

# Correlations Between Task-Related Activity and Responses to Perturbation in Primate Sensorimotor Cortex

JONATHAN R. WOLPAW

*Laboratory of Neurophysiology, National Institute of Mental Health,  
Bethesda, Maryland 20205*

## SUMMARY AND CONCLUSIONS

1. Monkeys were trained to maintain hand position against a range of constant forces. Short-latency responses to passive wrist extension or flexion, as well as short-latency responses to stretch of a single wrist muscle, were recorded from units in areas 4, 3, 1, and 2. These responses were compared to unit activity during active holding and during active movement.

2. Units related to active holding and to active movement were most common in areas 4 and 2. Three-quarters of these units displayed a specific correlation between their passive and active behaviors. Thus, a unit excited by passive extension was excited during active holding against extension force and excited during an active flexion movement. This behavior is similar to the expected concurrent behavior of muscle stretch receptors. By demonstrating that a significant number of task-related units give qualitatively similar responses to passive extension and passive flexion, the results appear to explain the disagreement among previous studies (5, 9, 36) in regard to area 4 behavior during active and passive movements.

3. Area 4 units responded similarly to passive wrist extension and electromagnetic stretch of a single flexor muscle occurring in the absence of wrist extension, indicating that muscle stretch was important in determining area 4 unit responses to passive movements.

4. The similarity of area 4 behavior to area 2 behavior in active and passive situations, along with the observation that area 2

responses to passive movements occurred several milliseconds earlier than those of area 4, emphasizes the importance of area 2 in motor performance and is consistent with significant area 2 mediation of area 4 responses.

5. Results support the hypothesis of an oligosynaptic transcortical pathway (22, 32, 34), beginning in large part with muscle stretch receptors. Furthermore, the correlation noted between short-latency responses to passive movement and task-related activity suggests that this transcortical pathway not only mediates responses to passive movement but may be responsible, to a significant degree, for task-related activity during undisturbed performance. Thus, active position maintenance and active movement were probably accomplished, at least in part, by increasing and decreasing the influence of this pathway on specific area 4 neurons and thereby producing the patterns of area 4 activity responsible for task performance.

## INTRODUCTION

The clear relation of the precentral gyrus (area 4) to movement and the equally clear relation of the postcentral gyrus (areas 3, 1, and 2) to somatosensory input have strongly affected studies of these regions. Thus, motoneuron and electromyographic (EMG) activity resulting from stimulation of area 4 has been intensively studied, and area 4 neuronal activity has been correlated with active movement and active position maintenance. In contrast, postcentral cortex unit activity has been precisely related to stimu-

lation of specific peripheral receptors. Its relation to motor activity remains largely unexplored in spite of the observation that stimulation of this region can produce movement (12, 58) and the more recent finding that corticospinal neurons reside here as well as in motor cortex (6, 20, 33).

The recognition that area 4 responds very quickly to a perturbation imposed during motor performance (5, 8, 36) has generated interest in the relationship between its sensory input and its motor output. The proposal by Koeze et al. (22) and Phillips (34) of a transcortical loop, an oligosynaptic pathway by which peripheral input generates compensatory area 4 activity, is supported by most (5, 9, 13, 32), though not all (24, 36), studies. That is, most studies have found that area 4 neurons that are active with active movement in one direction are usually excited by passive movement in the other direction. The observation that area 4 neurons do not respond to a perturbation if the task forbids compensatory movement (8, 10, 11) is an additional indication that short-latency peripheral input elicits compensatory activity. Such input could also be important in producing the task-related activity responsible for undisturbed performance. If this were the case, task performance would involve controlling peripheral access to area 4 neurons. Evaluation of this possibility requires knowledge of the specific aspect of peripheral input most important in determining area 4 response in a given situation, whether muscle stretch, joint rotation, tactile stimulation, or a combination of the three.

The prevalence and characteristics of postcentral task-related activity have only recently come under study (41). The relation of such activity to peripheral input and to concurrent area 4 activity requires extensive investigation. The role of the postcentral gyrus in mediating area 4 short-latency responses is unresolved.

The present study asked several questions about the relationship between task-related neuronal activity and neuronal responses to perturbations in both precentral and postcentral regions. The specific questions were: *a*) Do the responses of task-related area 4 neurons to perturbations tend to compensate for the perturbations, as

most studies report (5, 9, 13, 32) and, if so, can apparently contradictory findings (24, 36) be accounted for? *b*) Is muscle stretch, as opposed to joint rotation or tactile stimulation, an important determinant of area 4 responses? *c*) When does each area of the postcentral gyrus respond to perturbations in relation to the response time of area 4? *d*) Are task-related neurons found in the postcentral gyrus, and in what areas are they most frequent? *e*) How does postcentral task-related activity relate to postcentral responses to perturbations?

## METHODS

### *Training*

Each of four monkeys (*Macaca mulatta*) was seated in a primate chair. The right arm was snugly restrained above the elbow and at the wrist so that the elbow angle was fixed at 90°, and the right palm was strapped to a torque motor handle that moved in the plane of wrist extension and flexion. Because the handle was firmly strapped across the animal's palm, its fingers did not contribute to control of handle position. The absence of need for finger use and the lack of finger restraint minimized change in length of forearm finger muscles, as opposed to forearm wrist muscles, caused by passive and active movements. This design was intended to limit as much as possible the responsive and task-related neurons to those related to wrist movement, as opposed to just finger movement. The effects of a compensatory transcortical loop on neurons concerned primarily with finger movement might differ markedly, depending on whether the eliciting disturbance stretches finger muscles at the wrist joint or at the finger joints; thus these neurons could have greatly complicated data analysis. Similarly, fixation of the elbow angle was intended to exclude the majority of neurons responsive to movement about the elbow. These features helped to compensate for the usual absence of comprehensive receptive-field evaluation, which was impractical due to the experimental apparatus. Each monkey received liquid reward at pseudorandomly varying 3- to 6-s intervals for maintaining the handle in a middle zone of 6° (occasionally 12°), with its wrist neither flexed nor extended. Handle position was monitored by a potentiometer mounted on the motor shaft. A light signaled presence of the handle in the reward zone. The torque motor could apply extension or flexion constant background force to the handle, requiring continuous exertion by wrist flexors or extensors,

respectively, if the handle was to remain in the reward zone. The torque motor cycled through five levels of background force: zero, strong extension, strong flexion, weak extension, and weak flexion. Each level was maintained until the monkey earned 16 rewards. The force range was set to allow the monkey to perform the task indefinitely. Absolute amplitude of strong extension and strong flexion background force was usually 0.03 N. Weak extension and weak flexion were half this absolute amplitude. Animals readily mastered the task over the course of one to four daily 3- to 4-h exposures. One-half second before reward delivery, a 50-ms force pulse of fixed absolute amplitude (1.4 times that of strong background force) was superimposed on the background force. This caused a handle displacement usually between 10 and 20°, depending on the animal and background force. (In a prerigor mortis monkey cadaver arm, extension of this magnitude lengthened the muscle flexor carpi ulnaris by 100–200  $\mu\text{m}$ .) Eight extension and eight flexion pulses in pseudo-random order were delivered at each background force level. In the course of performance, animals frequently left the reward zone, either spontaneously or as a result of a force pulse. Return into the reward zone was defined as corrective movement if it did not occur within 100 ms following onset of a force pulse. This condition excluded immediate rebound after the force pulse.

### *Surgery*

After training, each monkey was prepared under Nembutal anesthesia for chronic single-unit recording by standard methods (7). A head holder was attached to bolts implanted in the skull to allow immobilization of the head during unit recording. A chronic recording cylinder was centered over the arm region of primary motor and somatosensory cortex on the left side. Cylinder placement was determined by stereotaxic coordinates, by the minimal visualization of sulci possible through the dura, and by evaluation of the sulcal pattern via digital markings on the disk of skull removed (54). A pyramidal tract-stimulating electrode was positioned in the left medullary pyramid. In each of two monkeys, a 2-g,  $3 \times 5 \times 20$  mm, coated (26) iron slug was implanted in the distal musculotendinous junction of the right flexor carpi ulnaris (FCU) muscle (4, 56).

### *Recording*

Animals resumed performance several days after surgery. Experimental design was identical to that during training except that a solenoidal coil encircled the forearm of each monkey with an implanted slug (4, 56). One to two seconds before force pulse delivery, a 100-ms (7-ms rise

time) DC current pulse passed through the coil. The pulse exerted a 70-g distally directed force on the slug, and thus stretched the FCU (25–50  $\mu\text{m}$ , rise time 50–75 ms, measured in a prerigor mortis monkey cadaver arm). The stretch caused no change in handle position as measured by the potentiometer, and appeared to be ignored by the monkeys. It often produced a tendon jerklike FCU EMG response with a latency of 10–14 ms (56).

Single-unit recordings were obtained from each animal over a period of 2–3 mo. Penetrations were made perpendicular to the plane of the cylinder with glass-insulated platinum-iridium microelectrodes (52). The electrode was slowly advanced as the animal performed the task. Unit background activity and responses to force pulses were monitored on-line by a raster display. For each well-isolated unit that appeared to respond to extension and/or flexion force pulses, unit activity and handle position were recorded on tape for one or more experimental cycles. A cycle consisted of the 5 background force levels with 16 force pulses (and 8 or 16 FCU stretch pulses) at each level. The interlocking of extension and flexion background force levels, as noted above, provided a check against change in unit behavior over time. For two monkeys, corrective movement activity (that is, unit activity occurring with movements into the reward zone) was also recorded, unless such corrective movement occurred less than 100 ms after the force pulse (this stricture eliminated rebound from the force pulse). During selected penetrations, small lesions were made by current passage to aid later histological analysis.

### *Histology*

On completion of recording, animals were killed by an overdose of Nembutal and were perfused with normal saline and 10% Formalin. Brains were embedded in celloidin, cut in the sagittal plane at 50  $\mu\text{m}$ , and stained for Nissl substance with thionine. Sections were examined and cortical areas identified according to the criteria of Powell and Mountcastle (37) (Figs. 1 and 2). The area 4/area 3a boundary was located by marked decrease in cortical thickness and disappearance of Betz cells. The area 3b/area 1 boundary was placed primarily on the basis of increasing differentiation and decreasing density of middle cortical layers. The area 2 boundaries were more difficult to place. For the area 1/area 2 boundary, the most helpful features were increase in cortical thickness and appearance of large pyramidal cells in layers III and V. Increase in clarity of lamination and position in the gyrus were used to locate the area 2/area 5 boundary. More laterally, the area 2/area 7 boundary was placed at the bottom of the intra-

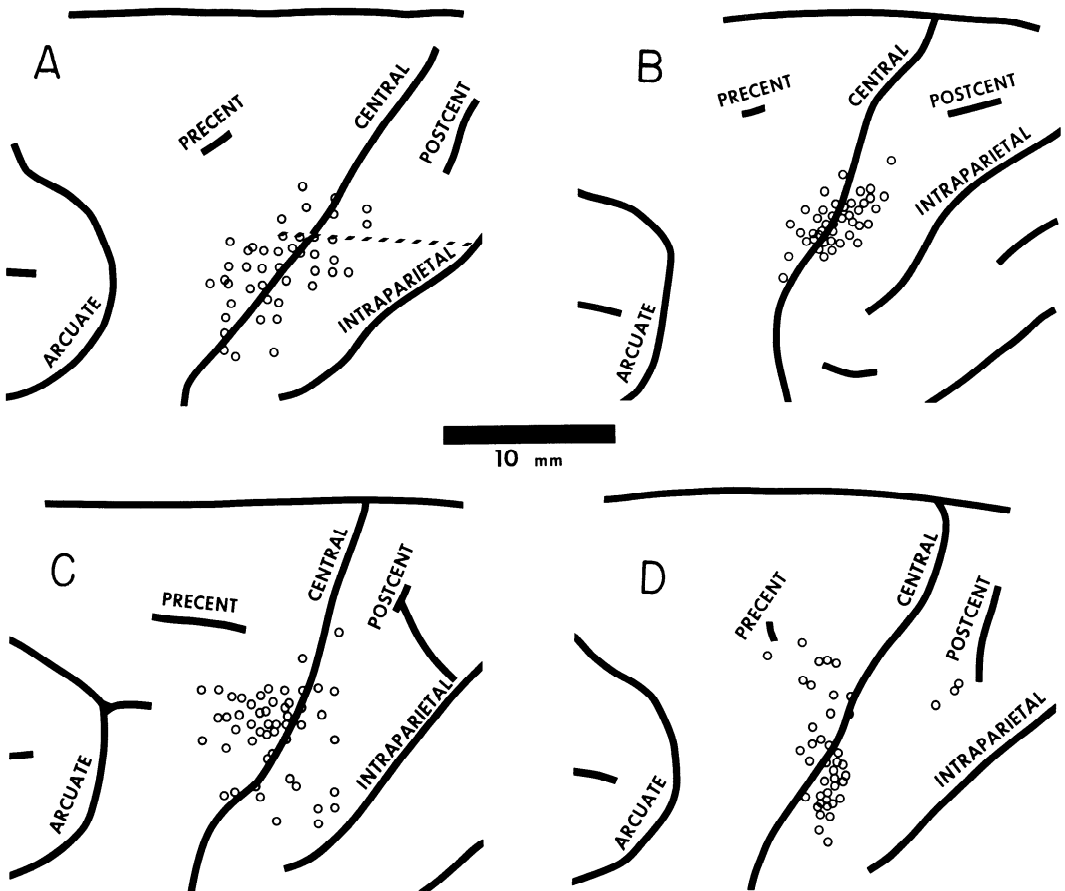


FIG. 1. Cortical surface maps of the four monkeys. Relevant major sulci are labeled. Circles indicate penetrations yielding units that responded to one or both force pulses within 60 ms. Dashed line in *A* gives the location of section shown in Fig. 2.

parietal sulcus, where transition from granular to homotypical cortex could be observed. The small size of area 3a and the uncertain cortical movement occurring with transdural penetrations did not permit a significant number of area 3 units to be confidently assigned to 3a or 3b. Thus this distinction was not made, and area 3a is included in area 3 in this report.

#### Data analysis

A PDP-12 computer analyzed and displayed single-unit activity and handle position in the form of peripulse and pericorrective movement rasters, histograms, and spike frequencies.

#### RESULTS

Data were obtained from 1,050 single units in the arm regions of areas 4, 3, 1, and 2. Analysis is confined to 504 units that responded to extension and/or flexion

force pulses with onset latencies of  $\leq 60$  ms, and for which sufficient data at multiple background force levels were available to determine whether unit activity was related to background force direction (that is, to position maintenance). Units that did not respond to either force pulse or responded only at latencies over 60 ms are not included in this analysis. For nonresponsive units, the presence or absence of task-related activity was not determined, since primary interest was in the relationship between force pulse responses and task-related activity. It was clear, however, that few, if any, nonresponsive units were task related. Maximum onset latency of 60 ms (8–10% of the 1,050 units first responded at latencies of 60–250 ms) ensured that initial response was due to peripheral events occurring

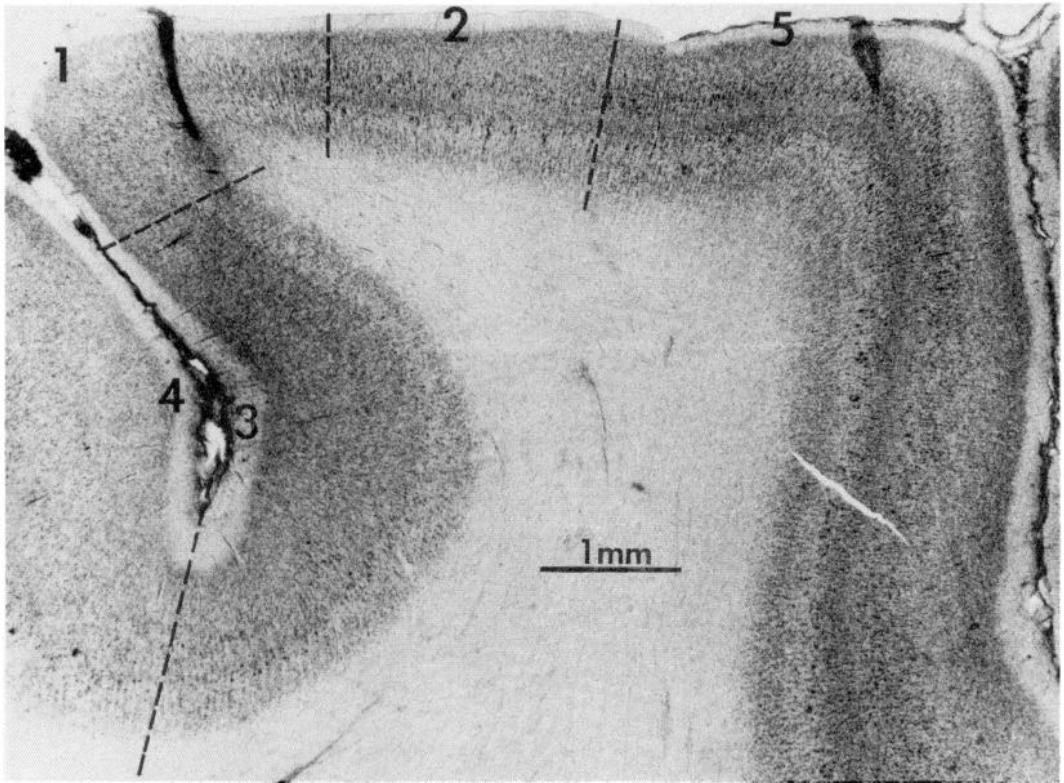


FIG. 2. Section across precentral and postcentral gyri in one monkey, showing division into areas. Location of section is given by dashed line Fig. 1A. Mark of a recent penetration is visible.

during initial displacement and was not solely due to events occurring during handle rebound, which began within several milliseconds of the end of the 50-ms force pulse. Onset latencies of all excitatory responses are shown by area in Fig. 3. Average latencies were 33 ms for area 4, 27 ms for area 3, 29 ms for area 1, and 30 ms for area 2. The three postcentral areas were not significantly different from each other [Kolmogorov-Smirnov two-sample test (40)]. Area 3 and area 2 responses were earlier ( $P < 0.01$  for each area) than area 4 responses, and area 1 responses were probably earlier ( $P < 0.05$ ).

Cortical maps of the four monkeys in Fig. 1 show penetrations from which these units were recorded. Surrounding regions were not fully explored, so the distributions probably do not indicate the full extent of the regions containing such units. Figure 2 is a sagittal section along the dotted line in Fig. 1A. It illustrates division into areas 4, 3, 1 and 2 (see METHODS).

#### Unit classification

Units were classified according to *a*) responses to extension and flexion force pulses, and *b*) task-related activity.

In all cortical areas, excitatory force pulse responses were 3 times as frequent as inhibitory responses. Units fell into three classes on the basis of the directional specificity of their responses: *a*) An absolutely specific unit was excited by one force pulse (flexion or extension) and/or inhibited by one force pulse (Fig. 4). *b*) A relatively specific unit (Fig. 5) was excited by both force pulses but gave a response to one at least 50% greater than its response to the other (response intensity was measured as the spike frequency in the 100 ms after pulse onset minus spike frequency in the 100 ms before pulse onset). It was not thought possible in most cases to quantify inhibition accurately; thus units inhibited by both force pulses were never labeled relatively specific. *c*) A nonspecific unit was

excited similarly by both pulses (one response was less than 50% greater than the other) or was inhibited by both pulses. Henceforth, the term exciting force pulse refers to *a*) the force pulse that excited an absolutely specific unit and/or was opposite to the force pulse that inhibited an absolutely specific unit, and *b*) the force pulse that most excited a relatively specific unit.

A unit was considered task related if it fulfilled at least one of two criteria. It was task related (to position maintenance) if its activity was clearly greater with background force in one direction than with background force in the other direction. It was task related (to corrective movement) if its activity increased during (and usually immediately before) corrective movement in one direction and decreased during (and usually immediately before) corrective movement in the other direction. (As noted above, immediate rebound after the force pulse did not qualify as corrective movement.) All 504 neurons were tested by the first criterion (relation to position maintenance) and 288 by the second (reciprocal relation to corrective movement). For units

classified as related to position maintenance, activity with background force in one direction averaged 3 times that with background force in the other direction.

In Table 1 are the units of each area divided according to the presence or absence of directional specificity and the presence or absence of task-related activity. Because the study concerned relationships between task-related activity and force pulse responses, the analysis focused on units that were both directionally specific and task related.

#### Area 4

Nearly two-thirds (64%) of area 4 units gave absolutely or relatively specific force pulse responses, and nearly half (49%) were task related to position maintenance and/or to corrective movement (Fig. 6). Ninety-three units were both specific and task related (Table 1).

For these 93 directionally specific task-related units, several strong correlations were evident between force pulse responses and directional activity. These correlations are presented in Fig. 7. First, for three-

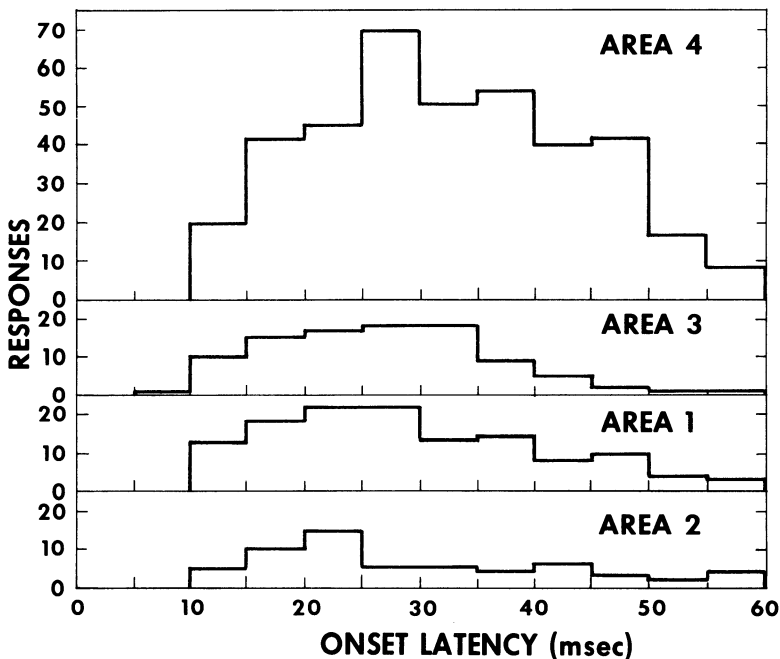


FIG. 3. Onset latencies of force pulse excitatory responses from areas 4, 3, 1, and 2. The three postcentral areas were not significantly different from each other. Area 4 was significantly later ( $P < 0.01$ ) than area 3 and area 2, and probably later ( $P < 0.05$ ) than area 1 (40).

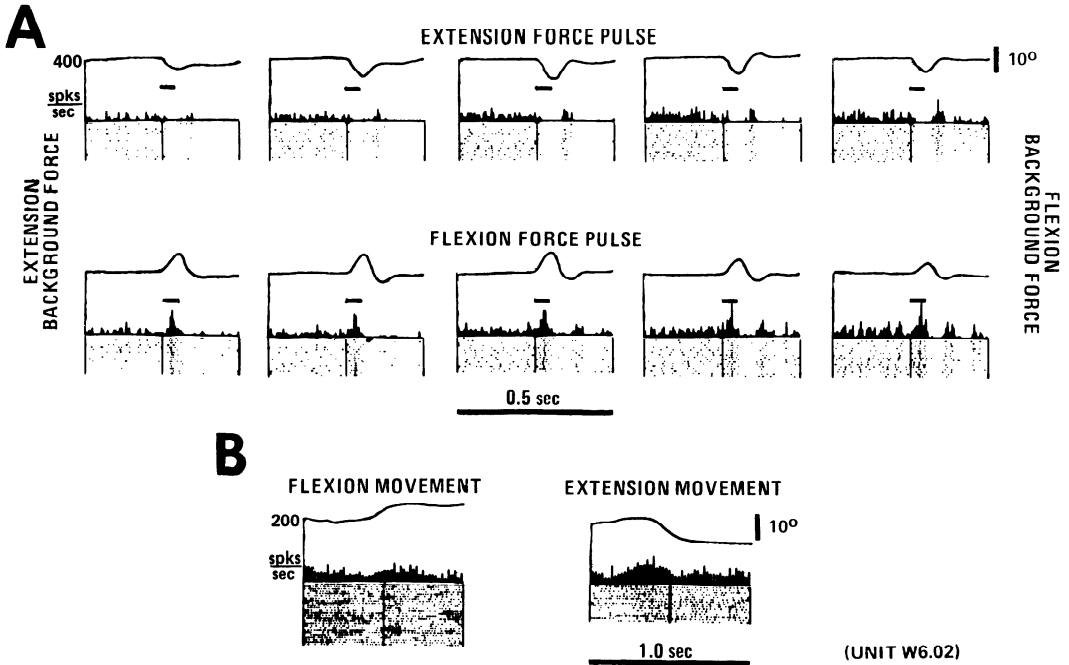


FIG. 4. *A*: responses of an area 4 unit to extension and flexion force pulses at all five background force levels. Each raster displays individual responses, while corresponding histogram shows average of individual responses in spikes per second. Force pulse onset is indicated by vertical line in middle of raster, and its duration is shown by bar just above histogram. Full sweep time, 500 ms; bin width, 5 ms. Trace above histogram is averaged handle position. Downward deflection indicates wrist extension; upward indicates wrist flexion. Background force levels from left to right are: strong extension, weak extension, zero, weak flexion, and strong flexion. Unit was absolutely specific. It was excited by flexion force pulse and inhibited by extension force pulse. Activity was greater with flexion background force. *B*: activity of same unit with corrective movement. In this display, vertical line in center of raster indicates entry into reward zone. (As noted, entry into reward zone occurring within 100 ms following onset of a force pulse was not considered corrective movement and is not included in data shown here.) Trace is averaged handle position. Full sweep time, 1 s; bin width, 20 ms. Flexion background force was present. Unit activity increased just before and during extension and decreased just before and during flexion. Thus, exciting force pulse was in same direction as background force associated with greater background activity and opposite in direction to corrective movement associated with increased activity.

quarters of units related to position maintenance, the direction of the exciting force pulse was the same as the background force direction associated with greater activity ( $P < 0.001$ ) (Fig. 7A). The unit in Fig. 4 is illustrative. It was excited by the flexion force pulse and inhibited by the extension force pulse and was more active in the presence of flexion background force. In terms of muscle groups involved, the group stretched by the exciting force pulse (the extensors) was the same group active during the background force direction associated with greater unit activity. Second, for three-quarters of units reciprocally related to corrective movement, the direction of the corrective movement associated with increased

unit activity was opposite to the direction of the exciting force pulse (Fig. 7B) ( $P < 0.001$ ). The unit in Fig. 4 is again illustrative. Its activity increased with corrective extension, and it was excited by the flexion force pulse. In terms of the muscle groups involved, the group active with corrective movement in the direction associated with increased unit activity (the extensors) was the same group stretched by the exciting force pulse. Third, these correlations were especially marked for the 30 units related to both position maintenance and corrective movement, such as the unit in Fig. 4. For all but five, the direction of the exciting force pulse was the same as the background force direction associated with greater activity

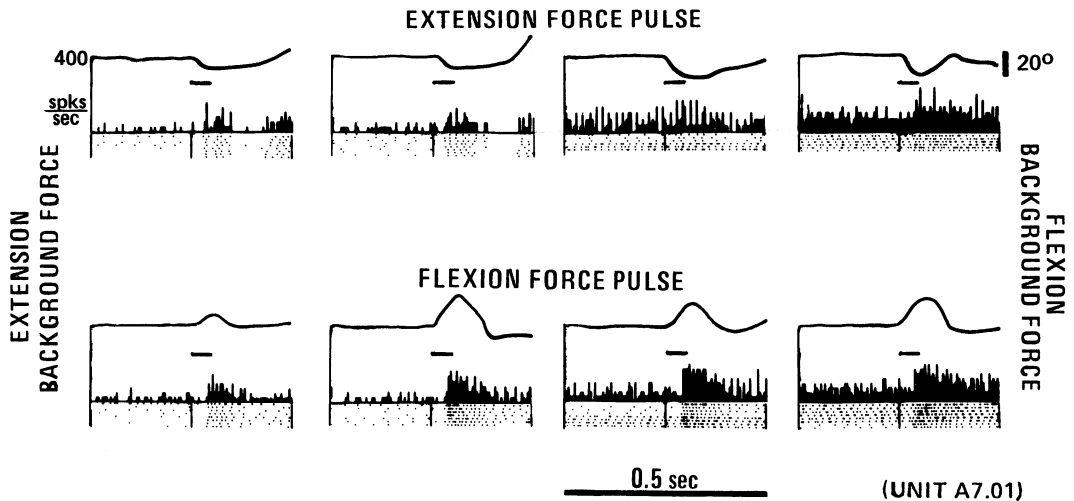


FIG. 5. Responses of an area 4 PTN (antidromic latency: 0.8 ms) to extension and flexion force pulses at four background force levels. Each raster displays individual responses, while corresponding histogram shows average of individual responses in spikes per second. Force pulse onset is indicated by vertical line in middle of raster, and its duration is shown by bar just above histogram. Full sweep time, 500 ms; bin width, 5 ms. Trace above histogram is averaged handle position. Downward deflection indicates wrist extension; upward indicates wrist flexion. Background force levels from left to right are: strong extension, weak extension, zero, and weak flexion (an adequate strong flexion level was not obtained from this unit). This relatively specific unit was strongly excited by flexion force pulse and weakly excited by extension force pulse. Its activity was greater with flexion background force. Recording sequence was interlocked as usual (zero, strong extension, weak flexion, and weak extension). Thus, periods of very high activity in the presence of zero and weak flexion background force were not contiguous.

and opposite to the direction of the corrective movement associated with increased activity. Thus, the muscle group stretched by the exciting force pulse was usually the same group active during the background force direction associated with greater unit activity and was usually the same group active during the corrective movement associated with increased unit activity. These data are summarized in Fig. 7C.

Half of the area 4 units were tested with pyramidal tract stimulation and 24 area 4 units were identified as pyramidal tract neurons (PTNs). Their antidromic latencies were 0.8–1.0 ms except for three, which were 1.6, 1.7, and 1.8 ms. Directionally specific, task-related PTNs displayed the same correlations described above. For five of five specific PTNs related to position maintenance, the direction of background force associated with greater activity was the same as the direction of the exciting force pulse (Fig. 5). For five of seven specific PTNs reciprocally related to corrective movement, the corrective-move-

ment direction associated with increased activity was opposite to the direction of the exciting force pulse. Finally, for four of four specific PTNs related to both position maintenance and corrective movement, the

TABLE 1. *Classification of units in each area*

Area	No. of Units		Task Related	Not Task Related
4	305	Spec	93 (31)	102 (33)
		Nonspec	55 (18)	55 (18)
3 and 1	153	Spec	18 (12)	56 (36)
		Nonspec	21 (14)	58 (38)
2	46	Spec	17 (37)	10 (22)
		Nonspec	11 (24)	8 (17)

Units in each area were classified according to the presence or absence of directional specificity of force pulse response and the presence or absence of task-related activity. Task-related units and specific, task-related units were significantly more common ( $P < 0.01$ ) in area 4 and in area 2 than in areas 3 and 1. Values in parentheses are percentages. Spec, specific; nonspec, nonspecific.



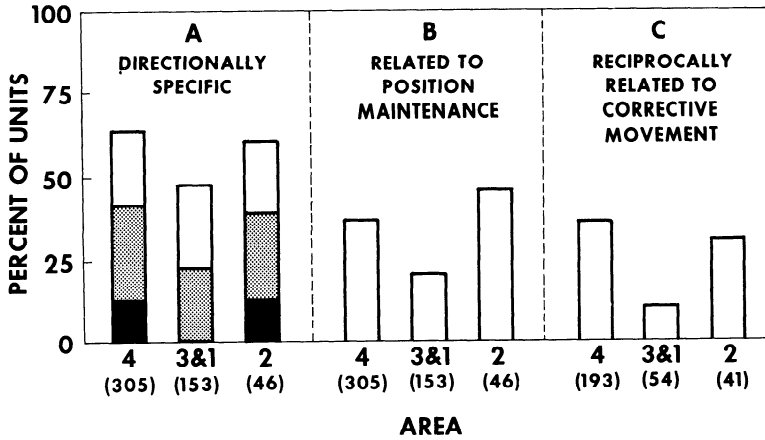


FIG. 6. Comparison of unit populations from areas 4, 3, and 1, and 2. Areas 3 and 1 were similar (see text) and thus were combined to simplify the figure. Number in parentheses below each column is total population on which column is based. A: entire column gives percentage of units that were specific, either absolutely or relatively. Solid and hatched sections together give percentages that were absolutely specific. Solid section gives percentages that were excited by one force pulse and inhibited by other. B: percentage of units related to position maintenance (i.e., activity dependent on background force direction). C: percentage of units reciprocally related to corrective movement (i.e., activity increased with active movement in one direction and decreased with active movement in opposite direction).

direction of the exciting force pulse was the same as the background force direction associated with greater activity and opposite to the corrective-movement direction associated with increased activity.

Electromagnetic FCU stretch data were obtained from 127 force pulse-responsive area 4 units in two monkeys. Fifty-six responded to FCU stretch. Each unit's FCU stretch response was compared to its extension and flexion force pulse responses in order to determine if it clearly resembled one as opposed to the other. The ability to draw such a conclusion was limited primarily to absolutely specific units since only response polarity (excitation or inhibition) and, to some extent, response latency could serve as criteria. Of 16 units for which a conclusion could be drawn, in all cases the FCU stretch response closely resembled the extension force pulse response and did not resemble the flexion force pulse response. Figure 8 shows three of these units. The close resemblance in form and latency of FCU stretch responses and extension force pulse responses is apparent. Units *B20.02* and *B31.08B* gave strong, short-latency excitatory responses to both FCU stretch and the extension force pulse and barely apparent, late ex-

citatory responses to the flexion force pulse. Unit *A50.01* was very rapidly inhibited by both FCU stretch and the extension force pulse, while it was rapidly excited by the flexion force pulse.

#### Areas 3 and 1

Directionally specific units and task-related units were significantly less frequent among the 153 units in these areas. The differences are displayed in Fig. 6 and Table 1. Furthermore, in contrast to area 4, the 18 units in areas 3 and 1 that were both directionally specific and task related displayed no dominant correlation between their force pulse responses and their task-related activity. This finding is shown in Fig. 7A. Ten units were identified as PTNs. Their antidromic latencies were between 1.5 and 2.8 ms and they resembled the general areas 3 and 1 population. Only four were specific and only three were task related.

#### Area 2

As shown in Fig. 6 and Table 1, directionally specific units and task-related units were as frequent in area 2 as in area 4, and significantly more frequent in area 2 than in areas 3 and 1. In addition, area 2 appeared to display the same correlations between force pulse responses and task-related

activity as did area 4. Figure 7A and B summarizes this result, while the unit in Fig. 9 is illustrative. This unit was excited by the extension force pulse and inhibited by the flexion force pulse, had greater background activity in the presence of extension background force, and increased its activity with corrective flexion and decreased it with corrective extension. Thus, for this typical area 2 unit, as for most area 4 and area 2 units, the direction of the existing force pulse was the same as the background force direction associated with greater activity and opposite to the direction of the corrective movement associated with increased activity. This unit was one of the few area 2 units tested with electromagnetic FCU stretch. As was the case with area 4 units, its FCU stretch response was similar to its extension force pulse response.

#### DISCUSSION

##### *Force pulse responses and task-related behavior in area 4*

For three-quarters of directionally specific task-related area 4 units, a force pulse in one direction affected the unit in the same way as background force in that direction and in the same way as corrective movement in the opposite direction. Thus, the unit in Fig. 4 was excited by the flexion force pulse, showed greater activity in the presence of flexion background force, and increased its activity with corrective extension. This finding is in agreement with most (5, 9, 13), but not all, other studies. Porter and Rack (36) found that, of units that were active when a monkey opposed a steady-state force and also responded to a force pulse in the opposite direction, 17 (68%) of 25 were excited by the force pulse and only 8 (32%) were inhibited. This finding appears to contradict that of this and previous studies (5, 9, 13). However, the present study, by documenting the considerable number of task-related area 4 units excited to some extent by force pulses in both directions, indicates that a considerable portion of their 17 excited units probably would have been excited as much or more by a force pulse in the same direction as the steady-state force. If the data of the present study are examined in a

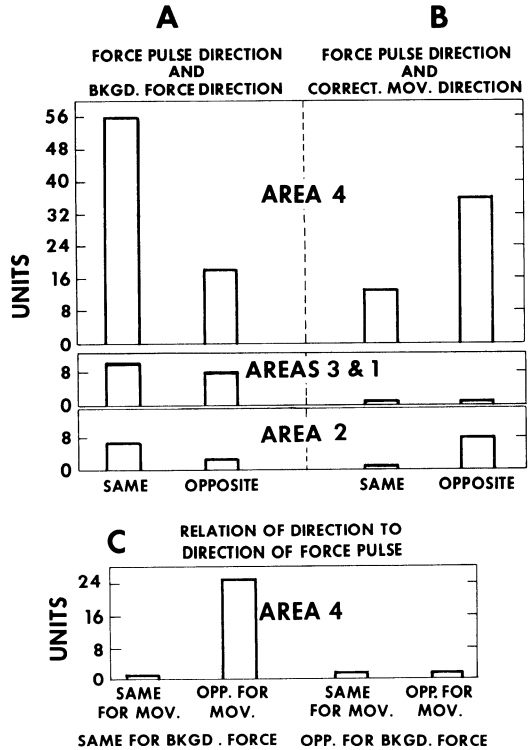


FIG. 7. *A*: units related to position maintenance. For units on left, direction of exciting force pulse was same as background force direction associated with greater activity. For units on the right, directions were opposite. *B*: units reciprocally related to corrective movement. For units on left, direction of exciting force pulse was same as corrective-movement direction associated with unit excitation. For units on right, directions were opposite. *C*: area 4 units related to position maintenance and also reciprocally related to corrective movement (these units also included in *A* and *B*). For units in first two columns (from left), background force direction associated with greater activity was same as direction of exciting force pulse, while for last two columns it was opposite. For units in first and third columns, corrective-movement direction associated with increased activity was same as direction of exciting force pulse, while for second and fourth columns it was opposite (see text for discussion).

nearly identical way to that of Porter and Rack (36), by taking the units whose activity increased with background force in one direction and looking only at their responses to force pulses in the opposite direction, the result is similar to theirs: of 93 units responding, 52 (56%) were excited to some degree and 41 (44%) were inhibited. This result does not change the conclusion drawn from the full body of data, embracing

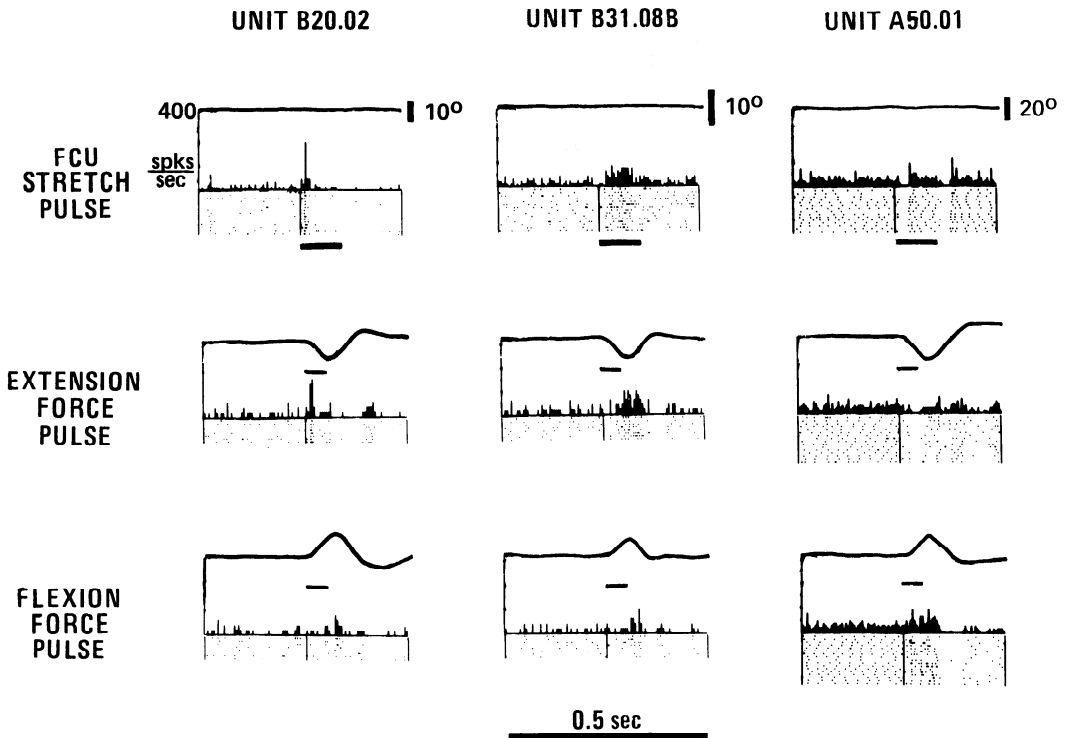


FIG. 8. FCU stretch and force pulse responses of three area 4 units. Each raster displays individual responses, while the corresponding histogram shows average of individual responses in spikes per second. Full sweep time, 500 ms; bin width, 5 ms. Stimulus onset is indicated by vertical line in middle of raster. Stimulus was either a 100-ms, 70-g FCU stretch (indicated by bar below raster) or a 50-ms extension or flexion force pulse (indicated by bar just above histogram). Trace above histogram is averaged handle position. Downward deflection indicates wrist extension; upward indicates wrist flexion. Background force was zero. Unit on left responded in 15 ms to both FCU stretch and extension force pulse. It did not respond within 60 ms to flexion force pulse. Middle unit responded strongly and similarly to FCU stretch and extension force pulse, while giving a weak, post-60-ms response to flexion force pulse. Unit on right was initially inhibited by both FCU stretch and extension force pulse, while it was excited by flexion force pulse. Note its off-response to FCU stretch. For all three units, the FCU stretch response closely resembled the extension force pulse response in form and latency, although FCU stretch produced no detectable handle displacement, and it did not resemble the flexion force pulse response.

responses to both force pulses: that over 75% of the units were excited only by, or excited more by, a force pulse in the same direction as the background force associated with greater activity. Thus, up to the present, all studies that imposed passive movements during the course of active performance support the conclusion that area 4 short-latency responses to imposed disturbances tend to promote compensatory movement, and therefore they are consistent with the transcortical loop hypothesis (22, 34). In contrast, Lemon et al. (24) compared area 4 unit response to passive manipulation when monkeys were quiescent to unit behavior during active performance and found that most units behaved

similarly with active and passive movements in a given direction. However, the dependence of area 4 responses on instruction (8, 10, 11) and the dependence of muscle spindle and joint receptor sensitivities on muscle tone (2, 3, 14, 15, 18, 31, 43-47) make it difficult to compare unit behavior in quiescent animals to unit behavior in active animals. Furthermore, the study deals with the full responses of units to passive movement, not just the short-latency responses.

If short-latency area 4 responses to an imposed disturbance are produced by a pathway that is also important in determining area 4 task-related activity during undisturbed performance (22, 32, 34), then only certain types of peripheral input could

be primarily responsible for the area 4 responses. It is difficult to imagine how input relating to joint angle could similarly affect an area 4 unit whether the joint was being extended by an extension force pulse, flexing during a flexion corrective movement, or remaining fixed during opposition

to extension background force. Cutaneous receptors could conceivably account for the three situations, but cutaneous input to area 4 has to date appeared sparse (25, 57). While the behavior of muscle spindles with active and passive movements depends on the muscles and the task, considerable evi-

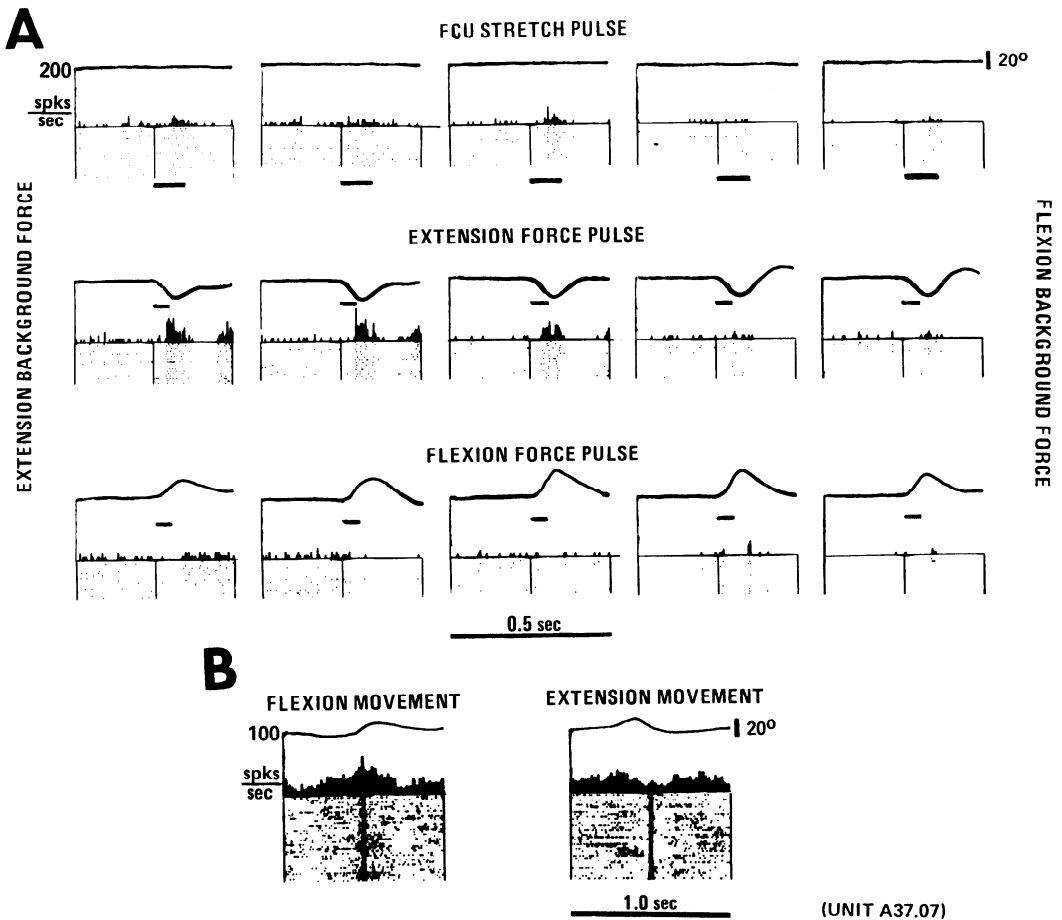


FIG. 9. *A*: responses of an area 2 unit to FCU stretch and to extension and flexion force pulses at all five background force levels. Each raster displays individual responses, while corresponding histogram shows average of individual responses in spikes per second. Stimulus onset is indicated by vertical line in middle of raster. Stimulus was either a 100-ms 70-g FCU stretch (indicated by bar below raster) or a 50-ms extension or flexion force pulse (indicated by bar just above histogram). Full sweep time, 500 ms; bin width, 5 ms. Trace above histogram is averaged handle position. Downward deflection indicates wrist extension; upward indicates wrist flexion. Background force levels from left to right are: strong extension, weak extension, zero, weak flexion, and strong flexion. Unit was excited strongly by extension force pulse and weakly by FCU stretch and was inhibited by flexion force pulse. Excitatory response was greater in presence of extension background force. Activity was greater with extension background force. *B*: activity of same unit with corrective movement. In this display, vertical line in center of raster indicates entry into reward zone. (As noted, entry into reward zone occurring within 100 ms following onset of a force pulse was not considered corrective movement and is not included in data presented here.) Trace is averaged handle position. Full sweep time, 1 s; bin width, 20 ms. Strong extension background force was present. Unit activity increased just before and during flexion and decreased just before and during extension. Thus, exciting force pulse was in same direction as background force associated with greater background activity and opposite in direction to corrective movement associated with increased activity.

dence (2, 3, 18, 31, 43–47) indicates that, in a context similar to that of this study, these receptors are capable of accounting for the predominant area 4 correlation between force pulse responses, position maintenance behavior, and corrective movement behavior. Other receptors sensitive to muscle stretch and/or muscle tension, Golgi tendon organs (47), and some joint capsule receptors (14, 15), should also be capable of accounting for this correlation. Recent work (16, 27, 51) has demonstrated considerable input to area 4 from muscle stretch receptors. The close similarity in the present study between area 4 unit response to wrist extension and to stretch of a single flexor muscle in the absence of wrist extension indicates the importance of the muscle stretch component in determining area 4 unit responses. Stretch of one (of five) wrist flexors provided a large proportion of area 4 neurons with information comparable to that provided by actual wrist extension. Tissues outside the FCU were jostled by its electromagnetically induced movement, and thus receptors outside the FCU were presumably stimulated. However, extra-FCU deep or superficial stimulation resulting from FCU stretch would probably not have closely resembled extension force pulse stimulation or not have resembled it more closely than it resembled flexion force pulse stimulation. Therefore, it probably could not account for the similarity of area 4 FCU stretch responses to extension, not flexion, force pulse responses (Fig. 8). The importance of muscle stretch in producing area 4 responses to force pulses suggests at least a partial explanation for the large number of directionally nonspecific and relatively specific units. Several studies have noted the moderate prominence in motor cortex of units giving the same response to both the onset and the offset of muscle stretch (16, 53). It may be that when a unit more active in the presence of extension background force was excited by a flexion force pulse, it was in fact giving an off-response to the transient decrease of extension force. This consideration and the presumed presence in area 4 of neurons concerned with regulation of intrafusal muscle fibers (9) may account for the

minority of task-related units that did not show the dominant correlation between force pulse responses and task-related activity.

The results support the hypothesis of an oligosynaptic transcortical loop (22, 34), beginning in large part with muscle stretch receptors. This loop appears to be important not only in determining area 4 responses to passive movements, but in determining area 4 task-related activity as well. If this is correct, then the animals did not accomplish position maintenance and corrective movement only by delivering excitation directly to area 4 from as yet undefined loci elsewhere in the brain. Rather, they performed these tasks, at least in part, by controlling the extent to which ongoing activity in the afferent, prearea 4, limb of this loop was allowed to reach the efferent limb, specific area 4 neurons, and thereby produce the pattern of area 4 activity responsible for task performance. Thus, according to this view, the activity produced in area 4 by an oligosynaptic transcortical pathway, probably originating largely with muscle stretch receptors, is capable of being used as a motor output for task performance. A companion study (55) provides further evidence for the importance of this mechanism in motor control by demonstrating appropriate correlations between force pulse response amplitude and background force direction.

A considerable number of area 4 force pulse-responsive units were not task related (Table 1), and a considerable number of task-related area 4 units did not display the predominant correlation between force pulse responses and task-related activity (Fig. 7). The first finding suggests that the short-latency input from a relatively focal limb perturbation has a wide distribution in area 4, probably reaching areas concerned with control of many different muscle groups. The second finding suggests that the activity produced in area 4 by this pathway does not bear a single, simple relationship to a limb perturbation. For example, there is some activity produced that might tend to increase rather than reduce the deflection caused by a perturbation. These possible implications are particularly interesting in

the light of recent studies by Marsden et al. (29, 30). Recording in man, they found that *a*) perturbation of one limb can produce a very-short-latency, possibly transcortical, EMG response in specific muscles of another limb, if such a response is conducive to better task performance (29); and *b*) a perturbation stretching one muscle group can produce a very-short-latency, possibly transcortical, EMG response in the shortened antagonist muscle group, if such a response is conducive to better task performance (30). These observations, together with those of the present study, suggest that a given focal input via an oligo-synaptic transcortical pathway can produce any of a wide variety of motor outputs, involving any of a number of limbs. Which, if any, output actually occurs in a situation depends on the demands of the task at hand. Presumably, in most situations a given input is permitted to produce significant motor activity at only a very small fraction of its area 4 destinations. At the rest it produces no activity or, if it is momentarily strong enough, it produces a transient response like those elicited from non-task-related units by the force pulses in the present study.

#### *Force pulse responses and task-related behavior in postcentral gyrus*

Task-related units (as well as directionally specific units) were more common in area 2 than in areas 3 and 1. The use of four monkeys and the distribution of penetrations make it difficult to ascribe this difference to sampling bias. The few task-related units in areas 3 and 1 displayed no clear correlation between force responses and task-related activity. Task-related area 2 units appeared to display the same correlation between force pulse responses and task-related activity found in area 4. Most, like the unit in Fig. 9, were affected in the same way by a force pulse in one direction, background force in the same direction, and corrective movement in the opposite direction. As noted above, such behavior resembles the probable concurrent behavior of muscle stretch receptors and does not resemble the behavior of receptors monitoring joint angle. Furthermore, while areas 3 and 1 respond mainly to superficial cutane-

ous input, area 2 responds mainly to input from deep receptors (21, 38, 49), including muscle stretch receptors (1, 39). Thus, the present findings suggest that in area 2, as well as in area 4, task-related activity and force pulse responses are in significant part a result of muscle stretch receptor input. The similarity of areas 4 and 2 emphasizes the need for further investigation of motor function in primary somatosensory cortex.

It is unlikely that the apparent correlation in area 2 between force pulse responses and position-maintenance activity could be ascribed to receptors responding to joint angle and the leeway of the reward zone. First, joint-angle sensitivity is significant only in the presence of muscle tension (14, 15), and thus force pulse responses should have been extremely dependent on the presence and direction of background force, which they were not. Second, input relating to joint angle alone could not account for the area 2 correlation between force pulse responses and corrective-movement activity.

It is also unlikely that a significant number of area 2 task-related units were in fact area 5 units. The correlation reported here between force pulse responses and active-movement behavior in area 2 is opposite to the correlation found in area 5 by MacKay et al. (28).

#### *Area 2 and area 4*

The course of the pathway responsible for area 4 short-latency responses to perturbation is not clear. It could ascend from the thalamus directly to area 4 (17, 23) or it could first pass through areas 3, 1, and 2, and/or area 5 (19, 42, 48, 50, 59). The latency data in Fig. 2 show that all three primary somatosensory areas respond early enough to mediate the area 4 responses. However, both areas 3 and 1 displayed less directional specificity and task-related activity than area 4. Furthermore, the fact that electromagnetic muscle stretch responses are earlier in area 4 than area 1 (53), and that they appear to contain information comparable to the force pulse responses, makes area 1 mediation less likely. In contrast, area 2, in its force pulse responses, in its task-related activity, and in the relation between the two, was similar to

area 4 except that its response latencies averaged several milliseconds less. These similarities, coupled with the indication that force pulse responses and task-related activity in both areas were largely a result of muscle stretch receptor input, are compatible with the possibility that the pathway to area 4 traverses area 2 as well as with the possibility that there are two parallel pathways, one slightly faster than the other.

The most anterior part of primary somatosensory cortex, area 3a, receives input from muscle stretch receptors (16, 35). Whether this area projects to area 4 in the primate is not clear (19, 59). In the present study, units from area 3a and the larger area 3b were of necessity combined. Thus any special characteristics of area 3a responses

were presumably obscured. For this reason, the study cannot address the question of the role of direct area 3a output to area 4, or of 3a output to area 4 via area 2.

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Address requests for reprints to J. R. Wolpaw at his present address: Division of Laboratories and Research, NY State Dept. of Health, Empire State Plaza, Albany, NY 12201.

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