

## INFLUENCE OF PROPRIOCEPTION ON MAP OF CORTICAL RESPONSES

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Many investigators have prepared maps of motor cortex responses to stimulation at different sites, but hitherto none has attempted to demonstrate the alterations that occur in cortical maps when the peripheral conditions (such as the initial position of the responding limb) are altered. That this position may alter the response to stimulation of a particular cortical site has been demonstrated by Gellhorn (1948, 1949) and Gellhorn & Johnson (1950*a*); the influence of proprioceptive conditions on a map of cortical sites has not been shown, however. Since proprioceptive reinforcement will make subthreshold cortical stimuli effective for a particular muscle group and reduce or abolish the reactivity of the antagonistic group it seemed possible that variations in the degree of proprioceptive activity would induce changes in the size of the cortical area from which a certain muscle or group of muscles can be activated at a given intensity of stimulation.

In the present paper examples of such maps will be given and described, and certain features of these maps will be discussed (see also Hyde, 1950).

### METHOD

In a series of eleven monkeys (nine macaques, two *Cynemolgi*) a number of cortical sites were stimulated and electromyographic responses recorded in six muscles at a time, with the contralateral leg fixated in the two conditions of (*a*) knee flexed and ankle dorsi-flexed as compared with (*b*) knee extended and ankle plantarflexed, the hip being fixated in a neutral position and toes being free throughout. The methods of stimulation (repetitive condenser discharges from a Goodwin stimulator) and recording were the same as in earlier publications from this laboratory.

In order to be sure that the cortex was relatively stable throughout the mapping, a number of different procedures were tried, of which the following was most satisfactory and was used in most if not all experiments of the present paper: four or five sites were stimulated with the leg in flexion, the same sites were then stimulated with the leg extended, and as a check the first of the sites would again be stimulated with the leg in flexion. If the first and last records of this (series) were quite similar, the series was considered valid.

Stimulation at 2 min intervals thus permitted recording from twenty-five sites in an hour, each site having 10 min between successive stimuli. The initial mapping was usually carried out with sites 3 mm apart, first a row anterior to the sulcus centralis and as near the mid-line as possible, then one 3 mm lateral, and so on, until the limit of responsiveness to the particular voltage was reached. If, in an attempt to extend the area, a higher voltage was employed at some sites, the same higher voltage was used on these sites with both leg positions. Subsequent tests were performed in order to fill in the gaps in the initial map, so that ultimately the entire excitable area would be covered at 1 mm intervals. This goal was not always realized before the death or decline of the animal; this accounts for the gaps in some of the maps.

The monopolar stimulating electrode mounted on a Horsley-Clarke instrument was moved millimeter by millimeter in an antero-posterior direction as well as laterally, and the relation of the various points to the principal sulci was indicated on a diagram. The data thus obtained made an accurate return to each site possible and permitted adequate recording of the spatial relationship of the stimulated points.

The maps were prepared with the actual location of the stimulated sites plotted on the diagram of the particular cortex under investigation. The amplitudes of the electromyographic responses were analysed and graded into four or five sizes; letters representing the muscles were plotted on the map, the size of the letter at any site being an indication of the size of the response, without reference to the latency of the response, either of the movement as a whole or of the particular muscles with respect to one another.

Ideally, maps of the motor cortex should perhaps be made with application of the same voltage (or current) to all stimulated sites, and in many of the animals examined it was possible to evoke responses of similar magnitude (though with varying representation of the different muscles recorded) from sites distributed throughout a widespread cortical area without changing the stimulus intensity. However, in order to evoke comparable responses from certain additional areas, especially anteriorly and medially, it was sometimes necessary to increase the voltage at some sites. In order to determine whether such a method really provides a representative picture of the response to stimulation of different cortical sites, each of several points was stimulated with a series of varying voltages. The results were analysed with respect to the relative e.m.g. amplitude of the different muscles at the sites, and it was concluded that the same relationship among the muscle responses was revealed independent of shifts in intensity from threshold to two or three times threshold. In Fig. 1, as an example, responses of four muscles to stimulation of a cortical site at several intensities are presented. As the voltage was increased from 2.6 V (*A*) to 5.7 V (*D*), the e.m.g. of each muscle increased, but semi-tendinosus (*H*) and tibialis (*T*) in each case gave a larger response than their antagonists. It was concluded that the method adopted was one of several which would give comparable and valid maps, with minor variations, of the cortical representation of different muscles (as revealed electromyographically).

## RESULTS

The experiment illustrated in Fig. 2 was one in which the condition of the animal (a *Cynemolgus*) was so constant that it was possible to obtain records of responses to stimulation of sixty-seven cortical sites, each with the two leg positions. The voltage used was either 4.2 or 4.9 V, and a frequency of 83/sec was employed throughout. This was one of the experiments in which both arm and leg muscles were recorded, in an attempt to determine the degree of overlap of arm and leg areas and the extent to which this overlap area was altered by proprioceptive changes. Where arm muscle responses were recorded the positions of wrist and elbow were varied, the position 'flexed' being with knee

flexed, ankle dorsiflexed, elbow flexed and wrist dorsiflexed; the position 'extended' being knee extended, ankle plantar-flexed, elbow extended and wrist volar-flexed. Fingers as well as toes were free; hip and also shoulder positions were kept constant throughout. On the maps of Fig. 2 are plotted

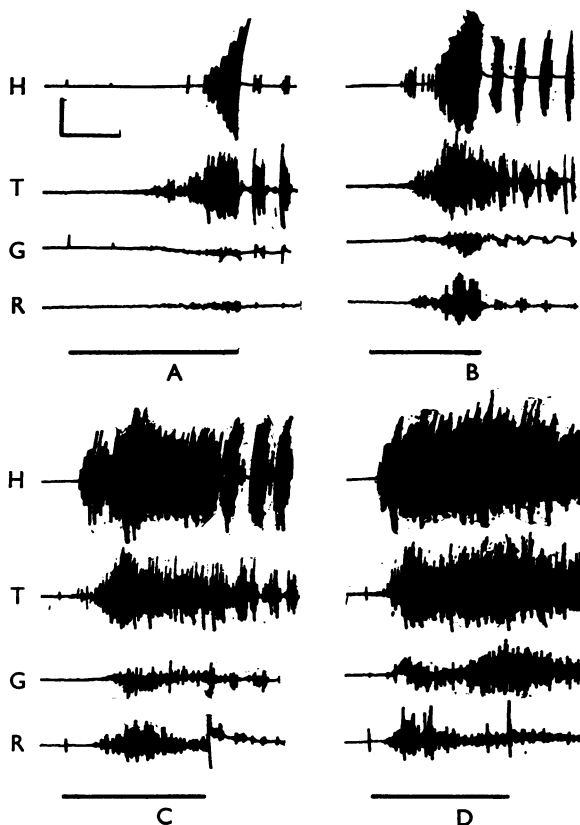


Fig. 1. Series of e.m.g. responses to stimulation of a cortical site at increasing intensities. Macaque 2-23-49. *H*, semitendinosus; *T*, tibialis anticus; *G*, gastrocnemius; *R*, rectus femoris. Site in leg part of area 4, left cortex. *A*, 2.6 V; *B*, 3.8 V; *C*, 4.7 V; *D*, 5.7 V. All 83/sec, pulse duration 7.7 msec, stimulus duration indicated by lines beneath e.m.g.'s. Hip fixated 90°, knee 100°, ankle 90°. Vertical calibration, 300  $\mu$ V. Horizontal calibration, 2 sec.

responses of two arm muscles, biceps brachii (*D*) and triceps (*A*), together with three leg muscles, gracilis (*L*), semitendinosus (*H*) and tibialis anterior (*T*), the leg muscles all being members of the 'flexor' group. One can see at a glance the considerable difference between the two maps, not only in overall area of responsiveness but particularly in type of movement as represented by these few muscles.

In the lateral part of the motor cortex (lower section of the figure) there is

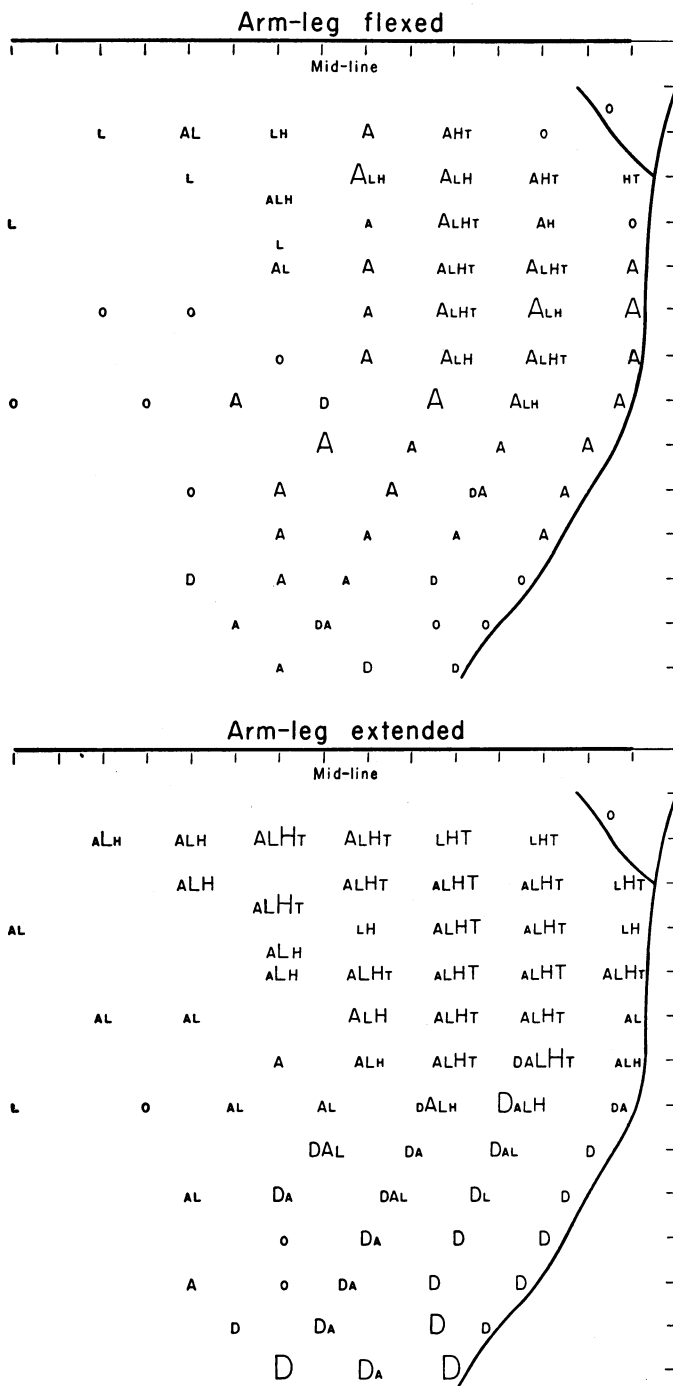


Fig. 2. Effect of proprioception on map of cortically induced responses, leg and arm. *Cynomolgus* 10-3-49, left hemisphere. Central sulcus indicates posterior border of stimulated area. 6 sec monopolar stimulation with 4.2-4.9 V, 83/sec, 7.7 msec pulse duration. Map above indicates responses obtained with flexed position: hip 90°, knee 70°, ankle 60°, shoulder 90°, elbow 80°, wrist dorsi-flexed to 30°. Map below indicates relative size of e.m.g.'s with limbs in extension: hip 90°, knee and ankle 160°, shoulder 90°, elbow 160°, wrist volar-flexed to 80°. Scale indicates millimetres on cortex. *D*, biceps brachii; *A*, triceps brachii; *L*, gracilis; *H*, semi-tendinosus; *T*, tibialis anticus. Relative e.m.g. amplitude indicated by size of letters. *O* indicates no response in any of the recorded muscles on stimulation of a site.

a marked shift in the representation of biceps and triceps muscles. The area from which the biceps response is obtained is greatly enlarged when the arm is fixated in extension, whereas the triceps area is enlarged with the arm held in flexion.

It is to be remembered that of the many muscles taking part in the cortically induced movement only two arm muscles are recorded here, so the map presents only a sample of the activity of the arm (and similarly of the leg also). This is the reason so many sites on the map show only a single responding muscle (e.g. the two rows just anterior to the central sulcus in the extended position favouring biceps brachii).

The three leg muscles mapped in Fig. 2 likewise show considerable variation in cortical representation in the two positions, all being excitable from more sites and to a greater amplitude when the leg is extended than with it held flexed. The gracilis (*L*) response is elicited from a more widespread cortical area than either tibialis (*T*) or semitendinosus (*H*); this area extends both anteriorly and laterally and is particularly noticeable with leg (and arm) in the extended position.

In the medial section of the motor cortex which shows an increased responsiveness of the flexor muscles of the hind leg in the extended position, the response of the triceps muscle is enhanced in spite of the fact that the arm was held in the extended position. This seems to indicate that in the area in which triceps brachii and leg muscles overlap in the cortex proprioceptive facilitation of the leg muscles may increase the responsiveness of all foci located in it.

The increased response of triceps at some medial sites in spite of the fixation of the elbow in extension would seem to be an example of the functional association of triceps-hamstrings mentioned by Bosma & Gellhorn (1947). It is significant that this increased response of triceps with elbow extended is limited to the hind-leg overlap area in Fig. 2.

A region of greatest excitability of tibialis (*T*) may be noted from 2 to 4 mm anterior to the sulcus and from the most medial site available for stimulation (2 mm lateral to mid-line in this experiment) extending about 5 mm laterally. This is the only region (except for one medial site on the sulcus) from which a tibialis e.m.g. was induced by stimulation with the leg flexed (ankle dorsiflexed); it is also the region in which the largest tibialis responses are noted with the leg extended, although in the latter position the number of sites from which a tibialis response is detectable can be seen to be extended especially anteriorly. Semitendinosus (*H*) responses are elicitable from a larger number of sites than tibialis, yet from fewer than gracilis; the responses are increased, as is the case with the other two recorded leg muscles, when the knee is extended and the ankle plantar-flexed.

Fig. 3 illustrates another experiment in a macaque in which arm and leg muscles were mapped; in this series of forty-three cortical sites, responses of four arm muscles and two leg muscles were recorded. The leg muscles tibialis anterior (*T*) and gracilis (*L*) are both 'flexors', and as can be seen there was



only one site where one of them (*T*) responded in the position of knee and ankle flexion. This does not mean that no hind-leg muscles were activated by stimulation of these sites with the leg flexed; but simply that neither of the particular muscles recorded responded under these conditions. As indicated in the map of responses with the leg and arm extended, there was a wide area, stimulation of which elicited responses in both tibialis and gracilis. These responses were mostly of small amplitude, the exception being the three most postero-medial sites where tibialis responses were larger than elsewhere.

Of the arm muscles there is a marked shift in biceps-triceps relations in the two positions; the biceps giving larger e.m.g.'s in response to stimulation of the lateral sites with the elbow extended, the triceps response showing less increase in its proprioceptively favoured position.

The small triceps responses seen at the most lateral sites with elbow extended are undoubtedly due to co-contraction as they accompany relatively large biceps responses and are absent when the triceps itself is favoured by elbow flexion.

It is interesting to note that in this experiment there was almost no overlap between the cortical hind-leg and triceps area. Consequently the change in the posture of the hind leg had little influence on the few triceps foci which were found in the *medial* part of the motor cortex (upper part of the figure).

Of the two more distal arm muscles, flexor carpi ulnaris is a member of the triceps complex (Bosma & Gellhorn, 1947), while extensor digitorum communis (*M*) is considered a member of the biceps complex (Gellhorn & Johnson, 1950*a*). The increased response in flexor carpi ulnaris at the more medial (triceps area) sites in position *A* (elbow flexed and wrist dorsi-flexed), compared with the opposite position, is even more pronounced than the shift in response of triceps itself.

Another series of cortical sites covering the medial part of the lateral hemisphere in an area of approximately 1 cm<sup>2</sup> was stimulated in the same animal, e.m.g.'s of six other hind-leg muscles being recorded. Of these, four are mapped in Fig. 4 where relative responses are shown at twenty-seven sites. The three 'flexor' muscles, semitendinosus (*H*), peroneus brevis (*P*) and extensor digitorum longus (*E*) responded to stimulation of a larger number of sites when they were proprioceptively facilitated by fixation of the leg in extension than with it held flexed; the opposite is true of the anti-gravity muscle, flexor digitorum longus (*F*), which was activated from fourteen of the stimulated sites with the leg flexed but from only five sites with the leg in extension. Not only was the area of 'representation' of the different muscles increased when the leg position stretched them, but also the amplitude of their responses shifted. The larger responses of semitendinosus (*H*) in extension of the leg, for example, are localized more strongly in the lateral row of sites near the arm area; whereas a study only of the map obtained in the flexor position of the leg would suggest that the semitendinosus representation was less in this





region than, for example, a little more antero-medially. Extensor digitorum longus (*E*) failed to respond at any site with the knee flexed and ankle dorsiflexed; yet stimulation of widely scattered sites, with proprioceptive facilitation, brought in a response of this muscle. The importance of attention to proprioceptive conditions in attempting to map the representation of a muscle in the motor cortex is demonstrated once more by these examples, which show that a distorted picture of a muscle's cortical area of representation might be obtained if either of the two maps were examined to the exclusion of the other.

The series of forty-six sites illustrated in Figs. 5 and 6 is from a macaque, records of responses in five hind-leg muscles being plotted in two maps: Fig. 6 illustrates two flexors, tibialis (*T*) and gracilis (*L*), and two extensors, gastrocnemius (*G*) and rectus femoris (*R*), while the relative responses of the two functionally opposed parts of biceps femoris are shown in Fig. 5. These responses were all recorded simultaneously in the six channels of the crytograph. Fig. 5 illustrates the relative shift in responsive area and in amplitude of e.m.g. between the two parts of the biceps femoris with the limb fixated in the two proprioceptively opposite positions. It is of some interest that the 'centres' of cortical neurones, stimulation of which induces the larger responses in the flexor part of the biceps femoris, are not in the same region of the cortex as are the 'centres' for the extensor part of the same muscle, further evidence that this muscle should no longer be considered a single anatomical unit (see also Sherrington, 1913; Gellhorn & Johnson, 1950*b*).

The map of the other four recorded muscles in this animal, Fig. 6, shows the shift in responsive areas and amplitudes between the flexors (*T* and *L*) which were excited from many sites with the leg extended and to a lesser degree with flexion, and the extensors (*R* and *G*) which showed an increase with the knee flexed and the ankle dorsiflexed. In general, the larger gracilis responses were obtained at the lateral sites while tibialis was better represented a few mm more medially. Gastrocnemius and rectus femoris had less obvious foci, but seemed to respond with greater amplitude from some of the more lateral sites.

One feature of the experiment which may not be obvious since the muscles are plotted on two pairs of maps is that there are only two sites where only a single muscle of the six responded in both proprioceptive positions. Stimulation at all other sites elicited a demonstrable e.m.g. in at least two, and more often three or more of these muscles. This animal had a relatively high threshold for cortical stimulation, 4.2 V being required to induce a relatively small response from most of the sites, a few requiring 4.9 V. With the small responses obtained, the difference in the number of sites from which a given muscle responded in the two proprioceptive conditions is marked, and the number of sites whose stimulation led to large or small e.m.g.'s also shows a definite shift.

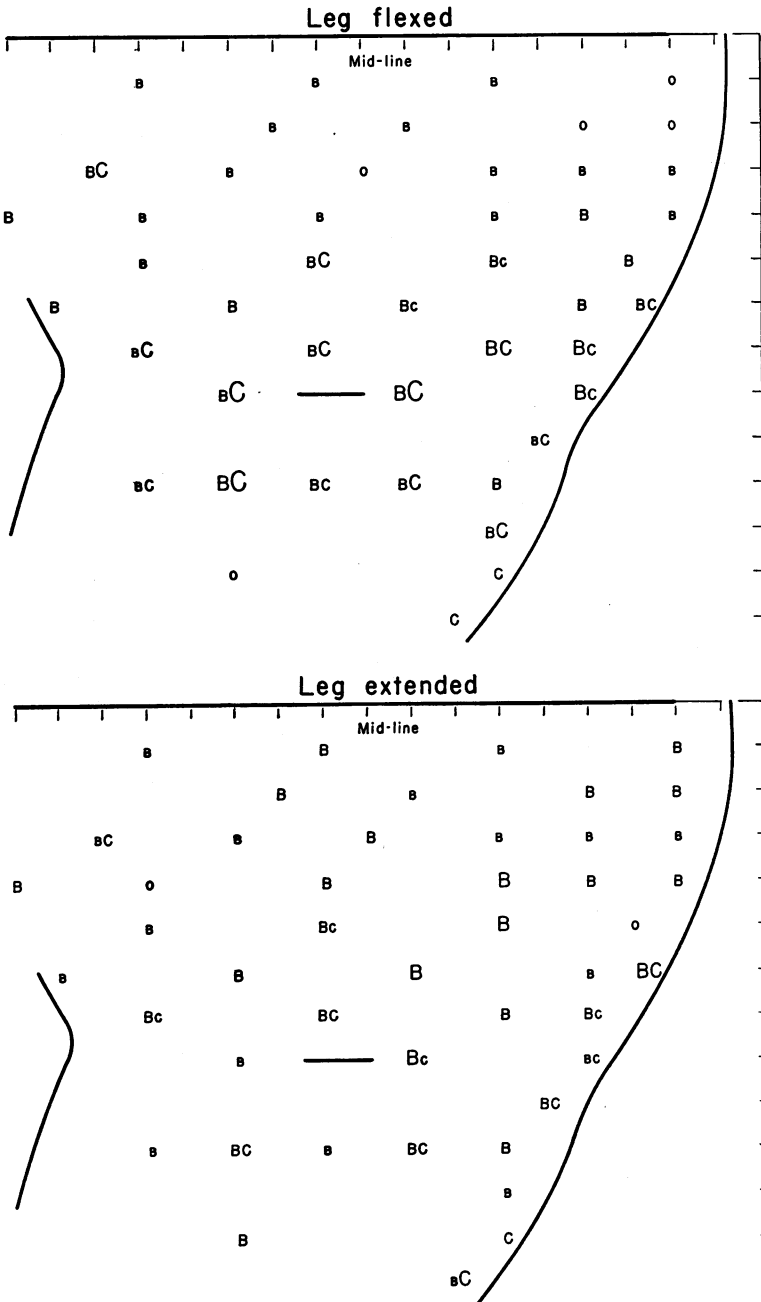


Fig. 5. Cortical representation of responses obtained in two parts of one muscle with two positions of the limb. Macaque 1-9-50, left hemisphere. Responses of two functionally opposed parts of biceps femoris induced by stimulation of the cortex. Central sulcus, on right, indicates posterior border of stimulated area. Superior precentral sulcus in centre of map; lower portion of inferior precentral gyrus on left. Monopolar stimulation for 3 sec with 3.5-4.9 V, 83/sec, 7.7 msec pulses. Elbow in extension throughout. Upper map represents responses with leg in flexion: hip 90°, knee and ankle 45°. Lower map, leg in extension: hip 90°, knee and ankle 150°. *B*, flexor part of biceps femoris; *C*, extensor part of biceps femoris; *O*, no response recorded in either part of the muscle.

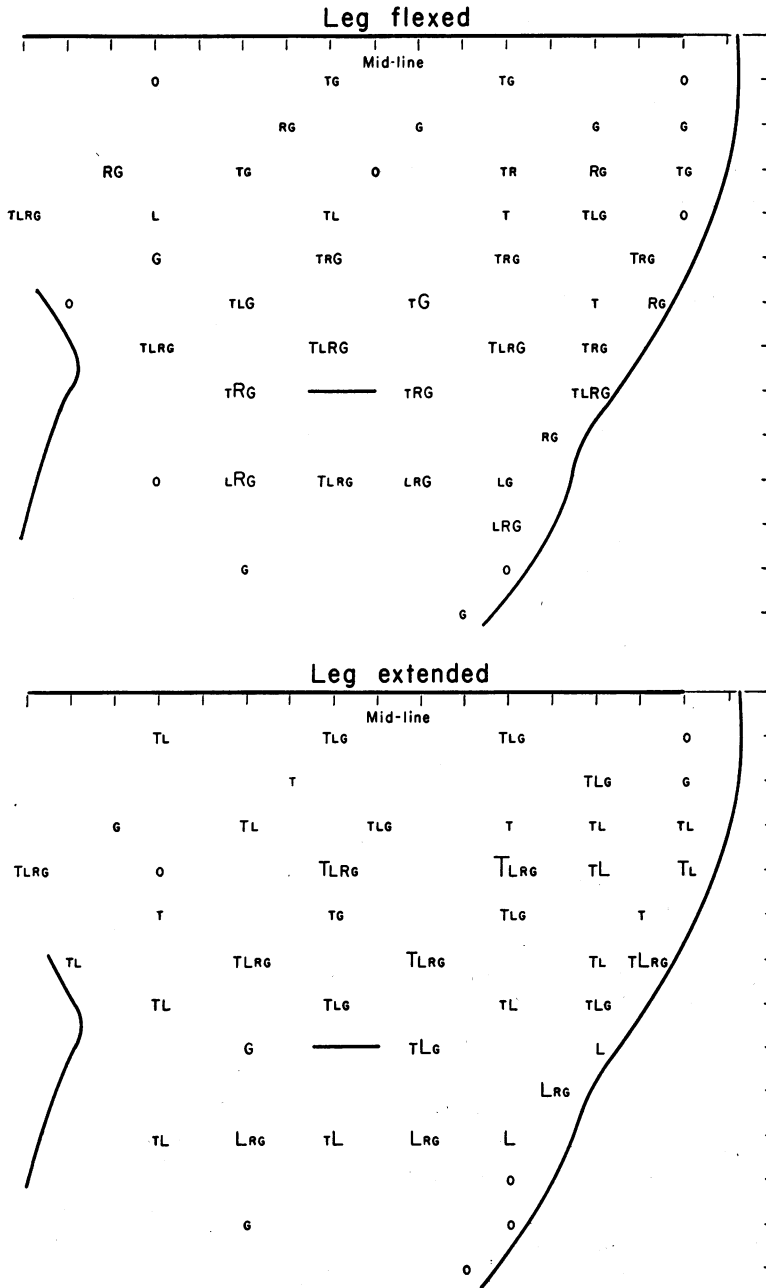
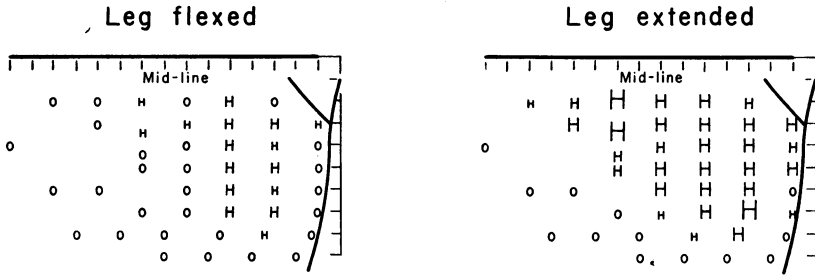


Fig. 6. Effect of proprioception on cortical maps, hind-leg area. Macaque 1-9-50, left hemisphere. Responses recorded simultaneously with those of Fig. 5. Central sulcus on right, inferior precentral sulcus on left, superior precentral gyrus in centre of maps. 3 sec monopolar stimulation with 3.5-4.9 V, 83/sec, pulse duration 7.7 msec. All records obtained with elbow in extension. Upper map, leg flexed: hip 90°, knee and ankle 45°. Lower map, extension of leg: hip 90°, knee and ankle 150°. *T*, tibialis anticus; *L*, gracilis; *R*, rectus femoris; *G*, gastrocnemius.

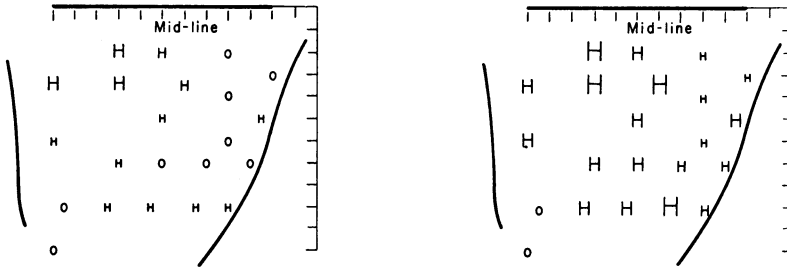
Individual variations in the location of foci of various movements have often been observed in studies on the motor cortex. This was likewise found in the present work since there was no consistency in the particular cortical area of 'representation' for any one of the hind-leg muscles from animal to animal. However, in spite of individual variations the effect of different postures of the leg on the extent of the area of cortical responsiveness is distinct. In Fig. 7 are shown three pairs of maps of semitendinosus response in different monkeys, two *Cynemolgi* and one macaque, each plotted for the two proprioceptive positions. The consistent shift in response, which increases with the knee extended (and ankle plantar flexed) is an obvious feature of the maps (left column compared with right), as is also the variation in foci of semitendinosus representation in the different experiments. A similar group of maps, with tibialis anticus responses from four macaques and two *Cynemolgi*, was prepared (not illustrated); over 200 sites in the two positions were examined. The same general features shown in Fig. 7 for semitendinosus emerged from the tibialis maps: (a) the widespread area from which responses in tibialis could be elicited with slightly suprathreshold stimulation; (b) the considerable effect of proprioceptive facilitation on this area and on the e.m.g. amplitude; and (c) the wide variation in area and in 'centres' of greater responsiveness from one animal to the next.

#### DISCUSSION

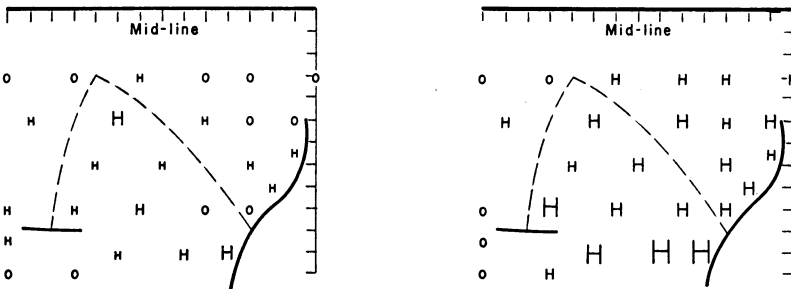
The experiments described in this paper show clearly that the area from which a given movement or the contraction of a muscle or group of muscles can be evoked depends to a large extent, other conditions being equal, on the posture of the limbs and on the degree of proprioceptive reinforcement which is present at the time of stimulation. The maps reproduced in Figs. 2-7 illustrate the effect: a muscle can be excited from more cortical sites, i.e. from a wider area of cortex and to a greater amplitude, with the limb fixated so as to stretch the muscle; as a result, the pattern of response or type of movement produced from any one cortical site may be quite different when the limb position is altered (see also Clark & Ward, 1937; Gellhorn, 1948, 1949; Gellhorn & Johnson, 1950*a, b*); consequently, the map obtained by stimulation in one position will be unlike that in another position. It is obvious that the recovery of motor functions following cortical lesions may be misinterpreted if the total area of cortical representation of an extremity had not been ascertained under optimal conditions before the operation (Gellhorn, 1953). Proprioceptive reinforcement and increase in cortical excitation as studied by Liddell & Phillips (1951) cause an increase in the area from which the contraction of a certain muscle can be elicited. However, the mechanism involved in the two procedures of activation may not be the same. If stimuli of greater intensity are applied to the cortex more neurones are activated at the cortical level, and this will



*Cynemolgus 10-3-49*



*Cynemolgus 10-17-49*



*Macaque 11-1-49*

Fig. 7. Relative representation of semitendinosus in motor cortex of three monkeys. Comparison of maps obtained with leg flexed and leg extended. *Cynemolgus* 10-3-49 as in Fig. 2. *Macaque* 11-1-49 as in Fig. 4. All scales represent millimetres of cortex. *H*, semitendinosus.

increase the number of responding motor horn cells and consequently augment the height of contraction and tension of the muscles. On the other hand, proprioceptive impulses resulting from fixation of one or more joints of an extremity will act on both the spinal (Loofbourrow & Gellhorn, 1949) and the cortical level (Gay & Gellhorn, 1949).

#### SUMMARY

1. The influence of proprioceptive impulses on the size and configuration of the cortical representation of an extremity has been investigated in the monkey.
2. It has been found that the initial position in which an extremity is placed or held has a large influence on the pattern of response to stimulation of any cortical site and also on the map of motor cortex responses. Stimulation of cortical sites with the leg fixed in extension gives one type of map; stimulation of the same sites with the limb held flexed gives a map differing in: (a) the size of the area (or number of sites) from which a contraction can be induced in a particular muscle; (b) the relative amplitude of that contraction at each site; and finally (c) the relative distribution of response to motor cortex stimulation.
3. Fixation of a muscle or group of muscles in stretch increases the cortical area from which contractions of these muscles in response to a standard stimulus can be elicited. This principle is valid for functionally distinguishable parts of a single muscle, the extensor portion of the biceps femoris giving a greater response to cortical stimulation with the knee flexed (and ankle plantar-flexed), the flexor part giving a larger amplitude of e.m.g. to stimulation of a larger number of cortical sites when the knee is held in extension. Moreover, extension of the hind leg leads to an increased area of responsiveness of triceps brachialis whose cortical foci overlap with those of the hind-leg muscles.

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