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MOTOR REPRESENTATION IN THE FRONTAL SULCI OF THE CAT‡

We were privileged to make our debuts in neurophysiology at Yale under the inspiring guidance of Professor John Fulton. While still very "wet behind the ears" we began together to study visceral and somatic motor representations throughout the frontal lobes of various experimental animals. Dr. Fulton was especially encouraging to us when we began to investigate the cortex hidden within the depths of frontal sulci. He pointed out that there was no reason to suppose *a priori* that the functions of cortex buried within the sulci were generically different from or less significant than those already attributed to the more accessible and therefore better known surface areas. Our first paper therefore included an analysis of the representation of respiratory movements within the frontal sulci of the anesthetized dog and monkey.[5] Although we extended observations relating to hidden cortex to other animals, including the chimpanzee, we recognized the desirability of mapping buried cortex systematically as an aid to preliminary localization during aseptic implantations of electrodes for later analysis in waking, freely moving animals without anesthesia. We considered that hidden cortex should be thoroughly explored in cats because of their general availability and their adaptability to the Horsley-Clarke stereotaxic apparatus.

Although many have emphasized the importance of taking hidden cortex into consideration in accounting for the total cortical representation in cats, there is as yet no schema available which indicates the general functional organization of this extensive and relatively inaccessible region. Some previous studies were helpful in supplying information relating to fragmentary parts of the hidden motor cortex (see Delgado, 1952, for a review of the literature[3]), but often these data were obtained after surgical ablation of one bank of the sulcus concerned. Surgical exposure of the surface of buried cortex has the advantage of direct observation of electrical placements, but

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has the disadvantage of imposing some circulatory embarrassment to the stimulated site and of limiting cortico-cortical relations which may be important in support of background activity as well as in the cortical organization of the motor response. We were fortunate in having access to a Horsley-Clarke apparatus whereby we could test responses to stimulation of carefully tapered bipolar concentric electrodes which penetrated the brain millimeter by millimeter. This technique is not itself free from some disadvantages, but we looked upon it as an improvement over surgical exposure and it did have the advantage of simulating conditions which are encountered during operative implantation of electrodes.

METHODS

Twenty cats, lightly anesthetized with Dial, were fixed to a Horsley-Clarke stereotaxic instrument and then suspended, instrument and all, from a horizontal bar, so that the four extremities were dangling and the lateral movements of the head and trunk could be readily detected. Twenty-gauge bipolar concentric probing electrodes, insulated except at the bared end of the shaft and tip of the internal electrode, were utilized for mapping millimeter by millimeter in successive vertical columns throughout the frontal lobes. By making use of both hemispheres, six to twelve such vertical tracts could be studied in each animal. Rectangular and thyratron discharge pulses were used for stimulation. Responses were detected visually and by palpation. Electrode tracts were identified by gross and microscopic brain sections, a paraffin-coated thread being placed in each of the successive electrode tracts during the experiment and removed again only after the brain had hardened.

RESULTS

Figure 1 is a diagrammatic synthesis of our data concerning the motor functions of the hidden cortical surfaces. In addition to the representations indicated, hind limb responses were obtained by stimulating the surface of the posterior sigmoid gyrus, forelimb and face responses by excitation of the anterior sigmoid gyrus, and movements of the face, tongue, mouth and eyes evoked from the anterior portions of the coronal and diagonal gyri. Moreover, the surface cortex around the middle portion of the coronal sulcus yielded trunk and hind limb movements. There appeared to be a continuum of motor representations which extend throughout both the surface gyri and cortex hidden within the sulci. Some cats, seeming to have less extensive representation of motor functions on the exposed surfaces of the hemisphere, proved to have greater than usual representation within buried cortex. Although slight variations from animal to animal occurred, there was a clear homology between one hemisphere and the other in each individual experimental animal. Certain facts relating to responses evoked from hidden cortex of the frontal lobe sulci in the cat seem worthy of detail:

Sulcus cruciatus: The cortex hidden within this sulcus is approximately 120 mm^2 in extent. In general, stimulation within this area yielded slow flexion of the contralateral hind limb. By employing currents only ten per cent above threshold for barely discernible responses, discrete individual movements which were characteristic for particular loci could be elicited. These involved motion of the pelvis, thigh, foot and paw, including the digits and claws. The movements were expressed in rotation, abduction, adduction, extension and flexion (the latter especially readily obtainable from the ventral bank of the sulcus), of the proximal parts of the limb, and digital extension, flexion or fanning, with claw presentation or retraction. Occasionally both hind limbs responded to cruciate sulcus stimulation; purely ipsilateral responses were rare. There were also points near the anterior extent of the cruciate sulcus which yielded pelvic tilting with or without accompaniment of hind limb movements. Nearby some loci gave combined movements of fore and hind limbs. Contraction of spinous muscles on the side opposite to the hemisphere stimulated caused trunk movements which sometimes spread to involve extension of the contralateral hind limb. In addition, tail movements were elicited by stimulation of the cruciate sulcus. These usually took the form of slow elevation from a relaxed dependent position to a nearly horizontal plane.

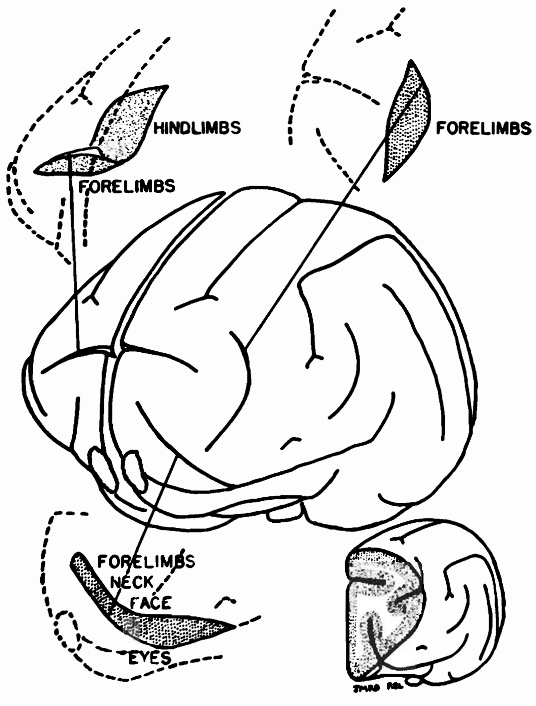

FIG. 1. Diagrammatic representations of motor functions of the hidden cortical surfaces. *Superior left:* sulcus cruciatus; *superior right:* sulcus coronalis; *inferior left:* sulcus presylvius; *inferior right:* diagram of the three sulci in a coronal section.

Cruciate sulcus movements were obtained quite consistently in all twenty cats and in the same pattern of representation within the sulcus. The anterior two-thirds of the sulcus had somewhat lower thresholds for response and evoked more prompt and imperious movements. Responses elicited from the posterior one-third of the sulcus tended to be less discrete, less uniform in timing and in the characteristics of motor display, and to be less readily fatigued.

Sulcus coronalis: There are approximately 80 mm^2 of hidden cortex within the two banks of this sulcus. Stimulation of the anterior portion induced lifting of the contralateral wrist and curling flexion of the paw. Sometimes contralateral flexion and ipsilateral extension were observed. Additional responses from different points within this region included pronation, supination, adduction and abduction of the contralateral or of both forelimbs. The posterior half of this sulcus required relatively higher intensities of stimulation and the responses were more complex and less consistent from trial to trial.

Sulcus presylvius: There are about 125 mm^2 of cortex enclosed by this sulcus. Since its course is practically vertical, electrodes can pass along its length from the base of the inverted "U" to its opening onto the anteroventral surface of the brain. Forelimbs are represented in the superior part of the sulcus, extension toward the topmost part and flexion a little deeper. Although most responses were contralateral, some were bilateral and, more rarely, ipsilateral alone. Rhythmic "pawing movements" were also evoked, the cycle being repeated again and again during continuous stimulation. Head turning was elicited below forelimb responses. In two animals, stimulation of the middle portion of the sulcus presylvius caused acceleration of respiration and gutteral vocalization.

Face representation is widespread throughout the inferior half of the presylvian sulcus. Facial responses here were lower in threshold than any other somatic movements obtained from deep or surface stimulation. The forward or upward movement of vibrissae had the lowest threshold of any facial response. In addition to tonic sustained movements of the vibrissae, rhythmic responses were often observed in which the whiskers twitched forward and then dropped more slowly backward, the rhythm varying from one to ten per sec. according to the applied stimulus strength. We referred to these as "vibrissae nystagmus." Vibrissae and eyebrow or vibrissae and forelimb responses occurred commonly from stimulation of single loci.

Eye movements, usually conjugate in the vertical or horizontal plane and usually accompanied by opening or closing of the eyelids or other facial movement, were elicited from the inferior part of this sulcus. An eye field functionally comparable to that of the monkey's area 8, however, appears to lie on the medial surface of the frontal lobe of the cat.[8, 11, 16] Pupillary dilatation occurred predominantly but not exclusively on excitation of the middle and inferior portions of the medial bank of this sulcus. Stimulation of the medial bank of the presylvian sulcus caused inhibition of respiration, resulting in shallow, slow respiration or arrest in the expiratory position. Confirming Hess, *et al.*,[9, 10] we found that the lower parts of the lateral bank of the sulcus yielded responses of the jaw and tongue, with some rhythmic movements, including opening and closing of the mouth, chewing, lapping, or swallowing. Swallowing usually accompanied lapping or chewing responses, but sometimes it occurred independently with a repetition of the swallowing sequence throughout the duration of stimulation. Occasionally there were isolated movements of the tongue such as curling or protrusion. At a few locations salivary secretion could be observed to increase distinctly during stimulation.

Although there were some variations in the maps of sulcus presylvius as analyzed in different cats, two features of the responses were remarkably consistent: the two hemispheres were closely matched in any one cat and the sequence of representation along the sulcus was the same throughout the series. Ascending the lateral column of the inverted "U" from its ventral to its dorsal parts, we found tongue, jaw, swallowing, vibrissae, face, eyelid and eye movements, neck and finally forelimb responses near the top of the "U." On descending the medial bank of the sulcus we encountered an extensive zone yielding forelimb movements, then pupillary and respiratory changes.

DISCUSSION

It has already been emphasized by several physiologists that functions probably do not stop abruptly at the margins of sulci or "jump across" to the opposite sulcal margin, but that they may continue within the hidden cortex in the depths of the sulcus. Stout, over forty years ago, attempted to explore the banks of the cruciate sulcus and did obtain discrete somatic responses which were different for the anterior and posterior banks of the sulcus. But he complained of the great difficulty of its exploration because of the location of an artery lying between the two lips of the sulcus.[20] Magoun, Ranson and Fisher stated in 1933 that "while only incidental information is furnished by the present series of experiments on the demarcation of the cortical motor area of the cat, the large number of responses obtained from buried cortex forming the lateral and dorsal wall of the presylvian sulcus is of interest."[17] Garol, in 1942, indicated that in the cat "There was no region from which responses of the trunk could be obtained until the intensity of the stimulus was sufficiently high to produce a spread of current and simultaneous movements of either the fore- or hind-limb or both. Such an area may lie in the depths of the *sulcus cruciatus*."[6] Sugar, Chusid and French explored the depths of the sylvian and lunate sulci in the monkey by making a surgical exposure of the buried cortical surfaces. They acknowledge the difficulties and disadvantages of this method.[2] Chusid, Mahoney and Robinson, also using surgical exposure techniques, investigated the motor functions of the hidden cortex in the frontal lobe of the dog,[1] and Wilbur Smith made a similar examination in the cat[18]; but apparently these studies were published only in abstract. Because of the inconveniences of mapping this infolded territory, Woolsey and his associates have given their principal attention to investigations of the more primitive brains.[21] In higher primates, Leyton and Sherrington found "the portion of the motor region which lies buried in the sulcus centralis and other fissures amounts to not less than about 35 per cent of the whole motor region."[15] Hidden cortex becomes a progressively larger fraction of the total cortex in higher mammals,[7] and it is reasonable to suppose that motor representation in man will eventually need to be understood in terms of the hidden as well as surface cortex.

Although our observations were confined to the overt responses which could be evoked by stimulation of the surface and depths of the frontal lobe, we are well aware that movements might be aroused by stimulation of regions that are essentially sensory in function. In fact, the higher thresholds, less confined and uniform (less evidently imperious) responses encountered in the posterior portions of the cruciate and coronal sulci suggested to us that we were stimulating what might be predominately "sensory fields." Our inclination is to consider all of the frontal lobe territory from which responses may be elicited, both superficial and deep cortex, as "sensorimotor" in character.

At times our penetrating electrodes were located in white matter from which motor responses were readily elicitable. Our report, however, has been confined to the identification or responses which were induced while the electrodes were in place within, or in close contact with, cortical grey substance. We have the impression that cortical responses, as contrasted with responses from white matter, are of lower threshold and exhibit a greater continuity of functional representation among adjacent points. In addition to providing useful information for the problem of electrode implantation, these data suggest to us the importance and dignity deserving in our consideration of the rôle of cortex buried within sulci. Rather than having this imply still another (fourth or fifth) motor zone, we would prefer to consider the entire sensorimotor region as being unitary and continuous over the surface and into the depths of the sulci as well.

SUMMARY

Cortex hidden within enclosed portions of the sulci cruciatus, coronalis and presylvius, has been stimulated electrically in twenty cats under Dial anesthesia by means of bipolar concentric electrodes directed stereotaxically so as to penetrate the frontal lobe millimeter by millimeter.

The hidden cortex forming the walls of these sulci in each hemisphere has a combined extent of more than three hundred square millimeters, an area comparable to the surface extent of the frontal lobe of the cat. Throughout subsurface cortex there is an important and essentially continuous "sensorimotor" region from which discrete somatic motor movements may be evoked.

Stimulation of the cortex within the cruciate sulcus yields movements of the contralateral hindlimb, trunk and tail. There is a small region of forelimb representation in the anterior part of this sulcus. Forelimb responses are also elicitable from the anterior part of sulcus coronalis. Within the sulcus presylvius there is an extensive motor representation of the anterior half of the animal: forelimbs near the top, head and neck movements, face, vibrissae, eyelid and eye movements, jaw, tongue, pupillary and respiratory responses as the orbital surface is reached. There are differences in representation within the opposing surfaces of each of these three sulci and each bank appears to provide a series of motor representations which are continuous with those encountered on stimulation of the surface gyri.

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