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Electromagnetic Muscle Stretch Strongly Excites Sensorimotor Cortex Neurons in Behaving Primates

Abstract. *Responses of single units in primary motor and sensory cortex of behaving primates to electromagnetic stretch of the muscle flexor carpi ulnaris are comparable in latency and intensity to responses to wrist extension. Thus, muscle stretch appears to be a major factor in cortical response to limb displacement during performance and probably has an important role in motor control at the cortical level.*

Single units in primary motor and sensory cortex respond quickly to limb displacement imposed during precisely controlled movements or postures (*1*). Such displacement rotates joints, stretches muscles, and moves other superficial and deep tissues. Knowledge of the part each form of stimulation plays in the cortical response to displacement is essential to understanding the role of peripheral feedback in motor control. Units which responded to abrupt displacement imposed during maintenance of a given hand position were studied for their responses to muscle stretch in the absence of joint rotation. Electromagnetic force, applied to an implanted iron slug, stretched a single muscle (*2*). The results support the hypothesis that muscle stretch is a powerful source of input to sensorimotor cortex in behaving primates and thus is probably a major factor in cortical control of performance.

Two monkeys (*Macaca mulatta*) were trained on a simple task. Each was seated in a primate chair, right elbow flexed to 90°, right arm restrained at elbow and wrist, and right hand held by a strap to a torque motor handle which moved in the plane of wrist flexion and extension. The monkey received liquid reward at 3- to 6-second intervals for maintaining the handle in a narrow middle zone of 10° with the wrist neither flexed nor extended. The presence of the handle in the correct zone was signaled by a light. The torque motor could apply flexion or extension steady-state torque to the handle, requiring exertion by wrist extensors or flexors, respectively, if the handle was to remain in the reward zone. One-half second before the reward was delivered, a 50-msec torque pulse, which produced an abrupt 10° to 20° displacement of the handle was superimposed on the steady-state torque. [In the arm of a cadaver that had not yet entered rigor mortis, extension of this magnitude stretched the muscle flexor carpi ulnaris (FCU) by 100 to 200 μm.] Both flexion and extension displacements were delivered in pseudorandom order. Reward was inevitable at the time of the torque pulse. Animals readily mastered the task.

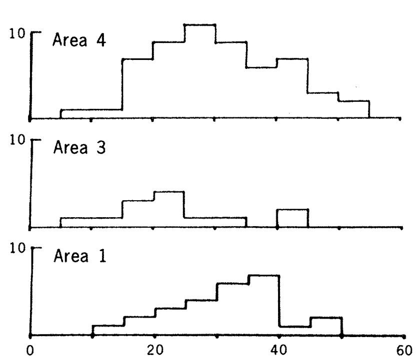

Fig. 1. Latencies of responses to FCU stretch of all initially excited units.

Under general anesthesia, a 2-g coated iron slug was embedded in the distal musculotendinous junction of the right FCU muscle (*2*), a head holder was bolted to the skull to allow the head to be immobilized, a recording cylinder was bolted over the arm region of motor and sensory cortex on the left side (*3*), and a pyramidal-tract stimulating electrode was positioned in the left pyramid.

Several days after surgery, animals resumed the task. The design was identical to that during the training period, except that 1 to 2 seconds before displacement a 100-msec (7-msec rise time) d-c current pulse was delivered to a solenoidal coil encircling the monkey's wrist. The pulse exerted a 70-g force, directed distally along the axis of the forearm, on the embedded slug, and thus stretched the FCU. This stimulus produced no detectable change in handle position, and the animals appeared to ignore it totally. (Pulse-induced movement of the muscle, measured in the cadaver arm at a point 5 mm proximal to the proximal end of the slug, was 75 μm, with a rise time of 50 to 70 msec. In the cadaver arm, at least half of this movement was due to movement of the entire forearm and thus did not represent FCU stretch.) Single-unit recordings were made from each animal over a period of 2 to 3 months. For each well-isolated unit that appeared to respond to flexion or extension displacements, unit activity and handle position were recorded for a full stimulation cycle (5 steady-state torque levels with 16 displacements and 8 or 16 FCU stretch pulses at each level). Selected penetrations were marked by d-c current passage. On completion of recording, animals were killed with Nembutal, and their brains were fixed, sectioned, and stained with Thionine.

Recordings were obtained from 301 responsive units in 81 penetrations in primary motor cortex (area 4), and the anterior part of primary sensory cortex (areas 3 and 1) (*4*). Of these, 296 responded to one or both displacements. The analysis is confined to the group of 255 (86 percent) that responded within 60 msec. In this group, 131 (51 percent) also responded to FCU stretch (73 of the 162 area-4 units, 20 of the 37 area-3 units, and 38 of the 56 area-1 units). They occupied a region extending along the central sulcus for at least 8 mm in one animal and 12 mm in the other. The distribution of units responding to both displacement and FCU stretch was the same as that of units responding only to displacement. The small size of area 3a, the large number of penetrations over several months, and the uncertain cortical vertical movement occurring with transdural penetrations did not allow most area-3 units to be confidently assigned to area 3a or 3b. Though the search stimuli were the displacements, recordings were obtained from five units that responded only to FCU stretch, three in area 4 and two in area 3.

Most units responded to FCU stretch with excitation rather than inhibition. Responses with very short latencies (≤20 msec) occurred in all three cortical areas (Fig. 1). Most responses (three-fifths in each of the three areas) were phasic (declining significantly in intensity before the end of the 100-msec stretch), rather than tonic. Phasic units often displayed OFF responses that were of the same polarity (excitation or inhibition) as their responses to stimulus onset, particularly in areas 3 and 1 (seven-tenths of phasic units) but also in area 4 (one-fifth of phasic units). Figure 2A shows FCU stretch responses and displacement responses of a unit in area 4. An FCU stretch produced a strong, 14-msec, ON response, similar to the extension displacement response, as well as a weaker OFF response. Figure 2B shows an area-4 pyramidal-tract neuron that responded within 15 to 20 msec to both the onset and offset of FCU stretch with strong inhibition followed by weak excitation. This response was similar to its response to extension displacement, and opposite to its response to flexion displacement. Of 15 identified area-4 pyramidal-tract neurons, four responded to FCU stretch. Figure 2C shows an area-3 unit that was one of five in areas 4 and 3 that responded only to FCU stretch, not to either displacement. Its OFF response was stronger than its ON response.

The FCU stretch responses resembled extension displacement responses in both form and latency. For 73 units excited by both FCU stretch and extension displacement, the responses were sufficiently more intense than spontaneous activity to allow accurate quantitation of response intensity (defined as spike frequency in the 100 msec following stimulus onset less spontaneous frequency). In area 4, the mean intensity of the FCU stretch response was 80 percent of that of the extension displacement response (median, 68 percent). In areas 3 and 1, the mean intensity of the FCU stretch response intensity was 87 percent of that of the extension displacement response (median, 35 percent). The disparities between means and medians were due to a number of units whose FCU stretch responses were several times as intense as their extension displacement responses. For 20 of the 73 units, the intensity of the FCU stretch response was greater than that of the extension displacement response. The five units responding only to FCU stretch were not included in this analysis.

Electromagnetic FCU stretch produced no detectable change in handle position; thus, the unit responses observed were not the result of joint rotation. Unit responses were equally prominent in the absence of background muscle activity; thus, they were not the result of change in joint capsule stretch (*5*). The stimulus appeared to be totally ignored by the monkey, and caused no visible disturbance in performance; thus, it was not painful. The slug was buried within the muscle and the major component of force was parallel to the long axis of the muscle and the forearm; thus, the unit responses were either a result of the stimulation of FCU stretch receptors, a result of the activation of receptors in other tissues jostled by the muscle's movement, or both. Two considerations suggest that stimulation of FCU stretch receptors was responsible for the bulk of the unit responses, particularly in area 4.

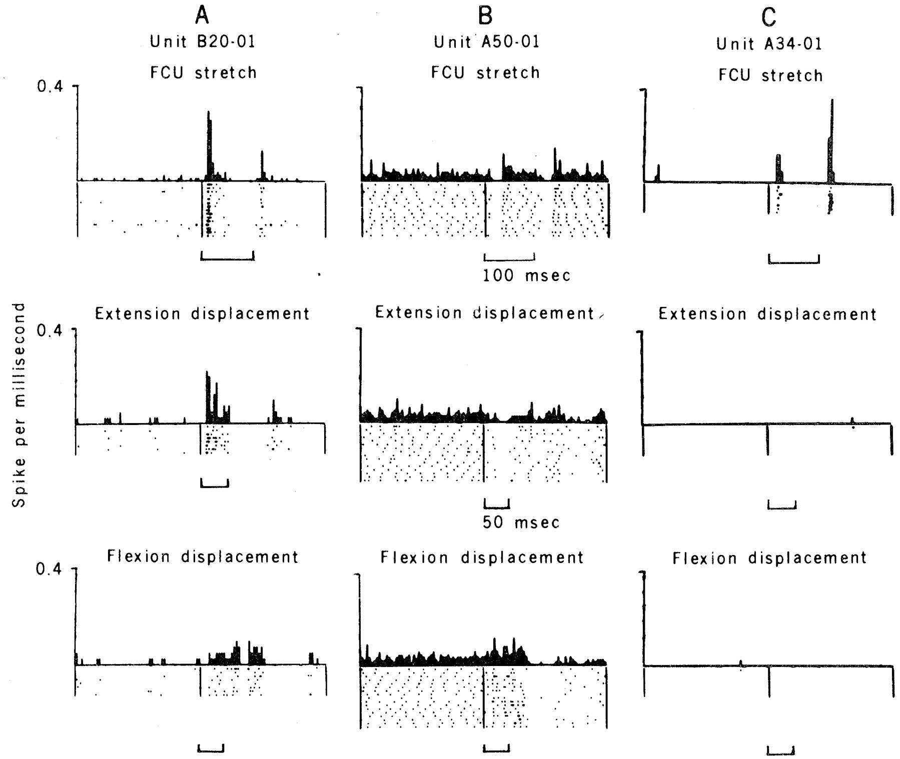

Fig. 2. FCU stretch and displacement responses of three units. The histograms are the averages of the individual trials shown in the rasters. The brackets represent the stimuli, either a 100-msec, 70-g FCU stretch, or a 50-msec extension or flexion displacement. (A) An area-4 unit excited by FCU stretch (ON and OFF responses) and by both displacements. The FCU stretch ON response and the extension displacement response are similar in form, latency, and intensity. The later activity after the displacements corresponds to handle movement resulting from rebound and repositioning by the monkey. (B) An area-4 pyramidal-tract neuron that responded with short latency (15 to 20 msec) phasic inhibition and subsequent weak excitation to both onset and offset of FCU stretch. This response is similar to its extension displacement response and opposite to its flexion displacement response. (C) An area-3 unit responding only to FCU stretch (ON and OFF responses), not to either displacement. Its OFF response is stronger than its ON response.

(i) Unit responses to electromagnetic FCU stretch closely resembled in form and latency their responses to extension displacement, which also stretched FCU. (ii) Studies in awake relaxed animals indicate that few units in area 4 respond to stimulation similar to that delivered to other tissues by FCU movement (*6*, *7*).

The data are in accord with results in acute anesthetized preparations (*8*, *9*) and awake relaxed animals (*6*) indicating that short-latency responses to muscle stretch occur in primary motor as well as primary sensory cortex. The predominance of phasic responses and the small magnitude of FCU stretch (< 75 μm in the cadaver) suggest that group 1A muscle afferents play a significant role. The large number of units giving both ON and OFF responses, also noted by Hore *et al.* (*9*), is in contrast to the behavior of the peripheral stretch receptors (*10*).

The most striking aspect of the data is the high proportion, in all three cortical areas, of displacement-responsive units that also responded strongly to FCU stretch. This result is particularly impressive since FCU is only one of 11 muscles (six flexors and five extensors) involved in wrist flexion and extension (*11*), and the FCU stretch by the slug (< 75 μm in the cadaver) was less than that by the extension displacement (100 to 200 μm). Combined with the similarity in latency and form between FCU stretch responses and extension displacement responses, the result implies that muscle stretch is a major factor in the short-latency response of area-4 units to limb displacement and suggests that such stimulation has a prominent role in motor control at the cortical level. At the same time, the high intensity of the cortical unit response to the stretch of a single flexor muscle implies that the motor cortex response is not proportional to the number of receptors stimulated. Thus the data do not support the hypothesis of a graded transcortical servo loop (*12*), unless one or more additional assumptions are made. One possibility is that the inputs from synergist muscles act in parallel, so that the stretch of any one is equivalent on the cortical level to the stretch of all. Another possibility, supported by units such as the one in Fig. 2C, is that movement of joints and other tissues, which was marked with the displacements, can inhibit the cortical response to muscle stretch.

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To Know with the Nose: Keys to Odor Identification

Abstract. *Successful odor identification depends on (i) commonly encountered substances, (ii) a long-standing connection between an odor and its name, and (iii) aid in recalling the name. The absence of any one ingredient impairs performance dramatically, but the presence of all three permits ready identification of scores of substances, with performance seemingly limited only by the inherent confusability of the stimuli.*

How many common substances can a person identify by smell? Estimates have varied from about 6 to 22 when subjects have had a single chance to identify each substance (*1-5*). For instance, 200 persons (physicians, nurses, medical students, and patients with normal olfaction) could identify an average of only 6 out of 12 odorants (*1*). The odorants included nine commonly recommended for neurological testing. For other sense modalities, the inherent confusability of stimuli seems to limit identification (*6*). The estimates for smell generally fall so low, however, as to suggest that factors other than inherent confusability limit identification. The four experiments reported here imply that sluggish acquisition and retrieval of odor names impede identification but that under the right circumstances confusability alone may set the upper limit. In the remarkably varied realm of odor quality, confusability poses only a minor limitation; when only this factor operates, persons can identify many odoriferous substances.

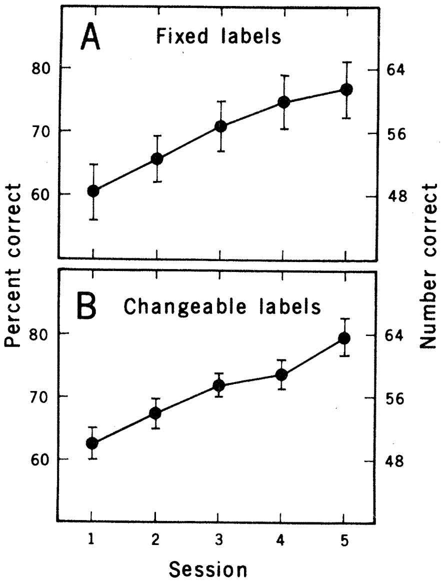

Fig. 1. (A) Percent correct and number correct when subjects sought to identify 80 substances with labels generated during previous inspection. Bars represent standard errors of the mean. (B) Similar to (A), except that the subjects had the option to change labels throughout testing.

In experiment 1, 12 women, blindfolded, sought to identify 80 commonly encountered, "ecologically valid" substances presented in irregular order from jars (*7*). Upon presentation of a substance, the subject first rated familiarity on a seven-point scale and then sought to name the substance. Average performance equaled 36 (range, 25 to 43). Moments after initial identification, the subject sought to "identify" the various substances again, but, on this occasion, sought to use only labels generated during the first exposure. Hence, in addition to asking how many substances a subject could identify veridically, the experiment looked at how consistently the subject could use her own labels, veridical or nonveridical. When incorrect on the second exposure, the subject received feedback regarding her previously generated label.