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Sensory and Motor Responses of Precentral Cortex Cells During Comparable Passive and Active Joint Movements

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SUMMARY AND CONCLUSIONS

1. In awake macaques trained to permit passive stimulation, we documented the adequate natural stimuli that reliably evoked responses in precentral motor cortex neurons. Seventy-five percent of the cells in leg and arm areas responded only to passive joint movement, 8% were activated by cutaneous stimulation, and 17% did not respond to the somatic stimuli tested. Half of the units with cutaneous input could also be activated by passive joint rotation. A small number of precentral neurons responded to complex visual stimuli, such as approaching objects or appearance of novel objects.

2. Of the precentral cells responsive to passive joint movement, over three-fourths responded only phasically during joint rotation and exhibited no tonic discharge related to joint angle. Two-thirds responded to movement of only a single joint. For most arm and leg joints, the numbers of neurons responding to flexion and to extension were approximately equal; some cells were activated by both flexion and extension of the same joint.

3. In exploring specific precentral regions, we found cells with input from different parts of a limb to be extensively intermingled. On the cellular level, we did not find somatotopic organization to be sufficiently precise and detailed to predict the response properties encountered in adjacent tracks, except in probabilistic terms. Nevertheless, successive neurons in vertical penetrations tended to respond to passive movements of the same joints.

4. The response patterns of precentral neurons, identified by anatomical location, adequate natural stimulus, and pyramidal tract projection, were documented during comparable active and passive elbow movements, with the forearm held in a cast. Response averages for each of the four ramp-and-hold movements indicated that the strongest neural activity occurred with active phasic movements. In these self-paced movements, changes in precentral cell activity preceded agonist muscle activity by an average of 159 ms and preceded the mean onset of postcentral cells (47).

5. Responses to controlled passive elbow movements with the arm restrained were usually consistent with the cells' adequate stimulus. Precentral neurons responding to passive elbow movement in one direction were about equally divided into those firing with active elbow movements in the same direction, the opposite direction, and both directions. Thus, we found no predominant relationship between the cells' peripheral input, as determined by their passive response, and their central input, as evidenced by early changes in activity before active movements. (However, recent evidence indicates that certain precentral output neurons, namely, reciprocally related pyramidal tract neurons (PTNs) (8, 15, 52), and cells that facilitate forelimb muscle activity (7, 18, 19) tend to respond to passive joint movements that stretch their coactivated muscles.)

6. Some precentral neurons responded to active and passive elbow movements in both directions. Most of these had adequate

stimuli restricted to elbow rotation; such neurons appear to be related to joint movement per se, independent of direction.

7. Differences between area 6 and area 4 cells related to elbow movements were barely significant. During active movements, average onset times of cells in areas 6 and 4 were essentially the same. A slightly larger proportion of area 6 cells responded to passive rotation of multiple joints, and during controlled elbow movements they more often exhibited complex response patterns.

8. These results, in conjunction with lesion and stimulation studies, are consistent with a sensory as well as motor role for precentral cortex neurons. Under passive conditions, the responses evoked by joint rotation and cutaneous stimulation may be utilized in perception of such stimuli, particularly in the absence of the more sensitive postcentral cells.

INTRODUCTION

Precentral "motor" cortex cells are commonly considered to function primarily in execution of active movements, just as postcentral "sensory" cortex cells are thought to be mainly concerned with the analysis and perception of somatosensory stimuli. Certainly the afferent neural connections from somatic peripheral receptors are relatively more secure and elaborated to postcentral cortex, whereas output pathways to motoneurons are more potent from precentral cortex. Experiments specifically designed to analyze the sensory responses of postcentral cells under passive conditions and the relation of precentral cells to active movements have reinforced this functional dichotomy. Nevertheless, such differences are largely a matter of degree; in fact, each of Woolsey's (54) symmetrically disposed simunculi in pre- and postcentral gyri simultaneously represents both sensory and motor maps. Moreover, corresponding regions in these maps are clearly interconnected (27, 28). Similarities between precentral and postcentral cortex become more evident when both are investigated under comparable conditions (11, 41, 54).

Behavioral evidence indicates that both voluntary motor activity and sensory perception involve a continual interaction between central and peripheral events. Motor responses are appropriately executed in the context of sensory information, and perception of sensory stimulation is influenced by central states. To understand the neural basis of these phenomena, it then becomes relevant to distinguish two separable sources of input to the underlying neurons: central and peripheral. The main sources of peripheral input to pre- and postcentral cortex cells are receptors in muscles, joints, and skin; their nature and location can be characterized by the neuron's response to adequate natural stimulation. Prior to onset of an active movement, the changes in cell firing that precede any muscle activity may be attributed to input from central sources, since they occur before any changes in stimulation of peripheral receptors produced by movement. After onset of an active movement, the cell's activity clearly represents a combination of these two inputs. To compare and contrast the central and peripheral input to precentral and postcentral cortex cells under comparable conditions, we documented their responses during similar active and passive limb movements (cf. Ref. 47).

The nature of peripheral receptors that may activate precentral cortex cells has been documented in greatest detail in anesthetized primates. Over a decade ago, Albe-Fessard and Liebeskind (1) reported that many precentral cells could be driven by passive joint rotation; peripheral dissection showed such responses to be mediated by muscle stretch. Recent attempts to identify the muscle receptors that may activate precentral cells have focused on primary and secondary spindle endings. In contrast to the potent input from primary spindle receptors to area 3a cells (23, 24, 43), the input from muscles to area 4 cells seems to derive more from secondary spindle receptors. Such conclusions follow from comparisons of the responses of cells in areas 3a and 4 to *1*) electrical stimulation of muscle nerves (43, 51), *2*) graded ramp and sinusoidal stretches of dissected muscle (24, 36, 43), and *3*) intravenous injection of succinylcholine (51). Nevertheless, some precentral cells receive input from primary spindle receptors (24, 36), and many receive

convergent input from different muscles (24, 51).

While detailed analysis of receptor sites required tissue dissection in anesthetized animals, adequate natural stimulation in intact primates has proved useful to identify the passive joint movements and/or cutaneous receptive fields that activate precentral cells (3, 17–21, 32–34, 40, 45, 53). In unanesthetized, behaving monkeys it is furthermore possible to investigate the active movement(s) in which a cell is involved and compare this with its natural stimulus. In a previous study, the movements in which each precentral cell was involved were characterized by operantly conditioning increased cell activity and observing correlated limb movements under unrestrained conditions (17); these cells often responded during passive and active movements of the same joints, but a variety of relations between sensory responses and correlated active movements were observed (17, 20). Recently, Lemon et al. (33) trained monkeys to perform an extensive sequence of forelimb movements that involved pulling a lever and reaching for food at varying positions. Observing the component of the active sequence in which the cell fired and comparing this with its adequate natural stimulus, they concluded that the effective active and passive movements often appeared to involve the same joint.

Such observations under conditions of relatively free movement provide useful qualitative indications of cell relations to a variety of movements, but do not permit quantitative measures of temporal response patterns. In contrast, experiments employing torque pulses applied during specific wrist movements have provided more quantitative data on precentral cell responses (8, 13, 15, 16, 52); however, the functional interpretation of such responses is often limited when the nature and location of the mediating receptors remain unidentified. Sensory responses to perturbations are clearly influenced by the ongoing or impending active movement (8, 15, 16, 52).

In this study we sought to document more completely the response patterns of identified motor cortex cells during comparable active and purely passive movements of a major forelimb joint, the elbow. Our objective was to determine whether any predominant relation exists between active and passive responses, since such relations would be relevant to hypothesized cortical reflexes during movement. Any relation between these response patterns and other identifiable characteristics, such as the neuron's adequate natural stimulus, its cortical location, and pyramidal tract projection, would also be of functional significance. To define the relative timing of cell and agonist muscle activity, EMG of biceps and triceps was recorded with each cell. To allow comparison between dynamic and static response components, all movements consisted of a phasic ramp followed by a static hold period. In contrast to elbow-related postcentral cortex cells documented under identical conditions (47), the precentral cells were typically more related to phasic movement and showed a greater variety of relations between active and passive responses.

METHODS

Training

Seven rhesus macaques were trained to allow passive handling of their limbs without struggling. Initially, all feeding was associated with handling of the monkey's arm, and food delivery was made contingent on increasing degrees of cooperation. To document cell responses during controlled elbow movement, we trained the monkeys alternately to flex and extend the elbow with the forearm held semiprone in a formfit cast hinged at the elbow through a potentiometer. In the cast the wrist was held fixed at 180° with fingers extended, while the elbow could be moved in a vertical plane between stops at 90° (extension) and 45° (flexion) (Fig. 1). A logic circuit rewarded alternate flexion and extension movements, each consisting of a phasic movement lasting less than 400 ms, followed by an uninterrupted static hold against the stop for at least 1 s. Successful performance of this ramp-and-hold sequence was indicated by a brief tone and was rewarded by delivery of 0.13 ml applesauce through a feeder tube in front of the monkey; a light also signaled that the opposite movement would be rewarded next. Monkeys were "shaped" to this terminal performance through gradual increases in elbow excursion and hold times.

Responses of precentral cells to natural stimulation were tested with the arm out of the cast, by passive movements of limb joints and brushing

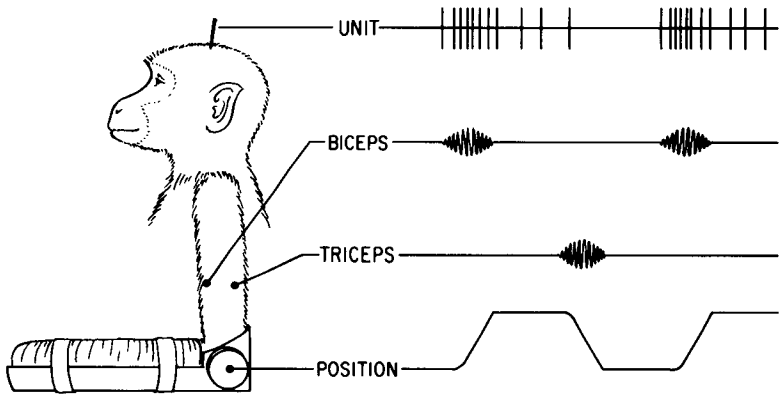

FIG. 1. Schematic representation of experimental conditions for documenting the relation of precentral and postcentral (47) neurons to elbow movements. To assure comparable movements in the primary rotational plane of the elbow joint, the monkey's left forearm was held semiprone in a cast, which pivoted in a vertical plane about the elbow axis. A resistive load was provided by a dashpot. With each cortical neuron, the activity of agonist arm muscles was recorded during both active and passive movements.

and touching the skin. In some cases, responses to visual stimuli were noted and characterized. Only those stimulus conditions that repeatedly elicited neural responses in the absence of overt movement or active resistance were considered to characterize the cells' adequate stimulus. Those cells whose responses were recorded during active elbow movements in the cast were also documented during comparable passive movements of the cast. These passive movements were confirmed to occur in the absence of recorded EMG activity or any other signs of active resistance.

Recording

As previously described (17, 20), single cortical neurons were recorded with tungsten microelectrodes within a 10-mm-diameter circular area centered over precentral cortex. EMG activity of biceps and triceps muscles was routinely recorded during active and passive elbow movements with implanted pairs of stainless steel wires led subcutaneously to a connector fixed to the skull. Concentric bipolar pyramidal tract (PT) stimulating electrodes were implanted 2 mm posterior to the intra-aural line and 2 mm lateral to midline; electrode placement was guided by the lowest threshold responses of thumb or fingers to a 50-ms train of stimuli at 500/s.

During recording sessions the monkeys sat isolated in an IAC sound-attenuating chamber and could be observed via a television monitor. A seven-channel FM tape recorder recorded activity of cortical units, biceps and triceps, elbow position, pulses triggered from unit action potentials, pulses synchronized with movement onset, and voice. The pulses identifying correct movements were timed to occur 1 s after the arm left the previous stop and were recorded only for those trials in which the criterion sequence of phasic movement followed by static hold were performed. Response averages were subsequently compiled by playing the tape recorder backward, triggering a Nuclear Chicago averager from the flexion or extension pulses, and averaging activity over a 2-s interval that straddled the phasic responses. This ensured that response averages were all aligned at the onset of criterion responses. Averages of position and full-wave rectified EMG activity were compiled at identical gains for active and passive responses; all time histograms of unit activity were compiled at the same gains unless otherwise noted.

To determine whether any of the recorded cells had detectable effects on covarying agonist muscles, spike-triggered averages of rectified EMG activity were compiled off-line (19). In this task, the phasic muscle activity occurring at movement onset was too brief and nonstationary to provide convincing evidence of spike-correlated effects; the amount of activity recorded was usually insufficient to allow observed effects to be confirmed by replicating the spike-triggered averages (18, 19).

Recording sites were histologically determined at the end of experiments; the position of the recording chamber was marked with respect to the perfused brain and recording tracks located in relation to surface features, using the polar coordinate system of the recording chamber. Serial sagittal frozen sections (40 μm) stained with cresyl violet were examined for location

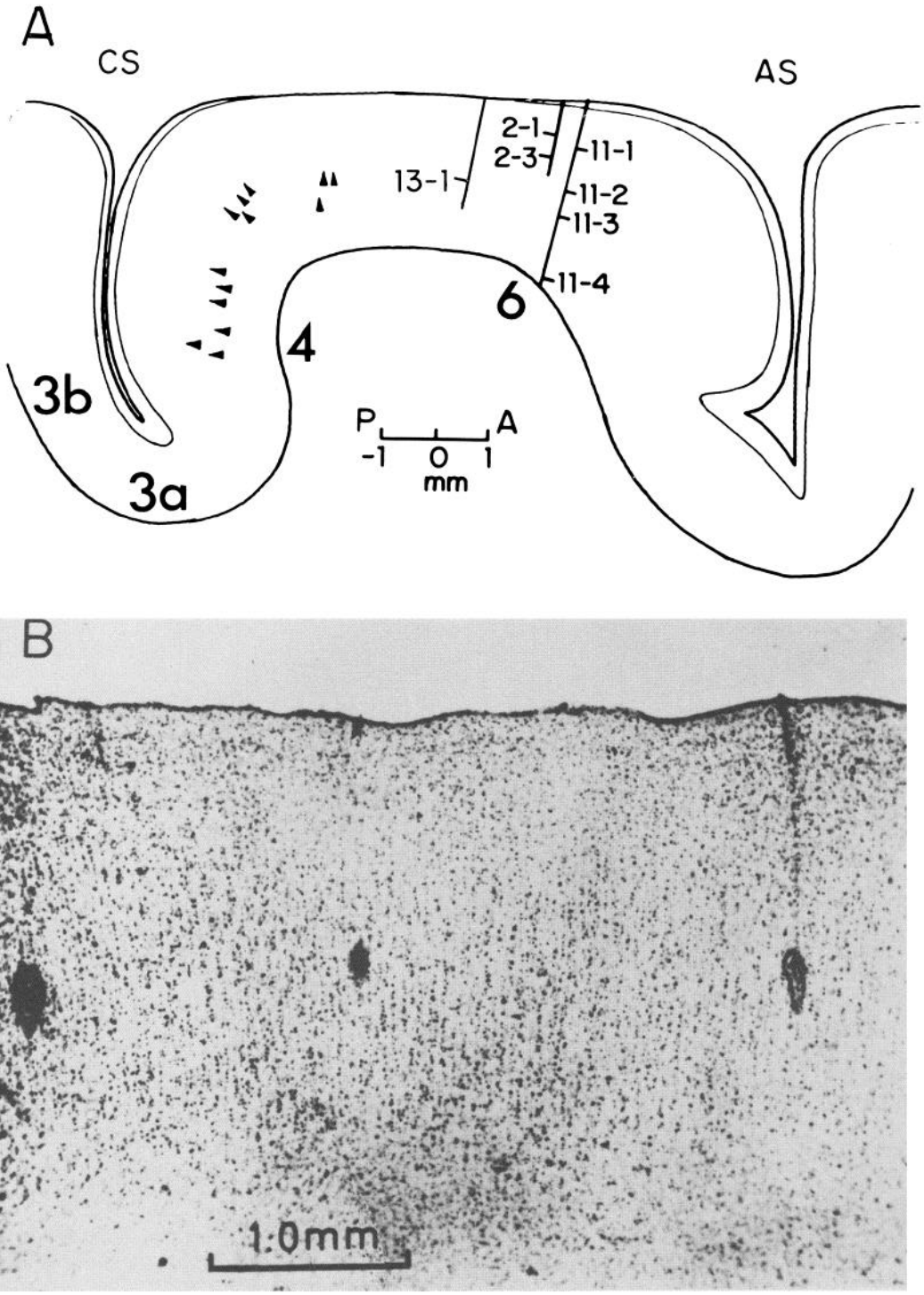

FIG. 2. *A*: location of precentral neurons whose responses during controlled active and passive elbow movements are illustrated in Figs. 3–7. Electrode tracks were projected onto the same sagittal plane; track 2 was 500 μm medial to track 11 and 700 μm lateral to track 13. Triangles represent the region of large Betz cells; areas in which cell cytoarchitecture matched Brodmann's criteria (4) are indicated by corresponding numbers. CS,

TABLE 1. *Sensory responses of precentral cells*

A. Modality of response

One Joint Only	Two Joints	Three Joints	Cutaneous + Joint	Cutaneous Only	Unresponsive	Total
Arm area						
112	37	13	8	11	62	243
(46)	(15)	(5)	(3)	(5)	(26)	(100)
Leg area						
129	56	4	12	6	16	223
(58)	(25)	(2)	(5)	(3)	(7)	(100)
Total						
241	93	17	20	17	78	466
(52)	(20)	(4)	(4)	(4)	(17)	(100)

B. Precentral cells responding to passive joint movements

Arm										
Finger		Wrist		Elbow		Shoulder			
Fl	Ex	Fl	Ex	Fl	Ex	Fl	Ex	Ab	Ad
6	5	15	12	43	47	42	36	8	8

Leg									
Toes			Ankle		Knee		Hip	
Fl	Ex	Ad/ab	Fl	Ex	Fl	Ex	Fl	Ex
13	21	20	56	65	28	49	3	5

A: number and percentage (in parentheses) of cells responsive to passive joint movements, cutaneous stimulation, and unresponsive to any tested input. *B*: number of cells responsive to passive flexion (fl), extension (ex), adduction (ad), and abduction (ab) of indicated joints.

of specific recording tracks and for electrolytic lesions made at certain recording sites (Fig. 2). The cytoarchitectonic areas in which units were recorded were identified by the criteria of Brodmann (4), as described also by von Bonin (in Ref. 6) and Jones and Powell (28).

RESULTS

Sensory responses of precentral neurons

In all, 466 precentral units in seven monkeys were characterized with respect to repeatable sensory responses to natural stimulation; 223 units were recorded in leg area (five monkeys) and 243 units in arm area (six monkeys). As summarized in Table 1, 351 units (75%) were driven by passive limb movement, 37 (8%) responded to cutaneous stimulation, and 78 (17%) were unresponsive to the somatic stimuli tested. Half of the cells responding to cutaneous stimulation could also be driven repeatedly by passive joint movement; the latter responses did not seem to be mediated by the cutaneous receptors, suggesting a convergence of cutaneous and proprioceptive input. Similar proportions of modalities were found in both arm and leg areas.

Responses of precentral cells to passive joint rotation typically occurred only during the phasic component of the movement;

central sulcus; AS, arcuate sulcus. *B*: electrolytic lesions made in three parallel tracks in precentral leg area 4, at a depth corresponding to the clear transition to spontaneously active cells related to hindlimb movements (5 μA, 10 s). Eleven additional lesions made in this terminal experiment were found at the same cortical depth, corresponding to cortical layer 5.

firing rates were usually not sustained during maintained joint displacement. Of 189 leg area units responding to passive movements, 148 (78%) responded only during phasic movements, 37 showed both tonic and phasic responses, and 4 fired at tonic rates proportional to joint angle. A similar predominance of dynamic responses was observed in arm area cells (Table 1). Two-thirds of the cells responsive to joint rotation were driven by only one of the major contralateral joints; some could be driven from two joints and a few responded to moving three or more joints. The proportion of cells driven by more than one joint was slightly higher in cortical area 6 than in area 4. Some cells responded to passive joint movement in both directions. In one monkey, responses to ipsilateral passive movements were tested systematically in the arm area where 39 of 147 cells tested responded to passive movements of both ipsilateral and contralateral joints. Most of these involved shoulder movements and in 19 cases, the ipsilateral response was movement of the same joint in the opposite direction as the contralateral joint (cf. Ref. 1).

Table 1*B* summarizes the total number of neurons responding to passive movement of each joint. The relative proportion of observed cells responsive to each joint does not reflect the cortical representation of these joints since the cortex was not systematically explored with an equally spaced grid of electrode tracks. In the arm area we preferentially searched for cells related to elbow movements and explored less extensively the bank of the precentral fissure where the wrist and fingers are more strongly represented (45, 48, 53, 54). Nevertheless, the relative proportion of responses to passive flexion and extension of each joint can be considered a significant comparison; except for the knee joint, there were roughly as many cells responsive to passive flexion of each joint as to passive extension. Of 29 pairs of adjacent cells thoroughly characterized in leg area, 15 pairs consisted of cells responsive to movement of the same joint in the same direction; for 8 pairs the second cell responded to movement of the same joint in the opposite or a different direction, and in 7 cases the 2 cells responded to input from different joints.

Cells with input from arm and leg were found most frequently in the regions indicated by published maps (53, 54). However, a finer grained somatotopic distribution of cells within these regions was not evident. As a typical example, when the 121 cells in leg area of one monkey were mapped within the area covered by the recording chamber, the cells responsive to toe ($n = 41$) and ankle ($n = 78$) were distributed evenly in an overlapping fashion over a 5-mm-diameter semicircle; 32 cells responsive to knee movements overlapped these in the medial quadrant. Similarly, in the arm area of one monkey, 181 cells responsive to passive wrist, elbow, and shoulder movements overlapped to a large extent in a 10-mm-diameter circular region.

The distribution of cell types at different cortical depths was also assessed in electrode tracks made perpendicular to the cortical surface in leg and arm areas. Cells in superficial layers (I–IV) typically had low spontaneous discharge, seemed less often clearly driven by passive movements, and tended to be weakly modulated during active movements. At a depth of 1.2–1.5 mm below the cortical surface, a clear transition occurred to spontaneously active cells with large action potentials; these were strongly modulated during active movements and more often driven by passive movements. To identify this transition layer, we made a systematic series of tracks in leg area of one monkey, placing 16 electrolytic lesions at this transition zone. With few exceptions, these lesions were found in cortical layer V (Fig. 2).

A small proportion of precentral cells responded consistently to complex visual stimuli. Of the 466 cells, 8 responded repeatedly when objects approached the monkey; since visual responses were not systematically tested, the true proportion of such cells may well be greater. Such visual responses were independent of the shape and nature of the moving object and its location within the visual field. In addition, some of these cells also responded to brushing the hairs over specific cutaneous receptive fields and gave the best "approach" responses when movement was directed toward these cutaneous fields. Similar movements of objects did not elicit responses when the monkey's vision was occluded. Such visual responses did not habituate and

could be demonstrated repeatedly for several hours; they were not accompanied by any recorded EMG activity or observable movement. These cells also fired repeatedly during active movement, and some were PTNs (e.g., cell *M12-3* in Table 2); they were encountered in both areas 4 and 6.

Responses during active and passive elbow movements

To document the response patterns of identified precentral cells during controlled joint movements, we recorded their activity during ramp-and-hold elbow movements with the forearm in a molded cast. Comparable response averages of unit and muscle activity and elbow position were compiled for equal numbers of active and passive movements. In each case the response average accurately reflected the pattern seen in individual trials, which typically were quite repeatable (Fig. 3). Table 2 summarizes the main features of the active and passive response patterns of precentral cells identified by cortical location, adequate stimulus, and pyramidal tract projection. To illustrate these response patterns, we chose several cells whose relative location in the precentral arm area of monkey *L* is shown in Fig. 2*A*.

Figure 3 illustrates a precentral neuron that responded during active and passive elbow movements in the same direction. Passive elbow flexion evoked a burst discharge during the phasic flexion movement; the static flexed position elicited a higher tonic rate, which adapted slowly. When the monkey actively moved the elbow, this cell also fired strongly with phasic flexion, becoming active just before biceps activity. When tested for responses to adequate natural stimulation (with the arm outside the cast), this cell could be driven by passive movements of numerous joints, including flexion of contralateral and ipsilateral elbows, hips, and ankles, abduction of contralateral shoulder, and flexion of ipsilateral wrist. In contrast to this unusually extensive convergence of peripheral input, most of the other precentral cells responsive to active and passive elbow movements in the same direction had adequate natural stimuli restricted to elbow movements (Table 2; cf. *L11-2* in Fig. 6).

A second group of precentral cells responded to passive joint movement in one direction and fired during active movements in the opposite direction. The example illustrated in Fig. 4 was recorded 400 μm below the cell in Fig. 3 in the same electrode track (cf. Fig. 2). This cell also responded with a burst to passive flexion of the elbow; it exhibited a negligible difference in tonic rate during maintained position. With active movements, the strongest response of this cell was an intense burst associated with active extension, beginning well before, and peaking with, onset of triceps activity. In contrast, the response pattern with active flexion consisted of a brief burst during the flexion movement superimposed on a longer suppression of activity beginning well before and lasting well beyond the phasic flexion movement. Similar patterns were observed for certain postcentral cortex cells (47), and suggest a centrally originating suppression of the phasic response during active joint movement. With the arm out of the cast, this neuron could be driven by passive elbow flexion and abduction of the shoulder.

Another cell responsive during active and passive movements in opposite directions is unit *L11-1*, recorded in a track 700 μm from the preceding one (Fig. 5). Like its neighbors, this cell responded phasically and tonically to passive flexion. During active extension it fired well before triceps, reaching a peak at EMG onset, and then becoming inactive as triceps activity increased. Such biphasic response patterns, perhaps related to changes in muscle activity, were observed in 20% of cases (Table 2). This unit also exhibited a reciprocal phasic suppression during active elbow flexion.

The next neuron encountered in this track also exhibited reciprocal response patterns during active flexion and extension. This non-PT neuron (*L11-2*) fired before active flexion and was suppressed before active extension (Fig. 6). Interestingly, the responses evoked by passive flexion and extension were similar to the active responses. With the arm out of the cast, the adequate excitatory stimulus for this cell was restricted to passive elbow flexion. Deeper in this track, a pyramidal tract neuron (*L11-3*) also fired with active flexion and responded to passive elbow flexion and extension (Table 2). It, too, was unresponsive to natural stimulation of any joint other than the elbow.

TABLE 2. *Responses of precentral cortex cells during active and passive elbow movements*

					Phasic Response				Tonic Response				Latency	
					Active		Passive		Active		Passive		Active	
Cell	Area	PT	NS	A-P	F	E	F	E	F	E	F	E	F	E
Elbow flexion														
F53-2	4	0.9	fE	S	++++	−/+	++	−/+	−	+	−	+	−480	−100
L2-1	6	0	fE, abS, fH, fiW	S	+++	0	++	−	−	+	+	−	−40	N
L4-1	4/6	1.3	fW	S	+	0	+	0	−	+	−	+	0	N
L11-2	6	0	fE	S	++/−	−−	+/−	−	0	0	−	+	−100	−100
L11-1	6	0	fE	O	−−/+	++/−−	++	0	+	−	+	−	−80	−300
F71-4	4	0.9	eW, adS	O	−	+++	+++	−	0	0	+	−	20	−60
L2-3	6		fE, abS	O	−/+/−	+++	++	0	0	0	0	0	−300	−360
F78-3	4	1.7	fE, f + eW, f + eS	O	−−/+	++	++	−	0	0	+	−	−200	−120
F68-2	4	0	fE	B	++	+++	+	0	0	0	0	0	−40	−280
F69-3	4	0.9	fE	B	+	+	+	0	0	0	0	0	−120	−180
F75-1	4	0	fE, fS	B	+++	++	+	0	0	0	0	0	−80	140
L10-1	4/6		fE	B	+	++	+	0	0	0	0	0	120	−240
E20-4	4		fE	M	−/+/−	−−/++	++	−	+	−	+	−	−320	120
Elbow extension														
F52-2	4	0	eE	S	0	+++	0	++	0	0	0	0	N	−220
F52-3	4	1.1	eE	S	−−−/+	+++	−−−	+	0	0	−	+	−300	−320
M10-1	4		eE	S	−	++	−	++	+	−	+	−	160	−220
M12-2	4		eE	S	+/−−/+	+++	0	+	0	0	+	−	−120	−120
M7-2	4		eE	S	−/+	++++	−	+	0	0	0	0	−180	−220
F29-1	4		eE, fW	O	+++	0	0	++	0	0	0	0	−200	N
D84-1	4	0	NCR	O	++/+++	−	−	+	+	−	++	−−	−120	−200
C136-4	4		S	O	−/+++	−	0	++	−	+	−	+	−320	−160
H30-1	4		eE	O	+++	+/−	−	+	−	+	0	0	−180	−340
F74-2	4	0	adS, fS, eE	B	+++	++	0	+	+	−	−	+	−280	−480
D94-4	4	0	S	B	+++	+++	0	+	+	−	0	0	−200	−100
M12-3	4	1.1	fS, vis. ap.	M	+++	−/++	0	+/−	+	−	+	−	−220	240
Flexion and extension														
F66-2	4		fE, eE	B	+++	+++	+++	++	+	−	0	0	−180	20
H28-2	4		eE	B	++++	++	+	++	0	0	0	0	−440	−180
E17-1	4	0		B	+	++	+	+	+	−	0	0	−60	0
L7-4	6	0	eE	B	+++	+	+	+	+	−	0	0	−220	−220
L9-1	4/6	0	fE, eE	B	++	+	+	+	0	0	0	0	−400	−180
L13-1	4/6	0	fE, eE	B	+++	+	++	+	0	0	0	0	−160	−280
F70-2	4	0.9	fE, eE	B	+/+	−/++	+	+	0	0	0	0	−300	−80
E19-4	4	1.2	S	B	++	+++/−	+	+	++	−−	0	0	−220	−220
L11-3	6	0.8	fE, eE	M	++	0	++	++	0	0	0	0	−40	N
M9-1	4		eE	M	−	+++/−	++	+/−	0	0	0	0	−40	−120
F77-2	4	0.9	fE, adS	M	−−/+	+++	+	+	−	+	0	0	80	−120
F31-2	4	0.9	fE, eE, pEJ	M	−	++	+	+++	0	0	0	0	−80	−240
Miscellaneous														
L10-3	4/6	0	fW		−−	−/+	+/−	−	0	0	−	+	−160	−140
L11-4	6	0	NCR		+/−	+/−	−	−	0	0	0	0	−200	−120
L12-1	6		NCR		+++	0	0	0	0	0	0	0	−160	N
H28-4	4		eE		+	+/+	0	0	0	0	0	0	−140	−360
C133-1	4		S		++++	0	0	0	0	0	0	0	−240	N
L7-3	6	0	NCR		−	+	0	0	0	0	0	0	−180	−100
F70-3	4	0	triceps tap		0	+	0	0	0	0	0	0	N	−100
H11-1	4		fE, triceps		+	0	−	0	0	0	0	0	20	N

Cells are grouped according to responses to passive elbow movement and are identified by monkey and track (as in Figs. 2–8). The cytoarchitectonic area in which neuron was recorded is given in second column; neurons located at the transition between Brodmann's area 4 and 6 are indicated by "4/6." PT gives antidromic latency in milliseconds; 0 indicates no PT response; blank indicates response was not tested. NS gives adequate natural stimulus with arm out of cast: f, flexion; e, extension; ad, adduction; ab, abduction; i, ipsilateral; vis ap, approach of visible object; NCR, no clear response; E, elbow; W, wrist; S, shoulder; H, hip, pEJ, pressure on elbow joint. Column A-P indicates whether the effective active elbow movement was in the same (S) or opposite (O) direction as the passive movement, or involved movements in both directions (B), or evoked mixed responses (M). The pattern of phasic and tonic responses observed in the response averages is summarized with +, indicating excitation, or −, indicating suppression. Number of symbols represents relative intensity of response (cf. Figs. 2–8). 0 indicates no difference in response. Latency column gives time of change in cell activity relative to onset of agonist muscle activity, for active flexion (F) and extension (E). Negative numbers indicate that cell activity changed before muscle activity. N, no response.

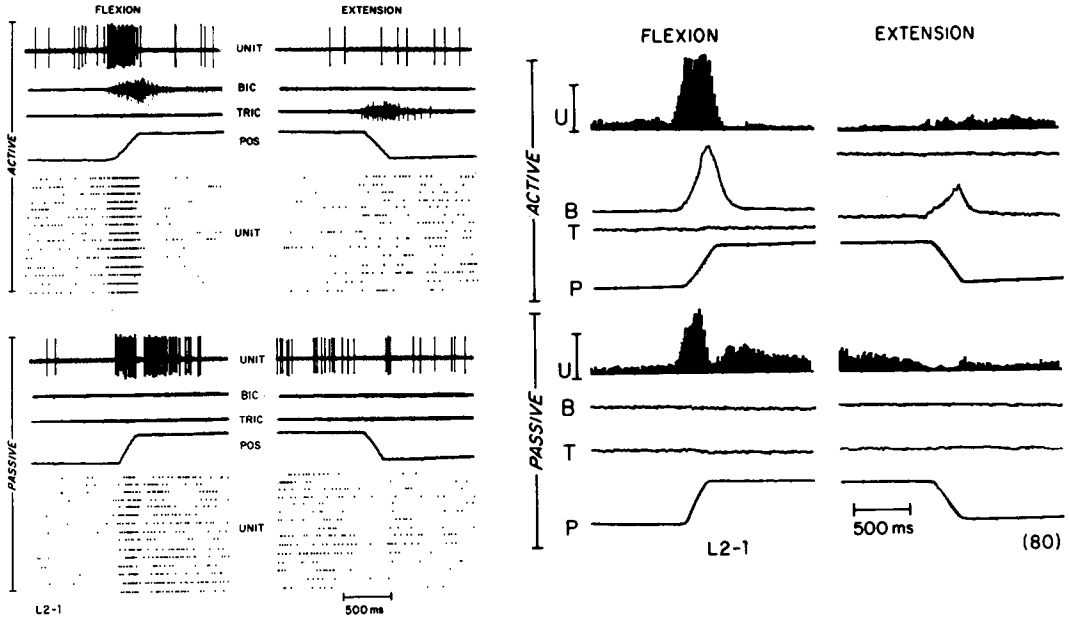

FIG. 3. Responses of precentral cell *L2-1* during active and passive elbow movements. At left are single trials and dot rasters of unit activity, illustrating the repeatability of successive responses. At right, response averages show the mean activity of this precentral unit (U), biceps (B), triceps (T), and elbow position (P). All averages were compiled at identical gains for 80 successive responses. Vertical bar in this and subsequent figures calibrates unit firing rate of 50/s.

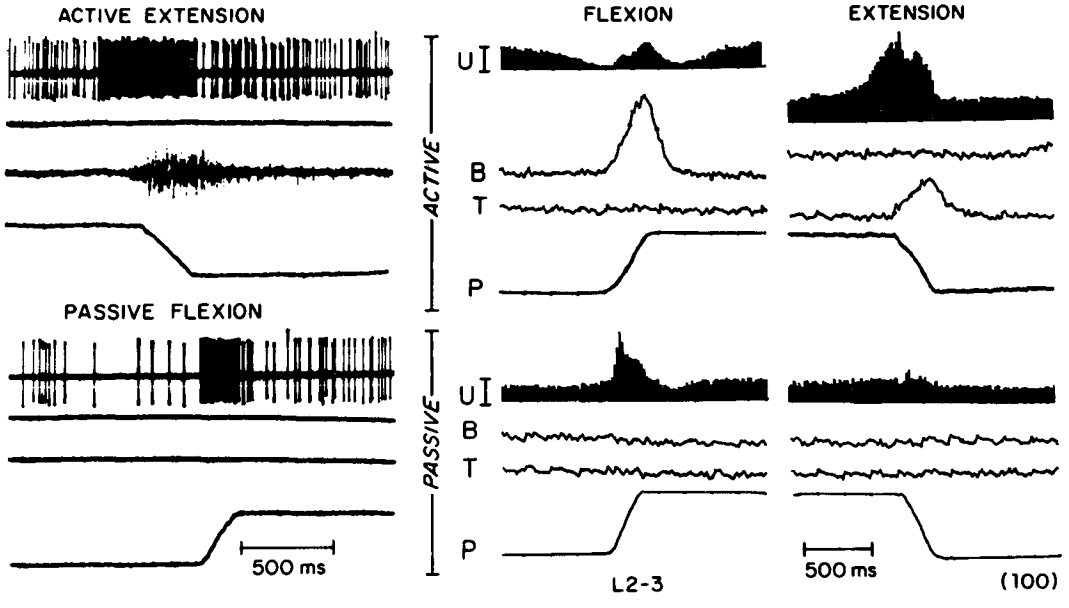

FIG. 4. Responses of precentral unit *L2-3* during active and passive elbow movements. Representative single trials at left illustrate unit and muscle activity during active extension and passive flexion. Timing of activity is documented in response averages at right, each compiled for 100 successive responses. Although the passive response average suggests a slightly higher tonic rate during maintained flexion, this difference was considered too small to be entered in Table 2.

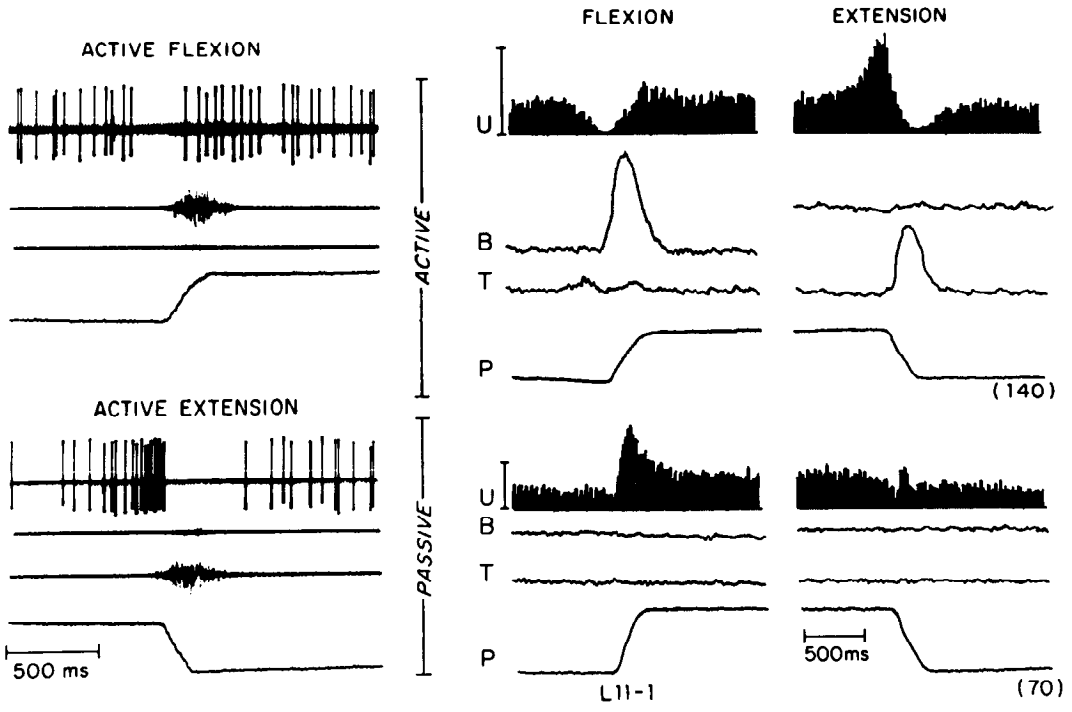

FIG. 5. Reciprocal response patterns of unit *L11-1* during active and passive elbow movements. Under passive conditions this neuron showed both a phasic response to flexion and a higher discharge in the flexed position (sufficiently strong and consistent to be entered in Table 2). Averages of active responses include 140 trials, of passive responses, 70 trials. Vertical bars calibrate firing rate of 50/s for both.

A third type of precentral neuron responded during active and passive elbow movements in both directions (Table 2). The example illustrated in Fig. 7 became active well before active flexion and extension; similarly, it was clearly driven by both passive flexion and extension movements. This non-PTN did not respond to any natural stimulation besides passive elbow movements; its response to passive extension was weaker than to passive flexion, but was too consistent to be ignored. It was encountered close to the transition zone between areas 4 and 6; similar bidirectional response patterns were found in both area 4 and area 6 neurons.

Finally, a small proportion of precentral cells exhibited a very simple response pattern: activation with active movement in only one direction and no passive response. Figure 8 illustrates such a cell (*C133-1*) recorded close to area 3a. Although it did not respond during passive movements of the arm in the cast, when tested for natural stimulation this cell did respond to squeezing triceps and deep tissue near the shoulder.

Table 2 summarizes the response patterns of the precentral cortex cells whose activity was averaged during comparable active and passive elbow movements. The cells are separated into four groups according to whether they responded to passive flexion or extension, or both, or neither; each group is further subdivided according to whether the predominant active response occurred with movements in the same direction (S), in the opposite direction (O), in both directions (B), or were more complex (M). As indicated, the cells responding to passive movement in one direction were about equally divided into three groups: those discharging during active movement in the same direction, in the opposite direction, and in both directions. In other words, the direction of effective passive movement did not predict the direction of effective active movement. In addition, a comparable number of cells responded to passive and active movements in both directions. While Table 2 includes only those cells documented during controlled arm move-

ments in the cast, these proportions are representative of a larger population of precentral cells qualitatively observed during active and passive joint movements in this and other studies (17, 34).

For most precentral cells, the strongest activity occurred during phasic active movements. The most common dynamic response was pure excitation (58%), which exceeded pure inhibition (10%), mixed responses (23%), or no response (9%). Patterns of mixed excitation and inhibition occurred more frequently with active movements (23%) than passive movements (6%). Compared with pure excitation or inhibition, mixed response patterns occurred slightly more often with area 6 cells (40% of responses) than area 4 cells (25% of responses). Mixed responses were somewhat more common for cells with input from joints other than the elbow (36%) than for neurons driven only by passive elbow movements (22%). Differences in tonic rate related to joint position were found in almost half of the cases of elbow movements in the cast; these appeared as often under active as passive conditions. When differences in tonic rate appeared under both active and passive conditions, they occurred more often with the same position for both (n = 7) than with opposite positions (n = 4). When phasic and tonic responses were comparable, they were as often in the opposite direction (n = 9) as in the same direction (n = 10).

Relative timing of cell and muscle activity

Table 2 also provides the onset times of precentral cell activity relative to onset of agonist muscle activity during active elbow movements. Onset time was identified as the first time bin in the response average in which activity clearly exceeded preceding base-line fluctuations, in a direction sustained over subsequent bins. Activity of the agonist elbow muscles, biceps and triceps, was routinely

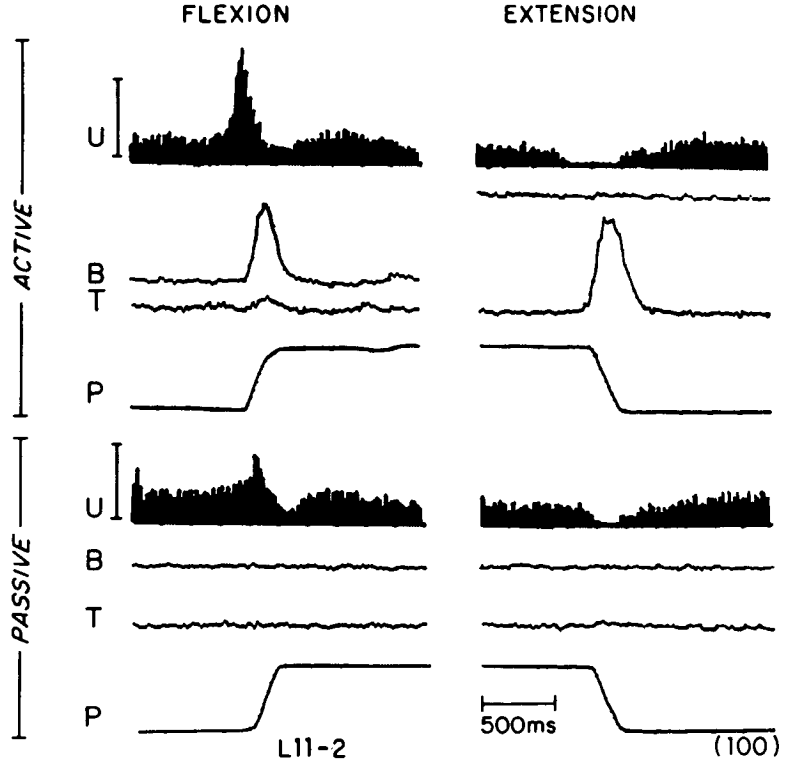

FIG. 6. Neuron *L11-2* exhibited similar reciprocal response patterns for both active and passive movements. The active pattern, involving a peak at onset of biceps activity, was the reverse of the pattern seen in superficial cell *L11-1* (Fig. 5) and similar to that of deeper cells *L11-3* and *L11-4* (cf. Table 2).

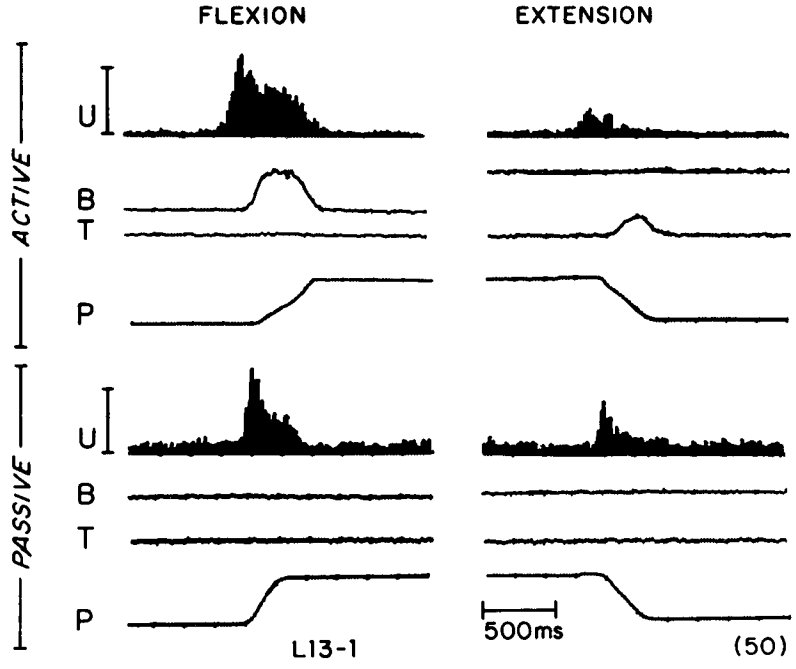

FIG. 7. Unit *L13-1* exemplifies precentral neurons that responded under all four conditions: active and passive flexion and extension. Although flexion responses were greater than extension responses, both appeared clearly and repeatedly and could also be demonstrated for passive elbow rotation with the arm outside the cast.

recorded and averaged during cell recording; the responses of other arm muscles were intermittently documented under the same movement conditions. When sampled separately, the synergistic agonist elbow muscles had identical onset times to within

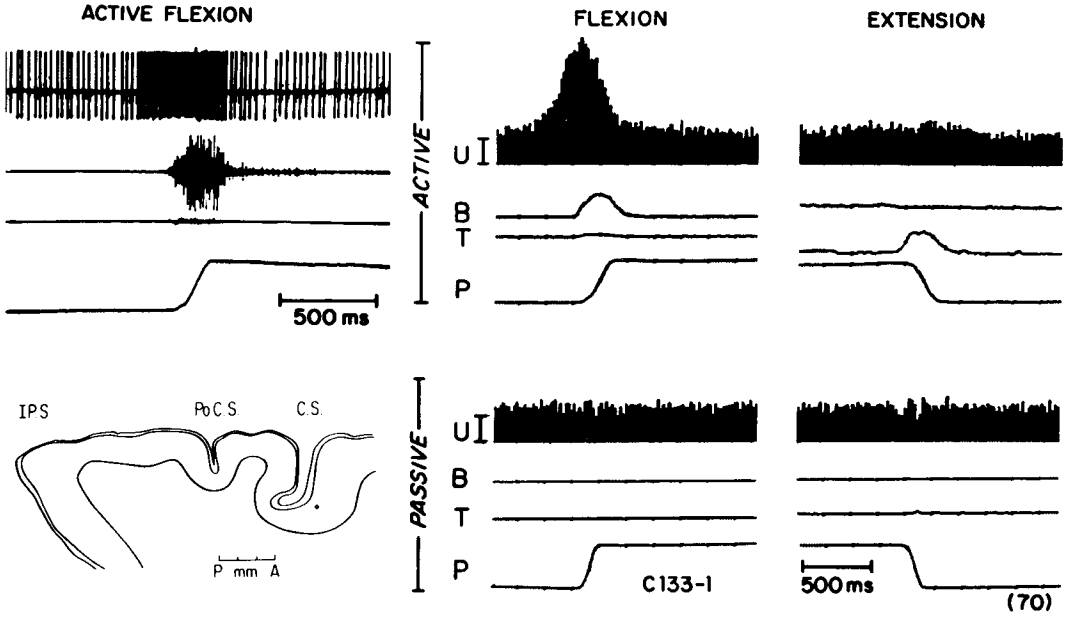

FIG. 8. Precentral area 4 neuron activated only before active flexion. The location of this cell in depths of the precentral bank is indicated at bottom left.

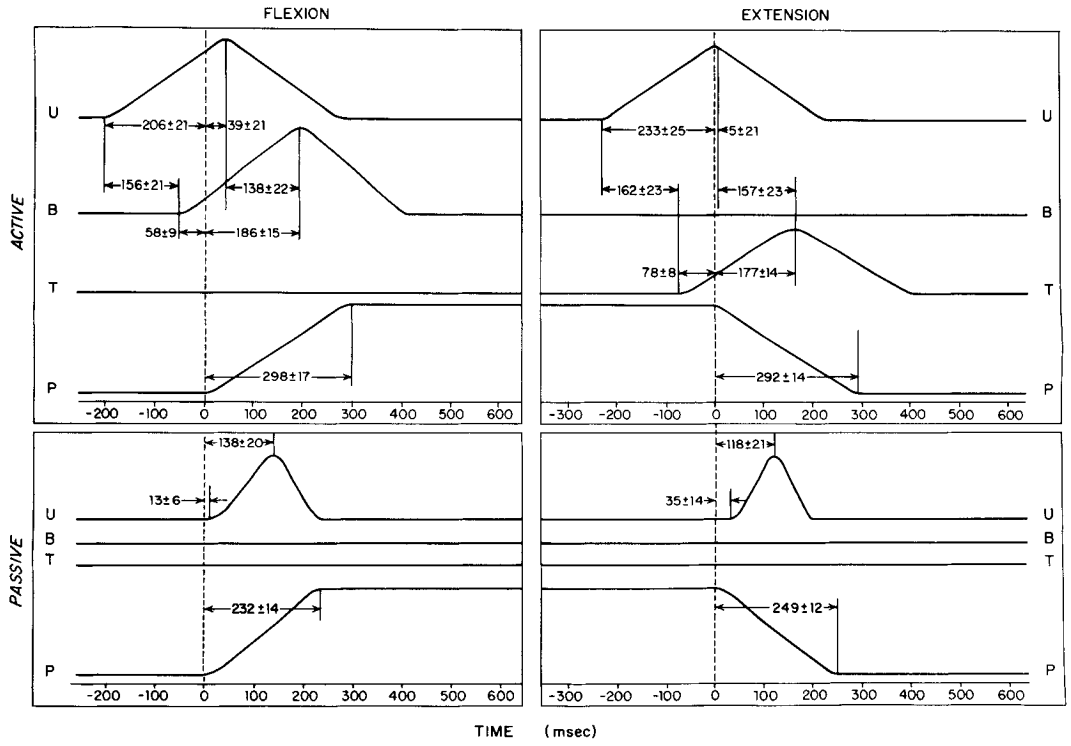

FIG. 9. Schematic summary of the average relative timing of precentral unit and arm muscle activity during active and passive elbow movements. Onset of movement is indicated by vertical dotted line through origin of abscissa. Numbers give mean ± SE of the relative times between indicated events, namely, onset and peaks of unit and agonist muscle activity and onset of movement. Values were computed from measurements of response averages of units in Table 2 (n = 38); since some cells were not activated during certain movements, means do not sum exactly. Although the relative timing of the indicated events is drawn to scale, the profile of activity is purely schematic.

20 ms (the resolution of the response averages); such coactivation was observed for the three elbow flexors—brachialis and biceps longus and brevis, and for the extensors—triceps medialis and longus. During elbow movements, activity of forearm, shoulder, and axial muscles was usually weaker or negligible; with few exceptions, these other muscles became active with or after the agonist elbow muscles. The relative onset times of other muscles during elbow movements are plotted in Fig. 10 of the accompanying paper (47).

Figure 9 schematically summarizes the mean relative timing of unit and muscle activity during elbow movements, as measured from response averages of the precentral cells in Table 2. For these self-paced active movements, changes in precentral unit activity began, on the average, well before agonist muscle activity (156 ms before biceps, 162 ms before triceps), and before onset of postcentral cells under comparable conditions (cf. Fig. 9, Ref. 47). The mean onset of area 6 cell responses (n = 15) preceded mean onset of area 4 cells (n = 56) by 9 ms, which was statistically insignificant. Peak unit activity preceded peak EMG activity by 138 ms for flexion and 157 ms for extension; by comparison, postcentral cells as a group showed peak discharge about 8 ms before peak agonist muscle activity (47).

DISCUSSION

Peripheral inputs to precentral cells

In unanesthetized monkeys, the effective natural stimulus for most precentral cortex cells was passive joint movement, usually of a single joint and often limited to rotation in one direction. Phasic joint movement was

typically more effective than maintained displacement. Such passive responses probably originate in muscle stretch receptors, although joint receptors could also contribute. In awake monkeys, the precise location and type of receptor was often more difficult to identify for precentral than postcentral cells, perhaps due to a greater degree of convergence of afferent inputs. In the precentral regions explored, relatively few cells responded to cutaneous stimulation; a larger proportion of neurons responsive to cutaneous input from the palm has been reported in the precentral bank in other studies (45, 48, 53). Our observations of the relative frequency of different types of sensory responses agree well with those reported by Lemon and Porter (34).

Regarding the degree of topographic organization of neurons in motor cortex, we have found Woolsey's (54) map (derived from movements evoked by stimulating precentral sites, and identical to the precentral sensory map of maximal evoked responses to peripheral stimulation) to be a useful predictor of where each body part is predominantly represented. However, on the cellular level, we found the distribution of cells in a given precentral region to be somatotopically arranged only in a statistical sense. In the precentral arm area, for example, we found more cells responsive to elbow movements than to any other single input; however, intermingled were numerous cells related to other regions and many cells apparently unrelated to any. Thus, somatotopic distribution on the cellular level was not sufficiently precise and detailed to use the responses encountered in one track to reliably predict the location of cells with input from adjacent somatic sites. Such an intermingling of cell types has also been reported by others (34, 40, 43, 48). In the most comprehensive mapping study to date, reconstructing the relative location of individual cells, Wong et al. found separate representations for distal and proximal limb regions, with substantial overlap at intervening borders (cf. Fig. 6 in Ref. 53).

In addition to neurons simply related to a specific peripheral locus, precentral cortex contains other cell types, some of which have also been encountered in other cortical regions. While the stimulus conditions activating some precentral neurons could be complex, the response properties of each cell could be repeatably demonstrated over many hours as long as the behavioral conditions were repeated. Some units responded much like cells in areas 2 and 5 to input from single and multiple joints (e.g., Fig. 3). A small proportion of precentral cells responded clearly and repeatedly to specific visual stimuli, such as objects appearing in view or moving toward the animal. Such visual stimulus conditions are strikingly similar to those activating posterior parietal cells, as described by Hyvarinen and Poranen (26). It seems likely that such precentral cells are interconnected with comparable neurons in other cortical areas. Recent anatomical studies have confirmed interconnections between precentral areas 4 and 6 with postcentral areas 2 and 5 (27, 28, 31). Many precentral cells were unresponsive to the stimuli tested and were not modulated during these movements; these may well be activated under other conditions. Thus, any notion that the precentral "motor" cortex consists only of neurons coactivated with individual muscles and responsive to sensory input from those muscles would be a serious oversimplification. Instead, diverse cell types appear to be intermixed, with only a relative predominance in any one cortical region.

In these studies, numerous electrode tracks were made perpendicular to the cortical surface, both laterally in arm area and medially in leg area. Some tracks, which were histologically confirmed to run parallel to the radial fibers, contained successive cells that responded to the same passive joint movements. For example, most cells in tracks 2 and 11 of monkey *L* responded to passive elbow flexion (Figs. 2–7). Such similarities in inputs to precentral cells in a vertical "column," also noted by others (34, 40, 45, 53), are probably the consequence of the radial orientation of afferent fibers.

The existence of relatively secure input from peripheral receptors to precentral cortex cells raises the question of its function. Such input is currently considered to provide feedback from peripheral receptors used in coordination of active movements (8, 13–15, 24, 32–34, 40, 42, 48). If this were its only function, the responses of these cells

to adequate stimulation under passive conditions would simply be an epiphenomenon—useful for characterizing their peripheral receptors but of no consequence to any sensory process. On the other hand, it seems entirely possible that the sensory responses of some precentral neurons could be used in the perception of passive movements (2, 22, 29, 30, 37, 41, 46). Since postcentral cortex cells appear to have greater capacity for coding cutaneous and static proprioceptive information than most precentral cells, they would probably contribute more to fine discrimination of those modalities. However, there is no evidence to indicate that the responses of precentral cortex cells to passive movements are inaccessible to perceptual mechanisms. On the contrary, electrical stimulation of the precentral gyrus of conscious man evokes sensations similar in quality and threshold to those evoked by postcentral stimuli; one-third of the cortical points from which Penfield and Boldrey (41) evoked somatic sensations in hand, arm, or shoulder were located precentrally. Ablation of precentral cortex in man and monkey commonly results in transient sensory deficits (6, 22, 30). Conversely, after removal of postcentral cortex, the ability to detect passive movement remains (2, 22, 30, 46), as do the peripherally evoked responses of precentral cells (29, 37). The recovery of greater proprioceptive capacities after postcentral ablation may well involve increased utilization of remaining sensory responses of cells in other cortical areas.

The argument that precentral cells could not contribute to sensation because they are located in motor cortex seems less than compelling in view of the fact that their function would depend more on their connections and interaction with other regions than on the location of their cell bodies in a predefined place. If precentral cortex participates in proprioception as well as motor functions, the relevant neurons may be separate subsets, each projecting to appropriate targets. Anatomical evidence that precentral cells projecting to postcentral and subcortical sites tend to aggregate in separate clusters, interspersed with cells projecting elsewhere (10, 27, 28, 31), suggests the possibility of interleaved sets of neurons subserving different functions. Alternatively, the same cells could be utilized in different combinations under different behavioral conditions (39). Thus, cells whose responses to passive stimulation contribute to proprioception may also be enlisted by central mechanisms generating active movements, but in such combinations as to direct their resultant output toward execution of the appropriate motor response. In either case, it seems possible that during passive movements the sensory responses of some precentral cortex cells could contribute to the perception of passive movements.

Relation between active and passive responses

During active movements, precentral cells integrate input from peripheral receptors and from central sources; the relation between these inputs is revealed by comparing each cell's passive response to natural stimulation with its response pattern during active movements. In agreement with observations of others (8, 15, 21, 33, 53), we found that most precentral cells driven by passive movement of a joint also fire during active movement of that joint; the effective directions may be the same or opposite or may involve movements in both directions.

Some precentral cortex cells were activated during passive and active elbow movements in the same direction (e.g., Figs. 4, 5, and 7). Peripheral receptors that could contribute under both conditions would be joint receptors and unloaded spindle receptors (cf. Refs. 38, 44). Postcentral cortex cells with confirmed input from elbow joint capsule or deep muscle receptors also fired during active and passive movements in the same direction (47). Since most of the precentral cells increased their activity well before the agonist muscles during active movements (Table 2), central input must drive these cells before onset of active movements. If such precentral cells contribute to agonist muscle activation during active movements, their peripheral input could provide a positive feedback, assisting the active movement.

Other precentral cells responded during active and passive movements in opposite directions (Figs. 6 and 8). Peripheral receptors activated under both conditions could

include Golgi tendon organs (38); with sufficient fusimotor coactivation, spindle afferents could also discharge during active contraction and passive stretch of their muscle (50). If these precentral cells contribute to activating the agonist muscles during active movement and respond to stretch of that muscle during passive movement, they could function as a component of a cortical stretch reflex (42).

We found as many precentral cells responding to active and passive movements in the same direction as in the opposite direction, both among PT and non-PT neurons (Table 2). Similarly, Lemon et al. (33) compared active movements in which precentral cells seemed to be related with their effective passive movement; they found more neurons driven by passive joint movements in the same direction (45 of 60) than in the opposite direction (13 of 60). Depending on the destination and postsynaptic effects of the cells' terminals, these active-passive relations are compatible with any relation between sensory input and final motor output. A more consistent relation between active and passive movements exists for those precentral cells whose output effects on muscles may be demonstrated by spike-triggered averaging (19); most of these cells, whose action potentials produce postspike facilitation of forelimb muscles, responded to passive joint movements, which stretched their target muscles (7, 19). Thus, specific subsets of cortical neurons with a common output projection do appear to have relatively consistent relations between sensory input and motor output.

Under different experimental conditions, the peripheral "input" to precentral cells has been assessed by their response to perturbations of the limb applied during performance of an active movement (8, 9, 15, 16, 52). Increasing the load during an active elbow movement in which the cell fired, Conrad et al. (8, 9) found that the most common response was an increased firing shortly after the torque pulse. Of 88 cells studied, 37 exhibited this pattern, which was in the direction "expected" if the cell was to function as part of the postulated "cortical load compensation reflex"; 17 cells responded in the reverse, "unexpected" direction; and 27 responded to perturbations in either direction. Evarts and Fromm (15) confirmed these response types and reported further that the perturbations evoked more intense responses during finely controlled movements than during ballistic movements. Wolpaw (52) has recently shown further that for some cells the intensity of the torque pulse response increased with the amount of background activity. Both studies reported that those precentral cells that were reciprocally related to opposite active movements typically responded more intensely to perturbations that opposed contraction of their coactivated agonist muscles (15, 52). Evarts and Tanji (16) perturbed a handle, which the monkey was prepared to either push or pull, and found that the response to the perturbation depended on the monkey's "set" to respond. Such altered responsiveness of precentral cells to limb perturbations applied during or before active movements are presumably related to changes in receptor sensitivity or altered transmission along afferent pathways. Although these activities may affect the magnitude of the response of perturbation, they do not appear to change its polarity (15, 52).

While many precentral cells respond to joint movement in only one direction, we also found a significant proportion responding to active and passive joint movements in both directions (Fig. 7). These may be similar to some precentral cells that were activated by both flexion and extension torque pulses (8, 9, 15, 52). Such cells might be assumed to be related in a simple synergistic way to some hypothetical limb muscle with identical response pattern. For example, certain distal or axial muscles could be coactivated with both flexion and extension of the elbow. However, such muscles are not likely to be stretched during passive movements in both directions. Indeed, many cells responsive to passive elbow movements in both directions did not respond to passive rotation of any other joints (Table 2). It seems likely that a "higher order" type of motor cortex cells exists, which is related to movements of a joint in either direction (20). Such cells are coactivated with both flexors and extensors of the joint and are driven by passive movements that stretch either set of muscles. Their activity may be related more to the

movement of a joint than to direction of movement.

Concluding comments

Having grouped the responses of precentral cells into a few simple categories, we must emphasize that this procedure seriously oversimplifies the diversity of response patterns actually observed. As indicated in Table 2 and the figures, even for a simple elbow movement, the response pattern of each cell is virtually unique. To what extent such individual differences may be neglected in favor of emphasizing those features consistent with simple conceptual schemes is open to question. The existence of a sufficient variety of cell types would provide an opportunity to document examples to support any particular functional hypothesis. Indeed, when Thach (49) statistically related motor cortex cell discharge to three different possible functions, he observed that "all the types of neuron that were looked for were found, in nearly equal numbers." Whether examples of specific types can be interpreted as representative depends on their relative predominance and the extent to which the numerous exceptions may be attributed to other factors, such as anatomical complexities. Certainly, the arrangement of primate forelimb muscles is so complex as to preclude any definitive functional interpretations of cortical cell activity. Moreover, the correlation between a given motor cortex cell and set of arm muscles may vary drastically, depending on behavioral conditions (20). Even those PTNs with sufficiently secure synaptic linkages to forelimb motoneurons to produce post-spike facilitation of EMG activity (19) often exhibit response patterns during ramp-and-hold wrist movements that differ substantially from the activity of their target muscles (7, 18). Similarly, on the sensory side, afferent fibers from peripheral receptors exhibit discharge patterns during active movements that are often quite unexpected on the basis of receptor type and location (35).

The fact that the nervous system is able to perceive stimuli and perform movements reliably utilizing such diverse and variable neural responses suggests that the ultimate explanation is unlikely to depend critically on the response patterns of any particular type of cell. The search for neural correlates of behavioral functions often assumes that such functions are recognizably coded in neural response patterns. Since behavior is the consequence of interaction between widely distributed neurons (25, 39), their individual response patterns need not resemble particular behavioral parameters any more than the spatial patterns on a holographic plate resemble the image produced by its proper illumination.

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