

Chapter 14

Functional Organization of Motor and Sensory Cortex: Symmetries and Parallels

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ABSTRACT

This chapter reviews several analogies in the functional organization of motor and sensory cortex cells and their representation of peripheral events. In precentral motor cortex, corticomotoneuronal (CM) cells, identified by spike-triggered averaging of electromyographic (EMG) activity, have been shown to affect a set of target muscles; this "muscle field" is the motor analogue of the receptive fields of sensory cortex cells — peripheral receptors that affect sensory cortex cells. In both cases, the peripheral fields can have excitatory or inhibitory components. The intensity of a peripheral event is also coded analogously: The ramp-and-hold motor responses are associated with a phasic-tonic discharge in most CM cells; the phasic component is related to onset of the torque ramp, and the tonic component is proportional to the level of static force exerted. This pattern is analogous to the encoding of a ramp-and-hold stimulus (cutaneous or proprioceptive) in sensory cortex cells by a phasic component proportional to the change of the stimulus and a static component proportional to its maintained intensity. Evidence for higher-order cells in motor cortex analogous to those in sensory regions is also described. It has become evident that motor and sensory cortex cells receive analogous convergences of peripheral and central input and have analogous functional loops with the periphery. These and other similarities between sensory and motor cortex may provide a common basis for the behavioral analogues of sensory perception and motor programming.

The neural circuitry of the cerebral cortex is evidently designed to process spatial and temporal patterns of neural activity underlying both sensory and motor functions. The organization of sensory cortical areas allows higher-order perceptual wholes to be extracted from diverse patterns of receptor activities; similarly, motor areas are organized to translate goal-directed motor programs into the appropriate coordinated muscle activity. The cortical functions of sensory perception and motor programming are quite analogous insofar as they involve the integration and coordination of the activity of diverse peripheral elements, namely, sensory receptors or motor units. The similar properties of these functions and their cortical representations suggest that sensory and motor behavior may involve comparable neural mechanisms. Recent evidence on the relation of primary motor cortex cells to muscles reveals a hierarchical representation of muscle activity in the motor cortex that is remarkably analogous to the representation

of receptor activity in somatosensory cortex. This chapter reviews current evidence on the hierarchical relation of primate motor cortex cells to limb muscles, with a view toward comparison with the representation of peripheral receptors in somatosensory cortex cells.

Analogous features of sensory and motor cortex cells are best brought out under experimental conditions in which the cortical neurons can be related to their respective peripheral elements, that is, passive stimulation of specific sensory receptors and active contraction of particular muscles. Normally, behavioral conditions are more complex, involving continual interaction between sensory and motor events, but even these interactions can be seen to involve analogous circuits.

BEHAVIORAL ANALOGUES: PERCEPTION AND PROGRAMMING

The neural mechanisms by which the nervous system extracts perceptual features from the diverse and changing patterns of receptor stimulation remain a challenging issue for integrative neurophysiology. We recognize an object effortlessly and immediately, despite drastic variations in the pattern of retinal stimulation it evokes: A familiar face can be recognized independent of its location, orientation, and expression. Similarly, a motor act can be coordinated to achieve a particular goal independent of the pattern of muscle activity required. One can draw the same picture, whether small on paper or large on a blackboard—indeed, whether executed with either hand. Despite the drastic difference in muscular activity in each case, the same motor program yields recognizably similar results. The linguistic capacities of the human cortex offer even more refined examples: The semantic meaning of a message can be recognized whether received through visual, auditory, or even tactile channels; conversely, the same message can be expressed through writing, speech, or gesture. The neural mechanisms underlying the processing of abstracted information, whether sensory or motor, have yet to be fully understood. They appear to involve neural activity propagating simultaneously among many distributed sets of cortical cells. The basic principles underlying such distributed parallel processing in large neural networks remain elusive and difficult to study. Yet we have reason to expect that the same mechanisms could explain the extraction of perceptual wholes in the sensory realm, the expression of volitional goals, and perhaps even the processing of abstract thought. Clues to understanding these mechanisms emerge from the analysis of hierarchical representation of sensory and motor events in cortical cells, which reveals some striking analogies in their functional organization.

HIERARCHICAL REPRESENTATION OF PERIPHERAL ELEMENTS

Primary and Secondary Cortical Areas

The functional roles of different cortical areas in motor and sensory behavior have been elucidated by three experimental strategies: analysis of the behavioral deficits produced by cortical ablation; mapping of the neural connectivity between

the cortex and the periphery through electrical stimulation; and correlation of the activities of single neurons with parameters of behavioral events. These different techniques are consistent in distinguishing primary and secondary cortical fields in both motor and sensory systems. In each case, neurons in the primary cortical areas are most directly linked to the corresponding peripheral elements: Ablation of primary cortex has the most severe functional consequences, and neural activity in primary areas most clearly codes for specific motor and/or stimulus parameters. Surrounding these primary cortical areas are multiple secondary areas in which neurons are less directly linked to inputs or outputs; their activity is related to events over larger peripheral fields and to more complex properties of peripheral events. The behavioral deficits produced by lesions in secondary areas are typically more subtle than those produced by lesions of primary areas.

As a specific example, Figure 1 illustrates the primary and secondary somatic sensorimotor maps of Woolsey (1958), based on experiments with anesthetized macaques. These maps represent two features simultaneously: the parts of the body whose movement can be evoked by electrical stimulation of the cortex, and the peripheral sites whose stimulation evokes maximal cortical potentials. The somatotopic maps in primary motor and primary sensory cortices resemble mirror images, similarly distorted to devote the greatest area to the distal extremities, in proportion to the density of peripheral receptors and the number of muscles. Anterior to the primary motor cortex lie multiple secondary motor areas, including the supplementary motor area illustrated here (MsII), as well as other premotor areas (Humphrey, 1979; Wiesendanger, 1981; Wise, this volume).

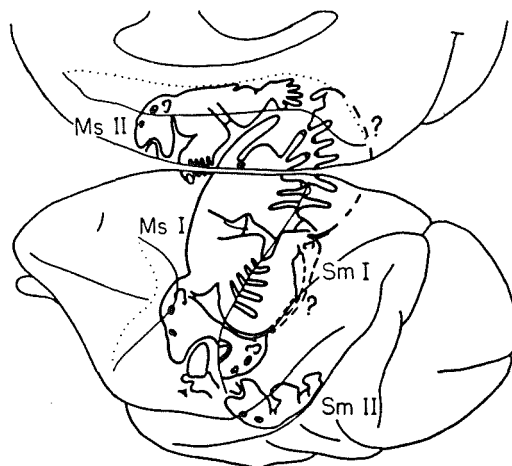


Figure 1. Schematic diagram of somatotopic organization of precentral and postcentral cortex of *Macaca mulatta*. Each figurine represents simultaneously a motor and a sensory map. As a motor map, each represents the part of the body in which movements are evoked by cortical stimulation at that site; the lowest thresholds are in the precentral motor-sensory I (*Ms I*) area. As a sensory map, each represents the part of the body whose stimulation evokes cortical potentials at that site; the largest potentials are evoked in the postcentral sensory-motor I (*Sm I*) area. Secondary motor-sensory (*Ms II*) and sensory-motor (*Sm II*) regions are shown as representative examples of secondary cortical areas. (From Woolsey, 1958.)

These secondary regions play a role in motor programming, as demonstrated by various types of apraxia produced by their ablation. Similarly, the posterior parietal cortex has multiple secondary sensory areas devoted to the elaboration and association of sensory events.

The functions of sensory perception and motor programming involve continual reciprocal interactions between the relevant primary and secondary cortical areas and between each of these and the periphery. The possibility that these interactions involve comparable mechanisms becomes plausible in light of recent evidence that primary sensory and motor cortex cells exhibit analogous hierarchical relations to their peripheral elements.

Muscle Fields of Corticomotoneuronal Cells

The motor cortex cells that have the most direct output effects on muscles can be identified in behaving primates by spike-triggered averaging of electromyographic (EMG) activity (Fetz and Cheney, 1980). These precentral cells produce a postspike facilitation of forelimb muscle activity, indicating that their action potentials increase the firing probability of motor units in their target muscles. The magnitude and timing of the strong postspike facilitation suggest that it is

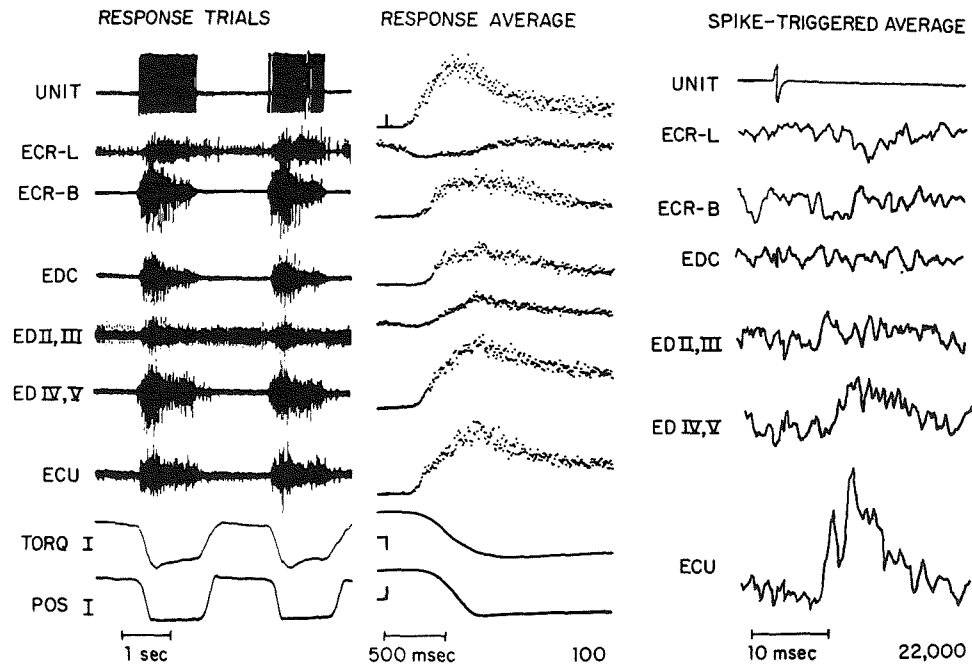


Figure 2. Response properties of a primate CM cell related to wrist extension. On the left, from top to bottom, are shown the activity of a CM cell, EMG recordings from six extensor muscles, and wrist torque and position during two successive ramp-and-hold wrist movements against an elastic load. The middle of the figure shows response averages of cell and rectified muscle activity aligned at the onset of wrist extension. On the right are shown spike-triggered averages of rectified EMG activity of extensor muscles. The large postspike facilitation in the extensor carpi ulnaris (*ECU*) appeared in the averages of 2000 events and identifies this as a CM cell. (From Fetz and Cheney, 1980.)

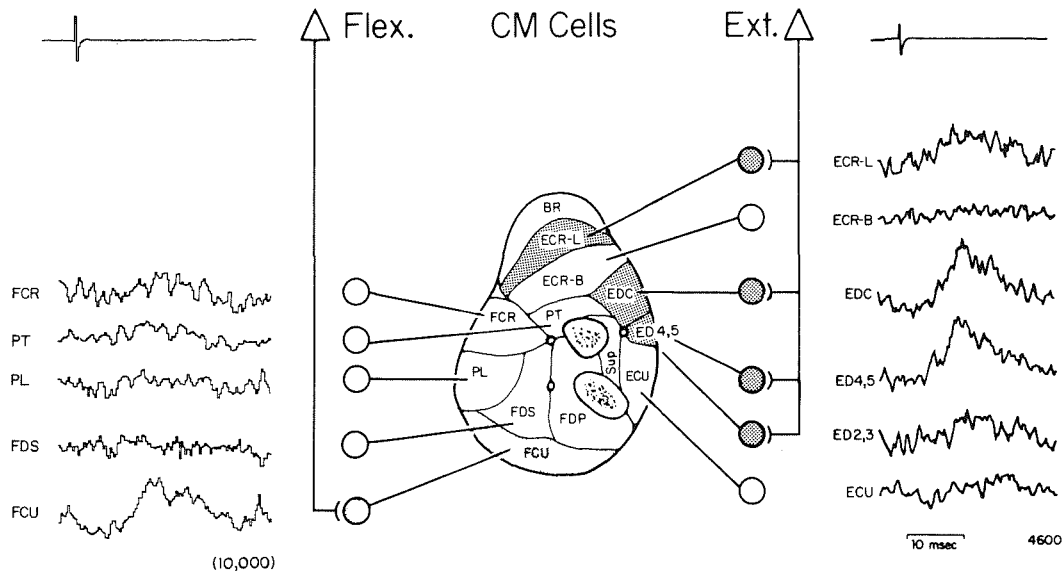


Figure 3. Muscle fields of two primate CM cells. The cross-section of the macaque forearm in the middle identifies the wrist and finger muscles. The spike-triggered averages of a flexor CM cell (*left*) and an extensor CM cell (*right*) show postspike facilitation of EMG activity in their target muscles. Muscles illustrated include the brachioradialis (*BR*), extensors carpi radialis longus and brevis (*ECR-L* and *ECR-B*), extensor digitorum communis (*EDC*), extensor digitorum four and five (*ED 4,5*), extensor carpi ulnaris (*ECU*), pronator teres (*PT*), supinator (*Sup*), flexor carpi radialis (*FCR*), palmaris longus (*PL*), flexors digitorum sublimis and profundus (*FDS* and *FDP*), and flexor carpi ulnaris (*FCU*).

mediated by monosynaptic corticomotoneuronal (CM) connections. Such cells often facilitate the activity of motor units in several target muscles; the set of muscles whose activity is statistically affected by the cell in a spike-triggered average has been called its "muscle field."

Figure 2 illustrates the activity of a CM cell that fired during wrist extension and facilitated activity of motor units in two of the six extensor muscles: the extensor carpi ulnaris (*ECU*) and the extensor digitorum four and five (*ED 4, 5*). The strength and latency of the postspike facilitation in these muscles are consistent with their mediation by monosynaptic CM connections. Other extensor muscles were also coactivated with the cell, but they showed no signs of being facilitated by this CM cell. Clearly, any number of muscles can be coactivated in a movement, so the identification of a functional linkage between cortical cells and muscles requires more stringent evidence than simple coactivation; the spike-triggered average is a convenient method of cross-correlating cell and muscle activity to reveal such a linkage.

Figure 3 illustrates the muscle fields of two other CM cells; the location of their facilitated target muscles is shown in a cross-section of the forearm. The flexor CM cell facilitated only one of the recorded flexor muscles, the flexor carpi ulnaris (*FCU*), while the extensor CM cell facilitated four of the extensors: the extensor digitorum communis (*EDC*); *ED 4,5*; *ED 2,3*; and the extensor carpi radialis longus (*ECR-L*). The strong postspike facilitation in *EDC* and *ED 4,5* identifies this as a CM cell; the weaker postspike facilitation in *ED 2,3* and *ECR-L*

may well be mediated by monosynaptic connections, as indicated in the diagram, although disynaptic links cannot be excluded. About half of the CM cells facilitated only one of the six coactivated synergist muscles; the rest facilitated two to six muscles. The mean size of the muscle field was slightly greater for extensor CM cells (2.5 muscles) than for flexor CM cells (2.1 muscles). In general, the magnitude of the facilitation produced by extensor CM cells tended to be stronger than that of flexor cells.

Anatomical and electrophysiological experiments provide additional evidence that CM cells can send divergent connections to motoneurons of multiple muscles. Injecting horseradish peroxidase (HRP) into axons of single corticospinal cells at the cervical level, Shinoda and his colleagues (1981) found that terminals of some corticospinal axons were distributed to many motoneuron pools in the cervical cord, including motoneurons of the median and ulnar nerve. Applying microstimuli in the lumbar ventral horn, Asanuma and his colleagues (1979) antidromically activated single corticospinal cells from multiple motor nuclei; moreover, adjacent pyramidal tract neurons (PTNs) were found to have many terminal projections in common.

The divergent effects exerted on multiple target muscles by a single CM cell can be considered the motor analogue of the convergent influence of multiple receptors on a single sensory cortex cell. Neurons in the somatosensory cortex respond to cutaneous stimulation over receptive fields that include large sets of contiguous mechanoreceptors. Other postcentral neurons, which respond to joint movement, fire over a range of joint angles wider than the individual peripheral afferents whose activity they integrate. Visual and auditory cortex cells are also driven by convergent input from spatially distributed sets of peripheral receptors. Thus CM cells, like neurons in primary sensory cortical areas, represent the activity of a spatially distributed set of peripheral elements.

In addition to facilitating coactivated muscles, the output from some CM cells can also contribute to suppression of antagonist muscles. Under normal conditions, spike-triggered averages of EMG can be computed only during the phase of movement in which the cells and the muscles are coactivated. Such experiments have tended to reveal postspike facilitation of synergist target muscles. However, two lines of evidence indicate that the same cells can also produce suppression of other muscles. Single-pulse microstimuli can be used to activate CM cells during both flexion and extension; single-pulse, 0.2-msec microstimuli of 5–10 μA are too weak to evoke overt muscle responses, but their subthreshold effects on motor unit firing probability can be revealed by stimulus-triggered averages of EMG. When delivered at the site of a CM cell during the phase of movement in which the cell is active, microstimuli evoke poststimulus facilitation in the cell's target muscles (Cheney and Fetz, 1977). Stimulus-triggered averages compiled during the opposite movement sometimes show that the same cells can evoke poststimulus suppression in antagonist muscles. Such reciprocal inhibition of antagonists of the cell's target muscles is evoked by microstimuli at about one-third of the CM sites. Poststimulus suppression occurs at a longer latency than poststimulus facilitation and requires a larger number of averages in order to be revealed, indicating that it is mediated polysynaptically.

Recent evidence indicates that the activity of even a single CM cell, evoked by glutamate during the phase of movement in which the cell is normally inactive,

can produce detectable inhibitory effects on the antagonists of its target muscles. Figure 4 illustrates an example of a CM cell that facilitated two extensor muscles, EDC and ECU. Evoking spikes during the flexion phase of movement with glutamate and compiling spike-triggered averages of the flexor muscles, Cheney et al. (1982) found postspike suppression in one of the flexor muscles, the palmaris longus (PL). In contrast to postspike facilitation, the suppression is

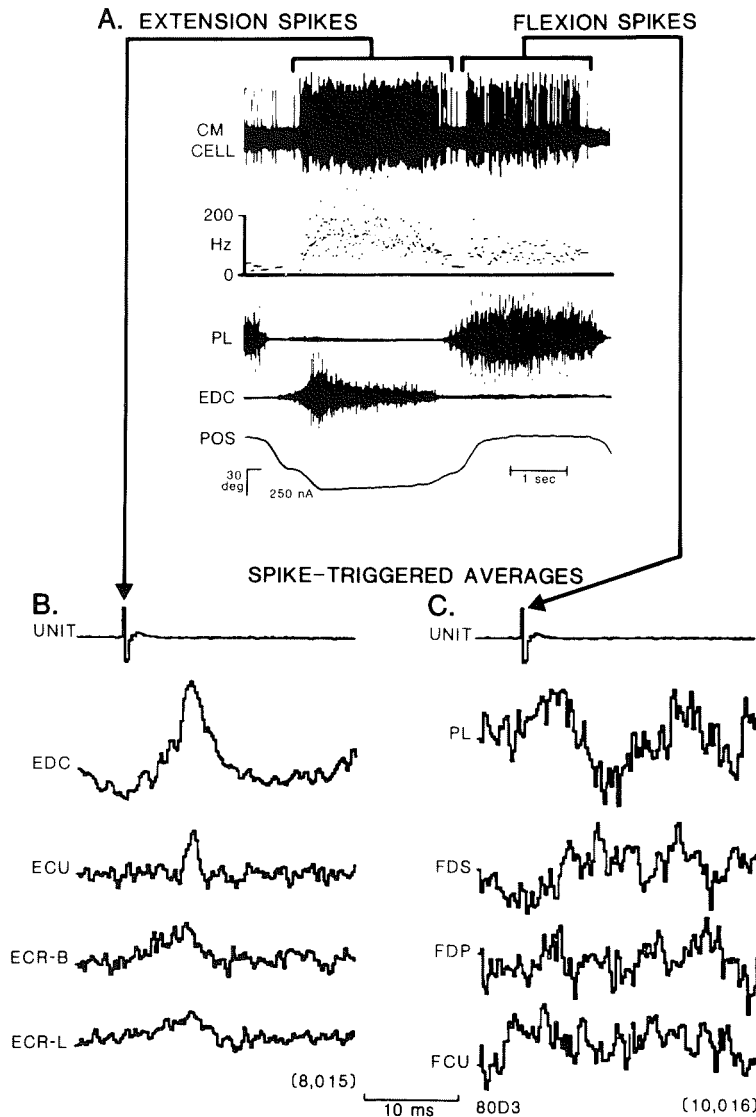


Figure 4. A: Recordings from an extensor CM cell that facilitated extensor muscles and reciprocally inhibited a flexor muscle. This cell normally fired only during wrist extension, but in this experiment was also activated during wrist flexion by intracortical injection of glutamate. B: Spike-triggered averages of extensor muscles during the extension phase showed postspike facilitation of EDC and ECU. C: Spike-triggered averages of flexor muscles showed postspike suppression of PL. Typically, postspike suppression was weaker and had a longer latency than postspike facilitation. (From Cheney et al., 1982.)

typically weaker and often of longer latency, as would be consistent with disynaptic mediation. A possible interneuron mediating this postspike suppression is the Ia inhibitory interneuron, which has been shown to receive convergent input from Ia afferents and PTNs (Jankowska et al., 1976).

Under current experimental conditions, the wrist muscles inhibited by CM cells have tended to be antagonists of the facilitated muscles. The number of CM cells that produce facilitation of EMG remains greater than the number that produce suppression. This is probably related to a sampling bias toward detecting linkages between coactivated cells and muscles. Moreover, polysynaptic linkages are less readily detected by cross-correlation than are monosynaptic connections (Fetz and Cheney, 1980).

Surprisingly, forearm flexor and extensor muscles are not affected equally by CM cells. Postspike facilitation tends to be stronger and more widespread in extensor muscles, whereas the poststimulus and postspike suppression effects are found predominantly in flexor muscles. A greater excitatory effect from the motor cortex on extensors may seem surprising, but this is consistent with clinical evidence that precentral strokes produce greater paresis in distal extensors. Functionally, this difference may be related to the greater capacity for differentiation of flexion movements in the digits. The ability to fractionate finger flexion may well involve the more specific excitatory muscle fields of flexor CM cells and the more numerous inhibitory linkages to flexor musculature.

If output effects mediated by disynaptic linkages are included, the muscle fields of CM cells may encompass inhibited as well as facilitated motor units. This would be analogous to primary sensory cortex cells whose receptive fields have inhibitory as well as excitatory components. Many postcentral neurons activated by cutaneous stimulation of their excitatory fields can be inhibited by stimulation of the surrounding skin (Mountcastle and Powell, 1959b; cf. Figure 7C). Even the simplest receptive fields of primary visual and auditory cortex cells commonly include inhibitory regions flanking an excitatory area. Thus, like their sensory cortex counterparts, many motor cortex CM cells can code suppression as well as excitation.

Somatotopic Maps

Maps of the cortical locations of cells responsive to input from different peripheral sites have become relatively detailed in sensory systems, largely because the cells' receptive fields can be characterized readily, even in anesthetized animals. Comparable somatotopic maps in the motor cortex of output sites to musculature may be surmised on the basis of stimulation experiments, but the resolution of details remains limited. Such motor maps generally show disproportionately larger areas devoted to distal rather than proximal musculature (Figure 1). Although the relative sizes of these cortical areas seem disproportionate compared with the sizes of their corresponding somatic regions, they are consistent with the greater number and finer capacities of distal muscles. In both the visual and the somatosensory cortex, the extent of the cortical area devoted to peripheral regions also appears to be proportional to the density of peripheral receptors rather than to the size of the peripheral regions per se.

Stimulation experiments that documented the lowest-threshold muscle response to cortical stimulation led to the notion that a given cortical site represents a

single muscle. It is now clear that microstimulation generates subthreshold output effects in many muscles; in fact, even a single CM cell may facilitate motor units in multiple target muscles. Thus, on the cellular level, the cortical representation of muscles often involves groups of muscles rather than single muscles.

Several lines of evidence indicate that neighboring CM cells have similar or identical muscle fields. In acute experiments, adjacent PTNs could be activated antidromically from the same motoneuron pools (Asanuma et al., 1979). In chronic studies, different CM cells encountered in a localized region often facilitated similar sets of muscles; the muscle fields of neighboring CM cells were either identical or differed by no more than one muscle. Consistent with this cortical organization is the observation that single-pulse microstimuli delivered near a CM cell facilitate the same target muscles that were facilitated in spike-triggered averages of the CM cell; the stimuli, however, produce a much stronger effect, suggesting that a group of CM cells with common target muscles is synchronously activated (Cheney and Fetz, 1977).

A given muscle, on the other hand, can be facilitated by CM cells distributed over fairly wide cortical regions. No obvious cortical distribution pattern of CM cells affecting a muscle has yet been delineated. Phillips and Porter (1964) found that the colony of CM cells that evoke monosynaptic excitatory postsynaptic potentials (CM-EPSPs) in a cervical motoneuron can be distributed over wide areas of cortex. Similarly, Jankowska et al. (1975) demonstrated that CM-EPSPs in lumbar motoneurons can be evoked from wide, irregularly shaped patches of cortex. Moreover, these regions could be separate for motoneurons of the same pool and overlap for motoneurons of different muscles. Taken together, the evidence suggests that each muscle is represented by CM cells scattered over diverse precentral sites, and that at each site a muscle is represented in combination with various others.

On the basis of this organization and from the fact that CM-EPSPs are subthreshold, we can surmise that the contraction of a single muscle in isolation involves the activation of all of its CM cells (as well as additional inputs from cells in other regions). The fact that CM cells have divergent connections to multiple target muscles would not preclude their participation in the isolated contraction of a common single muscle: Their effects on the additional target muscles would be subliminal. Thus, for motor as well as sensory cortex, the cortical activity associated with a spatially localized peripheral event would involve simultaneous activation of many neurons whose fields share the activated peripheral element, but which each represent additional elements.

Coding of Muscle Activity by CM Cells

To determine how the activity of CM cells is related to the initiation and maintenance of active muscle contraction, their firing patterns were examined during ramp-and-hold torque responses (Cheney and Fetz, 1980). Figure 5 illustrates the two most common patterns of CM cell activity associated with active torques about the wrist. During isometric ramp-and-hold responses, most of the CM cells (59%) exhibited a phasic-tonic firing pattern. The phasic-tonic CM cell fires a phasic burst of activity during the dynamic changes in force at the onset of movement, and codes the static force during the subsequent hold period in its tonic discharge.

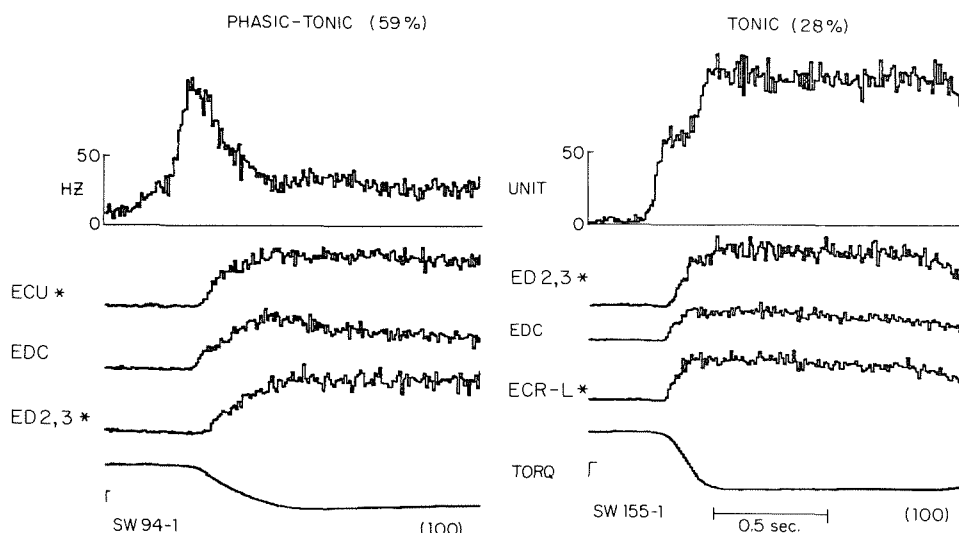


Figure 5. Firing patterns typical of CM cells during ramp-and-hold wrist responses. The firing pattern of most CM cells (59%) during ramp-and-hold torque trajectories was phasic-tonic (*left*): A phasic burst of activity preceded onset of movement, and tonic firing occurred during the static hold period. The second most common type of pattern (28%) was tonic (*right*); this involved steady activity throughout the hold period without any higher burst of activity at onset. The target muscles for these two cells are indicated by asterisks. These torque responses were isometric. (From Cheney and Fetz, 1980.)

The initial burst of cell activity usually begins well before the onset of activity in its target muscles (mean relative onset latency: 71 msec), and therefore contributes to the activation of the facilitated motor units. Since its onset precedes changes in peripheral activity, this phasic burst must originate from central sources. The magnitude of the phasic burst is often proportional to the rate of change of torque (Figure 6), a relation that has been documented previously for PTNs (Evarts, 1967, 1968; Smith et al., 1975). This burst is not simply related to overcoming the inertial loads in moving the hand, since it also appears during isometric responses, when the hand remains stationary. Thus, the phasic burst is a centrally driven discharge that contributes to the change in active force. In the burst, spikes with brief interspike intervals effectively excite the cell's target muscles, and when reciprocal inhibitory links are present, also help turn off their antagonists.

Besides contributing to changes in active force, the activity of CM cells also codes the intensity of static muscle force. During the static hold period, when the monkey maintains steady tension against an elastic load, most CM cells (87%) show a tonic, steady firing rate. Such steady discharge is characteristic of both phasic-tonic cells and the next most common type, tonic CM cells (28%), which show no phasic burst with the onset of movement (Figure 5). The tonic firing rate during the static hold period is an increasing function of the static torque exerted by the monkey; this relation has been observed previously for PTNs firing during wrist and finger movements (Evarts, 1968, 1969; Smith et al., 1975; Thach, 1978). Figure 6 shows that when the monkey exerted different levels of static torque at the same wrist displacement, the tonic firing rate of the

CM cell increased linearly over the upper torque range. Since this cell facilitated agonist target muscles, its activity contributed to the active force.

The phasic-tonic response pattern characteristic of most CM cells during ramp-and-hold active torques is quite similar to the response patterns evoked in many postcentral cells by the onset and maintenance of peripheral stimuli. Figure 7 illustrates the sensory responses of postcentral neurons evoked by ramp-and-hold proprioceptive and cutaneous stimuli (Mountcastle and Powell, 1959a,b). These neurons, in cortical areas 1, 2, and 3, responded to changes in joint angle or to pressures on the skin with a phasic burst at onset, followed by tonic discharge during maintained stimulation. For many joint cells, the level of tonic discharge was proportional to the maintained angular displacement, as shown for a thalamic cell in Figure 7D. Similarly, the sustained discharge of slowly adapting cutaneous neurons is proportional to the intensity of the tactile stimulus (Mountcastle and Powell, 1959b). In many cases the phasic burst at stimulus onset is proportional to the rate of change of the stimulus. Although the activity of motor cortex CM cells is centrally initiated during voluntary movement, whereas the activity of postcentral cells is evoked by peripheral stimulation, in both cases the cortical cells that are most closely linked to the periphery code changes in

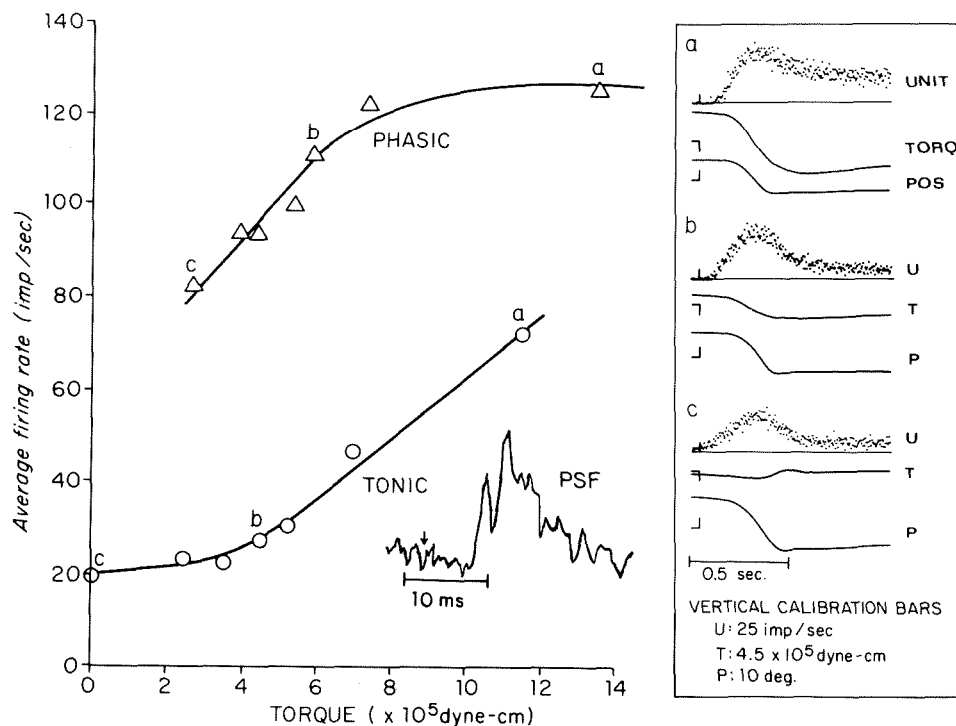


Figure 6. Relation between CM cell activity and active torque. Responses of an extension CM cell for movements into the same hold zone against different loads are shown on the right. The tonic firing rate during the static hold period was an increasing function of active torque, as plotted in the graph on the left. The phasic activity also increased as a function of the rate of change of torque. The inset shows the postspike facilitation produced by this CM cell in one of its target muscles. (From Cheney and Fetz, 1980.)

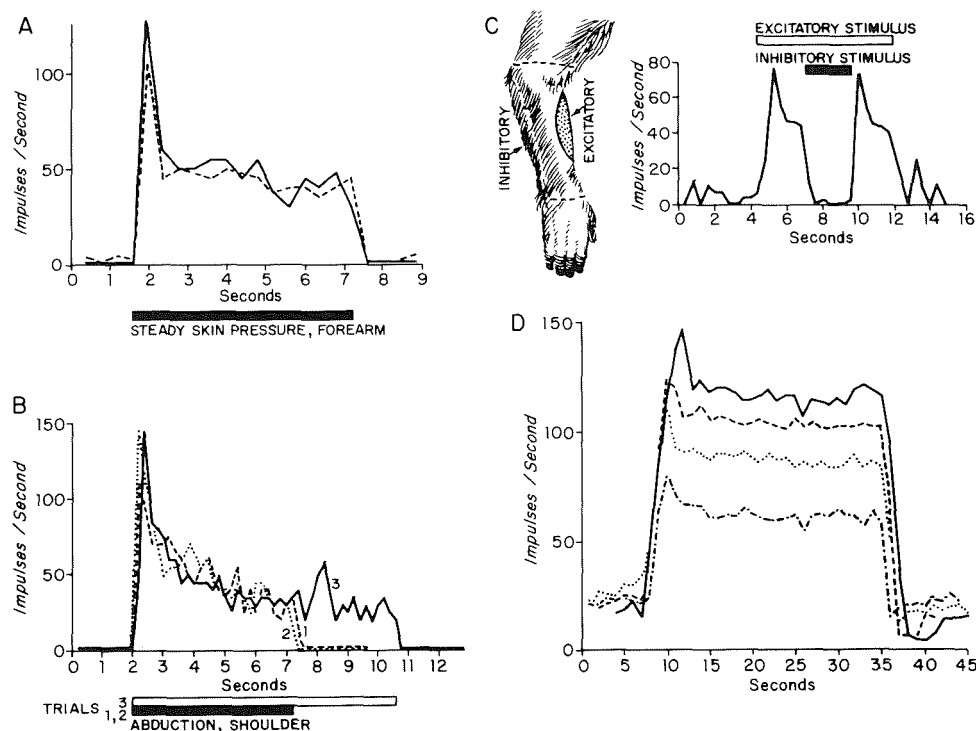


Figure 7. Phasic-tonic responses of cells in postcentral sensory cortex and thalamus evoked by peripheral stimulation. **A:** Response of an area 2 cortical cell to a steady pressure stimulus delivered to its receptive field on the contralateral forearm; two successive stimuli illustrate repeatability of the phasic-tonic response pattern (Mountcastle and Powell, 1959b). **B:** Response of a postcentral area 3 cell during abduction of the contralateral shoulder (Mountcastle and Powell, 1959a). **C:** Response of a postcentral cortex area 1 cell to stimulation in excitatory and inhibitory cutaneous receptive fields of the contralateral arm. Stimulation in the excitatory field generated a phasic-tonic pattern of discharge, which could be inhibited by stimulation in the inhibitory field (Mountcastle and Powell, 1959b). **D:** Response of a ventrobasal thalamic cell to passive knee extension. With identical velocities the knee was extended to angles (from upper line downward) of 180, 125, 100, and 80°. Note that tonic discharge increases in proportion to joint angle. (From Mountcastle et al., 1963).

the peripheral parameter by a burst at onset and code the static intensity by the rate of tonic discharge.

Higher-Order Relations to Muscle Contractions

Of the many neurons in the primary motor cortex, CM cells have the most direct links to motor units. Other motor cortex cells exhibit more complex firing patterns during the same ramp-and-hold movements, but such cells produce no postspike effects in spike-triggered averages of agonist muscles, indicating that they are not as closely linked to the agonist motoneurons. For example, many precentral cortex cells discharge phasically at the onset of movement, but show no tonic discharge during the hold period. Some of these may be related to phasically active muscles; others may be higher-order cells that contribute to the phasic component of CM cell discharge. Phasic motor cortex cells are analogous to

many somatosensory cortex cells that fire transiently only at the onset of a stimulus, adapting quickly to a firing rate of zero for static stimuli (Mountcastle and Powell, 1959a; Soso and Fetz, 1980; Gardner and Costanzo, 1981). Transient responses at stimulus onset are commonly seen in visual and auditory cortex neurons as well. Such transient responses often reflect transient input from rapidly adapting receptors, but may also result from inhibitory circuits and neural adaptation.

Some of the phasic precentral cells fire with both flexion and extension of a single joint (Fetz et al., 1980), as if coding primarily the onset of active joint movement, independent of its direction. Extrapolating further, one wonders whether even higher-order relations to muscle activity may be represented in motor cortex cells. Indeed, experiments designed to investigate the activity of motor cortex cells during the contraction of different sets of forearm muscles showed that many precentral neurons had response patterns related to remarkably diverse muscle groups. In these experiments, the monkey's forearm was held isometrically in a cast and the animal was operantly rewarded for isolated contractions of each of four muscle groups, the extensors and flexors of the wrist and elbow (Fetz and Finocchio, 1975). Figure 8 illustrates the responses of two

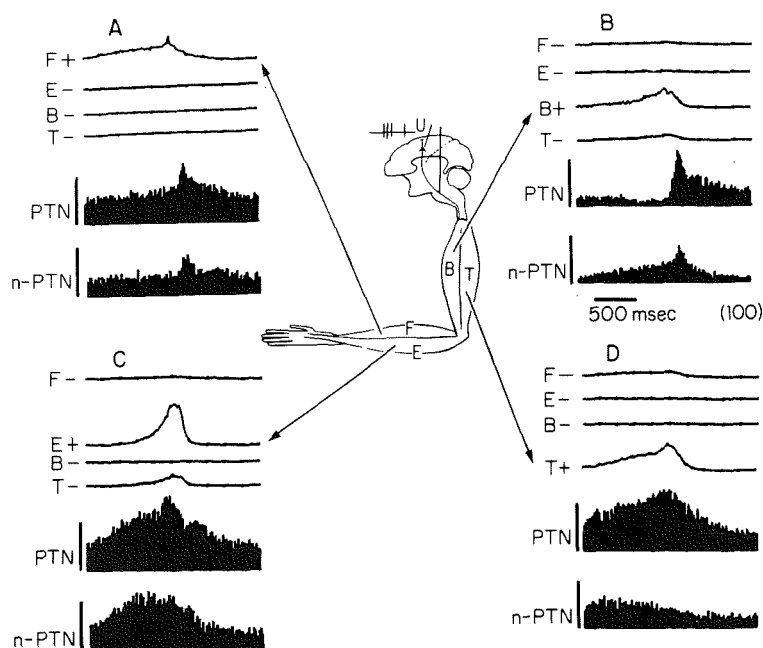


Figure 8. Higher-order relations of precentral motor cortex cells to isometric contractions of four sets of forearm muscles. Inset indicates recordings from wrist flexor (*F*) and extensor (*E*), biceps (*B*), and triceps (*T*). Response averages show isometric activity of muscles and two neighboring cells: a PTN and a n-PTN. These cells fired during contraction of the wrist and elbow extensor muscles (*C* and *D*). In relation to wrist and elbow flexor muscles, both cells fired a burst of activity as the muscle activity was decreasing (*A* and *B*). Compared with CM cells, these cells have a higher-order relation to muscle contraction: Spatially they are related to sets of muscles acting at different joints and temporally they exhibit an "off" response with the flexor muscles and an "on" response with the extensor muscles. Spike-triggered averages showed no correlational linkages to these muscles. (From Fetz and Finocchio, 1975.)

neighboring motor cortex cells recorded simultaneously; one was a PTN and the other a non-PTN (nPTN). In relation to isometric bursts of activity in the wrist extensor and the elbow extensor (Figure 8C,D), these units fired in association with the activation of the muscles. This pattern of coactivation with the muscle bursts could contribute to turning on the extensor muscles. In contrast, when the monkey activated the wrist or elbow flexors (Figure 8A,B), both units showed a peak of activity as the flexor muscles were turning off. Such "off" responses were characteristic of many other motor cortex cells in this region of area 4; they sometimes occurred in cells that also exhibited "on" responses with contraction of other muscles; one nPTN exhibited the same "off" response with all four muscles. These patterns of motor cortex cell activity may represent more complex relations to muscle activity than simple coactivation with a single set of synergists. The activity of such higher-order cells appears related to a larger spatial set of muscles, in this case pairs of antagonists acting at two different joints. Moreover, the temporal patterns reflect more complex changes in the activity of the muscles. These response properties are analogous to the responses of higher-order complex cells in the visual cortex that are affected by input from relatively large receptive fields and code more complex temporal patterns of stimulation within those fields than do simple cells (Hubel and Wiesel, 1965). Similarly, polyjoint cells in the posterior parietal cortex respond to passive rotations of multiple joints of the limbs; their activity represents convergent input from spatially diverse regions and codes more complex combinations of temporal patterns (Duffy and Burchfiel, 1971).

These observations may be considered in terms of a strictly hierarchical model of neural elements. In the sensory system, the representation of ever larger spatial fields in cells from peripheral receptors to primary cortex to association areas would be the consequence of the divergence of connections between successive cells. The extraction of more specific temporal features, such as the onset and offset of the stimulus, could be the result of several mechanisms: (1) temporal summation of input to relay cells, which assures that the most intense and most synchronous activity propagates furthest into the neural network; (2) interactions between excitatory and inhibitory neurons; and (3) neuronal adaptation, which reduces the response to sustained input. These features of a serial neural network would lead to the representation of larger receptive fields and the extraction of spatial and temporal derivatives of stimulus events at successively higher levels.

How plausible is it to consider the motor system to be analogously organized, with hierarchical levels of neurons coding the higher-order features of a motor response? Going centrally from motoneurons to primary motor cortex to secondary motor areas, representative cells do appear to be related to larger groups of muscles and to earlier stages of motor programming (Brinkman and Porter, 1979; Humphrey, 1979; Wiesendanger, 1981; Tanji and Kurata, 1982). In principle, a movement could be determined by the preceding neural activity in a strictly serial hierarchical network of cells in the motor system just as completely as a stimulus is represented by the subsequent activity it evokes in a serial sensory network. Yet a strictly serial hierarchy of cells in spatially separate regions of the motor system becomes implausible in view of the many reciprocal connections between cortical and subcortical regions. Although such interconnections preclude a strictly serial hierarchical network, a functional hierarchy of neurons involved in programming and execution remains likely.

FUNCTIONAL LOOPS

Peripheral Inputs to Precentral Cells

Figure 9 schematically summarizes some of the analogous features of the representation of peripheral elements in primary motor and sensory cortex cells. The target muscle field of CM cells is shown as the motor analogue of the distributed receptive field of somatosensory cortex cells. Each cortical cell codes a ramp-and-hold activation of peripheral elements by a burst of discharge at onset, followed by sustained discharge during maintained activity. These analogous properties involve similar relations to the periphery, despite the fact that the main flows of impulses are in opposite directions: Sensory input originates peripherally, whereas voluntary motor activity originates centrally. This simple picture must be extended to include feedback loops formed by reciprocal connections between the cortex and the periphery.

Motor output commands normally are generated in the context of continual feedback from receptors in muscles and skin. Peripheral input to many motor cortex cells is sufficiently potent to generate clear responses to passive joint movement or tactile stimulation (Rosen and Asanuma, 1972; Fetz and Finocchio, 1975; Lemon and Porter, 1976; Murphy et al., 1978; Fetz et al., 1980). This peripheral input to motor cortex cells usually originates in receptors that are closely associated with the muscles whose active contraction involves the cells. The duration of active movements such as those illustrated in Figures 2, 5, 6,

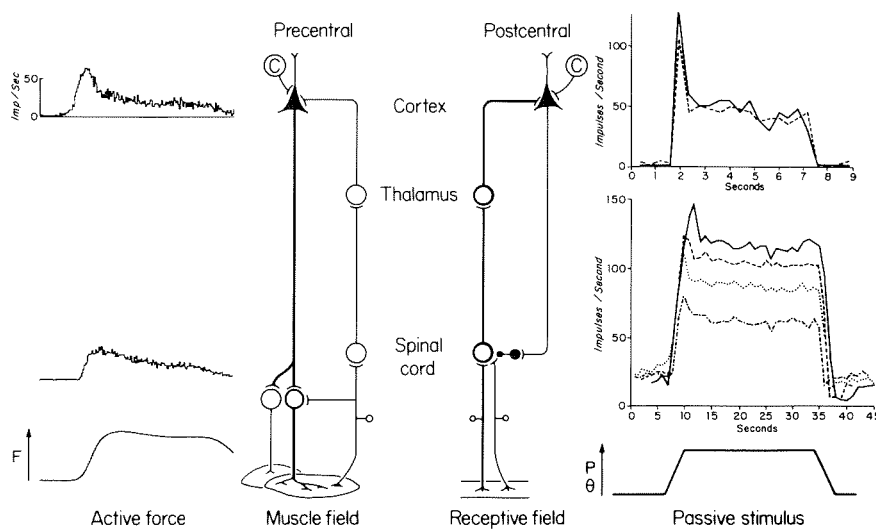


Figure 9. Analogous relations between precentral motor cortex cells and muscles (*left*) and postcentral sensory cortex cells and receptors (*right*). In each case the cortical cell is related to a spatially distributed set of peripheral elements, a muscle field or receptive field. The phasic-tonic response patterns of each cell code onset and intensity of the peripheral event (movement or stimulus). Loops with the periphery can also be considered analogous. In addition to peripheral input, both precentral and postcentral cells may receive centrally originating input, evident prior to voluntary movements, as indicated by cells labeled C. Records at right (from data of Mountcastle and his colleagues) show response of an area 2 cell to cutaneous pressure (*top*) and proprioceptive response of thalamic cell to knee extension (*middle*).

and 8 leaves ample time for the return conduction of impulses from peripheral receptors affected by the movements; during a ramp-and-hold movement CM cells show a tonic discharge throughout the hold period (Figure 5), which can be sustained by input from the peripheral receptors. When tested for responses to natural stimulation, most CM cells respond to passive joint movements that stretch their target muscles. Close input-output linkages between PTNs and muscles have been deduced from previous experiments (Rosen and Asanuma, 1972; Evarts and Fromm, 1978; Murphy et al., 1978; Sakai and Preston, 1978). In the baboon, motor cortex neurons have been activated by stretching specific muscles; interestingly, the discharge pattern of many PTNs evoked by passive ramp-and-hold stretch is also phasic-*tonic* or *tonic*, with the tonic discharge proportional to muscle length (Hore et al., 1976; Sakai and Preston, 1978). Thus, during active movement the response patterns of precentral cells must reflect inputs from the periphery superimposed on command signals from central sources. Indeed, the central command to a CM cell must be appropriately timed to sum with subsequent peripheral input so that the cell's resultant firing pattern contributes appropriately to sustain the movement. For example, if peripheral feedback makes an appreciable contribution to the tonic discharge of CM cells during ramp-and-hold movements (Figure 5), the central input could contribute primarily at the onset of movement. Thus, a sufficiently positive feedback loop through the periphery could transform a transient central command at movement onset into a sustained motor response.

Whether such a positive feedback loop has sufficient gain during voluntary movements to integrate transient central commands remains to be determined. Indeed, the net sign of the transcortical feedback loop—whether positive or negative—depends on two unknowns: the relative afferent contribution from different types of stretch receptors and the relative efferent effects of CM cells on alpha versus gamma motoneurons (cf. Evarts, this volume). If muscle spindles provide the main input to CM cells, which in turn activate motor units that unload the spindles, the feedback loop would be negative; this kind of loop would be appropriate for transcortical load compensation reflexes. The role of feedback to precentral cells has been amply discussed in relation to such transcortical reflexes, which act to overcome load perturbations (Phillips and Porter, 1977). The type of feedback received by PTNs and CM cells is certainly consistent with this hypothesis (Lemon and Porter, 1976; Evarts and Fromm, 1978; Murphy et al., 1978; Sakai and Preston, 1978; Cheney and Fetz, 1984).

Descending Control of Sensory Pathways

Just as motor cortex cells are situated in a functional loop that includes input from peripheral receptors, so also many sensory cortex cells form a comparable loop through descending connections, which may affect their input (Figure 9). It has become clear that the cerebral cortex can exert considerable influence on transmission along afferent sensory pathways via the pyramidal tract and other descending pathways (Towe, 1973). Postcentral sensory cortex cells affect spinal cord interneurons and dorsal column nuclear cells, both of which give rise to ascending projections (Coulter and Jones, 1977). The predominant effect of the pyramidal tract on cells transmitting input from cutaneous receptors to higher

centers seems to be inhibition (Fetz, 1968; Towe, 1973; Coulter et al., 1974) mediated by presynaptic inhibition of afferent fibers and by postsynaptic inhibition of relay cells. Thus, the activity evoked in these sensory cortex PTNs would result in suppression of subsequent input via the afferent pathway. This sort of negative feedback loop through postcentral cells might function to extend the range of stimulus intensities coded. The conduction times in these loops, 20–30 msec, would be fast enough to contribute to the adaptation of responses observed at the cortex. Another functional consequence of such a loop is the focusing of peripheral input on the dominant stimuli by suppression of the weaker surroundings.

Clearly, even such transcortical loops between peripheral elements and the cerebral cortex are oversimplified abstractions if they are imagined to operate independently. During normal behavior, the motor output affects the peripheral receptors that feed back into the sensory cortex and, conversely, some of the descending output from the postcentral cortex affects interneurons in the spinal cord that are involved in segmental reflex pathways. Moreover, the precentral and postcentral cortices are heavily interconnected at the cortical level as well (Jones et al., 1978). Such interactions explain the discovery of cells with similar response properties in the pre- and postcentral cortex. When tested under comparable behavioral conditions, neurons with comparable response properties are found to be widely distributed. Thus, under passive conditions many precentral cells, like most postcentral cells, respond to natural stimulation, and during active movements some postcentral cells, like many precentral cells, change activity prior to movement.

Central Input to Sensory Cortex

Just as precentral motor cortex cells receive input from both peripheral and central sources, so do many postcentral “sensory” cortex cells. Recent studies in behaving primates have revealed a centrally originating modulation of postcentral cells that changes their firing rates prior to active movements. Most of these postcentral cells also respond readily to passive joint rotation or cutaneous stimulation, as documented in inactive primates (Mountcastle and Powell, 1959a,b). With active movements this early modulation can occur well before the first signs of EMG activity; it may be excitatory or inhibitory. Figure 10 illustrates the activity of a postcentral area 2 cell during passive and active elbow movements. A phasic-tonic response pattern accompanied both passive and active elbow extensions; however, when the monkey actively extended the elbow, the amount of phasic activity was clearly reduced. The activity of this cell actually began to decrease prior to the agonist muscle activity, suggesting that the suppression originated centrally. The response pattern of this neuron is typical of many postcentral area 2 cells that responded to proprioceptive input from rotation of the elbow (Soso and Fetz, 1980).

Other postcentral cells increase their firing well before active movements, as do many precentral motor cortex cells. Fromm and Evarts (1982) found that many postcentral PTNs discharge before movement and have firing rates proportional to the active force. Depending on their projections, such PTNs may contribute to motor output as well as to sensory modulation. Jennings et al.

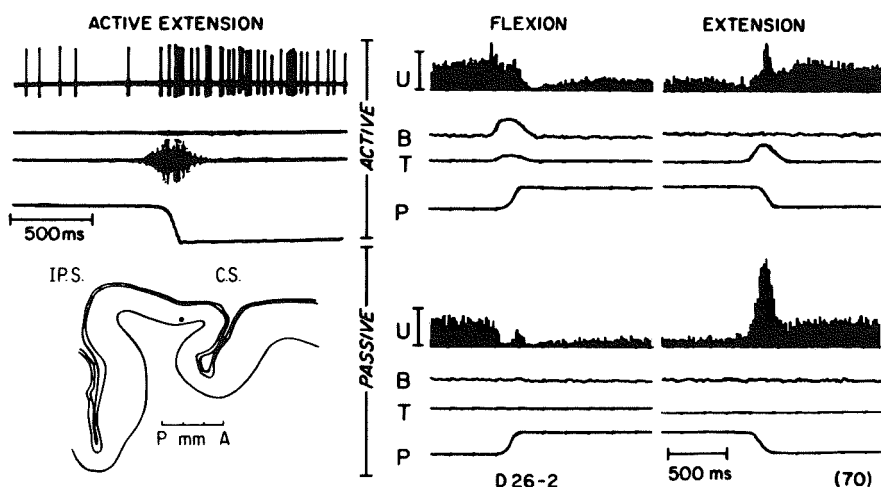


Figure 10. Response patterns of a postcentral area 2 neuron during active and passive elbow movements. During both passive and active elbow extension, the cell fired in a phasic-tonic pattern; however, during active movements the phasic component was clearly reduced. As in many other postcentral cells, this inhibition began before the active response and may be related to central suppression of the peripheral input. 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 the cell. I.P.S., intraparietal sulcus; C.S., central sulcus. Averages at right show unit activity (*U*), average rectified EMG of biceps (*B*) and triceps (*T*), and elbow position (*P*). (From Soso and Fetz, 1980.)

(1983) showed that the activities of many postcentral cells code active force as well as displacement; their response properties often resemble those of precentral cells. Thus, when precentral and postcentral cells are observed under the same behavioral conditions, similar cell types can be found in both areas. Of course, there are clear differences in the relative number of cell types and the degree of precision with which cells of each area code peripheral activity. Most postcentral cortex cells respond to finer gradations of passive stimulus parameters than do precentral cells; conversely, precentral cells contribute more effectively than postcentral cells to active muscle contractions. However, the observation of similar cell types in both the pre- and postcentral cortex suggests that such differences are more a matter of degree than an absolute dichotomy (Woolsey, 1958). Considering the full range of cell types in each area and the fact that stimulation of either area can generate movements or evoke sensation, it seems likely that precentral cortex and postcentral cortex may each participate in both motor and sensory processes.

SYMMETRIES AND PARALLELS

The list of analogies between sensory and motor cortex can readily be extended to include additional anatomical relations with subcortical centers, particularly their corresponding thalamic nuclei. Moreover, it has been suggested that the intrinsic cortical circuitry may involve similar neuronal "modules" replicated in

different cortical areas (Hubel and Wiesel, 1965; Mountcastle, 1979); such cell modules could provide similar local input-output processing for the neural activity propagating through each cortical region. Further structural and functional analogies are likely to emerge if the processing of sensory and of motor events involves comparable mechanisms.

The analogous properties discussed here may be divided into those that are parallels—similar in sensory and motor cortex—and those that represent symmetric opposites. The parallels include the similar receptive field properties of precentral and postcentral cells, the columnar arrangement of neurons with common inputs in both areas, the similar laminar organization of cortical cells, and so on. On the other hand, the receptive fields of sensory cortex cells represent the symmetric inverse of the muscle fields of CM cells, insofar as cortical inputs are coded analogously to outputs. The symmetric representation of spatial fields of peripheral elements by cortical cells is clearly the result of convergent input connections to sensory cells and divergent output connections from precentral CM cells. Less obvious, perhaps, is the reason for analogous coding of onset and intensity of peripheral events in phasic-tonic discharge patterns, since the sources and targets of this activity are quite different. The behavioral functions of sensory perception and motor programming also involve opposite causal relations to their peripheral correlates. These higher-order integrative functions may be subserved by symmetric neural mechanisms but, given the extensive interactions involved, they must also involve the parallel properties of sensory and motor cortex.

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