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Responses of Identified Cells in Postcentral Cortex of Awake Monkeys During Comparable Active and Passive Joint Movements

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SUMMARY AND CONCLUSIONS

1. In awake rhesus macaques trained to allow passive somatic stimulation without active resistance, we documented the adequate natural stimuli of single neurons in postcentral cortex. Thirty-six percent of the neurons sampled in areas 1, 2, and 5 responded to cutaneous stimulation, and 43% responded to manipulation of "deep" tissue and/or joint rotation; 10% were activated by other, more complex stimuli; and 11% were unaffected by any of the stimuli tested. The deep cells either responded to stimulation of single joints (shoulder, 33%; elbow, 20%; wrist, 6%), or of multiple joints (14%), or they responded to palpation of muscles and rotation of associated joints (27%).

2. The cortical distribution of postcentral cells tended to be statistically compatible with previous accounts (38, 45) insofar as posterior regions (areas 5 and 2) tended to have a higher proportion of deep cells than anterior regions (areas 1 and 3b); also, distal receptive fields tended to be more common in lateral regions. Different types of cells were sufficiently intermixed that the responses encountered at a given site were far from predictable. Nevertheless, cells in the same vertical penetration tended to respond to either cutaneous or deep stimulation.

3. Activity of postcentral cortex cells, identified by adequate stimulus and cytoarchitectonic locus, was documented during comparable active and passive elbow movements with the forearm held in a cast. Response averages of ramp-and-hold movements revealed both the phasic activity associated with elbow movement and tonic activity during the static hold. "Elbow joint" cells, whose adequate stimulus was passive rotation of the elbow only, as well as direct manipulation of the elbow joint, tended to discharge phasically and tonically during active and passive elbow movements in the same direction; however, active movements often produced additional response components. Similarly, "elbow muscle" cells, driven by muscle palpation and elbow rotation, also fired during active and passive elbow movements in the same direction. The phasic response of many of these deep elbow-related cells was less intense during active movements than during comparable passive movements. "Polyjoint" cells, which received input from other joints in addition to elbow, tended to discharge during controlled elbow movements in a manner consistent with their natural response to elbow rotation, but some exhibited additional response components during active movements. "Shoulder" cells, which responded to passive rotation of the shoulder joint, also fired during controlled active and passive elbow movements, tending to discharge most intensely during active flexion. "Cutaneous" cells, with receptive fields on hand, forearm, or upper arm, tended to respond ubiquitously to active and passive flexion and extension; in contrast to deep cells, their phasic responses were less directionally selective and they less frequently exhibited tonic discharge with maintained elbow position.

4. With active elbow movements, the

firing rate of many postcentral cortex cells changed well before activation of contralateral arm muscles. Relative to onset of agonist elbow muscles, activity of postcentral neurons changed on the average 61.4 ms earlier; and a third of the changes preceded agonist muscle onset by 100 ms or more. Mean onset times did not differ appreciably for deep and cutaneous cells, nor for cells in areas 1 and 2. Such early changes in neural activity during these self-paced elbow movements suggest a centrally originating input to these postcentral neurons. Responses of certain elbow joint and muscle cells appeared to be reduced before active elbow movement, indicating central inhibition. Other deep cells showed evidence of central excitation well before agonist muscle activity. Cutaneous cells exhibited relatively little evidence of central or peripheral inhibition of phasic responses during active movements. Depending on their projections, postcentral neurons that become active before agonist muscles may participate in generation of active movements.

INTRODUCTION

Cells in postcentral "sensorimotor" cortex may play significant roles both in perception of proprioceptive and tactile stimuli and in the neural mechanisms underlying generation of active movements. The sensory responses of postcentral cells have been most thoroughly documented in paralyzed or anesthetized animals (5, 11, 12, 34, 36, 38, 39, 42, 45, 48, 60). Mountcastle and Powell (38, 39) divided postcentral neurons into two major classes, cutaneous and deep, on the basis of their responses to natural stimulation. Of particular relevance to our study were the cells responsive to passive joint rotation, which have been suggested to subserve kinesthesis—i.e., motion and position sense (38). Such cortical cells responded phasically to passive joint movement, and 80% also fired tonically to maintained angles. For postcentral cortex cells the effective joint angles (60–90°) were generally wider than those of peripheral afferent fibers from joint capsules (10–30°) (51, 52) and more often extended into intermediate angles, i.e., beyond the extremes of the angular range that activate most joint capsule afferents (6, 22, 23, 51, 52). Direct dissection revealed that relevant receptors for postcentral "joint cells" were located in tendon grooves, joint capsules, and pericapsular tissue (36, 38, 39).

Current controversies concerning the relative contributions of muscle and joint receptors to kinesthesis remain similar to those of the last century (1, 49; for recent review, cf. Ref. 33). Investigators using a variety of techniques (4, 19, 30, 46, 57) all agree that denervating or anesthetizing capsular and pericapsular tissues leads to the loss of position sense. However, sensations of motion survive articular insensibility (19, 57). Since vibrating isolated tendons apparently produces no movement sensations (32), the origin of these sensations may well be extramuscular as well as extraarticular.

That muscles may affect joint capsule receptors is now well established (22, 35). Additional psychophysical evidence that kinesthetic sensitivity is more acute for active movements than for passive movements (40) suggests that voluntary movements may enhance proprioceptive perception. To further assess the potential role of different types of postcentral neurons in proprioception, we have documented the activity of cells with identified natural responses during comparable active and passive movements of the elbow.

In addition to their input from peripheral receptors, as determined under passive conditions, parietal cortex cells may well be influenced by central circuits during the generation of active movements. Precentral and postcentral gyri are heavily interconnected (27–29, 41, 59) and posterior parietal cells in areas 5 and 7 discharge before active limb movements (31, 37). Evarts (14, 15) reported very few postcentral cells to be activated before rapid forelimb movements, and concluded that most were probably activated by peripheral input. Parietal field potentials preceding active movements, however, suggest effects on postcentral cells prior to self-paced voluntary movements (7, 10). Since stimulating postcentral cortex in the absence of precentral cortex can evoke movements (20, 62) and since some postcentral cells project to spinal levels (9), their activity may contribute to

the generation and control of motor output. To evaluate this possibility we carefully analyzed the timing of postcentral cell responses prior to initiation of active movements. We found that many neurons in areas 2 and 1 changed their activity well before onset of agonist muscle activity, suggesting that central as well as peripheral inputs may affect these cells during active movements (53, 54).

METHODS

Six rhesus macaques (*Macaca mulatta*) were operantly trained to alternately flex and extend the left elbow joint with the forearm held in a cast. A correct response consisted of a phasic movement followed by maintained position for at least 1 s. If the position was not sustained for at least 1 s or if the direction of movement was not opposite that of the preceding response, reinforcement (0.13 ml applesauce) was withheld and that response was excluded from data analysis. To maintain successful performance, the monkeys were kept at 85–95% of ad libitum body weight, which constituted mild food deprivation. The form-fitting cast holding the monkey's forearm was hinged at the elbow joint through a potentiometer monitoring position. A resistance to motion was provided by a dashpot linked to the cast. Stops limited the extent of movement between elbow angles of approximately 45° (flexion) and 100° (extension).

The monkeys were also trained to relax during passive movements of the manipulandum and to permit stimulation of skin and rotation of joints without active resistance.

Recording procedures were identical to those previously described (17), except that the 10-mm-diameter circular recording chamber was centered over postcentral cortex (2 mm posterior to bregma and 18 mm lateral).

In three monkeys, bipolar stimulating electrodes were stereotaxically implanted in the brain stem pyramidal tract (PT) or the medial lemniscus. PT electrode placement was guided during surgery by evoking contraction of hand and foot muscles. Under halothane anesthesia, thresholds were on the order of 1 mA and ranged from 0.3 to 3 mA for detectable muscle twitches. Electromyographic (EMG) activity of biceps and triceps was routinely recorded with either *1*) permanently implanted stranded stainless steel wires, *2*) temporarily implanted transcutaneous electrodes, or *3*) electrodes fastened to the skin over the biceps and triceps muscles. These three procedures were confirmed to produce equivalent EMG recordings (53).

During recording experiments, the monkeys were placed in a sound-attenuating, electrically shielded chamber. As the animals performed their arm movements, cortical neurons were isolated with tungsten microelectrodes advanced with a Trent-Wells remote-controlled microdrive. Amplified signals were displayed on oscilloscopes and monitored with a Grass AM5 audio monitor. Data recorded on a Honeywell 5600 FM tape recorder included activity of the cortical unit, biceps and triceps, pulses triggered by the unit action potentials, elbow position, and delayed trigger pulses occurring 1 s after the onset of each successful trial.

Response averages were compiled with a Nuclear-Chicago model 7100 data retrieval computer by playing the recorded data backward and triggering the averager with the delayed pulses. Since the delayed pulses always occurred 1 s after the onset of each successful response, the resulting 2-s averages had the beginning of every movement in register at the center of the display. Aligning averages on movement onset was important to establish the relative timing of neural events preceding the movement. Time histograms of the unit pulses yielded the neurons' average firing rates; arm position and rectified EMG activity were also averaged for each neuron. Response averages were compiled with identical gains for four conditions: active flexion, active extension, passive flexion, and passive extension. To produce comparable passive elbow movements, the experimenter moved the monkey's arm in the cast. Such passive movements were recorded only during periods of EMG silence.

Before recording unit data, we tested the neuron's responses to peripheral stimulation by manipulating skin, muscles, and joints of the arm to determine the natural receptive field of the unit as specifically as possible. In general, cutaneous and deep modalities could be readily distinguished, and cutaneous receptive fields could be unambiguously defined. Whether deep cells responded to joint or deep tissue manipulation was sometimes difficult to determine. Cells were classified as elbow joint cells if they responded to elbow rotation and to direct manipulation of the elbow joint, but not to muscle palpation. In contrast, neurons responding to muscle manipulation and joint rotation but not to joint capsule deformation were categorized as "deep muscle" units. Such a distinction between joint and deep tissue manipulation was more difficult to make for units responding to manipulation of the shoulder. The categories and techniques used in this study are similar to those previously described by others (38, 39).

At the end of the recording experiments, the animals were perfused with physiologic saline followed by 10% Formalin. Ink marks cor-

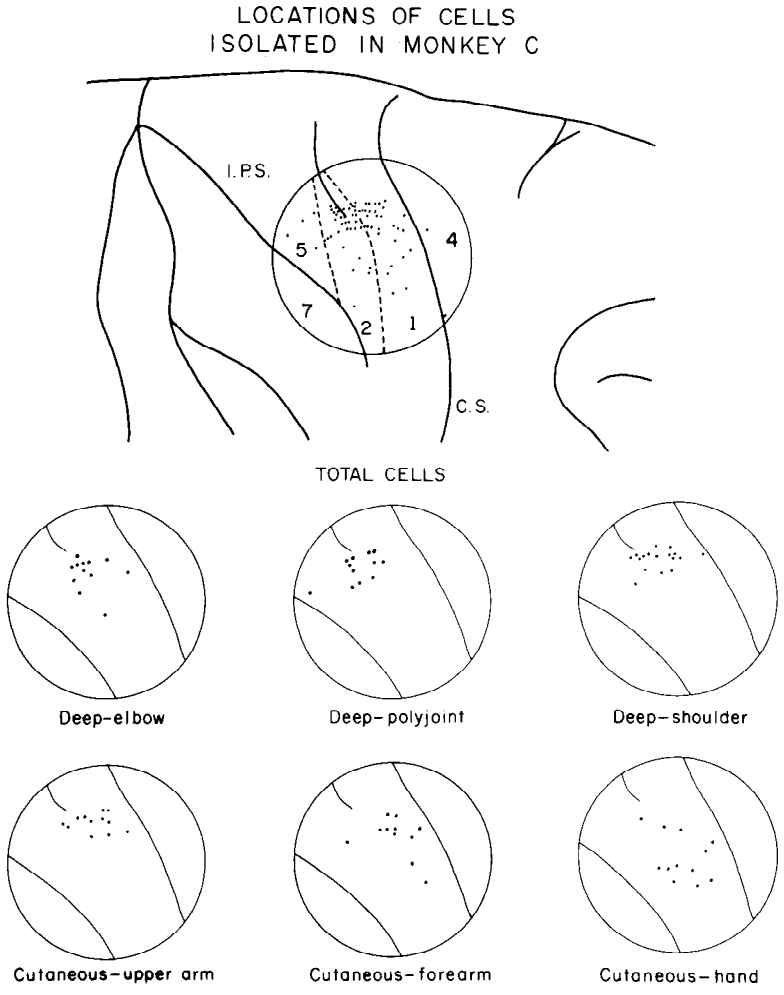

FIG. 1. Relative cortical location of cells recorded in monkey *C*. Each dot represents an electrode penetration in which identified units were isolated. Numbers refer to cytoarchitectonic areas of Brodmann (3). Locations of cells of specific modality and receptive-field location are plotted separately below. IPS, intraparietal sulcus; CS, central sulcus.

responding to extreme coordinates of the microdrive map were placed in the cortex. The fixed brain was then removed from the skull and photographed. Sagittal frozen sections were cut at 40 μm and stained with cresyl violet. Recording sites were located on the stained sections with reference to the polar coordinate system of the recording mount. In addition, microlesions (10 μA for 10 s) were sometimes produced through the microelectrode at particular sites, and their location subsequently reconstructed. Cytoarchitectonic areas were identified by the criteria of Brodmann (3) and Powell and Mountcastle (44).

RESULTS

Of 320 postcentral cortex cells tested for responses to adequate natural stimulation, 36% had cutaneous fields on either the forearm (22%) or upper arm (14%), and 43% responded to deep stimuli applied to the contralateral arm. The latter group was divisible into cells responsive to rotation of wrist (3% of total), elbow (8%) or shoulder (14%) joints, to movement of several joints (6%), or to muscle palpation (12%). Ten percent of the 320 cells responded to other, more complex stimuli, and 11% could not be activated by any form of stimulation tested. Figure 1 illustrates the relative cortical locations of cells in these categories for one monkey and indicates the cytoarchitectonic fields in the region explored. Neurons with distal cutaneous receptive fields tended to

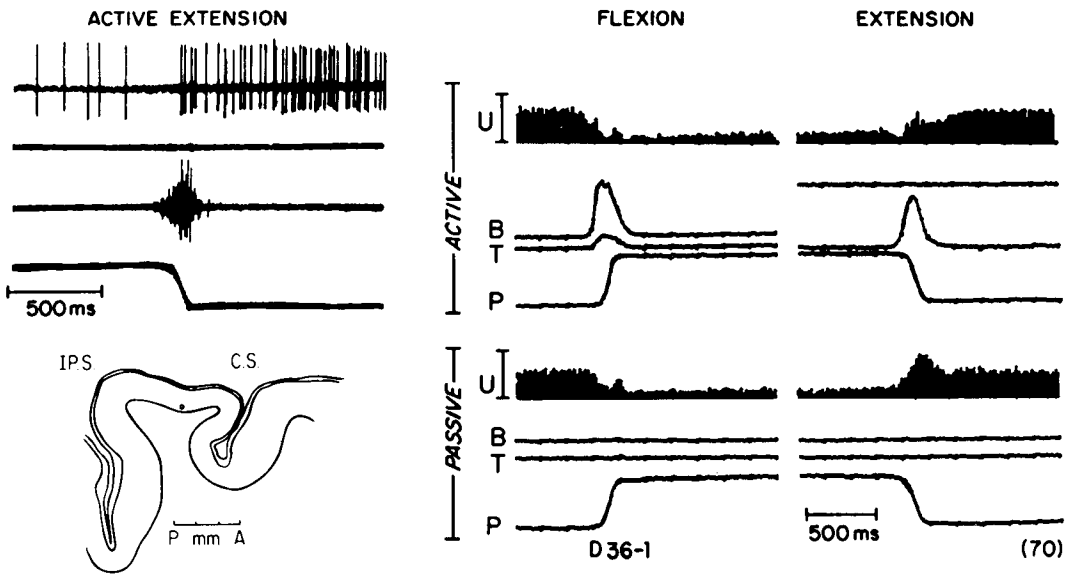

FIG. 2. Responses of elbow joint unit *D36-1* during active and passive elbow movement. Top left illustrates single active extension response showing, from top to bottom, activity of unit, biceps and triceps, and elbow position. Bottom left illustrates reconstructed location of cell in deep layer of area 2. CS, central sulcus; IPS, intraparietal sulcus. Averages at right show time histogram of unit activity (U), average rectified EMG of biceps (B) and triceps (T), and elbow position (P), at same gains for 70 responses each. Vertical calibration represents firing rate of 50/s in this and subsequent figures. This unit exhibited distinct differences in tonic discharge, but the only phasic excitation large enough to be entered in Table 1 was the response to passive extension.

be located more laterally in this region than those with proximal fields. The proportion of deep cells to cutaneous tended to be statistically greater in more posterior areas. However, the different cell types were quite thoroughly intermingled over the area studied.

In view of previous reports that postcentral cells are segregated into columns according to modality (38, 45), we reviewed all electrode tracks containing two or more responsive cells; 70% of these tracks contained only cutaneous or only deep cells. Moreover, successive cells in a track had similar receptive-field locations. Of those penetrations that contained both cutaneous and deep cells (and three or more cells), all but one exhibited pure separation of modalities; i.e., the first cells responded to one modality, and all the subsequent cells to the other. Most tracks were approximately perpendicular to the cortical surface; nevertheless, the above observations pertain to all penetrations, unselected for orientation.

Elbow joint cells

We identified 27 postcentral units as elbow joint cells. Besides responding to flexion (n = 14) or extension (n = 11) of the elbow, or both (n = 2), these cells were also activated by direct manipulation of the elbow joint, but they were not activated by palpation of any muscles or by cutaneous stimulation. (However, three elbow joint cells could also be inhibited by cutaneous stimulation.) Of these 27 units, 14 responded only phasically during elbow movements while 13 also exhibited tonic discharge related to maintained joint angle.

Response averages of active and/or passive elbow movements with the forearm held in the cast were obtained for 16 elbow joint cells. Figure 2 illustrates the response pattern of an elbow joint cell that responded with a burst when the elbow was passively extended and also exhibited a higher tonic rate during maintained extension; such phasic and tonic responses were observed both when the arm was manipulated outside the cast and during passive movements with the arm in the cast. During active elbow movements this neuron also fired at higher tonic rates when the elbow was in the extended position; however, in contrast to the passive case it exhibited relatively little phasic response during active extension movements. This

cell was recorded in a deep layer of area 2. Similarly, the elbow joint cell in Fig. 3, recorded more superficially in cortex of another monkey, also responded phasically and tonically to passive elbow extension. When the monkey made comparable active extension movements, both the phasic and tonic responses were smaller. In fact, the firing rate of this neuron began to decline before the onset of triceps activity associated with active extension movements.

The response patterns of these 16 elbow joint cells (summarized in Table 1) are largely consistent with those predictable on the basis of their responses to natural stimulation of the elbow. Of the 10 cells that exhibited different tonic discharge for flexed and extended positions in the cast, 7 exhibited the higher rate with the elbow displaced in the direction of the effective passive movement; the 3 exceptions all occurred during active movements. Five elbow joint cells did not show discharge related to passive displacements within the angular range of the cast, although two of these fired tonically for greater elbow angles outside the cast. The neurons' phasic responses during passive movements in the cast were also consistent with natural stimulation for 7 of the 10 cells; the 3 exceptions were neurons that responded during passive movements of the cast in both directions. Surprisingly, when the monkey actively moved the elbow, only 7 of 16 elbow joint cells exhibited consistently greater phasic responses in the same direction as the effective passive movement. Again, most of the exceptions were cells that responded the same way for phasic movements in both directions. Thus, during the controlled movements of the arm in the cast, the responses of most elbow joint cells included those predictable on the basis of natural stimulation, but sometimes included additional responses as well.

Muscle cells

We classified 37 units as muscle cells because they responded to manipulation of specific arm muscles but not to squeezing or pressing the joints. Of these, 24 cells also responded to passive joint rotation that either stretched the relevant muscle ($n = 21$) or shortened it ($n = 3$). Of these 24 units, 7 exhibited tonic discharge related to joint angle; the rest responded only phasically

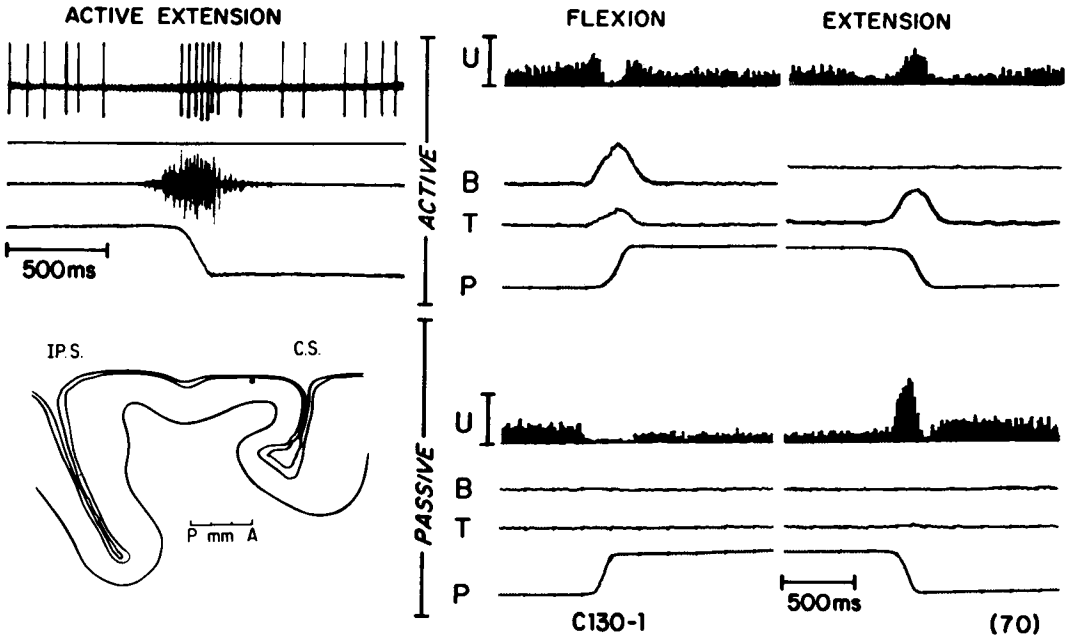

FIG. 3. Responses of elbow joint unit *C130-1* during active and passive elbow movements. This cell responded to direct palpation of elbow joint but not to palpation of arm muscles. In contrast to its passive response pattern, during active extension its phasic response was reduced and preceded by a drop in activity. Under active conditions, differences in its tonic discharge with flexed and extended positions were negligible.

TABLE 1. *Responses of postcentral cortex cells during active and passive elbow movements*

Cell	Area	Natural Response	Phasic				Tonic				Latency	
			Active		Passive		Active		Passive			
			F	E	F	E	F	E	F	E	AF	AE
Elbow joint cells												
C42-3	2	ΔfE	+	0	−	−	+	−	0	0	80	N
C39-1	2	fE, ΔfE	++	−/+/−			0	0			−40	0
C110-1	2/5	fE, ΔfE	++	+/−	+	0	+	−	0	0	0	−40
D25-1	1/2	fE, ΔfE	+	0	+	0	+	−	+	−	220	N
H24-1	1	fE, ΔfE	−	−			0	0			−100	0
C13-1	2	eE, ΔeE	−	++			−	+				
C50-5	1	eE, ΔeE	−	−	−	0	+	−	0	0	−20	40
C95-1	2	eE, ΔeE	++	+/+	−/+	+	0	0	−	+	−180	−200
C130-1	1	eE, ΔeE	+/−/+	−/+/−	−−	++	0	0	−	+	60	−120
D36-1	2	eE, ΔeE	−	0	−	+	−−	++	−−	++	0	N
C44-1	2	eE, ΔeE	+	+/−/+			−−	++			−280	−120
C32-2	2	ΔeE	+/+	+/+	+/+	+/+	0	0	0	0		
C42-2	2	ΔeE	−/+/−	−−/+	+/+	+/+	0	0	0	0	100	−120
D46-1	1/2	ΔeE	−	+	−	+	+	−	0	0	−160	−20
D26-1	2	ΔfE, ΔeE	+/+/+	+			0	0			−180	−140
C29-3	2	ΔfE, ΔeE	+	+			+	−				
Muscle cells and joint-muscle cells												
C102-1	2	TRIC, fE	+++/+	++	+	0	−	+	++	−−	−280	−280
D33-2	2	TRIC, fE	+	0	+	−	+	−	+	−	60	N
D40-2	1	BIC, ΔeE	+	+/+	+	++	−	+	−	+	0	−340
G8-1	1	BIC, ΔeE	+++	++	−	+/−	0	0	0	0	−80	20
*D25-2**	1/2	TRIC, eE	+/−	++	−	++	−−	++	−−	++	80	−40
*D26-2**	2	TRIC, eE	−	+	−	++	−−	++	−−	++	280	100
C129-1	1	Deltoid, ΔadS	++	−	−	+	0	0	0	0	120	140
Polyjoint cells												
C29-4	2	ΔfE, ΔfW ΔfS, ΔfiE	+	0			0	0				
C73-1	2/5	ΔadS, ΔeE ΔeS	++	0	0	+	0	0	0	0	−80	N
C76-1	5	ΔfS, ΔeiS Visual	−/++	0	0	+	0	0	0	0	−40	N
C105-1	2	abS, eE, eW ΔeE, ΔfiS	+/−/+	++	−	++	−	+	−	+	−160	80
D50-1	1	ΔfS, ΔfE ΔfW	+/++	+	+/+	++	0	0	0	0	40	0
G32-1	2	ΔeE, ΔadS ΔfW	+	++	+	++	−	+	−	+	−140	−20
Shoulder cells												
C48-4	1	ΔadS, ΔfS	+	−	−/+	+	+	−	0	0	−20	−100
C55-2	2	Pressure	++	+/−	+	+	0	0	0	0	−180	−320
C66-5	2	ΔadS	−/+++	−/+	−/+	+	−	+	0	0	0	−100
C82-1	1	ΔadS	+++	−/+	0	+/−	+	−	0	0	−180	−160
C97-1	2	lat rotS	+/+	−/−	+	0	+		+	−	−80	20
C97-2	2	lat rotS	++/+	++/+	+	+	0	0	0	0	20	0
D50-2	1	fS	−/+	+/+	+	++	0	0	0	0	−60	0
D51-2	1	ΔfS	++	++	+	+	0	0			−40	−200
G10-3	1	ΔfS	+++	++/++			0	0			−100	−160
H2-1	1	adS	+/+/+	0			0	0			80	N
Wrist cells												
C40-1	2	eW	0	+++	0	+	+	−	0	0	N	−20
D60-1	2	fW, eW	++	+/+	+	+	−	+	+	−	−180	−140

TABLE 1—*Continued*

Cell	Area	Natural Response	Phasic				Tonic				Latency	
			Active		Passive		Active		Passive			
			F	E	F	E	F	E	F	E	AF	AE
Cutaneous cells												
C146-1	1	Hand	++	0			−	+			40	N
D7-5	1	Hand	+++	++			0	0			−200	−120
G3-1	2	Hand	0	+	+	+	0	0	0	0	N	−200
C118-1	1	Forearm	0	++			0	0			N	120
C131-1	1	Forearm	+	+++	+/+	+/+	−	+	0	0	20	−200
C131-3	1	Forearm	−/+	+	+	−/+	+	−	0	0	−20	−40
C143-1	1	Forearm	−/+/−	−−	−	−	−	+	0	0	−180	20
D22-1	1	Forearm	+	+++	+	0	0	0	−	+	200	−180
D7-1	1	Forearm	+++	+++			0	0			−160	−180
D7-5	1	Forearm	+++	++			0	0			−200	−120
D14-1	1	Forearm	++	+			0	0			−40	−120
D17-2	1	Forearm	++	+/+	+/+	+	0	0	0	0	−80	−120
D42-3	1	Forearm	+/+	+	+	+	−	+	−	+	−100	−120
D43-2	1	Forearm	++	++/+	+	+	0	0	0	0	−140	−200
D45-1	1	Forearm	+	0	0	+	−	+	0	0	100	N
G3-2	2	Forearm	+	+/+	+	+	0	0	0	0	180	−40
G25-1	1	Forearm	+	++	0	0	0	0	0	0	−80	−120
G49-2	1	Forearm	+++	0	0	+	+	−	0	0	−60	N
C51-1	1	Upper arm	++	−/+			+	−			0	0
C130-2	1	Upper arm	++/−	++/−−	++	+	−	+	++	−−	20	−80
D19-7	1	Upper arm	++	+++	+	+	0	0	+	−	−160	−200
D9-1	1	Upper arm	+/+	+	+	+	−	+	+	−	−60	260
D17-1	1	Upper arm	+/+	++	+	0	0	0	+	−	−100	−120
D40-1	1	Upper arm	0	+/+	+	+	−	+	−	+	N	−80
G10-1	1	Upper arm	+/−	+/−	0	−	0	0	0	0	−20	0
D49-1	1	Shoulder	+/+	+/+	+	+	0	0	0	0	−140	−180
D51-1	1	Shoulder	0	+	0	++/+	0	0	0	0	N	0

Neurons are grouped on the basis of their adequate natural stimulus. The cell column identifies neurons by monkey and track. The Brodmann (3) cytoarchitectonic area in which the cell was recorded is given in the second column; double numbers indicate location in transition zone between areas. Natural response indicates adequate stimulus or the location of cutaneous receptive field. f, greater tonic discharge in flexed position; Δf, phasic discharge during flexion movement. e, Δe, same for extension. ad, adduction; rot, rotation; i, ipsilateral; E, elbow; S, shoulder; W, wrist. Response patterns during active and passive flexion (F) and extension (E) are given separately for phasic responses during elbow movement and tonic responses during maintained position. + indicates excitation above base-line levels, − indicates suppression, and 0 indicates no appreciable change. +/+ indicates two distinct peaks of activity. Latency of onset of change in unit activity relative to onset of agonist muscle activity is given in milliseconds for active flexion (AF) and extension (AE); negative numbers indicate unit onset precedes muscle onset; N, no response. * Joint-muscle cells.

during movement of the joint. The effective muscles for the 37 cells included intrinsic hand muscles (n = 1), forearm muscles (n = 7), biceps (n = 5), triceps (n = 12), shoulder muscles (n = 9), and axial muscles (n = 3). Typical of the muscle cells for which response averages were compiled is unit *C102-1* (Fig. 4). This neuron was activated phasically by taps anywhere on the triceps muscle belly and tonically by pressure at the medial margin between triceps and humerus. In addition, it was driven both phasically and tonically by passive flexion of the elbow joint, both out of the cast and during controlled movements. When the monkey made active movements, this area 2 cell began to fire well before both flexion and extension, becoming active about 280 ms before biceps and triceps.

The response patterns of five muscle cells are summarized in Table 1. Of the first four, related to biceps or triceps, three had higher tonic rates for the passive elbow position that stretched the effective muscle. Excitatory phasic responses of all cells were stronger for the passive phasic move-

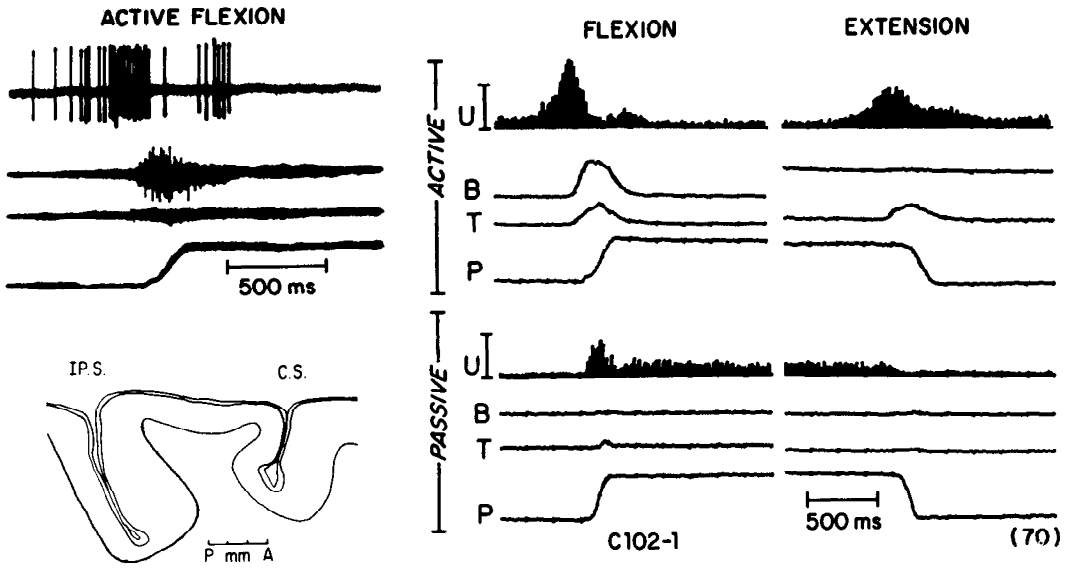

FIG. 4. Responses of muscle unit *C102-1* during elbow movements. This area 2 cell responded to taps on triceps muscle and passive flexion of the elbow. During active movements it began firing well before agonist muscle activity for both flexion and extension; such early discharge appeared consistently in all single trials.

ment that stretched its effective muscle. During active movements, three of the muscle cells also exhibited greater phasic responses for those movements in which that muscle was stretched.

Joint-muscle cells

Two neurons were classified as joint-muscle cells because they were so extremely sensitive to both elbow joint and palpation of triceps muscle that they could not be called exclusively joint or muscle cells. During natural stimulation, unit *D25-2* responded phasically and tonically to elbow extension as well as manipulation of the elbow joint and triceps muscle. During movements in the cast this unit exhibited clear phasic and tonic response during elbow extension, whether active or passive (Fig. 5). A neighboring cell, unit *D26-2*, exhibited similar responses to natural stimulation. However, when the monkey actively extended the elbow, its phasic response was clearly less than that during comparable passive extension (Fig. 6). A slight reduction in activity before active extension is apparent in the response average.

Polyjoint cells

The 19 polyjoint cells responded to rotation of two joints (n = 10) or more (n = 9). Nine of these exhibited bilateral convergence of input from the corresponding joint on both sides of the body; 15 responded only phasically during joint rotation and 4 had tonic discharge related to maintained angle. Typical of the complex convergence on polyjoint cells was unit *C76-1* (area 5), which was excited by flexion and inhibited by extension of the contralateral shoulder. Similar movements of the ipsilateral shoulder produced the opposite responses. The unit was also inhibited when a hand was waved in front of the monkey's eyes at a distance of about 1 m.

The response averages obtained for six polyjoint units during elbow movements exhibited patterns that were basically consistent with each cell's response to natural stimulation of the elbow (Table 1). For example, unit *C105-1* from area 2 responded phasically and tonically to extension of the elbow, as well as to rotation of wrist and both shoulders; with contolled elbow movements in the cast it responded relatively consistently during passive and active elbow extension (Fig. 7).

Shoulder cells

We classified 45 units as shoulder cells because they responded to manipulation of the shoulder joint tissue, i.e., muscles and/

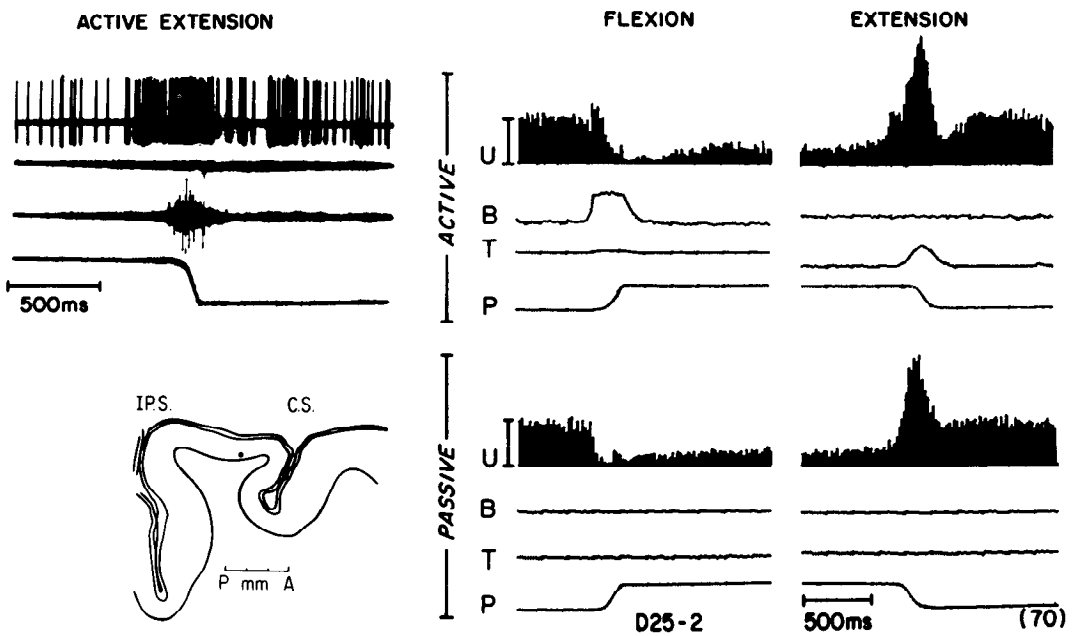

FIG. 5. Responses of joint-muscle unit *D25-2*. Out of the cast this area 2 cell responded to palpation of triceps and elbow joint. Its discharge during active extension was somewhat greater than during comparable passive extension.

or joint capsule. Five responded only to pressure in the region of the joint capsule but not to movement of the shoulder joints. The remaining 40 responded to joint motion (22 of these also responded to pressure in the shoulder joint region). The three principal

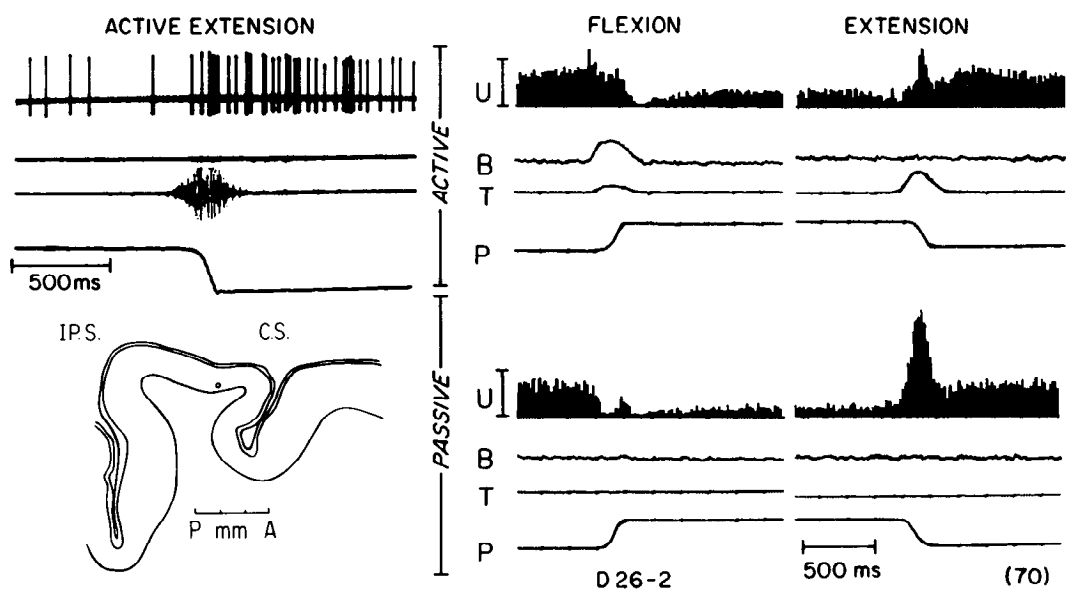

FIG. 6. Responses of joint-muscle unit *D26-2*, whose natural response was similar to that of unit *D25-2*. It was located 100 μm medial and posterior to unit *D25-2*. During active extension, its phasic response was comparatively reduced; the response average indicates that its activity decreased before active extension, but the magnitude of this suppression was too small to qualify for entry in Table 1.

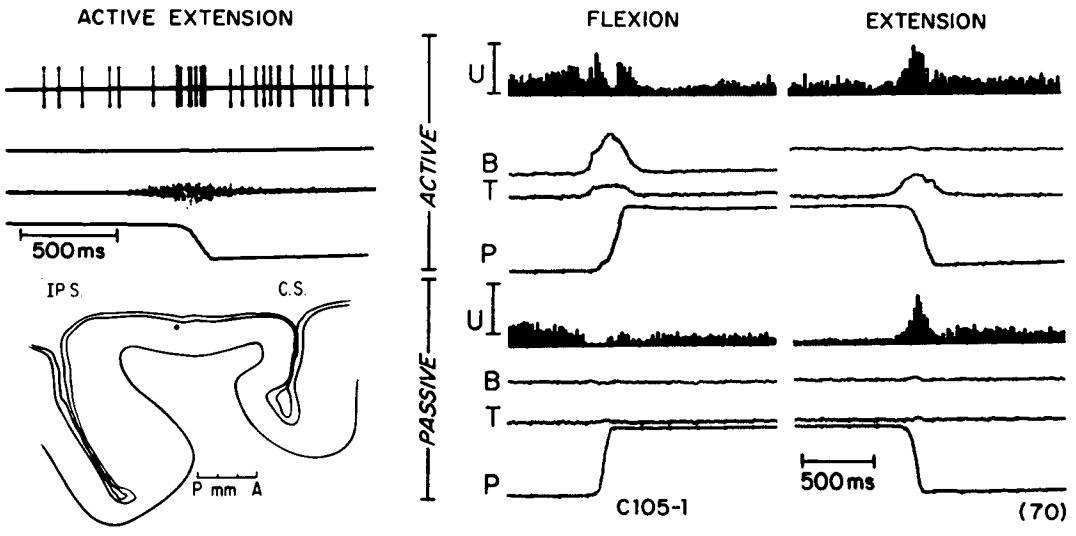

FIG. 7. Responses of polyjoint cell *C105-1*, which responded to abduction of shoulder, extension of elbow, and extension of wrist, as well as flexion of ipsilateral shoulder. In the cast it responded to active and passive elbow extension, phasically and tonically. The double peaks during active flexion may represent activity related to input from other joints.

directions of shoulder joint motion (flexion-extension, abduction-adduction, medial-lateral rotation) were equally represented in the sample. Twelve cells responsive to shoulder joint rotation also exhibited tonic rates related to shoulder angle.

Response averages during elbow movements were obtained for 11 shoulder cells (Table 1). As a group, shoulder neurons discharged more during active elbow movements than during passive movements; many were more strongly related to active flexion than extension, possibly because raising the forearm required more effort. Phasic excitation was largest during active flexion movements, and phasic suppression occurred more often during active extension movements.

Wrist units

Seven wrist units were driven by passive wrist rotation, either extension (n = 5), flexion (n = 1), or both (n = 1). Two were also driven by pressure on the wrist. The response patterns of two wrist units averaged for 70 cycles of active and passive elbow movements showed responses during similar elbow movements (Table 1).

Cutaneous cells

We observed 116 cutaneous cells, which were activated by brushing hair and touching skin over receptive fields located in the hand (n = 32), forearm (n = 39), upper arm (n = 31), or shoulder (n = 14). At least one cell also had a demonstrable inhibitory field, although this was not rigorously tested for all cells. Response averages during elbow movements were obtained for 28 cutaneous units with receptive fields on the hand (n = 3), forearm (n = 15), upper arm (n = 8), or shoulder (n = 2). Although the response patterns of several cutaneous cells during active and passive elbow movements could be easily interpreted on the basis of stimulation of the receptive fields during these movements, most of the observed patterns were too complex to be analyzed so simply. Unit *17-2* (Fig. 8) illustrates several features typical of the cutaneous cells. Its receptive field included the lower half of the forearm and extended proximally around the elbow joint. With the forearm in the cast this unit responded during all four phasic movements, but showed no consistent differences in tonic discharge related to elbow position. For the two phasic movements in which the cast would be expected to exert the most pressure on the receptive field, active extension and passive flexion, the response pattern consisted of two distinct peaks of activity. These peaks seemed related to the onset and

termination of the passive flexion movement, but clearly preceded the onset and termination of the active extension. Since triceps activity generates the active force during extension, pressure on the receptive field should occur during triceps activity; the response pattern of this cell clearly did not show such a simple relation to triceps.

With the arm in the cast, the activity of many cutaneous units was less intense than was anticipated on the basis of their brisk responses to natural stimulation out of the cast. Six cells with receptive fields on the lower arm had distinctly reduced spontaneous rates and had diminished evoked responses while the arm was held in the cast.

Most of the 27 cutaneous cells in Table 1 responded during phasic movements; a difference in tonic discharge rate related to position appeared in about one-third of cases (11/27 active and 7/20 passive cases). The strongest responses occurred during active phasic movements and generally weaker responses were evoked by passive phasic movement. In contrast to the joint muscle cells, most cutaneous cells responded positively during movements in both the flexion and extension direction.

Other units

The responses of 17 units did not fit any of the preceding categories. Four were driven from cutaneous fields on the face or thorax, seven responded to deep pressure exerted on hand or thenar muscle regions, and six had complex receptive fields such as ipsilateral joint movements or approach of visible objects. Of the 320 postcentral cells tested, 36 were not driven by any peripheral stimulation.

Response patterns during active and passive movements

The response averages compiled during active and passive elbow movements (Table 1) reveal some significant differences between the response patterns of cells driven by natural proprioceptive (deep) stimulation and those driven by cutaneous stimulation. Many deep cells were preferentially activated by phasic movements in only one direction and were either inhibited or unresponsive during phasic movements in the opposite direction; in contrast, most of the cutaneous cells were activated during both phasic flexion and extension. Moreover, a greater proportion of deep cells exhibited higher tonic firing rates during one

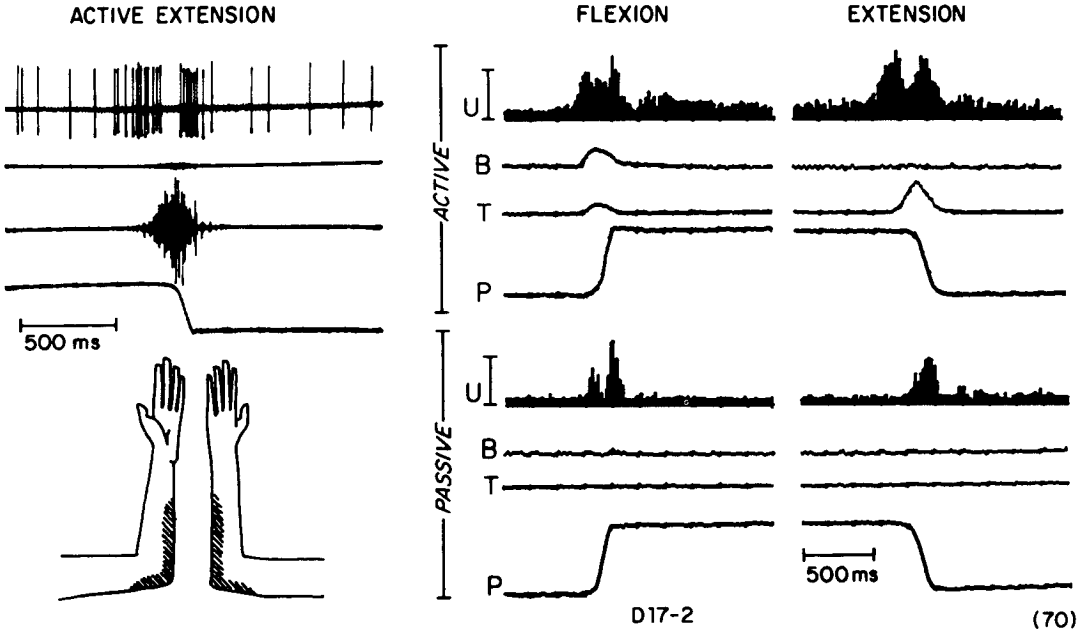

FIG. 8. Responses of cutaneous unit *D17-2*, which responded to brushing hairs over the receptive field illustrated in bottom left.

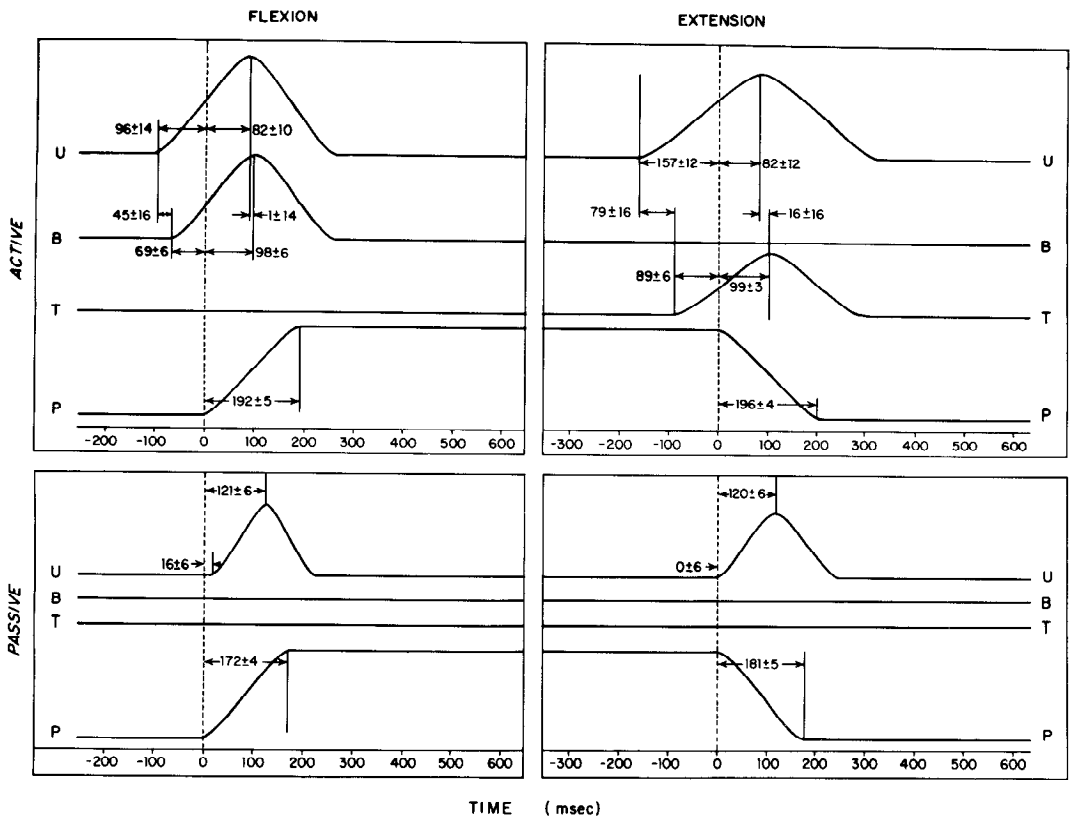

FIG. 9. Schematic summary of average relative timing of unit and muscle activity and elbow position for the postcentral cortex cells in Table 2. Means and standard errors were obtained from measurements of response averages (n = 72). Vertical dotted line represents movement onset, and arrows indicate relative onset times and peaks of unit and muscle activity. Except for location of onset and peak, the time course of activity is not intended to accurately represent the population response; when multiple peaks occurred, the first was taken. On the average, during active movements the postcentral cells began firing later than precentral cells (cf. Fig. 9 in Ref. 17) but earlier than muscles.

of the two maintained positions, whereas cutaneous cells showed relatively less differences in tonic discharge with position. Thus, the deep cells gave more directionally selective responses for both phasic movements and static positions.

Deep cells that responded during active movements in one direction usually responded to passive movements in either the opposite or the same direction. In contrast, cutaneous cells were activated during movements in both directions, whether passive or active. Finally, deep cells more often exhibited a suppression of activity before active movements in contrast to cutaneous cells, which usually exhibited only excitation.

Relative timing of postcentral cells and movement

Figure 9 schematically summarizes the mean latency differences between onset and peaks of activity of postcentral units and agonist muscles and elbow position during elbow movements in the cast. These means and standard errors were derived from response averages of 72 postcentral cells. While passive movements usually evoked unit activity within the first 20 ms after movement onset, during active movement many postcentral cells became active over a broader range of latencies, including times before movement onset. Changes in postcentral cell activity began, on the

average, 61.4 ± 17.8 ms (mean ± SE) before onset of agonist muscles; mean unit onset was slightly earlier for active extension (78.9 ± 15.6 ms) than active flexion (45.2 ± 15.8 ms). These means did not differ significantly for cutaneous and deep cells, nor did the mean onset of cells in area 2 differ appreciably from those in area 1.

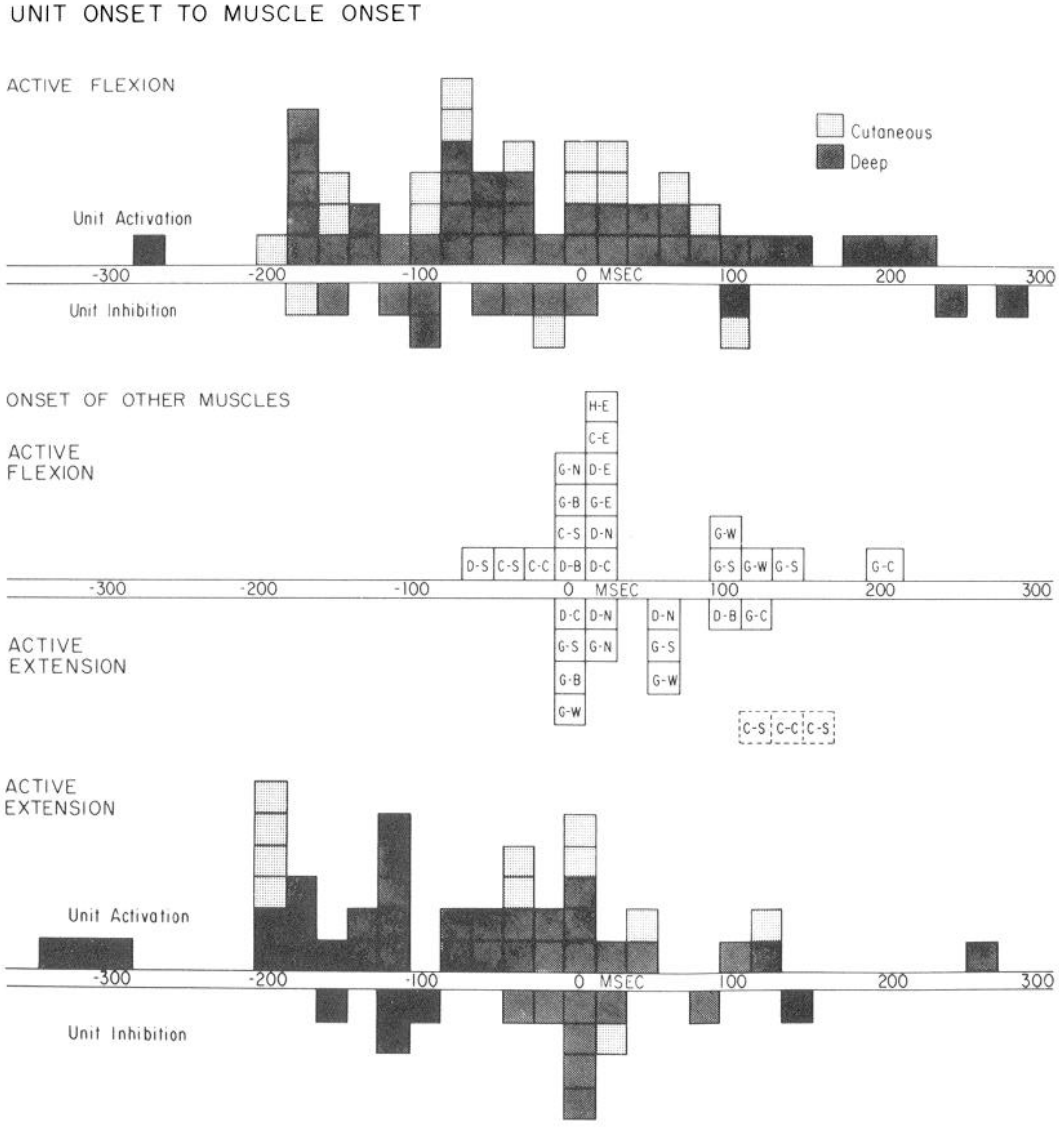

FIG. 10. Relative timing of onset of unit activity and beginning of EMG activity, measured from response averages of postcentral units. Abscissas indicated time in milliseconds with respect to the beginning of agonist EMG activity (biceps for flexion and triceps for extension). Negative values indicate times preceding the begining of EMG activity. Top and bottom histograms represent onset time of postcentral unit activation (upward) or suppression (downward) with respect to the beginning of biceps (top) or triceps (bottom) EMG activity. Middle histogram represents the onset time of EMG activity in different forearm muscles with respect to the beginning of biceps (upward) or triceps (downward) EMG activity. The first letter in each block designates monkeys from which the muscle was recorded, and the second letter designates the muscle. E, elbow (brachialis and brachioradialis); C, chest (pectoral); B, back (paraspinal); W, wrist (flexors and extensors); N, neck (sternocleidomastoid); S, shoulder (teres major and minor, deltoid, trapezius). The dashed histogram blocks represent muscles that were silent during active extension.

Figure 10 plots the onset times of different postcentral cells relative to onset of agonist muscle activity during active movements. It also shows the relative onset times of other representative forearm and trunk muscles. In general, other muscles showed much less activity during elbow movements than the agonists, and with three exceptions all other muscles became active with or after onset of the agonist muscles. The histograms show that during active movements, approximately one-third of the postcentral cells changed their activity 100 ms or more before agonist muscle activity. Such early onset occurred equally for deep and cutaneous cells. Neurons that responded during active movements in both directions showed no clear correlation between onset times during flexion and extension—i.e., early onset in one direction did not correlate with early onset in the opposite direction.

DISCUSSION

The major purpose of this study was to document the response patterns of postcentral "sensory" cortex cells during controlled active and passive elbow movement and to interpret those patterns in the light of the cells' responsiveness to natural stimulation. Such comparisons are relevant to evaluating the possible role of postcentral cells in proprioception and to understanding the relative importance of peripheral and central input during active movements.

On the basis of their responses to natural stimulation, we could divide most postcentral neurons into two major groups, cutaneous and deep, in accordance with previous studies. Powell and Mountcastle (45) further classified some of their deep units as responsive to stimulation of joint capsules, periosteum, muscle fascia, and peritendinous connective tissues. Such fine determination of receptor location proved impossible in our study, primarily due to limitations in the amount of probing possible with an intact, responsive animal. Without dissection, it was not possible to distinguish whether muscle cells were driven by stretch receptors or connective tissues. Similarly, cortical joint units could have been activated from several peripheral sites, including articular connective tissues such as tendon grooves, periosteum, joint capsules, ligaments, and pericapsular connective tissues. Connective tissues typically contain a triad of encapsulated, unencapsulated, and free endings. The highest concentration of such proprioceptive triads is found in regions with the most connective tissue stress, such as joint capsules, ligaments, and muscle attachments to periosteum, but tendon sheaths, retinaculae, fascia, and intramuscular and interosseus membranes are also innervated (25, 43, 47, 50, 55, 56). Receptors at any of these sites could provide input to cortical muscle cells as well as joint cells.

In our alert monkeys, the passive responses of most postcentral cortex units to natural stimulation were consistent with those previously described (5, 11, 12, 34, 38, 42, 45, 61). Cutaneous units were more numerous in anterior parts of the postcentral gyrus, in agreement with Mountcastle's and Powell's (38, 45) observation that the proportion of deep units was greater in area 2 than in area 3b. Most cells responding to cutaneous stimulation had distal receptive fields; in contrast, the majority of cells driven by deep tissue stimulation responded to movement of proximal joints. Since our primary goal was to document response patterns during active and passive elbow movements, we preferentially sought well-isolated task-related cells in the arm area. Consequently, our sample of neurons is too selective to address the issues of somatotopic organization, which have been more comprehensively investigated by others (11, 34, 39, 42, 45, 60–62). Nevertheless, in systematically exploring the arm region we encountered distributions of cells such as those illustrated in Fig. 2. Minor discrepancies with the various maps proposed by others may be due to the fact that our monkeys were unanesthetized, to differences in cytoarchitectonic criteria and projection methods and to the acknowledged variance in arm representation between individual monkeys (34).

Neural mechanisms of position-motion sense

Postcentral cells responsive to passive joint movement have been suggested to mediate position and motion sense. To what

extent are the results of the present study consistent with this hypothesis? The joint cells all responded phasically during joint movement; 80% also discharged tonically, at rates related to joint position. The 16 elbow joint cells documented during controlled active as well as passive movements responded to phasic elbow movements in either one direction ($n = 14$) or both ($n = 2$) (cf. Ref. 38). The 14 unidirectional cells also exhibited tonic discharge. With the arm in the cast, the strongest passive responses usually occurred in the same direction as the effective natural elbow rotation (Table 1); however, some cells also exhibited a response during phasic passive movements in the opposite direction, perhaps due to pressures exerted by the cast. Thus, with minor exceptions, responses to passive movements in the cast agreed with responses to adequate natural stimulation. However, during active elbow movements many elbow joint cells responded in a way different from that expected on the basis of their natural response. Some of these discrepancies occurred in their tonic discharge during maintained elbow positions. Three of six cells responded tonically during active movements of the arm in the cast, but not to passive angular displacements outside the cast. All three exhibited higher tonic rates during active flexion even though two of these had responded to phasic extension out of the cast. Such tonic responses could have been due to a different distribution of tissue tensions during active movements in the cast.

Other deviations from the expected pattern occurred during active phasic movements. Only half of the 14 unidirectional elbow joint cells gave a greater excitatory response during active movements in the effective direction. The remainder exhibited comparable or complex responses for active movements in both directions. Two factors may have contributed to this result. The appearance of additional responses during active movements in the direction opposite the effective passive direction could have been due to peripheral inputs; the greater stresses occurring during active movements might have stimulated the relevant receptors during movements in either direction. In several cases such increases in cell activity began before muscle activity, suggesting the possibility of centrally originating excitation during active movements. A second factor equalizing the phasic flexion and extension responses is the reduction of the phasic response in the effective passive direction during active movements. Although the movement trajectories were comparable, many elbow joint cells fired less intensely during active than during passive movements (Figs. 2, 3, 6). These observations indicate that during active elbow movements the response patterns of many elbow joint units no longer reflected a simple relation to elbow angle or rotation.

Psychological studies comparing kinesthetic perception during active and passive joint movements suggest a greater ability to make proprioceptive discriminations during active movements. Paillard and Brouchon (40) reported significantly greater accuracy in matching position of an actively moved arm than a passively positioned arm. Similarly, subjects could match the position of their index fingers more accurately after active than after passive displacement of the hand. In these studies it made little difference whether the position had been maintained actively or passively, suggesting that the relevant information was derived from the dynamic phase of movement and was not obtained during self-maintained postures. Paillard and Brouchon (40) also found that passive displacements were consistently overestimated. In contrast, the elbow joint cells in this study responded more strongly and selectively with passive than active elbow movements. The apparent discrepancy could simply be related to the differences in behavioral conditions. Our monkeys merely had to move their arms rapidly between two stops but were not required to make fine kinesthetic discriminations, whereas in psychological studies, subjects were attempting to maximize their perception of proprioceptive cues and could well have used their muscles toward that end. Muscle tensions clearly affect the responses of joint capsule afferents (22, 35, 52) but not the activity of ligament afferents (51, 52). Indeed, the observed variability in response patterns of postcentral joint cells during active movements might reflect a sensitivity to muscle tensions and is consistent with

the possibility that in psychophysical tests, the muscle activity could be adjusted to maximize the responses of such cells to joint angle.

Besides the cortical joint cells, the postcentral deep muscle units, which could be driven by muscle palpation (as well as joint rotation), also exhibited clear and consistent movement-related response patterns (Table 1). Muscle palpation and tapping is an effective stimulus for stretch receptors but may also activate sensitive Ruffini and paciniform receptors located in the periosteum and fascia (25, 26, 36, 50, 51). Consequently, we cannot conclude that the effective receptors for deep muscle cells were stretch receptors. However, by our definition these neurons did not respond to direct stimulation of pericapsular tissues. The responses of elbow-related deep muscle cells during passive and active movements in the cast were consistent with their responses to natural stimulation (Table 1); such cells could also subserve position and motion sense, and could also contribute to sensations of "effort," "force," or "resistance" (1, 19, 33).

The cells responsive to natural stimulation of the shoulder joint did not exhibit response patterns clearly correlated with elbow movements in the cast. On the whole, the shoulder joint cells responded most strongly during active flexion movements, probably related to contraction of shoulder girdle muscles during biceps contraction (confirmed by EMG recording).

Most cells with cutaneous receptive fields responded to active and passive movements in either direction. They rarely exhibited different tonic responses for different positions and those that occurred were generally weak. Thus, under conditions of this experiment the capacity of cutaneous cells to code kinesthetic information quantitatively appears limited. Interestingly, several cutaneous cells with forearm receptive fields were less active with the forearm placed in the cast; this may well reflect the effects of afferent inhibition.

The responses of polyjoint cells agree with descriptions of cells in area 5 that respond to rotation of multiple joints of both contralateral and ipsilateral limbs, with maximal activation by coordinated limb movements (12, 48). In general, all polyjoint cells shared these properties; a minor difference was that only 4 of 19 units exhibited tonic responses to maintained angles. Two units responded to visual stimulation (37, 48). During controlled elbow movements, the six polyjoint cells that were documented showed patterns consistent with their responses to natural stimulation of the elbow.

Central input to neurons of primary somatosensory cortex (SI)

Input from peripheral receptors may account for much of the postcentral unit activity during active and passive movements, but does not explain the changes in cell activity that preceded active movements. Although these cells may receive tonic peripheral input during the hold periods, such static input cannot account for the phasic changes in neural activity that precede onset of muscle activity. Approximately one-third of the postcentral cells changed activity 100 ms or more before agonist EMG discharge (Fig. 10). Such early discharge was found in cells of all modalities and receptive-field locations.

An obvious hypothesis to account for such early changes is that the cells were affected by peripheral receptors stimulated by early contraction of nonagonist muscles. However, recordings of other distal and proximal muscles during these movements revealed that most became active after the agonists; the few that preceded agonist contraction began 20–60 ms earlier, insufficient to account for the even earlier changes in unit activity. Some cells, like unit *C102-1* (Fig. 4), had already reached maximal firing rates when muscle activity was just beginning. Moreover, the possibility of sensory input from the other body regions that could be stimulated earlier in the sequence was tested and not confirmed by natural stimulation. Most cells that fired before active elbow movements derived their sensory input from receptors restricted to contralateral forelimb; for example, unit *C102-1* responded only to triceps palpation and passive elbow flexion, yet fired well before triceps and biceps EMG under active conditions.

It seems probable, then, that during active

movements many postcentral cortex cells were also affected by centrally originating input. Such an interpretation is consistent with comparable interpretations of the early responses of precentral motor cortex cells. Earlier reports of "readiness potentials" recorded over parietal areas before active movements (7, 10) had already suggested this possibility. The present results confirm that such early activity is also observable in postcentral cortex neurons.

After reviewing the reasons for expecting early discharge in postcentral neurons, Evarts (13–16) reported that he found relatively few postcentral cortex cells whose activity changed prior to a rapid reaction-time response. Several differences in experimental conditions may account for these different results. While Evarts' monkeys performed ballistic flexions and extensions of the wrist or rapid push-pull movements of the arm in response to a visual stimulus, our monkeys performed a self-paced sequence of alternating elbow movements, which apparently involved more prolonged recruitment times prior to muscle activation, as indicated also by earlier onset of precentral cells (17). Besides differences in the speed of the movements, the self-initiated responses could conceivably involve different neural mechanisms than reaction time responses to a stimulus; in the latter case the monkeys attended a visual stimulus that triggered rapid ballistic movements that were largely "preprogrammed." Another significant variable may be the cytoarchitectonic area: many of our early onset cells were recorded in areas 2 and 1, while Evarts may have sampled more cells in area 3b, which receives a greater direct input from dorsal column afferents (11, 42). The fact that many posterior parietal cells in areas 5 and 7 change activity prior to directed reaching movements (31, 37) suggests that central input may become increasingly important relative to peripheral input in the more posterior parietal areas. This would be consistent with a greater interconnection of posterior areas with precentral cortex (27, 28, 41).

Bioulac and Lamarre (2) also observed postcentral cell activity prior to active limb movements, but found that such early activity was abolished by deafferentation. They conservatively concluded that such early responses might have been due to peripheral input. Alternatively, their deafferentation could also have eliminated a sufficient amount of peripheral facilitation to reduce the early responses to central input.

The modulation of postcentral cortex cells before active movements could be produced by several means. Primary sensory cortex neurons may be directly affected by input from precentral cortex areas 4 and 6 as well as posterior parietal cortex area 5 (27, 29, 59), all of which contain cells exhibiting early changes. Early activity could also be relayed via thalamus from cerebellum and basal ganglia. Central modulation of sensory input at the dorsal column nuclei and dorsal horn have also been demonstrated (8, 18, 24, 58). Transmission through dorsal column nuclei appears to be suppressed up to 200 ms before EMG activity (8, 18), which could contribute to early suppression of postcentral cells.

These early changes in postcentral cell activity may function in relation to either sensory or motor mechanisms, depending on destination of the cells' projections (29). Since movements may be evoked by stimulating SI, even in the absence of motor cortex (20, 62), it is clear that the output of some cells can eventually facilitate motoneuron activity. The cells with early activation (e.g., Fig. 4) could well contribute to motor responses, much like comparable precentral cells. Although we tested the pyramidal tract projection of many postcentral cells, only one antidromic response was identified; why the postcentral PTNs (9, 29) should be so difficult to identify physiologically (cf. also Refs. 14, 15) remains a mystery.

If the responses of postcentral cells are interpreted in terms of coding of sensory input, the central modulation during active movements might serve to compensate for self-initiated stimulation. Interestingly, many joint and muscle cells responsive to passive elbow movement exhibited reduced phasic responses during active elbow movements. Although some of the reduction occurring during the movement may be attributed to afferent inhibition or altered stimulation of receptors, the decrease in

activity prior to agonist muscle activity suggests a central inhibitory mechanism. In contrast, postcentral cells with cutaneous input exhibited little evidence of reduced responses during active movements. Although some cutaneous cells showed evidence of afferent inhibition by a reduction of their spontaneous and evoked activity when the arm was placed in the cast, this effect should be comparable for active and passive movements. The fact that most cutaneous cells exhibited greater phasic responses during active than passive movements suggests that their excitatory input overrides any afferent or central inhibition.

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