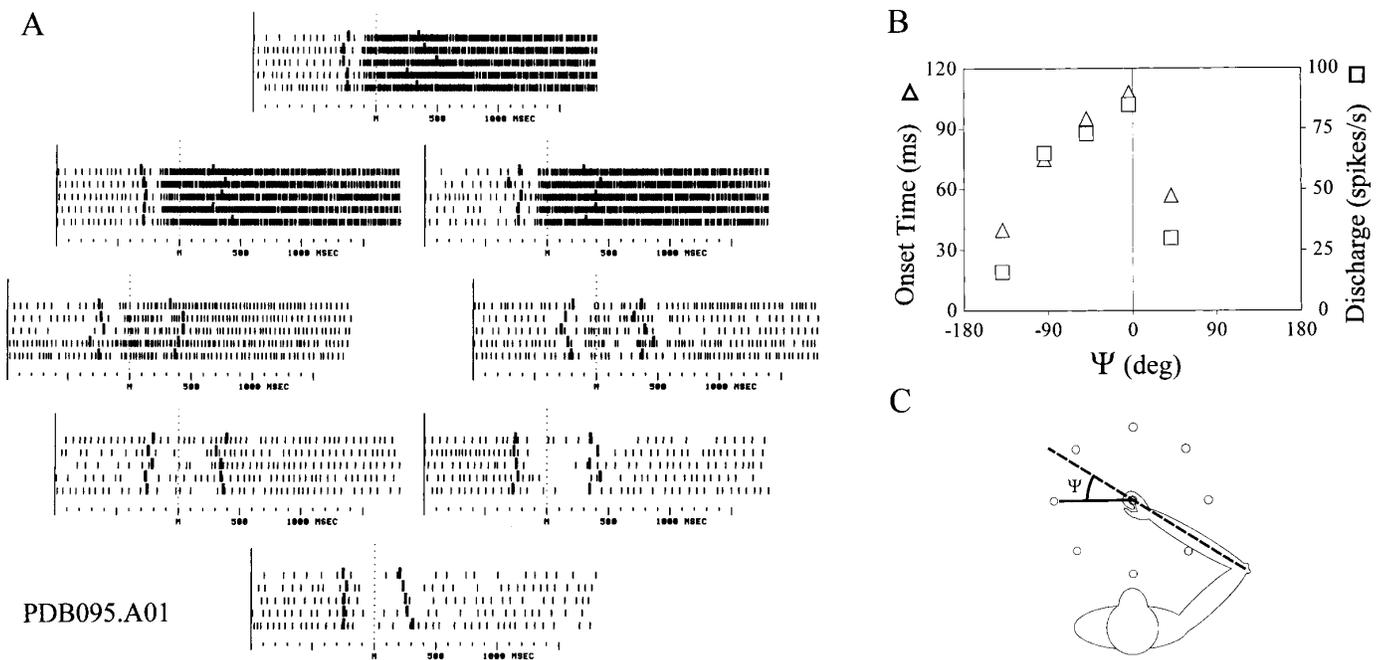
A

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B

C

FIG. 3. Activity of a motor cortical cell for movements in different directions. *A*: each raster illustrates the discharge of a cell responsive to passive elbow movements (score = 1) for 5 repeat trials to each target. M denotes the start of movement, whereas the thicker bars before and after the M denote the target light onset and the end of movement, respectively. *B*: onset time (triangles) and absolute magnitude (squares) of cell discharge both varied with the direction of movement, as defined in *C*. Results are displayed only for movements in which cell discharge increased during the reaction time. *C*: diagram of the approximate position of the 8 target lights and the starting position of the monkey's hand. The direction of movement was defined relative to the initial forearm orientation, Ψ.

correlation was the same as observed for the corresponding muscle agonist pair. For example, the averaged discharge of shoulder extensor cells was greater than that observed for elbow extensors for movements at $-150°$. The reverse was true for movements at $-50°$; the average discharge of shoulder extensor cells was less than observed for elbow extensor cells (squares in Fig. 2). A similar coupling with movement direction was observed for the ratio of the magnitude of EMG of the shoulder extensors and elbow extensors.

Changes in onset time between shoulder and elbow cells also demonstrated dependencies with movement direction. For two of the four agonist pairs, differences in onset time of shoulder and elbow cells were significantly correlated

TABLE 1. *Correlations between agonist activity and direction of movement,* Ψ

Agonist			Muscles		Cells	
Shoulder	Elbow	Variable	*n*	*r*	*n*	*r*
Extensor	Extensor	M	25	−0.85*	8	−0.95*
		OT		−0.44†		−0.02
Flexor	Extensor	M	9	0.66†	6	0.91*
		OT		0.87*		0.86*
Flexor	Flexor	M	12	−0.71*	7	−0.88*
		OT		−0.71*		−0.80†
Extensor	Flexor	M	9	0.87*	3	0.45
		OT		0.72†		−0.42

n is number of observations; *r* is linear correlation between variable and direction of movement, Ψ. M, relative magnitude of agonist activity: log (EMG shoulder/EMG elbow); OT, difference in agonist onset time: shoulder-elbow (ms). * $P < 0.01$. † $P < 0.05$.

with movement direction (Fig. 2*D*; Table 1). In both cases, the sign of these correlations with movement direction were similar to that observed for their relative magnitude of discharge and similar to that observed for the onset time and relative magnitude of EMG of the corresponding shoulder and elbow muscles.

Because of the limited number of movements analyzed in this preliminary study, data were pooled across all hemispheres. This approach, in fact, tended to reduce the correlations between agonist variables and movement direction. For example, no significant correlation was observed between the onset time of shoulder extensors and elbow extensors when data were pooled across the three hemispheres (squares in Fig. 2*D*). However, analysis of the onset differences on a hemisphere-by-hemisphere basis demonstrated some coupling with movement direction. For the two hemispheres with three observations in which the shoulder extensors and elbow extensors were first active before movement (agonist cell groups), the average correlation between changes in onset time and movement direction (after *z* transform) was -0.95 ($P < 0.01$). Similarly, within hemispheric comparisons for the other movement variables with Ψ also tended to generate higher average correlations than observed for data across all hemispheres (data not shown).

DISCUSSION

Previous studies on the activity of motor cortical cells during reaching have focused largely on the relationship between cell discharge and variables related to the global goal of the task, such as the direction of hand movement

(Caminiti et al. 1990; Fu et al. 1993; Georgopoulos et al. 1982; Kalaska et al. 1989; Schwartz 1992; Scott and Kalaska 1995, 1997). The purpose of the present study was to illustrate an alternative framework to interpret motor cortical activity during reaching based on coordinated motor patterns at the shoulder and elbow. The results show that the onset time and relative magnitude of EMG of muscles spanning the elbow and shoulder can be described by the use of simple rules based on the direction of movement relative to forearm orientation, as seen in human movements (Karst and Hasan 1991). Correspondingly, motor cortical cells related to the shoulder and elbow show similar changes in their onset time and magnitude before movement, suggesting that descending commands from motor cortex can provide the sorts of information required to select motor patterns at the shoulder and elbow to initiate reaching movements. The comparisons between motor cortical cells and proximal arm muscles was limited to the reaction time phase of the task when movement-related afferent feedback from the periphery to the spinal cord is minimal.

These results extend previous findings on the covariation of motor cortical discharge with the onset and magnitude of muscle activity during single-joint movements (Evarts 1968; Fetz et al. 1989; Humphrey 1972) to situations involving multijoint movements where the temporal and spatial activity patterns of muscles and cells related to a joint must be carefully coordinated with those acting at another. For a reach and grasp task, Murphy et al. (1985) demonstrated that the onset time of cell activity in motor cortex related to the proximal arm was earlier than the onset time of cell activity related to the distal arm and thus reflected differences in the onset time of EMG for proximal and distal arm muscles associated with the reach and grasp phases of the task. They found no differences in the onset time of cells related to the shoulder and elbow, but only studied movements in a single direction. Variations in onset time of cells related to the shoulder and elbow were evident in the present study because movements were analyzed in many different directions. The present results also agree with studies on gait modifications in cats where the discharge of individual pyramidal tract neurons in motor cortex covary with changes in the discharge pattern of different groups of flexor muscles (Drew 1993; Widajewicz et al. 1994).

Recent motor theories suggest that descending commands from motor cortex provide global information related to the whole limb, such as the direction of hand movement, and that coordinated motor commands to muscles are developed only at the spinal level (Bizzi et al. 1991; Georgopoulos 1996). The present results do not support the notion that motor cortical cells only regard the limb as a functional whole. Rather, the present results suggest that basic attributes of the discharge of motor cortex cells (onset times and intensity) covary with movement direction as is observed for the EMG of proximal arm muscles, indicating that motor cortical descending commands are capable of providing specific details of the motor output at different joints during multijoint movements.

The nonuniform distributions of preferred directions for shoulder- and elbow-related cells described in this study contrast sharply with previous studies that show roughly uniform distributions of preferred directions for motor corti-

cal cells during reaching (Caminiti et al. 1990; Georgopoulos et al. 1982; Schwartz et al. 1988). These earlier studies focused largely on shoulder-related cells when monkeys made reaching movements using a natural arm orientation in which the elbow remained below the level of the shoulder. Under these conditions, the distribution of preferred directions for shoulder-related cells tends to be uniform (Scott and Kalaska 1997). In contrast, the distribution of preferred directions for shoulder-related cells is bimodal when the arm is abducted and reaching movements are performed with the arm moving largely in the horizontal plane. This change in the distribution of preferred directions appears to reflect important differences in the kinematic and kinetic features of shoulder movement when reaching movements are performed using different arm orientations (see Scott and Kalaska 1997).

This study demonstrates striking parallels between specific aspects of the activity patterns of motor cortical cells that respond only to passive movement at a single joint and the behavior of muscles acting at that joint. While the focus of the present article was to illustrate the behavior of motor cortical cells that receive sensory input from only one joint, these results should not be interpreted as evidence that individual motor cortical cells control movements only at a single joint. The observed similarities between the motor cortical cells and muscles described here do not prove that such cells directly control the behavior of these muscles, nor exclude the possibility that such cells influence the activity of muscles acting at other joints. Furthermore, cells that responded equally to passive movement of the shoulder and elbow (''multijoint'' cells) had a uniform distribution of preferred directions and thus appeared to reflect a compromise between the bimodal and orthogonal distributions associated with the shoulder- and elbow-related cell populations. These multijoint cells emphasize the point that motor cortical cells likely influence a portion of the peripheral motor apparatus that often spans more than one joint. Although such multijoint cells likely play an important role in coordinating movement at both joints, more controlled experiments are required to elucidate their potential function during reaching.

The magnitude of motor cortical cell discharge tended to be coupled with its onset time before movement (Fig. 3) and has been described qualitatively before (Georgopoulos et al. 1982). Such magnitude-time coupling has also been observed in the discharge of cells in superior colliculus (Munoz and Wurtz 1995; Sparks and Mays 1980) related to oculomotor control and may reflect a basic feature of neuronal processing related to sensorimotor signals and transformations. Such coupling is present in the activity of proximal arm muscles (Karst and Hasan 1991; Wadman et al. 1980) and may actually help, in some cases, to linearize hand movements in space (Wadman et al. 1980). Therefore this relatively simple relation between the onset time and magnitude of motor cortical cell discharge may represent a basic feature of neuronal processing that aids in transforming signals related to the spatial location of a target into appropriate temporal and spatial patterns of motor output to initiate reaching movements.

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