Amplitude of Responses to Perturbation in Primate Sensorimotor Cortex as a Function of Task

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SUMMARY AND CONCLUSIONS

1. Monkeys learned to maintain hand position against a range of background forces. Short-latency responses to passive wrist extension or flexion were recorded from units in areas 4, 3, 1, and 2. Response amplitude was studied as a function of background force direction (extension or flexion).

2. For 40% of the precentral and postcentral responses, response amplitude depended on constant force direction. For these dependent responses, amplitude with background force in one direction averaged 2.8 times amplitude with background force in the opposite direction.

3. Units for which background activity varied with constant force direction were designated task related. Dependent responses from area 4 task-related units were usually larger when background activity was greater and when background force direction matched the direction of the passive movement.

4. Dependent responses from area 4 task-related units occurred significantly later than nondependent responses from the same units.

5. Since most area 4 task-related activity was explicable as a result of peripheral input via the same oligosynaptic path mediating area 4 responses to passive movements (32), the present findings imply that area 4-task-related activity may result in large part from centrally mediated change in the access of short-latency peripheral input to area 4 units.

6. The dependence of responses from non-task-related area 4 units and from non-task-related and task-related postcentral units showed no dominant correlation with background activity or with background force direction. Their dependence appeared to require no explanation other than a change in peripheral input with change in background force direction.

INTRODUCTION

During motor performance, task-related neuronal activity is found in primary somatosensory cortex, particularly area 2, as well as in primary motor cortex, area 4 (20, 32). In area 4 and apparently also in area 2, task-related activity correlates with the short-latency response to a perturbation (3, 6, 9, 32). Thus, three-quarters of the units excited by an imposed wrist extension are more active during position maintenance against extension force and more active immediately before and during an active flexion movement (32). In terms of the muscle groups involved, the group stretched by the perturbation that excites the unit is usually the same group active during isometric opposition to the force direction associated with greater unit activity and also the same group active during the active movement associated with increased unit activity. Unit behavior in these three situations, perturbation, position maintenance, and active movement, is thus comparable to the probable concurrent behavior of muscle stretch receptors (1, 2, 12, 16, 25–29). This similarity, combined with evidence that muscle stretch receptors project to both areas 4 and 2 and with evidence that muscle stretch alone supplies information to area 4 comparable to that supplied by all elements of a perturbation (see Ref. 32 for review), supports the hypothesis that short-latency peripheral input, due in large part to muscle stretch, exercises important control over area 4 and area 2

during ongoing undisturbed performance as well as during a perturbation (14, 18, 19). If short-latency peripheral input is in fact important in the production of task-related cortical activity, then motor control may involve adjustment of the access of such input to cortical neurons. That this is the case is suggested by studies (4–6) indicating that whether an area 4 neuron gives a short-latency response to a perturbation often depends on whether the task under way requires or forbids a compensatory movement. The present study explored the question of such change in access by investigating the amplitude of precentral and postcentral unit responses to a perturbation as a function of the task under way at the time.

METHODS

Experimental procedures fully described elsewhere (32) are summarized, whereas the choice of a force pulse of fixed amplitude and duration as the perturbation is discussed in detail.

Each of four monkeys (Macaca mulatta) was seated in a primate chair, right arm restrained so that the elbow angle was fixed at 90° and right palm strapped to a torque motor handle that moved in the plane of wrist flexion and extension. The monkey was rewarded for maintaining the handle in a middle zone, with its wrist neither flexed nor extended. The motor applied 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. It cycled through five levels of background force: zero, strong extension, strong flexion, weak extension, and weak flexion. One-half second before reward delivery, a 50-ms force pulse of fixed absolute amplitude was added to the background force. Eight extension and eight flexion force pulses in pseudorandom order occurred at each background force level. Following training, each monkey was prepared under Nembutal anesthesia for chronic single-unit recording from the arm region of motor and somatosensory cortex on the left side (4, 31). 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 five background force levels with 16 force pulses at each level). The interlocking of extension and flexion background force levels (noted above) served as a check against change

in unit behavior over time. An off-line PDP-12 computer analyzed and displayed single-unit activity and handle position as peripulse rasters and histograms. During the final week of recording prior to killing the animal by an overdose of Nembutal, small lesions were made by current passage through the microelectrode to aid histological analysis. Thionine-stained, 50-μm sections were examined and the cortical areas identified according to the criteria of Powell and Mountcastle (21). This procedure and the criteria utilized have been fully described (32).

Ideally, the perturbation would have produced the same stimulation of peripheral receptors at all background force levels. Changes in cortical unit responses could then have been ascribed to central mechanisms. Such an ideal perturbation was not obtainable. Two basic choices were available: a force pulse of fixed amplitude and fixed duration with degree of displacement determined by the interaction between the pulse and the monkey, or a fixed displacement produced by a servo-controlled motor exerting a force of magnitude varying with opposition encountered. For several reasons the first option was selected. First, preliminary observations made it clear that obtaining a standard displacement would often require more force when the perturbation was in the same direction as the background force than when it was in the opposite direction. Thus, with a standard displacement, activation of muscle stretch receptors—probably the single most important source of input in the present context—would have been greater when the directions matched (1, 2, 12, 16, 25–29). Since it was anticipated that matching of the directions might produce, on a central basis, a larger response to a standard perturbation from task-related units, it seemed probable that use of a fixed displacement would complicate interpretation of the results, for it could be said that the larger response was simply due to the greater activation of muscle stretch receptors. In contrast, obtaining the same result with a perturbation of fixed force and duration would be more convincing evidence for central regulation, for the larger unit response would occur in response to a perturbation of fixed force, fixed duration, and equal or lesser displacement. (This was frequently the case for area 4 task-related units. See Fig. 4, flexion force pulse response.) Second, the effects of displacement on joint receptors are very dependent on muscle tone (10, 11). Thus a fixed displacement would have done little to stabilize joint receptor activation. Third, the responses of the most important cutaneous receptors, those located in the hand and directly affected by handle and strap pres-

sure (15), should have been more closely dependent on the force of the perturbation than on the degree of displacement.

RESULTS

The data comprise recordings from 416 units from areas 4, 3, 1, and 2, which were excited by flexion and/or extension force pulses within 60 ms. Limitation to units that responded by 60 ms meant that for analyzed units the initial response was due to peripheral events occurring during the 50-ms force pulse, not to events occurring during handle rebound, which started within several milliseconds of force pulse termination. Eighty-eight other units showing only inhibitory responses within 60 ms were not included in this study since, in these cases, response amplitude was not readily quantifiable. Units were judged to be task related if their background activity (that is, their activity during position maintenance) was clearly dependent on background force direction (32).

Classification of responses

Of these 416 units, 163 gave an excitatory force pulse response to either the extension or flexion force pulse, while 253 gave two excitatory responses, one to each force pulse. Thus the data comprise a total of 669 excitatory force pulse responses. Each response was classified according to whether or not its amplitude was dependent on the direction of background force on which it was superimposed. Amplitude was measured as the spike frequency in the 100 ms after pulse onset minus frequency in the 100 ms immediately preceding pulse onset (thus the effect of task-related change in background activity was eliminated). The fixed 100-ms response analysis period was chosen to avoid the subjective decision of exactly when a unit's response ended. In a few cases, when responses were early, brief, and very well defined, a 50-ms period was used. It was recognized that both the animal's initial muscular response to the pulse and handle rebound could have affected unit activity within 100 ms. However, the inaccuracy introduced into measurement of force pulse response amplitude by these factors was judged to be minor for the vast majority of units, and was

tolerated in order to obtain a completely objective measure of response amplitude. For 257 responses from 209 units, amplitude was clearly dependent on background force direction. For these responses, amplitude with background force in one direction averaged 2.8 times amplitude with background force in the other direction. Dependent responses comprised about 40% of all responses in each of the four cortical areas. Figure 1 shows dependent responses to the extension force pulse from three different units.

These 257 dependent responses were separated according to whether they came from area 4 or postcentral units, and were classified as shown in Table 1. Areas 3, 1, and 2 are considered together since their results were not noticeably different. First, the dependent responses were put in two groups: responses from task-related units and responses from non-task-related units. Each group was then divided into those responses that were larger when background force direction matched force pulse direction (force-matched responses) and those that were larger when the directions were opposite (force-unmatched responses). Figure 1 shows three dependent force pulse responses from three units. All three are extension force pulse responses. The first two are larger with extension background force; they are force-matched responses. The third is larger with flexion background force; it is a force-unmatched response. This classification was done for the entire population of dependent responses and also for the population of dependent responses that were each the only force pulse response or the significantly larger (≥50% greater, see Ref. 32) force pulse response produced by a unit. For example, the extension force pulse response of the unit in Fig. 2 and the flexion force pulse response of the unit in Fig. 3 were in this category. The Fig. 2 unit responded only to the extension force pulse, while the Fig. 3 unit responded to both extension and flexion force pulses, but gave a significantly larger response to the flexion force pulse. The results of classification of this subclass are presented in parentheses in Table 1, next to the numbers resulting from classification of all the dependent responses. Finally,
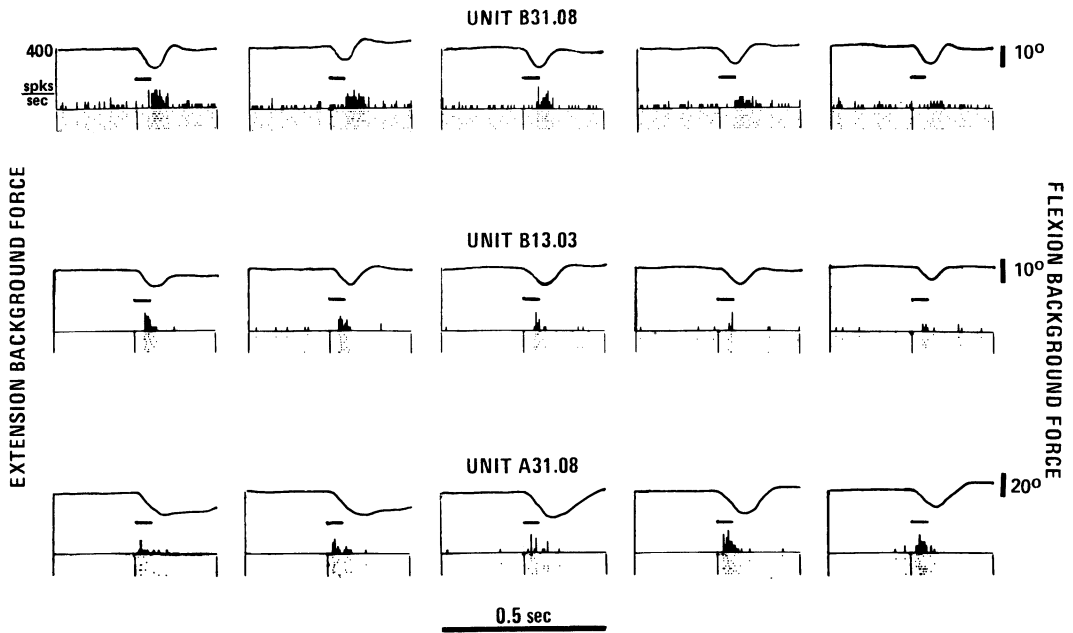
FIG. 1. Extension force pulse responses of three units at all five background force levels. Each raster displays individual responses, while corresponding histogram shows average of individual responses in spikes per second. Force pulse onset is indicated by vertical line in middle of raster, and its duration is shown by bar 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. For these units, force pulse response intensity was clearly dependent on background force direction. For area 4 unit in *B31.08* and area 3 unit in *B13.03* force pulse response was greater when background force was in same direction as force pulse. These responses were force matched. For area 3 unit in *A31.08* force pulse response was greater when background force was opposite in direction to force pulse. This response was force unmatched.

dependent responses from task-related units were divided into those that were larger when background activity was greater (activity-matched responses) and those that were larger when background activity was less (activity-unmatched responses). The task-related units in Figs. 2 and 3 display activity-matched responses. (Note that, as

TABLE 1. *Classification of area 4 and postcentral dependent force pulse responses*

	Responses		Force Matched	Force Unmatched	Activity Matched	Activity Unmatched
Area 4	141	Task related	35 (23*)	27 (8)	41*	21
		Not task related	42 (17)	37 (22)		
Postcentral	116	Task related	16 (12)	18 (9)	15	19
		Not task related	36 (11)	46 (7)		

Postcentral consists of areas 3, 1, and 2. Task related indicates that responses were produced by task-related units, units with background activity varying with background force direction. Force-matched responses were larger when background force direction matched direction of force pulse. Activity-matched responses were responses from task-related units that were larger when background activity was greater. A number in parentheses comprises a subset of immediately preceding number. A response qualified for this subset if it was only or significantly larger response of a unit; that is, if unit was excited only by force pulse producing that response and not by opposite force pulse or was excited significantly more by force pulse producing that response (32). * Significant ($P < 0.01$) majority of population. Thus 23 is significantly larger than 8, and 41 is significantly larger than 21.
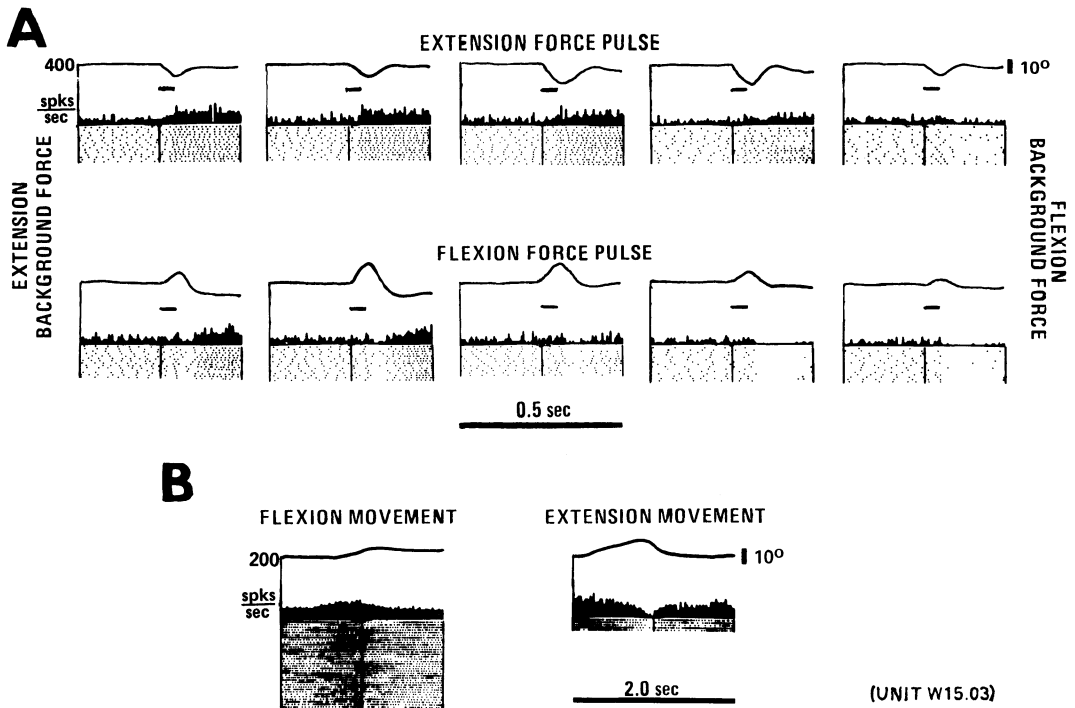
FIG. 2. *A*: responses of area 4 task-related unit to extension and flexion force pulses at all five background force levels. Each raster displays individual responses, while corresponding histogram shows average of individual responses in spikes per second. Force pulse onset is indicated by vertical line in middle of raster, and its duration is shown by bar 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 by extension force pulse and inhibited by flexion force pulse. Both background activity and extension force pulse response were greater in presence of extension background force. *B*: activity of same unit with active corrective movement. In this display, vertical line in center of raster indicates entry into reward zone (as noted in Ref. 32, immediate rebound after the force pulse was not considered corrective movement). Full sweep time, 2 s; bin width, 20 ms. Strong extension background force was present. Unit activity increased before and during corrective flexion and decreased before and during corrective extension.

described above, the subtraction of pre-pulse spike frequency in calculating response amplitude kept task-related background activity from distorting the measurement of response amplitude.)

Characteristics of response dependence

A slight majority (55%) of area 4 responses were force matched while a slight majority (55%) of postcentral responses were force unmatched, but this difference is of questionable significance. As noted above, displacement by the force pulse tended to be less in the force-matched situation. It averaged 80% of the displacement occurring in the force-unmatched situation, and displayed considerable inter- and intraindividual variability. This varia-

tion appeared to exert at most a slight effect on the proportion of responses that were force matched. It was estimated that change in force-matched displacement from its minimum of 60% of force-unmatched displacement to its maximum of 95% of force-unmatched displacement increased by 10 the percentage of responses that were force matched.

Except for the data from area 4 task-related units, the results summarized in Table 1 show no striking correlations. The amplitude dependence of non-task-related area 4 responses or of task-related or non-task-related postcentral responses does not appear consistently related to matched or unmatched background force direction or to matched or unmatched background activity.
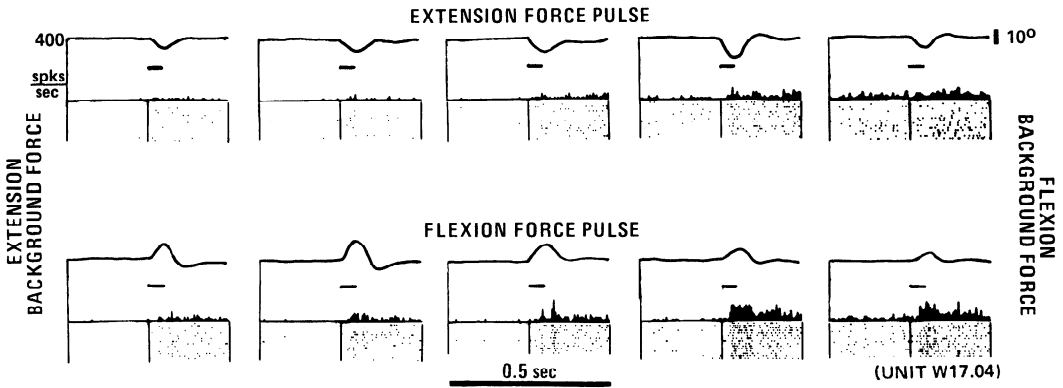
FIG. 3.   Responses of an area 4 task-related unit to extension and flexion force pulses at all five background force levels. Each raster displays individual responses, while corresponding histogram shows average of individual responses in spikes per second. Force pulse onset is indicated by vertical line in middle of raster, and its duration is shown by bar 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 by both force pulses but was more excited by flexion force pulse (32). Background activity and both force pulse responses were greater in presence of flexion background force.

In contrast, the dependent responses from area 4 task-related units displayed several strong correlations. First, two-thirds of these responses, a significant ($P < 0.01$) majority, were larger when background activity was greater. They were activity matched. The units in Figs. 2 and 3 are illustrative. The unit in Fig. 2 was more active with extension background force and gave a larger extension force pulse response in the presence of extension background force. This response was the beginning of a prolonged (at least 250 ms) period of increased activity. The important point in the present context is that the initial response, that occurring within 50 or 60 ms, was itself much larger in the presence of extension background force. (As shown in Fig. 2B, this unit was also related to active corrective movement. As expected (32) in area 4 or in area 2, for a unit excited by the extension force pulse and more active with extension background force, it increased its activity with corrective flexion and decreased it with corrective extension.) The unit in Fig. 3 was more active with flexion background force and gave larger extension and flexion force pulse responses in the presence of flexion background force. Second, of those responses that were each the only or the significantly larger response produced by a unit, a significant ($P < 0.01$) majority, 23

(74%) of 31, were larger when background force direction matched force pulse direction. Thus the unit in Fig. 2 responded only to the extension force pulse, and this response was larger in the presence of extension background force. The unit in Fig. 3, while responding to both force pulses, gave a much larger response to the flexion force pulse, and this response was larger in the presence of flexion background force. Thus, for task-related area 4 units, dependent responses were usually larger when background activity was greater, and dependent major responses were usually greater when the direction of the force pulse matched background force direction. The unit in Fig. 3 illustrates another feature of dependent responses from area 4 task-related units. Thirteen task-related area 4 units gave dependent responses to both force pulses. For 10 of those 13 units, both responses were greater with the same background force direction.

Dependent responses from task-related area 4 units were significant in another way: they were relatively late. Figure 4 compares the latencies of these 62 dependent responses to the latencies of the 71 nondependent responses obtained from area 4 task-related units. The dependent response distribution is significantly later ($P < 0.01$) (22). Dependent response latency averaged

37 ms, while nondependent response latency averaged 28 ms. This striking latency difference was not present between dependent and nondependent responses from postcentral task-related units.

DICUSSSION

The results demonstrate that for many units in areas 4, 3, 1, and 2, the amplitude of response to a perturbation of fixed force and fixed duration imposed during position maintenance is dependent on the direction of the background force being opposed. The results also indicate that dependent responses from area 4 task-related units display certain distinctive features. This finding is the more interesting, for it supports the view that central gating of peripheral access to area 4 units is a significant mechanism in motor control.

Response dependence of non-task-related units

Precentral and postcentral responses to the force pulses were presumably a result of the muscle stretch, joint rotation, and skin deformation produced by the force pulses. With a force pulse of fixed amplitude, activation of receptors sensitive to joint rotation would have depended on the background muscle activity (10, 11) and on the degree of displacement. Receptor activation due to deformation of the skin should have varied inversely or directly with displacement, depending on whether a receptor was affected by the pressure of the handle or

by the resulting movement, respectively. Activation of muscle stretch receptors should have increased with background muscle activity and with displacement (1, 2, 12, 16, 25–29). Since displacement was usually greater when muscle activity was less (see above), the nature of the dependence of muscle stretch receptor activation on background force direction cannot be readily inferred. In sum, dependence of peripheral receptor activation on background force direction was probably significant and presumably accounted for much of the amplitude dependence of cortical unit responses. Central gating of peripheral input may have played a role also. However, the population of dependent responses from non-task-related units displayed no distinctive features or special correlation with background force that might suggest central gating.

Response dependence of task-related units

The response dependence of postcentral task-related units displayed no special features. It did not differ from that of non-task-related units. There is no reason to presume that it resulted from any other than changes in peripheral receptor activation. In contrast, for area 4 task-related units, dependent responses were usually larger when background activity was greater, and a dependent response to the most exciting force pulse was usually larger when force pulse direction matched background force direction. Thus, the unit in Fig. 2 was active
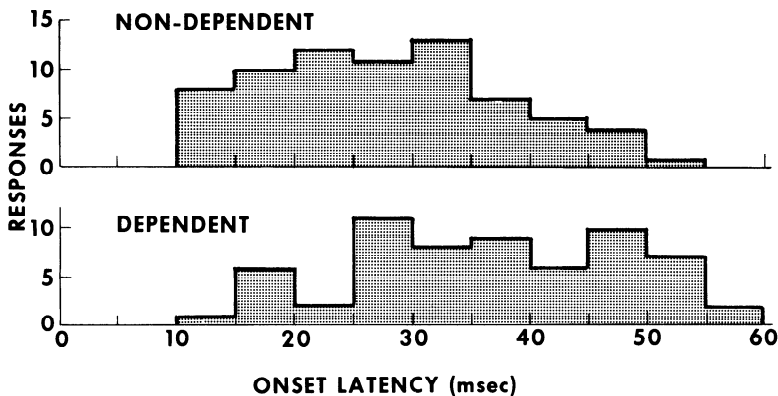

FIG. 4.   Onset latencies of force pulse excitatory responses from area 4 units related to position maintenance. For responses in upper histogram, amplitude was not dependent on background force direction. For responses in lower histogram, amplitude was dependent on background force direction. Dependent responses are significantly later ($P < 0.01$) than nondependent responses (22).

with extension background force, was excited by the extension force pulse, and was most excited by it in the presence of extension background force. It is possible that this kind of dependence was due to change in activation of peripheral receptors. However, such response dependence was not evident in the general population of precentral and postcentral units. To explain its presence in this limited population as a result of peripheral change would require that these units received their input from a specific subset of peripheral receptors. For example, if units were responding to input from muscle spindles, α-γ coactivation might well account for the fact that responses to the most exciting force pulse were usually force matched. However, another aspect of the data indicates that this possibility is probably an insufficient explanation for the special response dependence of these area 4 task-related units. When both force pulse responses from a unit were dependent on background force, both were usually larger with the same background force. Peripheral input would be unlikely to change with background force in the same way for both force pulses. This similar dependence is more easily explained on a central basis. It appears that the response dependence of area 4 task-related units often resulted from change in the access to these units of peripheral input and that access to most varied with their task-related activity. The substantial minority of dependent responses from these units that did not show the dominant correlations may have been affected by change in peripheral input or by differing central gating.

Peripheral access and motor control

As discussed in the INTRODUCTION, for most area 4 task-related units, the correlation between task-related activity and short-latency responses to a perturbation suggests that the afferent pathway producing the latter is also important in producing the former, and that much of the crucial input is supplied by muscle stretch receptors (32). These conclusions are in accord with the

hypothesis of a transcortical loop functioning during undisturbed performance as well as in response to a perturbation (14, 18, 20, 32). The present data add to the credibility and clarity of this position. Not only does short-latency somatosensory input correlate with task-related activity in area 4, but the access of that input to area 4 is similarly correlated. Thus it is possible to propose that when an area 4 unit, such as those in Figs. 2 and 3, is more active with a given task, it is more active because it has been made more accessible to somatosensory input from the relevant limb. For example, the background activity of the unit in Fig. 3 was greater with flexion background force. The fact that force pulse responses were also greater with flexion background force supports the hypothesis that the greater background activity was due to greater peripheral access to the unit, that activity produced by somatosensory input served as motor output.

The mechanism controlling access remains to be identified. The longer latency of the dependent responses from area 4 task-related units, shown in Fig. 4, suggests that the dependent responses may be produced by a pathway different from that responsible for the nondependent responses. Whether the path mediating the dependent responses traverses the cerebellum or is influenced by it (17) and whether it traverses the postcentral gyrus (though similar, apparently centrally mediated, dependence was not evident postcentrally) require investigation.

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